# Facing change: forms and foundations of contemporary adaptation to biotic invasions

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## Abstract

**Ongoing adaptation in native populations to anthropogenic change both facilitates and challenges ecologically appropriate and sustainable management. Human disturbance promotes adaptive responses at the genomic, individual and population levels. Traits vary widely in whether adaptation occurs through plasticity or evolution, and these modes interact within and among traits. For example, plasticity in one trait may be adaptive because it permits homeostasis and lessens the intensity of selection in another. Both opportunity and catastrophe generate adaptive responses. Recently evolved adaptations characterize the responses of many native species to biotic invasions. Several well-known examples involve native phytophagous insects colonizing introduced plants. For example, our studies of North American and Australian soapberry bugs on nonindigenous plants demonstrate both diversifying and homogenizing contemporary evolution. Modes of adaptation differ among traits and populations and as a function of the host on which they develop. The genetic architecture of the evolving adaptations involves a substantial degree of nonadditive genetic variation. One important consequence of contemporary adaptation may be an enhanced capacity of native communities to provide *adaptive biological control* of invasive species. Conservation scientists may manipulate adaptation to achieve conservation goals, but must also decide how deeply they wish to attempt to control the phenotypes and genotypes of other species.**

*Keywords*: adaptation, biological control, conservation, contemporary evolution, invasion, soapberry bug

## Introduction

Human actions and population growth do more than alter the local and global carrying capacities of other species. By modifying the challenges organisms face, and the resources they have to address them, we alter their behavioural, physiological and evolutionary circumstances. Sometimes, the impacts of factors such as novel predation or habitat change may be so swift or thorough that there is little possibility for adaptive response, with extinction being the result. At the other extreme, change benefits some organisms by providing them with expanded or improved habitats. Selection may actually be relaxed, or evolutionary diversification released, as a result. Between these extremes, many populations are likely experiencing

selection in new directions and at new intensities, and the degree to which populations respond adaptively may have an important influence on their capacity to survive over the coming decades and millennia. Moreover, such evolution will alter biotic communities by changing the dynamics of interspecific interactions (Thompson 1998; Hairston *et al*. 2005; Strauss *et al*. 2006a). Because these outcomes are inevitable, understanding the probability of, and capacity for, adaptation in affected populations should be a growing focus of conservation biology.

Evolutionarily significant environmental change is caused by many human activities, including the elimination and conversion of habitats, poisoning, over-harvesting, species introductions and climate change (e.g. Vitousek *et al*. 1997). Among these, species introductions may be especially dynamic because they generate new biological interactions (e.g. O'Dowd *et al*. 2003). Nonnatives interact in ecological webs as predators, pathogens, parasites,

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competitors, mutualists or hosts (e.g. Mitchell *et al.* 2006). Nonindigenous populations that establish and spread by successful reproduction and recruitment of subsequent breeding generations may become prominent in the native biota and may be designated 'invasive' (Parker *et al.* 1999; Richardson *et al.* 2000). Invasive species may become numerically and ecologically dominant to native populations (Davis & Thompson 2000; Crooks 2002).

On the other hand, only a small proportion of introduced species become invasive (Williamson & Fitter 1996), suggesting that interactions with natives may control their establishment and spread. Consistent with this inference, disturbed habitats that lose native species are more susceptible to invasion by nonindigenous taxa (e.g. Elton 1958; Davis *et al.* 2000; Rejmanek *et al.* 2004). Nonindigenous organisms may establish in disturbed habitats by accessing resources left unused by reduced resident taxa (Levine *et al.* 2004; Fargione & Tilman 2005), or because they are better adapted to using human-altered habitats (e.g. Burke & Grime 1996; Strauss *et al.* 2006b). Phylogenetic meta-analyses with plants indicate that colonizers with native relatives share preadaptive defences against native herbivores (Ricciardi & Ward 2006), while at the same time, successful colonists appear more likely to become invasive if they lack close relatives in the native flora (Strauss *et al.* 2006b), perhaps due to reduced competition for a particular niche.

In addition, nonindigenous species may escape natural enemies during introduction, giving them a competitive advantage over native species that are regulated by native competitors or enemies (e.g. Colautti *et al.* 2004; Joshi & Vrieling 2005; Stastny *et al.* 2005). Thus, as an introduced species transitions into a community, the ecological circumstance of the invasion (called 'niche opportunity' by Shea & Chesson 2000), as well as the invading population's genetic history (Darwin 1859; Strauss *et al.* 2006b) and phenotypic potential (the range of phenotypes a population is capable of expressing across all environments; Carroll & Watters in press) may influence the options available to the newcomers.

