

The evolutionary consequences of biological invasions

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Abstract

A major challenge of invasion biology is the development of a predictive framework that prevents new invasions. This is inherently difficult because different biological characteristics are important at the different stages of invasion: opportunity/transport, establishment and spread. Here, we draw from recent research on a variety of taxa to examine the evolutionary causes and consequences of biological invasions. The process of introduction may favour species with characteristics that promote success in highly disturbed, human-dominated landscapes, thus exerting novel forms of selection on introduced populations. Moreover, evidence is accumulating that multiple introductions can often be critical to the successful establishment and spread of introduced species, as they may be important sources of genetic variation necessary for adaptation in new environments or may permit the introduction of novel traits. Thus, not only should the introduction of new species be prevented, but substantial effort should also be directed to preventing the secondary introduction of previously established species (and even movement of individuals among introduced populations). Modern molecular techniques can take advantage of genetic changes postintroduction to determine the source of introduced populations and their vectors of spread, and to elucidate the mechanisms of success of some invasive species. Moreover, the growing availability of genomic tools will permit the identification of underlying genetic causes of invasive success.

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Introduction

The ecological consequences of human activities have long been recognized, but we know little about the evolutionary impact of anthropogenic changes to the environment. One major form of anthropogenic global change is the widespread introduction of non-native species (reviewed in Elton 1958; Williamson 1996; Mooney & Hobbs 2000). In addition to negative economic and ecological impacts (Parker *et al.* 1999; Pimentel *et al.* 2000), the process of invasion can exert novel selective pressure on both the introduced species as well as the species they interact with

in the new environments (Mooney & Cleland 2001; Lee 2002). These evolutionary consequences of invasions are underappreciated but they likely influence the success and impact of invasive species and, in turn, should play a role in the strategies developed to control them (Sakai *et al.* 2001). If we are to preserve biodiversity in the wake of accelerating rates of species invasions (Cohen & Carlton 1998), or develop a predictive framework for the process of invasion (Kolar & Lodge 2001), it is imperative that we understand the role played by evolutionary forces before, during and after the introduction of species to new ranges.

When species are introduced to a new range they may experience an array of new selective pressures and simultaneously act as novel selective agents on native taxa in the invaded ecosystem. Thus, conditions are favourable for rapid evolution of both the invaders and the species they interact with in the new range. Compared to processes such as natural dispersal or long-term competitive or predatory interactions among species with a coevolutionary

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history, the ecological shuffling associated with biological invasions is extraordinarily rapid and can be geographically widespread. Thus, in many cases both the native and introduced species must adapt quickly or risk extirpation. For example, when species are introduced to an environment that is abiotically unsuitable, they may lack the genetic variation required for rapid adaptation to the new circumstances. Likewise, native species in an invaded habitat may lack defences to a newly introduced predator, competitor or pathogen due to the absence of a coevolutionary history between the two (e.g. Payne *et al.* 2004; Schlaepfer *et al.* 2005).

It is also important to remember that biological invasions occur as a multistage process that includes the acquisition of a propagule in its native range, transport of that propagule to a new range, and the introduction, establishment and spread of the invader in the new habitat. Each stage of this process poses new challenges and imposes different types of selection (Sakai *et al.* 2001). Each stage thus acts as a filter, weeding out species that lack the characteristics needed for survival or the variation necessary for adaptation to novel selection pressures.

In this review, we discuss the role of evolutionary processes in biological invasions in the context of the different stages of this process. Specifically, we examine the importance of the following evolutionary mechanisms: (i) preadaptation of invasive species in their native range; (ii) evolution of invasive species in their introduced range; and (iii) introduced species as a selective force on native species. We propose that taking an evolutionary approach to the study of biological invasions will provide important insights into both mechanisms of success and their consequences. Moreover, we argue that the efficacy of future strategies for the prevention and control of invasive species will hinge on an understanding of the evolutionary processes that are involved in successful invasions.

