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SPECIAL ISSUE

Evolution in biological invasion

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Natives adapting to invasive species: ecology, genes, and the sustainability of conservation

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Abstract Contemporary anthropogenic evolution is common. Biological invasions are an especially dynamic form of novel selection. This paper considers how native species evolve in response to biological invasions and the potential consequences of such evolution. Among numerous recent cases, the most widely reported instances are of phytophagous insects shifting onto introduced host plants. For example, our studies show that in North America and Australia, soapberry bugs evolved substantially after colonizing introduced hosts. Such cases permit close estimation of evolution's direction and rate, and we have used cross-rearing studies of derived and ancestral-type populations to measure changes in reaction norms and performance tradeoffs. Different fitness traits have followed very different paths in evolving to their current phenotypic values. Our hybridization studies show that the genetic architecture of these adaptations involves a surprising degree of non-additive variation (epistasis, dominance). The importance of non-additive genetic variation in rapid evolution will be clarified as more studies take advantage of similar situations. As appreciation grows for the deep contemporary interplay of evolution and ecology, debate about qualitative terms describing evolution's rate will become less relevant. From a conservation standpoint, contemporary evolution in native species presents challenges for ecologically appropriate and sustainable management. Evolving natives and invaders may reconfigure contemporary and future communities. Adaptive evolution may also enhance native communities' capacity to control invasive populations.

Keywords Rapid evolution · Soapberry bug · Biological invasion · Conservation · Genetics

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Japanese honeysuckle (*Lonicera japonica*) was introduced into the eastern United States for horticulture 200 years ago and began naturalizing widely by the early 1900s. With the introduction of other East Asian honeysuckles that similarly became abundant environmental weeds (Hartman and McCarthy 2004), hybrid swarms of complex parentage developed (Rehder 1947). In 1997, native North American tephritid fruitflies were discovered infesting wild, hybrid East Asian honeysuckles in Pennsylvania (Schwarz et al. 2005). In their native ranges, the introduced honeysuckle taxa are hosts for Asian *Rhagoletis*, but no infestation of introduced or native *Lonicera* by *Rhagoletis* has been previously reported from North America.

Genetic analyses of the flies newly parasitizing *Lonicera* fruit showed them to be a monophyletic group overlapping with the invaders' geographic distribution. Yet they were not identifiable to a known *Rhagoletis* taxon; instead, they have a unique allelic mixture formed through the hybridization of two native fly taxa: *R. mendax*, which uses native blueberry fruit (*Arctostaphylos*), and *R. zephyria*, which uses native snowberry fruit (*Symphoricarpos*). Due to its hybrid origin, the new taxon differs genetically and appears to be reproductively isolated from its parental taxa. The Lonicera fly is regarded as a new species (Schwarz et al. 2005) that "suddenly" evolved as a host specialist in response to swift ecological changes rendered by Asia-native plants invading North America.

The rapid origin of a new species in response to a nonnative weed reveals the biological complexity of invasion issues and the implications of evolutionary responses to global change. The major factors destroying Earth's biodiversity are describable in simple terms: destruction comes from eliminating and converting habitats that kills individuals and prevents reproduction. Poisoning, over-harvesting, species introductions and climate change further alter habitats, disintegrate natural communities, alter niches and reduce carrying capacity (e.g., Cox 2004; Diamond 1989). When resources change in form, distribution and abundance, they create new niches, affect competition, eliminate enemies and recast the landscape for surviving taxa. These ecological changes raise the possibility that adaptive evolution, emerging from the demographic chaos suffered by 'refugee taxa,' will prove to be foremost in altering the form and structure of species and communities in the coming years, decades and millennia. A chief result of efforts to secure sanctuary for species and biota will be to provide raw material for such evolution. Accordingly, a principal challenge of conservation biology is to predict and manage the structure of communities that have unprecedented assemblages of juxtaposed, and rapidly evolving, remnant species (Carroll 2007; Strauss et al. 2006a).

The human-influenced geographic shuffling of organisms is probably the most biologically dynamic of anthropogenic 'global change' phenomena. Nonindigenous (a.k.a. 'nonnative' or 'introduced') species are populations of organisms not native to a particular habitat. If established populations of a nonnative species grow and spread due to successful reproduction and recruitment of subsequent generations into the breeding population, that species may become prominent in the native biota, or 'invasive' (Parker et al. 1999; Richardson et al. 2000). Invasive species may become numerically and ecologically dominant to native populations (Crooks 2002; Davis and Thompson 2000).