Adaptive changes in both native and exotic taxa may determine how communities reconfigure as a result of invasion (Vermeij 1996; Yoshida *et al.* 2003; Cox 2004; Lambrinos 2004; Strauss *et al.* 2006a; Carroll 2007a, b; Lee *et al.* 2007). However, not all organismal responses, whether phenotypic or genotypic, are reliably adaptive (Box 1). This paper considers the diversity of ways in which native species may respond to introduced taxa, and the potential evolutionary and demographic consequences of such responses. Among the questions it considers is 'can a native community that initially permits an invasion then evolve quickly enough to control it?' While explored in theory over the decades, the importance and prevalence of evolutionary change as an agent of ecological significance have only recently begun to become widely appreciated (Thompson 1998; Hairston *et al.* 2005; Carroll *et al.* 2007). I present interrelated examples of invasive plant species currently spreading in Australia and North America, to which native insects show increased adaptation. I describe the ecological, phenotypic and genetic bases for this contemporary adaptation, evaluate the ecological and conservation consequences of ongoing change, and consider the potential for active evolutionary management of interacting species.

## A forest-invading vine

On the Australian continent, the transformation of introduced plants into weeds that invade its natural environments is recognized as a problem of great ecological and economical significance. Of the approximately 28 000 plant species brought to Australia in the past two centuries, about 10% have become environmental weeds (e.g. Groves *et al.* 2003). That percentage far exceeds the 1% 'rule' for naturalization quoted in temperate studies (e.g. Kowarik 1995) and suggests that areas of Australia resemble tropical oceanic islands in their vulnerability to plant invasions. The majority of its invaders are descended from horticultural introductions (Martin 2002).

Balloon vine, *Cardiospermum grandiflorum*, is a tendril climber in the soapberry family (Sapindaceae) native to warm habitats from southern Mexico to southern Brazil. In the American tropics, balloon vine species support a small community of seed-eating insects from three orders that have overcome the plants' cyanide-based defences (Carroll & Loye 1987, 2006). Due to the curious inflated seedpods and attractive appearance, balloon vine is planted as an ornamental in many warm areas of the world. It was introduced in eastern Australia in about 1920 from unknown sources and it almost immediately naturalized. Range expansion was relatively slow until the 1960s but then accelerated and appears to continue within watersheds. It grows on a diversity of soils and is especially abundant along rivers, where it may cover native and other vegetation in uninterrupted stands several kilometers in length (Carroll *et al.* 2005a). In addition to governmental declaration as an 'environmental weed' in many areas of eastern Australia (Batianoff & Butler 2003), it is recognized as an invader of serious ecological consequence in South Africa (Olckers 2003) and the Cook Islands (Meyer 2000).

Heteropteran 'true' bugs of the subfamily Serinethinae are specialists on seeds of the Sapindaceae and hence are called soapberry bugs (*Jadera, Leptocoris, Boisea*). Balloon-vine species are attacked by soapberry-bug species worldwide (Carroll, unpublished). One bug species, *Jadera haematoloma*, is particularly effective in gaining access to the seeds within the inflated capsule by virtue of its greatly elongated mouthparts (Carroll & Boyd 1992). This is the only species known to regularly attack the seeds while they

### Box 1  Sources of phenotypic variation in human-altered environments

Trait values differ as a result of the environment, as a result of evolved genetic differences, or both. Both environmental and genetic variation can lead to phenotypic changes that are adaptive (or not) in human-altered environments. Fig. 1 shows the influence of such variation on the probability of population persistence ('+' positive, '−' negative). Developmental flexibility and behavioural plasticity may enhance the performance of individuals in changed circumstances. For example, threatened prey species may learn to avoid introduced predators by associating novel signals with the threat (Griffin & Evans 2003).