The evolution and preadaptation of introduced species in their native range, prior to introduction

In general, the species that become successful invaders are not a random sampling of biodiversity. Instead, successful invaders are predicted to be species that, in their native ranges, have evolved traits that predispose them to be transported by humans and successfully survive the selection regimes encountered during transport, introduction, establishment and spread. These predictions are borne out by analyses of invasive vs. noninvasive species. In pines (*Pinus*), for example, successful invaders possess characteristics associated with effective dispersal and increased propagule pressure: high growth rates, consistent and regular reproduction, and small seed masses (Rejmanek & Richardson 1996; Grotkopp *et al.* 2002). Similarly, many other invasive

plants possess adaptations for long-distance dispersal that likely increase the probability of being transported by humans, either deliberately or inadvertently (reviewed in Levin 2006). By increasing propagule pressure not only do these adaptations increase the probability of introduction, but the continued introduction of additional propagules after establishment can facilitate invasiveness by reducing potentially harmful Allee effects, increasing genetic diversity, introducing novel genotypes and phenotypes, and permitting further adaptive evolution (see below).

Similar characteristics are often observed in invasive animals. Many invasive ant species, for example, nest ephemeraly and have a temporally and spatially fluid colony structure, which allows them to rapidly move their colonies in response to changing environmental conditions (e.g. rising floodwaters, the appearance of a temporary food resource; Holway & Case 2000; Holway *et al.* 2002a). When associated with humans, however, this habit translates into frequent introduction to new locales, as the ants colonize items that are transported by humans (such as trash, soil or potted plants), often across long distances (Suarez *et al.* 2001; Suarez *et al.* 2005). Moreover, many invasive ants are characterized by a polygyne colony structure, where multiple reproductive queens are present in each colony. Thus, when colony fragments are accidentally moved by humans, there is a high probability that the propagule will contain reproductive individuals, and thus be viable in the new habitat (Hee *et al.* 2000; Tsutsui & Suarez 2003); whether these characteristic are overrepresented among invasive ants relative to ants as a whole remains to be tested.

Having a shared history with humans may also make a species more likely to invade new environments (Elton 1958). In addition to being preadapted to human modified landscapes, a close association with humans increases the probability of transport through a variety of anthropogenic vectors (Crooks & Suarez 2006). For example, many introduced insects in North America come from Europe where they have coevolved with human land practices for hundreds of generations and many potential host genera are similar between the regions (Elton 1958; Sailer 1978). Interestingly, ant invasions into North America do not follow this pattern (Suarez *et al.* 2005).

When attempting to predict where potential invaders will be successful, it would be useful to assess how well conditions in the native range (which have driven the historical evolution of the species) match conditions in a potential introduced range. Because introduced propagules may be more likely to succeed in habitats similar to those they evolved in, in depth knowledge about both ranges may allow for more accurate predictions. Unfortunately, for many invasive species we know little about their ecology or genetics in native populations.

The evolution of introduced species in their introduced range

Although some species may possess traits that preadapt them to becoming biological invaders, these traits alone are unlikely to explain their success. Most invasions progress along a timeline that includes a significant 'lag phase' (Crooks 2005) soon after introduction. Although this lag phase may simply result from a pattern of exponential growth and expansion of an initially small population (Crooks 2005), another possibility is that it represents a time during which adaptive evolution to conditions in the new range is occurring, and invasive expansion only occurs after some evolutionary breakthrough is achieved. For example, genetic changes may occur that release these populations from the lag phase, including events such as secondary (or multiple) introductions from the native range or elsewhere in the introduced range, hybridization or the spontaneous acquisition of novel genetic traits (through, for example, chromosomal or gene duplication).