Disturbed habitats may lose constituent species and are more susceptible to nonindigenous taxa (e.g., Davis et al. 2000; Elton 1958; Rejmanek et al. 2004). Nonindigenous organisms may become established in disturbed habitats by accessing resources left unused because resident taxa are reduced (Fargione and Tilman 2005; Levine et al. 2004), or because they are better adapted to disturbed habitats than are residents (e.g., Burke and Grime 1996; Strauss et al. 2006b). Whether in disturbed habitats or not, nonindigenous species may, during introduction, escape natural enemies in ways that give them a competitive advantage over residents regulated by activity at higher tropic levels (e.g., Colautti et al. 2004; Joshi and Vrieling 2005; Stastny et al. 2005). Thus, as an introduced species transitions into a community, the ecological circumstance of the invasion, as well as the invading population's genetic history, may influence niche opportunities available to the newcomers.

Invasive species necessarily exist within biotic communities, and thus play many parts in ecological webs. They can be predators, pathogens, parasites, competitors, mutualists or hosts (e.g., Mitchell et al. 2006). Certain prominent examples highlight interactions in anthropogenic communities. For example, controlling invasive rabbits by introducing the *Mxyoma* virus in Australia involved well-documented gradients of virulence and resistance evolution (Fenner and Ratcliffe 1965). In Guam, the introduced brown tree snake, *Boiga regularis*, eliminated native birds and shifted to lizard prey (Fritts and Rodda 1998). However, we are just beginning to appreciate the breadth of ways in which invasive species may alter native communities and how quickly they may do so. As chronicled perturbations, invasion events offer increasingly commonplace opportunities to test ideas about how communities assemble (Strauss et al. 2006a). As researchers exploit more of these opportunities, we will better understand how invasive species integrate into new communities.

This paper examines how native species may evolve in response to biological invasions and the potential consequences of such evolution. Evolutionary changes in both native and exotic taxa may determine how communities reconfigure following invasion (Cox 2004; Lambrinos 2004; Strauss et al. 2006a; Vermeij 1996; Yoshida et al. 2003). This paper also reviews work about rapid evolution in an insect seed predator in response to introduced plants, describes the ecological and genetic bases for its ongoing adaptive evolution and evaluates ecological and conservation consequences of such fundamental change in species.

Phylogeny and ecology in invasions of native communities

Colonists from biologically distant locales that survive and reproduce in a new habitat will form a variety of relationships with natives. How those relationships develop depends on a variety of factors. The colonists' degree of pre-adaptation may strongly influence how quickly their population grows and the form and strength of their interactions with natives. Pre-adaptation may mean that a colonist can readily find resources, escape from enemies or avoid abiotic perils. For example, Strauss et al. (2006b) found that in California, grasses with few close relatives in the native flora were more likely to invade than were those with many close relatives, implying that resources were more available (or risks lower) for genetically distant colonists. The relatively more novel genotype-by-environment interactions represented by new genera (rather than species in a genus already present) colonizing a habitat may represent an instantaneous "niche-creation" process.

In such cases, where colonization succeeds due to low levels of competition with natives, impacts on native communities may (at least initially) be slight. Colonist populations may then grow until interspecific competition for one or more resources becomes important. To the extent that colonists have certain advantages over natives (e.g., enemy-free space), they may out-compete them and become deleteriously invasive.

The hypothesis that invaders may prosper due to "escape from enemies" has been especially well examined in plants (e.g., Mitchell et al. 2006). Any organism that colonizes a new place has necessarily passed through chance and mortality filters during transport and establishment; its familiar biological associates may not have had similar opportunities or success. In particular, dependent associates occupying higher trophic levels may be especially vulnerable to extinction even if they travel with their hosts. Plants arriving in new locales may therefore be exposed to fewer species of insect herbivores and pathogens than previously and in comparison to native plants in the new locale (Agrawal et al. 2005; Colautti et al. 2004; Keane and Crawley 2002; Mitchell et al. 2006). Consequently, invaders may have competitive advantages over ecologically similar natives.

Successful invaders may benefit from other advantages as well. For example, some of their attributes may be unusually effective in their new environments, whether due to a functional coincidence or to the absence of historical coadaptation with the new neighbors. The devastation of behaviorally naïve island faunas by introduced vertebrate predators is an example of the former. For the latter, Callaway and Ridenour (2004) propose the 'novel weapons' hypothesis, suggesting (with respect to plants) that competitors in the habitat of origin evolved tolerance to allelopathic compounds, while those in the new range have not. This hypothesis also relies on coincidence, i.e., that in some cases, colonists' vulnerabilities will by chance be less significant than the native community's reciprocal vulnerabilities.