Nonetheless, cue-dependent trait expression may be disrupted in altered environments. Changed circumstances may also present individuals with signals that induce maladaptive actions or phenotypes. Misleading signals, or 'evolutionary traps' (Schlaepfer *et al.* 2005), range from such phenomena as the attraction of nocturnal insect to artificial lights, to native predators attacking toxic toads introduced to Australia (Phillips *et al.* 2006) and birds nesting preferentially in less productive habitats formed by invasive plants (Misenhelter & Rotenberry 2000). These examples show that altered habitats induce naïve organisms to make mistakes,
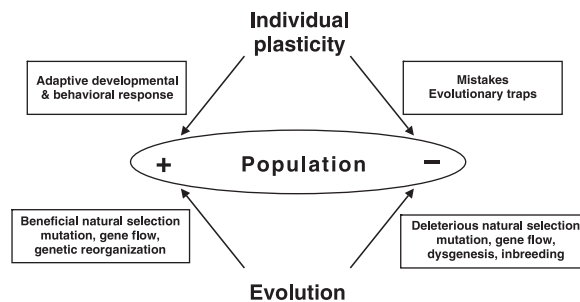


**Fig. 1** Fates of populations via individual and evolutionary responses to environmental change. Adaptive responses that increase the probability of population persistence may be induced or genetically based; they may also operate simultaneously, and plasticity may evolve as well (e.g. Carroll & Corneli 1999; Pigliucci 2001). Adaptive change is not guaranteed (Price *et al.* 2003; Ghalambor *et al.* 2007).

though the prospect remains that learning may permit individuals to extract themselves from traps as well. Even when adaptive, plasticity at one juncture may later constrain adaptive options (Weinig & Delph 2001).

Like environmentally induced phenotypic variation, genetic sources of phenotypic variation may also be a double-edged sword from the standpoint of population persistence (Fig. 1). For example, while differential survival and reproduction in altered habitats may result in adaptive evolution in heritable traits, hard selection may undermine fitness increments by dangerously reducing population size (e.g. Stockwell *et al.* 2003). In rapidly or unpredictably changing environments, local adaptation may have reduced value with respect to population viability. Indeed, responses to natural selection may be against the interests of the species as a whole (Ferriere *et al.* 2004). Likewise, mutations may be beneficial or deleterious, but may in general be too infrequent to commonly play a role in tipping an imperiled population toward survival or extinction. In contrast, changes in the frequencies of extant alleles, whether through selection, gene flow or inbreeding, may strongly impact population persistence (e.g. Hedrick & Kalinowski 2000; Garant *et al.* 2007). Such effects may be positive if they increase the frequencies of beneficial alleles. A particularly interesting concept is the founder-flush model, which postulates that the altered allele frequencies of bottlenecked populations may be magnified through inbreeding to create derivative populations with frequencies far different from those of the parental population (Willis & Orr 1993; Goodnight 2000). Such novel genotypes may theoretically express unprecedented phenotypes resulting from novel gene–gene (dominance, epistasis) interactions, though the conditions in which they are expected to be important are under debate (e.g. Naciri-Graven & Goudet 2003; Turelli & Barton 2006). Unanticipated, recently evolved dominance and epistatic variation is highlighted later in this paper. Likewise, stress-augmented phenotypic (and genotypic) variation may place genes in novel developmental environments and contribute both to reduced fitness and to adaptive evolutionary potential (Badyaev 2005).

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are still in the undehisced capsule, prior to wind or water dispersal (although few of the *c.* 65 soapberry-bug species have been studied).

In Australia, there are five soapberry bug species associated with the native sapindaceous flora, and one of these, *Leptocoris tagalicus*, commonly occurs on balloon

vine in the area of invasion (Carroll *et al.* 2005b). Previous results showed that North American soapberry bugs have evolved substantial adaptations to introduced sapinds over periods of less than 100 generations (< 30 years; Carroll 2007a). This led us to predict that the Australian native bug might similarly adapt to invasive balloon vine,

and that such phenotypic change might result in enhanced predation on balloon-vine seeds (Carroll *et al.* 2005c). I will review North American result first, in order to provide context for assessing the potential for *adaptive biological control* of balloon vine in Australia.

## Evolution to exploit introduced plants in native soapberry bugs

The extent and magnitude of contemporary evolution in the North American soapberry bug *Jadera haematoloma* is remarkable in several respects. Already widely diversified into host races on native sapinds, during the past half century these insects have evolved races on introduced sapinds. These derivative populations appear to be as differentiated from their ancestral races as are the latter from one another (Carroll *et al.* 1997; Carroll 2007a). Changes in morphology, physiology, life history and behaviour greatly enhance the descendant populations' abilities to exploit the seed resources from the introduced host plants.