Clearly, a variety of new selective pressures and challenges are encountered by species when they are introduced to a new geographical range. This occurs because the new habitat (and the species in it) exerts novel forms of selection, and also because selective agents in the native range, such as parasites and predators, are left behind (Mitchell & Power 2003; Torchin *et al.* 2003). Thus, the survival and proliferation of introduced propagules may require adaptive evolution to the new environment. This is aided, in some cases, by human land-use practices that create disturbed habitats within which invaders can out-compete native species (Elton 1958; Hobbs & Huenneke 1992; Fausch *et al.* 2001; Holway *et al.* 2002b).

In some cases, sufficient genetic variation for adaptive evolutionary change may not be present in newly introduced populations because introduced species typically pass through a period of small population size; the resulting populations may experience a concomitant loss of genetic diversity (a genetic bottleneck; Chakraborty & Nei 1977; Nei *et al.* 1975). The survival and adaptation of introduced species in the face of this challenge has been referred to the paradox of invasion biology (Allendorf & Lundquist 2003): how is it that species can be so successful against native species that are adapted to their surroundings despite the problems associated with small population sizes and a lack of genetic diversity?

As predicted by Nei *et al.* (1975) and Carson (1990), losses of genetic diversity during introduction are often modest, or even absent, particularly if the bottleneck is brief or population growth rapid, or if the propagule is large. Moreover, under some circumstances population bottlenecks may increase the genetic variance available to selection as balanced epistatic variance is converted to additive genetic variance (reviewed in Carson 1990). In a recent

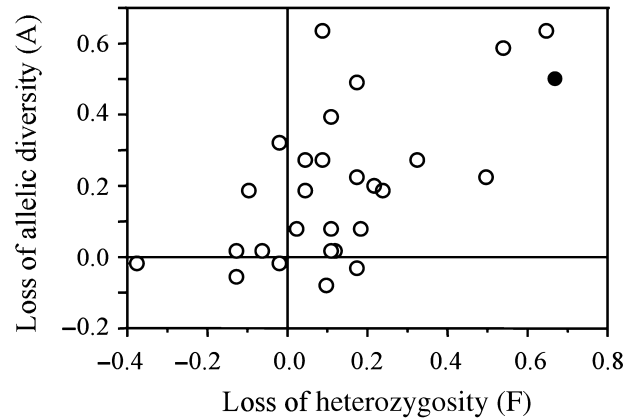


Fig. 1 Examples of reductions in genetic diversity measured as loss of allelic diversity (*y*-axis) and loss of heterozygosity (*x*-axis) associated with species introductions where data was available from both the native and introduced range. The closed black circle represents data from the Argentine ant (*Linepithema humile*). Data from Wares *et al.* (2005).

review by Wares and colleagues (2005) the authors compiled data from studies in which molecular tools were used to estimate genetic diversity in both native and introduced populations. Of the 29 animal species examined, most introduced populations retained 80% or more of the genetic variation present in native populations (Fig. 1). In some cases, substantial genetic diversity may be retained if the introduced population quickly grows to substantial numbers. In Britain, the introduction history is well-known for some populations of the invasive marsh frog, *Rana ridibunda* (Beebee 1981). In one case, introduced populations were initiated by as few as 12 founding individuals, and the resulting population served as a source for a later introduction to a different site. Surprisingly, genetic analysis revealed that these populations lost little or no genetic variation relative to frogs sampled from the original, native range (Zeisset & Beebee 2003). This pattern likely stems from the rapid growth and expansion of introduced *R. ridibunda* populations — this species is considered to be the most successful introduced amphibian in Britain (Zeisset & Beebee 2003).

Although natural selection may well be the primary evolutionary force acting in biological invasions, other evolutionary mechanisms, such as genetic drift and admixture, might also cause important genetic or phenotypic changes in invasions (Clegg *et al.* 2002). For example, genetic drift might be the best explanation for the relatively haphazard patterns of morphological evolution during an introduction of the common chaffinch (*Fringilla coelebs*) to New Zealand (Baker *et al.* 1990). Alternately, admixture of introduced individuals descended from different source populations could cause morphological evolution during an invasion. Introduced populations of *Anolis* lizards in

North America, for example, are characterized by genetic patterns consistent with multiple introductions from different locations in the native range (Kolbe *et al.* 2004; Kolbe *et al.* 2007). Moreover, morphological differentiation among introduced populations appears to be a product of differential admixture from this handful of sources (Kolbe *et al.* 2007).