If a nonindigenous species prospers and becomes common, it may become a resource for natives. This will be influenced by the degree of pre-adaptation in the native community. At one extreme, an example of a complete lack of such pre-adaptation is the case of invasive *Opuntia* cactus in Australia, where more than 150 years since introduction, no native insects have adopted this member of a plant family novel to the biogeographic realm (Moran 1980). An intermediate scenario is posed by invasive European *Silene* in North America. Compared to its ancestral range, on the new continent, this taxon experiences less damage from natural enemies. An apparent consequence has been the evolution of reduced enemy resistance and increased growth and reproduction over the past 200 years (Wolfe et al. 2004). Yet introduced plants may also experience insect attack at rates similar to those of related natives (Agrawal and Kotanen 2003) and may even evolve increased tolerance to herbivory (Stastny et al. 2005). Lastly, proof that close interactions may develop between invaders and natives became evident when introduced members of the soapberry family (well represented in Australia) became sufficiently important to a native seed-feeding insect within about 40 years of naturalizing to select for morphological changes (Carroll et al. 2005a below).

Evolution in response to invasion

Whether a native population evolves in response to an invader depends on attributes of both the invader and the affected natives. Not only must the invader have a strong ecological impact, but it also must affect different genotypes nonrandomly (Strauss et al. 2006a). The ecologically catastrophic invasions of North America by the European fungal pathogen *Cryphonectria parasitica*, cause of 'Chestnut Blight' in native *Castanea dentata*, and the Asian fungal pathogen *Ophiostoma ulmi*, cause of 'Dutch Elm Disease' in *Ulmus americana*, are two examples of vast mortality events that lack clear evidence of selection and consequent evolution in victims. Compared to their population peaks when hosts were still abundant, those pathogens are now rare, yet still controlling their hosts.

In contrast, should a recently arrived community member harm members of a native population more than others without decimating the population, and that difference is due to genetic differences among natives, evolution may result (e.g., Kiesecker and Blaustein 1997). Similarly, evolution may occur if some genotypes benefit from invasion when a new species directly or indirectly supports their propagation. Adaptive evolution may be especially rapid in natives pre-adapted to colonize invaders, as when herbivores successfully adopt novel plants that are phylogentically related to their native hosts. Genotypes better pre-adapted to the changed circumstances may produce rapidly expanding lineages that quickly refashion the traits associated with exploiting the new resource (e.g., Carroll 2006; Carroll et al. 1997). Of course, genetic differences among individual invaders will likely interplay with such differences in natives, predicting evolutionary and coevolutionary dynamics within and between both classes of organisms. This natural, but more complex, eventuality has yet to be thoroughly explored.

The most common examples of evolution in response to invasion are of two contrasting trophic types (Strauss et al. 2006a). The first involves prey (principal examples are native anurans, fish and crustaceans) evolving in response to introduced predators. Here, interesting questions arise: can evolution protect populations from extinction? How does evolution interact with prey population dynamics? The second trophic relation involves native herbivores (mainly insects) evolving because of interactions with introduced plants. These herbivores colonize a new resource in their midst, one that is of sufficient value to permit persistence while simultaneously selecting for altered trait values. Here the question is not one of extinction, but one of diversification and perhaps speciation. Two interesting questions arise in these cases: How does preference for, and performance on, a new host influence gene flow with populations on nearby native hosts? And how may such interactions impact host specialization in both populations?

In cases of introduced predators, anti-predator adaptations include morphological and behavioral changes that reduce the probability of mortality. Kiesecker and Blaustein's example (1997) showed phenotypic difference between larval native frogs ('tadpoles') of western North American *Rana aurora* inhabiting ponds invaded by, versus free from, their predaceous eastern North American congener, the 'bullfrog' *R. catesbiana*. Native tadpoles from invaded ponds altered their behavior to avoid potential predation when exposed to bullfrogs' chemical cues, but those from uninvaded ponds showed no response. The defensive response evolved during the 60 years between the predator's invasion and the time of the study.