From a scientific standpoint, ecological shifts of this type are particularly valuable when the history of the shift is documented or inferable, and when the derivative populations can be directly compared to those that remain relatively unaltered in their prior condition (e.g. Singer *et al.* 1993; Feder *et al.* 2003). That combination of circumstances permits the testing of hypotheses about the rate and direction of evolution (Carroll & Boyd 1992; Carroll *et al.* 2001). The ability to 'cross-rear' populations reciprocally on native and introduced host plants, for example, is important in several ways (Box 2). The resulting phenotypes reveal the genetic and environmental (rearing-host) contributions to the observed differences between races. That in turn permits determination of the extent to which racial phenotypes are induced, evolved or both. In addition, rearing ancestral-type races on introduced hosts simulates the phenotypes of the first generation produced by the original colonists. Those phenotypes serve as the baseline for describing the actual extent and direction of evolution that has occurred. Reciprocal rearing likewise permits the estimation of the evolved loss of performance on the native host, a process that may be important to the evolution of both host specialization and reproductive isolation among host-associated populations (e.g. Nosil *et al.* 2005).

We have cross-reared and hybridized races of Florida soapberry bugs (*J. haematoloma*) that occur on the native balloon vine (*Cardiospermum corindum*) and the Asian flamegold (or 'goldenrain') tree (*Koelreuteria elegans*), an ornamental commonly planted from about 50 years ago (Carroll & Boyd 1992; Carroll *et al.* 1997, 1998, 2001; Carroll 2007a). 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), and hence we conclude that they retain the ancestral condition. Flamegold represents an abundant new resource, and we predicted that its differences from the native would favour a variety of new trait values related to host utilization.

In the laboratory, we reared bugs from two populations of each race on seeds of each host in order to compare responses (reaction norms) in beak length, body size, survivorship, development time and fecundity. Both within and among traits, the direction and magnitude of the mean responses to rearing on the alternate hosts were not closely correlated. Trait means, and the slopes of the lines connecting them, varied in all possible directions and combinations. For example, adults from both 'native host populations' were smaller-bodied when reared on the exotic host, with beak length also declining (the direction also favoured by selection on small fruit) in one, but stable in the other. In contrast, in the reciprocal comparison with populations of the derived race, developmental stabilization (canalization) of beak length was not evident, such that body and beak size declined similarly in all derived bugs reared on the native host (Carroll *et al.* 1997). That plasticity in beak length is in the opposite direction to that of natural selection and would impede the reverse host shift simulated in the experiment.

Response diversity during adaptation is further illustrated in the reduced survivorship and development rate of the native host race when reared on the introduced host. Assuming these performance decrements resemble those experienced by the original colonists, that initial developmental stress has been overcome genetically. These traits in the derived population have now evolved to their former (ancestral) values via counter-gradient selection (Carroll *et al.* 1997, 2001). This is the opposite situation to the parallel diminution of beak length and body size in the ancestral-type race described above, in which plasticity concordant with selection may have facilitated the race's ultimate evolutionary response (*sensu* Price *et al.* 2003; West-Eberhard 2003; Grether 2005; Ghalambor *et al.* 2007). Taken together, it is evident that a combination of plastic responses, adaptive reaction norms and pleiotropically generated, potentially maladaptive tradeoffs have come into play during adaptation to the new resource. Our current viewpoint is about 100 generations into the process, and the adaptation that has produced the derived race has an overriding genetic basis. Yet the cross-rearing experiment suggests that the interaction of plasticity and selection created a complex 'network' of pathways that the traits followed towards adaptation.