Social insects, which include many successful invasive species, may be particularly sensitive to microevolutionary changes during and after introduction. Not only do these species often have a relatively small number of reproductive individuals, but the hymenopteran social insects also possess small effective population sizes as a consequence of their haplodiploid genetic system. Moreover, the system of complimentary (single-locus) sex determination (CSD) in the hymenoptera may make them particularly vulnerable to losses of genetic diversity. Because heterozygotes at this locus become females and hemizygotes and homozygotes become males (Crozier 1977), high levels of allelic diversity are necessary for this system to operate properly (Beye *et al.* 2003). One consequence of having a small founding population followed by inbreeding is the production of diploid males. Diploid males are often sterile and can impose a huge cost to the colony (Zayed & Packer 2005). Evidence for diploid male production in introduced social insects has been detected in nearly 40 species of Hymenoptera (Cook 1993; Crozier & Pamilo 1996), including in introduced populations of *Polistes* wasps (Liebert *et al.* 2004; Liebert *et al.* 2005), the honeybee (*Apis mellifera*, e.g. Drescher & Rothenbuhler 1964), the Argentine ant (*Linepithema humile*, Tsutsui *et al.* 2003), and the red imported fire ant (*Solenopsis invicta*, Ross & Fletcher 1985).

Hybridization within and among species

When multiple introductions of a species occur, introduced populations may attain higher levels of genetic diversity than native populations. This is particularly likely when the sources of introduced propagules are genetically divergent native populations. Accordingly, a number of genetic studies have shown that intraspecific hybridization among successively introduced populations may provide the genetic variation necessary for adaptive evolution to occur, and may thus be a critically important determinant of invasive success (Ellstrand & Schierenbeck 2000). For example, Chen *et al.* (2006) used microsatellite markers to show that both genetic diversity and the number of private alleles are higher in some introduced *Rhagoletis completa* populations, suggesting that multiple introductions have occurred. Similarly, Roman (2006) used cytochrome oxidase I (COI) mitochondrial DNA (mtDNA) sequence data to show that a recent northward range expansion of introduced the European green crab (*Carcinus maenas*) in the northeastern United States was probably caused by a

secondary introduction of *C. maenas* from the native range. Finally, Kolbe and colleagues (Kolbe *et al.* 2004) show that introduced populations of the lizard, *Anolis sagrei*, are more diverse than natives. Future research demonstrating the benefits of increased genetic diversity in introduced populations is still needed to determine its role in invasion success post-establishment.

Equally importantly, individuals in these populations may possess alleles in combinations that do not exist in the native range, thus increasing the likelihood of novel epistatic interactions or the expression of new phenotypes. In a recent study of the invasive reed canarygrass, *Phalaris arundinacea*, Lavergne & Molofsky (2007; reviewed by Novak 2007) conducted population genetic analyses of native and introduced populations from both the centre and the periphery of each range. These data showed that introduced populations, regardless of their location, had higher levels of genetic diversity than native populations and possessed many alleles that were not seen in the native populations sampled. Also notable is the fact that the vast majority of multilocus genotypes in the introduced range were not seen in the native range, indicating admixture among multiple genetically different introductions.