Evolution in native prey over surprisingly few generations implicates very strong selective mortality. Yet rapid evolution also means that the predator-prey interaction may, by the time a study is conducted, already be ecologically different from when the most intensive selection took place. Experiments that intentionally introduce predators prove that rapid evolution may ensue across the first few generations (e.g., Losos et al. 2004; Reznick et al. 1997). A largely unexplored area is the degree to which evolutionary change in prey may influence their population dynamics with respect to predation. Yoshida et al. (2003) showed that prey evolution can determine predator-prey dynamics. Hairston et al. (2005) built on that result to suggest that 'rapid' evolution should be defined ecologically, i.e., evolution is rapid if it significantly influences a measure of ecological performance.

Phytophagous insects' colonization of new host plants has been studied as an evolutionary force since before biotic invasions' conservation impact was widely appreciated (e.g., Bush 1969; Carroll and Boyd 1992; Singer et al. 1993; Tabashnik 1983). Nonetheless, for a novel plant to become selectively important, it must often be abundant. Accordingly, some of the best examples of rapid evolution in phytophagy do not strictly involve host invasions, but rather crop plants (e.g., Malausa et al. 2005) or horticultural plantings that were colonized before naturalization (e.g., Carroll and Boyd 1992; Filchak et al. 2000). The introduced population's size may be especially important when the introduction is in close proximity to native hosts, but less so when insects discover new hosts in allopatry. Feeding or oviposition preference should be a key trait if gene flow to and from populations on native hosts may otherwise prevent differentiation. Such concerns have fueled the decades-long controversy about the probability that sympatric speciation could be prominent in nature. Microgeographic differences do exist in preference among host-associated populations (e.g., Dres and Mallet 2002; Nosil et al. 2006). Host-associated populations have also rapidly differentiated in other fitness traits, including morphology, development, survivorship and life history (e.g., Carroll et al. 1997, 1998, 2005a; Singer et al. 1993; Thomas et al. 1987).

Evolution in soapberry bugs in response to introduced and invasive plants

Soapberry bugs are brightly colored, aggregating seed predators in the Hemipteran sub-family Serinethinae (Rhopalidae), a worldwide group of three genera and about 70 species specialized on the plant family Sapindaceae (Carroll et al. 2005a). The Sapindaceae, or 'soapberry' family, is mainly tropical and includes fruits like lychee and longan, plus maples (*Acer*) and soapberry trees (*Sapindus spp.*). Populations of the soapberry bug *Jadera haematoloma*, which use two native North American sapinds, have been differentiating since they colonized three sapinds introduced into their range over the past 50 years (Carroll and Boyd 1992; Carroll et al. 1997).

Our experimental studies focused on bugs within Florida, where the native host, balloon vine (*Cardiospermum corindum*), occurs in the far south of the state. The goldenrain tree *Koelreuteria elegans* (ssp. *formosana*) was planted in central Florida 5 decades ago. This ornamental has naturalized, and Florida regards it as a potentially serious environmental weed. In addition to having smaller fruit (Carroll and Boyd 1992), the introduced tree's seeds have more fat and less protein (Carroll et al. 1998), an alternate cyanolipid seed-defense (Siegler and Kawahara 1976) and larger production numbers over a much briefer annual period of seed production (Carroll et al. 2003b).

Because bug populations on the native balloon host now closely resemble museum specimens collected before *K. elegans* was introduced, we regard modern populations as an 'ancestral-type' race, meaning that we infer that they are genetically similar to the population that gave rise to a 'derived' race on *K. elegans*. This adaptive derivation process took place over about 100 generations or fewer (Carroll and Boyd 1992).

We explored performance evolution by cross-rearing bugs from each race on the dehisced seeds of either host species. For example, when reared on the new host versus the native host, derived bugs mature 25% faster, are 20% more likely to survive and lay almost twice as many eggs. Fecundity is twice that of ancestral-type bugs reared on either host, while eggs are 20% smaller. At the same time, performance loss on the original, native host evolved at a similar rate and often in a symmetrical manner (Carroll et al. 1997, 1998, 2001, 2003a, b). These evolved performance contrasts may have contributed to selecting for the considerable differences that evolved in host preference (Carroll et al. 2003a), although it is unlikely that individuals would encounter more than one of the two host species due to their strongly allopatric distribution. Faster evolution and greater fecundity likely enhance reproductive success in the annually cycling habitat that the new host's seed crop represents. Part of that change has been through the increase of a flightless, rapidly cycling morph (Carroll et al. 2003b), and so a pre-existing genetic basis for a phenotypic life flight/life history discontinuity may have predisposed the ancestral population to adapt quickly to the challenges posed by the new host.