A thorough genetic examination of multiple introductions is the recent study of the honeybee, *Apis mellifera*, using > 1100 single nucleotide polymorphism (SNP) loci (Whitfield *et al.* 2006). This species, native to Africa, Europe and Asia, was first introduced (deliberately) to the New World in the 1600s, and it has since become the leading pollinator of many plants, including a number of agriculturally important crops (Delaplane 2000). Historical records suggest that the first introduced hives were 'German black bees', the subspecies *A. m. mellifera* (Sheppard 1989). Since then, however, a number of other subspecies have been introduced, including the 'Italian' bees, *A. m. ligustica* and *A. m. carnica* (Sheppard 1989), and the infamous African 'killer' bee (*A. m. scutellata*), which was accidentally released in Brazil in 1956 (Sheppard & Smith 2000; Schneider *et al.* 2004). The spread of Africanized honeybees since their introduction has been a cause for concern for human health, apiculture and agriculture. The SNP analysis of Whitfield and colleagues examined 14 subspecies in the native range (including the aforementioned four) and showed that native populations fall into several well-defined, genetically distinct groups. Assignment of introduced bees to these native populations revealed that, for the most part, they are a genetic amalgamation of the successive introductions of various subspecies. Interestingly, the introduction and spread of Africanized honeybees (*A. m. scutellata*) has affected some parts of the genome more than others – alleles descended from *A. m. mellifera* have been retained at far higher rates than alleles descended from *A. m. ligustica* or *A. m. carnica*. Because the SNPs examined reside within expressed genes, these types of genome-wide

SNP-based studies offer great hope for teasing out genes of functional importance for interesting phenotypes, including behaviours, morphologies and life histories associated with invasive success.

Another potential source of genetic variation is hybridization between introduced and native species in the new range. In the San Francisco Bay area, for example, four different species of *Spartina* cordgrass have been introduced from native ranges in Europe, Chile and the Eastern seaboard of North America (Ayres *et al.* 2004). Since their introduction, some of these species have spread widely and, in some cases, have hybridized with the native cordgrass, *S. foliosa* (Daehler & Strong 1997). Genetic studies using chloroplast DNA markers, for example, have shown that the introduced *S. alterniflora* has hybridized with the native *S. foliosa* (Anttila *et al.* 2000), resulting in highly invasive clones that then displace the native parental species (Gray *et al.* 1991). In Great Britain, hybridization between the native *S. maritima* and the introduced *S. alterniflora* has given rise to the allopolyploid invasive *S. anglica*. Although this invasive reproduces clonally, and thus has virtually no interindividual genetic variation, it possesses extremely high levels of within-individual genetic variation and heterosis as a result of its hybrid origin (Ellstrand & Schierenbeck 2000).

Although it is clear that interspecific hybridization can occur between both introduced and native species as well as between two different invaders, it is difficult to estimate the relative frequencies of these events. However, work by Stace (1991) documenting the 2834 plant species that occur in the British Isles provides some insights (reviewed by Abbott 1992). Of this number, Stace estimated that 1264 (~45%) are introduced species and 21 (~2%) are the product of hybridization between two different introduced species. About 62% of these hybrids have some documented level of fertility. Moreover, 70 species were judged to have arisen from hybridization between an introduced plant and a native species, and four resulted from hybridization between a hybrid and a native species. Nearly half of the hybrids between a native and introduced plant showed some evidence of fertility.

Introduced species as a selective pressure on native species

There is a rich and voluminous body of research documenting the negative consequences of invasive species on native taxa in their introduced ranges (Parker *et al.* 1999; Mack *et al.* 2000). However, studies that examine the nature and strength of selection exerted by the invaders are rarer. Recent studies of an introduced crab illustrate the selective force that invasive species can bring to bear on native species and demonstrate how adaptive responses may act to ameliorate this selection. The blue mussel, *Mytilus edulis*,

is native to the east coast of North America where it is preyed upon by several species of crabs, including the long-established European green crab, *Carcinus maenas*. Mussels from throughout the range display an inducible defence to the presence of this crab predator – the mussels grow thicker shells when exposed to waterborne cues that indicate the presence of the crabs (e.g. Leonard *et al.* 1999). These thicker shells likely provide greater protection from attacks by the crabs. More recently, however, another non-native crab species, the Asian shore crab (*Hemigrapsus sanguineus*), has become established in the region (McDermott 1991). Mussels that co-occur with *H. sanguineus* in southern New England display the same inducible defence in the presence of *H. sanguineus*, but mussels from farther north (in allopatry with *H. sanguineus*) do not (Freeman & Byers 2006). These data suggest that in the short time since the Asian shore crab's introduction the southern mussels have evolved the ability to detect and respond defensively, whereas the naïve mussels have not (Freeman & Byers 2006).

In some cases, invasive species can radically alter abiotic and biotic characteristics of ecosystems, thus changing the strength and form of selection on the species therein (e.g. O'Dowd *et al.* 2003). The presence of some invasive grasses, for example, can alter fire frequencies in their introduced range, thus producing changes in community composition and nutrient cycling, and further altering the frequency of future fires (reviewed by D'Antonio & Vitousek 1992; Brooks *et al.* 2004). Other invasive plants can exude toxic chemicals into the soil, thus creating conditions that are intolerable for sensitive native plant species (Bais *et al.* 2002; Bais *et al.* 2003). Invasive vertebrate 'ecosystem engineers' can similarly cause extreme ecological changes (Wright & Jones 2006). The large-scale perturbations of fundamental habitat characteristics likely produce myriad simultaneous shifts in natural selection for all species involved, and we are only beginning to understand the nature and extent of the evolutionary responses.

Mutualism and facilitation

Mutualism and facilitation are becoming widely recognized as important evolutionary forces that contribute to the success of invaders (Simberloff & Von Holle 1999; Richardson *et al.* 2000; Bruno *et al.* 2003). Native species that facilitate one another, for example, may be able to better resist invaders (Bruno *et al.* 2003). In contrast, facilitative and mutualistic interactions among introduced species can lead to invasional meltdown: more severe ecological impacts than those expected if the invaders did not synergistically interact with one another (Simberloff & Von Holle 1999).

The growing number of empirical studies on facilitation and invasion illustrates an impressive array of possible interactions and potential for selection. Direct interactions

include animal-mediated pollination and seed dispersal, animals and plants modifying habitats in ways conducive to other organisms, and symbioses among plants and mycorrhizal fungi and among plants and nitrogen-fixing bacteria (Simberloff & Von Holle 1999; Richardson *et al.* 2000). Indirect interactions are also diverse and are documented from terrestrial, freshwater and marine environments (Simberloff & Von Holle 1999; Adams *et al.* 2003; Levin 2006). In a marine embayment in California, for example, Grosholz (2005) found that the introduced European green crab (*Carcinus maenas*) indirectly facilitates the introduced gem clam (*Gemma gemma*) by preferentially preying on native clams (*Nutricola* spp.) that normally outcompete the non-native clam in the absence of the crab. Whether direct or indirect, mutually beneficial interactions may develop between species that share no evolutionary history (Bach 1991; Grosholz 2005) or involve invaders that evolved together but were introduced into a new environment at different times only to be eventually reunited (Richardson *et al.* 2000; Adams *et al.* 2003). These examples strongly suggest that examination of coevolutionary relationships between introduced species and the species they interact with (either native or also introduced) will be fruitful areas for future studies.