Rearing contemporary bugs from the native balloon vine on seeds of the introduced goldenrain tree perhaps recreates how early colonists responded to the new host 5 decades ago, evoking a scenario of pioneers founding a population that performs weakly, yet persists as a colony of poorly adapted phenotypes. Directional selection among survivors transformed the population through the evolution of new trait values, which now map as adaptive reaction norms that are the reverse of the previous. The form of adaptation differed widely among the traits studied. For example, developmental stress appears to be an affect of the host shift that countergradient selection overcame to return some traits to their former ancestral values, such as survivorship and development time (Carroll et al. 1997; Grether 2005). In contrast, the developmental response of body size to the new host plant is ultimately favored by selection, suggesting a promotional role of plasticity in moving the population toward a new adaptive peak (Ghalambor et al. 2007). Egg size appears unaffected by the developmental host, but that the native host loses performance in the other traits is probably a pleiotropic epiphenomenon to the adaptive evolution.

The successful colonization of, and adaptation to, the introduced host was likely promoted by several factors. Most fundamentally, in its native Taiwan, the goldenrain tree is the principal host of the native soapberry bug *Leptocoris vicinus* (the accepted identification of that species as *L. augur* in Taiwan appears to be incorrect [Carroll, unpublished data]. Soapberry bugs do not attack many sapind genera (e.g., Carroll et al. 2005b), but the goldenrain tree's ready adoption by *Jadera* in North America may have been phylogenetically facilitated by its history in East Asia. Moreover, no other seed predator colonized *Koelreuteria*, and as plantings matured, large crops of uncontested seeds would have become available. Strong early population growth might have been important in creating a demographic buffer, permitting colonists to withstand the stresses to which they were least pre-adapted. Rapid population growth is a common attribute of contemporary cases of adaptive evolution in colonists (Reznick and Ghalambor 2001; Reznick et al. 2004) and may be important in multiplying beneficial alleles rare among colonists. It could also generate new, beneficial gene–gene interactions (epistatis) and, ultimately, new genes (via mutations, which appear in proportion to population size), permitting further evolution. Altogether, these circumstances may have permitted relatively free natural 'experimentation' on the evolutionary path to adapted, derived phenotypes (Carroll 2006). Pre-adaptation provided sufficient developmental plasticity to permit survival and reproduction on the new host, bridging what otherwise might have been a fatal valley in the adaptive landscape and catalyzing rapid evolution in the likely absence of significant mutation (below; Ghalambor et al. 2007).

Remarkably, the goldenrain tree race consists of bugs that appear to have differentiated more deeply in terms of genetic organization than might be anticipated from their recently evolved phenotypic values. Contrary to theoretical expectations, nonadditive genetic variation (epistasis, dominance) underlies much of the differentiation among host races (Carroll 2006). That surprising finding suggests a role for multilayered genetic changes early in the process of adaptive population differentiation, a result inconsistent with gradual accumulation of point mutations. One speculative interpretation is that novel, selectively favored phenotypes resulted from formerly neutral variation, now expressed for the first time in genotypes in new host environments (sensu Badyaev et al. 2005). Another is that small, initial colonist populations might differ so much from their parental populations in allele frequencies that overrepresented, chance novel combinations would generate new gene–gene interactions (epistasis), leading to unprecedented phenotypes, with a small but important proportion adapted to the new environment: a founder-flush scenario (e.g., Regan et al. 2003).

While Florida's *J. haematoloma* populations shifted from native *C. corindum* to *K. elegans*, in the south-central US, the shift was from native *Sapindus* to introduced *K. paniculata* (from China) and introduced *C. halicacabum* (pan-subtropical). These host-associated races differentiated in patterns similar to those observed in Florida (Carroll and Boyd 1992; Carroll and Dingle 1996; Carroll, unpublished data). Taken together, these events portray unfettered rapid adaptation on a continent-wide scale. Yet such changes are not inevitable. To illustrate that point: in coastal Texas and the Bahamas (near Florida), soapberry bugs on native hosts have failed to colonize *K. elegans*, and massive seed crops go unutilized (Carroll, unpublished data). In those regions, the first steps toward adaptation, and consequent diversification, have not even begun, while in nearby locales, tremendous functional changes have already evolved.

Lastly, the patterns of adaptation we found in North America led us to explore the conservation significance of contemporary evolution in soapberry bugs of Australia, where invasive sapinds are a more serious environmental problem. Australia's native sapindaceous flora probably include about five times the number of host species as does that of North America and is much more widespread. The five recognized species of *Leptocoris* soapberry bugs together range over most of the continent, and it is possible that additional, host-based species remain to be fully distinguished (Carroll et al. 2005b).