A case study — Argentine ants

It is now well-established that introduced populations of the Argentine ant passed through a genetic bottleneck during introduction and establishment and consequently lost substantial amounts of genetic diversity (Fig. 1, Suarez *et al.* 1999; Tsutsui *et al.* 2000; Giraud *et al.* 2002). This loss of genetic diversity has led to increased levels of genetic homogeneity in introduced populations relative to native populations, which has contributed to widespread cooperation and the formation of massive 'supercolonies' (Tsutsui *et al.* 2000; Giraud *et al.* 2002). Multiple studies have shown that in their introduced range, Argentine ant colonies can be orders of magnitude larger than colonies in the native range. For example, studies by Tsutsui *et al.* (2000), Heller (2004), and Pedersen *et al.* (2006) all show that colonies in their native Argentina vary from just a few meters in diameter (e.g. occupying a single tree) to many hundreds of meters long (Fig. 2). In contrast, studies of introduced populations in California, Europe, Australia and New Zealand have all documented a unicolonial colony structure, characterized by the formation of massive 'supercolonies' across tens or thousands of kilometres (Fig. 2, Tsutsui *et al.* 2000; Giraud *et al.* 2002; Suhr 2004; Corin *et al.* 2007). Both lab and field research suggests that the lack of intraspecific aggression over such large spatial scales in introduced populations may contribute to the success of invasive ants (Holway *et al.* 1998; Holway & Suarez 2004). However, the short-term ecological benefits of unicoloniality may be

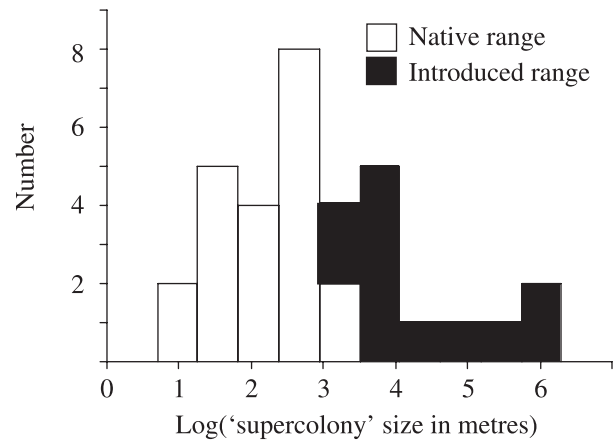


Fig. 2 Distribution of Argentine ant colony sizes in the native and introduced ranges. Data from Tsutsui *et al.* (2000), Tsutsui *et al.* (2001), Heller (2004) and Pedersen *et al.* (2006).

eventually outweighed by long-term consequences of having low levels of genetic diversity, such as an inability to adapt to environmental variation or a novel disease (Queller 2000). Interestingly, introduced Argentine ants in the southeastern United States are characterized by colonies of intermediate size and possess higher levels of genetic diversity than other introduced populations (Buczowski *et al.* 2004), consistent with the known history of Argentine ant introductions in North America: first to the southeastern United States, then later to California (Suarez *et al.* 2001). Although a recent study has proposed redefining the term 'unicolonial' to include the smaller colonies of the type found in the native range (see Table 1 of Pedersen *et al.* 2006), it is clear that the distribution of colony sizes in the two ranges are nearly nonoverlapping (Fig. 2). Thus, we view this proposal as misguided and unnecessarily confusing.

Argentine ants have been introduced by humans to more than 30 countries worldwide (Suarez *et al.* 2001). Almost everywhere that Argentine ants have been established, native ants are markedly reduced in diversity (Holway *et al.* 2002a). This sensitivity to Argentine ants is not distributed across species randomly. Instead, ants with the largest body sizes are lost and those able to coexist with Argentine ants are among the smallest in the community (Holway & Suarez 2006). Some of the most susceptible species include harvester ants, which are important seed predators and dispersers (Christian 2001; Carney *et al.* 2003) and a food source for horned lizards (Suarez *et al.* 2000). Thus, loss of these species has consequences for the evolution of the resident flora (Christian 2001) and specialist predators (Suarez *et al.* 2000; Suarez & Case 2002), and may change the competitive structure of ant communities (Sanders *et al.* 2003).

The flood plains in the vicinity of the Rio Uruguay and Rio Parana in northern Argentina include the native range

of Argentine ants and at least six other ant invaders (including *Solenopsis invicta*, *S. richteri*, *Wasmannia auropunctata* and *Pheidole obscurithorax*) that have established populations in the United States and elsewhere. This pattern suggests that particular features of this region may preadapt resident species to become damaging invaders elsewhere. For example, these communities are characterized by relatively high species diversity, many competitively dominant ant species and large-scale natural disturbances in the form of regular flooding (LeBrun *et al.* 2007). Studying the selective pressures of environments such as these that are the source for many invaders will shed light on how characteristics that confer invasion success can evolve.