Keen to explore multiple continents, horticultural escapees *K. elegans formosana*, and another Neotropical balloon vine, *Cardiospermum grandiflorum*, have invaded eastern coastal Australia over the past several decades (Carroll et al. 2005c). They colonized riparian and disturbed forest habitats, and are now expanding inland into intact moist forests. Balloon vine is regarded as a serious environmental weed (Batianoff and Butler 2002) and is abundant in many areas, whereas the goldenrain tree is still a perceived threat and relatively rare. To determine whether Australian soapberry bugs are adapting to invading sapinds in the manner of North American *Jadera*, we began by measuring beak length as a function of host in *Leptocoris tagalicus*. This bug species appears to occupy the invaders more reliably than it does its main native host in the invasion region, the woolly rambutan tree (*Alectryon tomentosus*; Carroll et al. 2005b, 2006). Woolly rambutan has much smaller fruits than the balloon vine (which are inflated like those in the native Florida species), but its fruits are larger than those of the goldenrain tree. These plants have many other differences of potential significance to specialized seed predators.

Because morphological size characteristics are easy to measure, in 2004 we sampled beak length and thorax width (a measure of overall body size) of approximately 1,000 adults across the three hosts to test for adaptive differentiation among host-associated bug populations. In both sexes, the grand mean beak length of the 12 populations on balloon vine was greater than the means for all 10 populations on native rambutan (Table 1; $P < 0.002$ in Wilcoxon rank-sum test of population means; thorax widths did not differ significantly; Carroll et al. 2005a). Developmental data from cross-rearing experiments showed that bugs from lines collected from the invasive host had longer beaks irrespective of the rearing host, indicating that host-associated population differences in beak lengths of wild bugs are genetic (Carroll et al. 2005a).

In contrast, thorax width was substantially smaller in eight populations from planted (rather than naturalized) goldenrain trees (Table 1). While beak length is, as predicted, much shorter on goldenrain trees, we have not yet tested whether that difference has a genetic basis or is induced by the developmental host. The reduced body size suggests that development is impaired on the new host, but we cannot yet distinguish evolutionary versus developmental hypotheses in this case.

Both the main effect 'host' and the covariate 'thorax width' significantly affect beak length (Table 2). In addition, the effect of the interaction of thorax width and host differs among host-associated populations, which indicates that the relation between thorax width and beak length differs among them. While the collection locale, within host, is also significant to the analysis, comparing the *F* ratios shows site variation within hosts to be much less important than the host species itself (Table 2).

To understand the history of change further, we measured beak length and body size in museum specimens collected between 1920 and 2000. Because *Koelreuteria* is rare compared to *Cardiospermum*, which is extensively naturalized, and *Alectryon*, which is common in moist rainforests, we anticipated that beak elongation would be more likely to appear as a trend from older to more recent collections. No host data accompany these museum specimens, and later collections may include bugs from any host. In females, beak length of the 16 post-1965 individuals averages more than a half-millimeter longer than that of 6 comparable individuals collected before 1965 (7.41 ± 0.35 versus 6.81 ± 0.35 mm, $P < 0.003$ in Wilcoxon rank-sum test; Carroll et al. 2005a). Thorax width has not changed significantly (3.41 ± 0.10 versus 3.39 ± 0.15 mm, respectively), indicating that the change in beak length results from developmental reorganization rather than just an overall body-size increase. Results for males are similar (Carroll et al. 2005a).

How does this evolutionary change interact ecologically with invasive balloon vine? In one experiment, we exposed unattacked balloon vine seed capsules to laboratory-reared females from either balloon vine or native rambutan. Females of both histories attempted to feed with equal frequency, but the balloon vine bugs (with their longer beaks) successfully fed on 75% more seeds over a 1-week period (Carroll et al. 2005a), suggesting that the balloon vine-adapted bugs' longer beaks permit them to attack invaders' seeds much more efficiently. Balloon vine is probably so abundant that increased selection from more efficient seed predation will not be strong enough to measurably influence fruit-size evolution yet. However, if the ability of *L. tagalicus* to kill seeds continues to increase, it may soon become a potent selective agent. In addition, from a practical standpoint, because of propagules' general importance to recruitment in an expanding population, and for establishing new subpopulations in new habitats, this insect's ability to serve as an effective indigenous biological control agent may also be evolving.