A case study — cane toads

The case of the introduced cane toad (*Bufo marinus*) provides a fascinating example of how invaders can be both a source and subject of natural selection in their introduced ranges. This species, native to Central and South America, was first introduced to Australia in 1935, and has since caused a litany of problems, including declines in both the prey of the toads as well as predators, which are often susceptible to the cane toad's toxins (e.g. Crossland 2000; Smith 2005). In the introduced range, the availability of uncolonized habitat at the periphery of the toad's distribution appears to have selected for faster, longer-legged toads at the invasion front. This was also supported by the observation that long-legged toads move faster over short distances, and dispersed farther than short-legged frogs over the course of a three-day mark-release-recapture study (Phillips *et al.* 2006). Similarly, the investigators showed that a chronosequence of frogs passing by a spatially fixed sampling location showed that long-legged frogs were the first to pass by, followed later by the shorter-legged toads. Finally, using historical records over a 60-year period, Phillips *et al.* (2006) also showed that average leg length was longest initially, then later became shorter. Thus, some introduced populations have evolved faster locomotion and the corresponding physical features that permit it, although the genetic basis for this change remains unclear.

As expected, native species (those not extirpated) have also evolved in response to the strongly selective pressure exerted by introduced cane toads. Since consumption of highly toxic cane toads is often fatal to native snakes, the introduction of the toads has led to the rapid evolution of reduced gape size in two species of Australian snakes (Phillips & Shine 2004). Similarly, compared to naïve snakes, populations of the native Australian black snake (*Pseudochis porphyriacus*) that coexist with cane toads have evolved greater physiological tolerance to the toads' toxin and avoid them as prey items more often than naïve snakes (Phillips & Shine 2006).

Policy implications and future directions

Given the potential for both the rapid adaptive change of invasive species and the evolutionary consequences of their invasions, it is imperative to consider microevolutionary processes in research and policy concerning biological invasions. Understanding the role of evolution in the success of invasive species will only be possible through a careful comparison of species in both their native and introduced populations. However, for many invasive species little to no research has been conducted on native populations, and for some species the native range has not yet been identified. Similarly, long-term studies are needed to investigate changes in species post establishment (Strayer *et al.* 2006). Ideally, data should be collected over long periods of time (years, perhaps decades), which may not be realistic given the relatively short nature of grant funding cycles. However museum collections are an ideal resource for this endeavour (Suarez & Tsutsui 2004). For example, Zangerl & Berenbaum (2005) used herbarium samples collected over a 150-year period to show phytochemical shifts in wild parsnip (*Pastinaca sativa*) introduced to the United States from Europe. Specifically, they found an increase in the plant's production of toxic furanocoumarins coincided with the introduction of the parsnip web worm — a major coevolved herbivore from the parsnip's native range.

It is obvious, and widely accepted, that introductions of new species should be prevented by monitoring and early eradication. However, as discussed above, the success of some invasive species may also depend on acquiring genetic variation after initial establishment. Therefore monitoring programs should be established to both detect new species introductions but also to prevent continued movement of previously established species. Moreover, simply establishing a base of knowledge regarding the identity of species being moved by humans would be an impressive and much-needed step forward. Current efforts to develop a predictive framework for invasion success rely on comparing traits held in common among known invasive species. However, to identify factors that contribute to invasion success, it is necessary to know not only why certain introductions succeed but also why others fail (Simons 2003; Lester 2005; Suarez *et al.* 2005). For this reason also, we strongly suggest the initiation of programs to inspect cargo and document all species that are being transported by humans even if they are not known to have established populations outside of their native range.

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