Discussion

Contemporary evolution in response to anthropogenic change appears to be increasingly common (e.g., Palumbi 2001), and biological invasions will be a chief

Table 1 Beak length differences among host-associated populations of the Australian soapberry bug *Leptocoris tagalicus* are illustrated by mean values[1] for females

Trait	*Cardiospermum grandiflorum* (*N* = 12; nonnative)	*Alectryon tomentosus* (*N* = 10; native)	*Koelreuteria elegans* (*N* = 8; nonnative)
Beak length	7.43 ± 0.15	7.11 ± 0.11	6.78 ± 0.72
Thorax width	3.42 ± 0.06	3.36 ± 0.07	3.15 ± 0.17

[1] Values (mm) are grand means of (*N*) population means for each host sampled. This insect occurs on two nonnative host species with fruit sizes that straddle that of the principal native host in their introduction/naturalization region

Table 2 ANCOVA of host-associated variation in female beak length as an effect of thorax width (an indicator of body size), host, their interaction and site of collection (within host)

Source	DF	Sum of squares	*F* ratio	Prob > *F*
Thorax width	1	13.434203	124.2766	< 0.0001
Host	2	6.260163	28.9556	< 0.0001
Site [host]	29	5.321542	1.7582	0.0105
Thorax width × host	2	0.843199	3.9001	0.0209

Size values were log-transformed for analysis theater in which such evolution plays out. Certainly, there is evidence of invasive species evolving in response to selective differences between their current and former environments (e.g., Lee 2002; Phillips et al. 2006; Siemann and Rogers 2003; Wolfe et al. 2004). Such evolution may in fact be important to the process of invasion. The substantial time lag between when some species are introduced and when they be become invasive is often thought to represent a period during which evolution occurs to the point that invasion becomes possible (Kowarik 1995). Moreover, work by Phillips et al. (2006) on limb elongation in invasive *Bufo marinus* toads in central Australia indicates that evolution may be taking place in response to the toad's 'evolving experience.' In other words, novel aspects of genotype-by-environment interaction, which may develop as peregrinating genotypes become more common as they spread into additional unoccupied habitats, may continue to generate new, derivative selective environments that create yet more evolutionary change. Hence, the 'before-versus-after' invasion dichotomy may be oversimplified, because invasive species' evolutionary trajectories could remain indefinitely dynamic as they continue to expand their geographic ranges, and as their host communities respond ecologically and evolutionarily. Thus, the impacts of invasive species will continue to develop because many recently introduced species have not yet, but soon may, find a successful combination of genetic and environmental opportunity, and those that are already invasive may continue to alter their relationships within native communities.

Evidence for native evolution in response to invasions is interesting and abundant. It indicates that an invader has had sufficient impact, positive or negative, on at least one native population to alter the selective environment. That is a scientifically valuable phenomenon because it offers the opportunity to examine processes involved in the assembly and re-assembly of biotic communities in a manner that would otherwise not often be possible. While too many biological invasions will be seriously disruptive and often reduce local biodiversity, conducting basic science on the demographic, ecological and evolutionary processes at work will be greatly useful in laying the foundation of the emerging field of evolutionary conservation management.

Strauss et al. (2006a) found more than 30 published cases of evolution in response to invasion. Herbivory on novel hosts and novel predator-prey associations were the most common, but competition, disease and other parasitism were also represented, as was at least one case of an indirect effect (Smith et al. 1995). The most evident cases will be those in which selection is altered by either great destructive influences or great opportunity. The strongest negative effects, e.g., novel predation, disease or competition, may not generate direct evolutionary legacies in invaded communities if they eliminate native populations before evolution can rescue them (e.g., Parchman and Benkman 2002). On the other hand, decimating invasions will doubtless have lasting indirect influences on community evolution, but these may take more time to occur and be more difficult to link to their causes. In contrast, when invaders become abundant new resources for natives, selection to take advantage of opportunity need not be as strong to result in detectable evolution if the overall effect is population growth. Between those extremes, discerning evolution may require intensive observation and careful experimentation. More refined and co-evolutionary relationships such as new mutualisms may, on average, take longer to evolve (Mitchell et al. 2006). That last possibility is of particular concern because specialized biotic relationships are those that may most readily disappear due to invader disturbance, and disturbed communities may come to include greater proportions of transient generalists (Rodland and Bottjer 2001). Yet the Lonicera fly example that opens this paper is an instance of the surprisingly rapid evolution of an extreme specialist (Schwarz et al. 2005), and new specializations in soapberry bug populations are increasing the phenotypic and, likely, the genetic diversity of the clade (Carroll 2007).

Key to understanding evolutionary change in invasive and native species, directly and indirectly, will be means by which to integrate ecological and evolutionary analyses (Hairston et al. 2005; Lambrinos 2004). Building from Thompson (1998), Hairston et al. (2005) proposed that rapid evolution be defined as "a genetic change occurring rapidly enough to have a measurable impact on simultaneous ecological change." In other words, the adaptive products of selection must influence that ongoing selection as a result of their evolutionary change. The authors refer to this as the "convergence of ecological and evolutionary time." Their analytical approach is to assess the mutual influence of ecological and evolutionary impacts. Assessing those effects will depend on a clear and quantitative understanding of causal relationships, something that may be difficult to obtain in circumstances less 'microcosmic' than the copepod/fish and island finch/seed examples they dissect. Other cases will often involve more complex, community-level interactions, including the presence of many indirect, ramifying interactions (sensu Mitchell et al. 2006). Taking a prospective approach, which anticipates native evolution, may lead us to make early measurements in more complex biological systems and thus to generate baseline data that would ultimately permit incisive analyses.

The ecological definition proposed by Hairston et al. (2005) is important because it is a clear formalization, but it may be too restrictive in at three least ways. First and simplest, it precludes assigning such qualities as 'rapid' in non-ecological discussions comparing evolutionary rates. This concern is likely resolvable by context, however. Second and more importantly, it is difficult to imagine cases of rapid evolution due to biotic processes in which there actually is no feedback on the selective agent, even when we fail to measure it. It is true that biologically remarkable and scientifically informative adaptive evolution may occur in response to introduced enemies or resources with little evident influence on the invaders. In cases where novel enemies drive a native population to extinction, any differential survival and reproduction among genotypes before extinction implies likely influence on some aspects of the introduced species, whether behavioral, energetic or subtly demographic. Similarly, new resources, such as introduced plants that alter native herbivores' lives, may appear to suffer little ecological feedback from those insects during the invasion process. Documenting any such effects may require years of labor-intensive data collection and complex analyses (e.g., Fagan et al. 2005), such that evident evolution might only qualify as 'rapid' only years after genetically based phenotypic change is noted. Moreover, community-level responses to such change, e.g., extinction or evolution, may become evident only after evolution occurs. Predators altered by evolution in now-extinct prey, for example, may differ significantly in their interactions with other prey species due to that alteration, just as natives' phenotypic evolution in response to new resources may in theory influence their interactions with other native and introduced community members. The third difficulty is that while these examples meet the Hairston et al. (2005) criterion of considering the ecological consequences of evolutionary change, they call into question the utility of relying on a requirement of simultaneous action.

Understanding causality, its temporal structure and its spatial behavior will be central to the evolutionary synthesis of conservation practices and sustainability issues. Invasive species biology is an excellent venue for such efforts because of its community context and need for both preemptive action and long-term study. Adding evolution to conservation invokes the familiar exhortation to include more natural history in management planning, but with more challenging requirements. Yet, to the extent that evolution is predictable, and central to the creation of biodiversity, we must harness its power to ameliorate damage and reconstitute species and ecosystem functions. For example, as agricultural science does, practices to control invasive species should use resistance-management planning. Likewise, gene flow can be manipulated to influence rates of local adaptation (Stockwell et al. 2003), and selection may be promoted to protect native communities by fostering evolution of invasion-resistant species (Carroll et al. 2005a).

Like adaptation itself, evolutionary management will sometimes need to balance severe tradeoffs. Retaining genetic diversity is a cardinal goal of conservation management, but selection to improve fitness in changing conditions is likely to reduce genetic variation. Conservation tactics could thus be conflicting: practices preserving genetic variation to protect long-term evolutionary potential may directly impede current adaptive processes (Stockwell et al. 2003). Learning to balance such competing goals will require substantial experimentation. It is certain that biological invasions will offer many such opportunities.

As global change phenomena become more potent and appreciated, I predict that dialogue throughout the field of evolutionary ecology will soon become dominated by discussions of systems in which evolution is ongoing, directional and non-reversing. Community and conservation ecology will likewise become microevolutionary disciplines. When that happens, concerns about issues such as 'slow versus fast' evolution will likely be superceded as we work from more unified perspectives and positions about the problems and opportunities to be addressed.

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