Genetic models of adaptive evolution assume that multiple, independently acting genes of small effect (additive genetic variance) provide the raw material for sustained evolutionary responses to selection (e.g. Roff 1997). In

## Box 2 Evolutionary analysis with reciprocal comparisons

Testing hypotheses about population differences across environments benefits from a focus on traits whose values likely influence fitness in each. Reaction norms measured within populations can be contrasted and compared in several ways to explore the rate and structure of ongoing adaptive evolution.
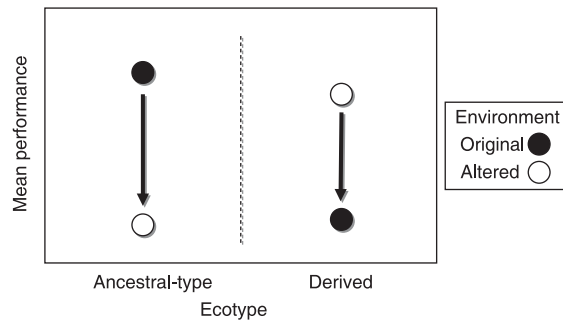


1 Evolution of reaction norms during the transition from an ancestral phenotype in the original environ-ment to the derivative state in the altered environment. Performance in each environment is indicated by the closed (original environment) or open (altered environment) circles. In this hypothetical example, each ecotype performs better in its current environ-ment, with the arrows linking each to their performance when experimentally exposed to the alternative environment.
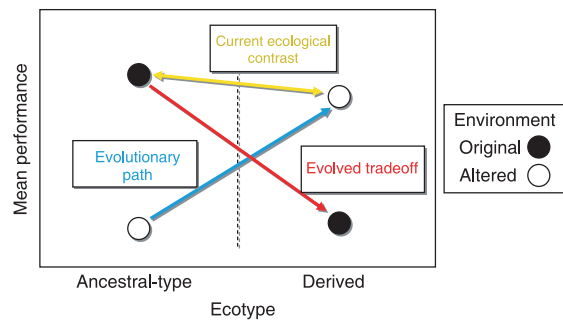


2 Three types of inferential links between reaction norms of the two populations in panel A. By itself, the current ecological

(or 'populational' or 'phenotypic') contrast is devoid of genetic information. The simplest explanations for the performance similarity between environments are that the phenotype is strongly canalized, or the environments differ trivially. The evolutionary path shows performance is *not* canalized, and reveals the true course of evolution. The reciprocal cross shows that the loss of performance of the derived population in the original environment (tradeoff) is at least as great as the increment in the new. (Based on Carroll *et al*. 2001.)
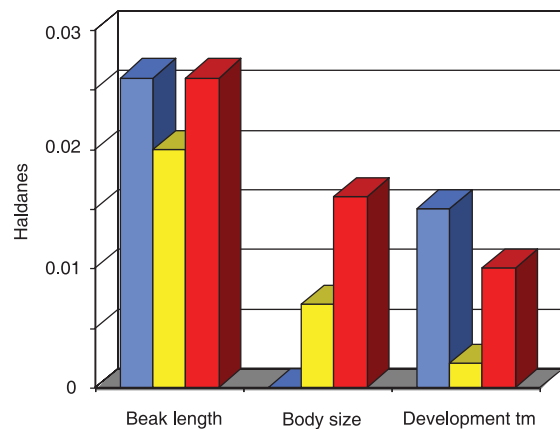


3 Within and among traits that are evolving in soapberry-bug host races, the rates (in haldanes) and structure of evolutionary change differ substantially. The colours scheme for the evolutionary path (blue), current ecological contrast (yellow) and evolved tradeoff (red) matches that of panel B above. Beak length in the ancestral population is relatively un-affected by the host, but is much shorter in the derived population, especially in bugs reared on the native host. Thus the evolved tradeoff slightly exceeds the evolutionary path, and both exceed the current ecological contrast. Body size (measured by thorax width) is smaller in the derived race, but no more so than the decrement from rearing the ancestral race on the introduced host. A reciprocal host effect in the derived race means that the tradeoff appears to have evolved, in contrast, substantially. For development time, current values are very similar, but host-based tradeoffs in both populations reveal that substantial evolution has taken place to restore a development time close to the original. Without reciprocal rearing, that 'cryptic' counter-gradient evolution would be undetectable.

terms of evolutionary time scales, it is difficult to know whether 100 generations (maximally) of genetically based adaptation to new hosts in soapberry bugs represents 'sustained' directional evolution. However, some of the trait means have shifted two-to-three standard deviations. To examine the genetic architecture of the evolving adaptations in the soapberry bugs, we compared the traits in purebred, hybrid and backcrossed phenotypes of each race reared on the seeds of the native or the introduced host. We used a goodness-of-fit test of scaled generation means and variances

to assess models of additive, dominance, epistatic and maternal effects ('joint-scaling' statistical analysis, Mather & Jinks 1982). Surprisingly, only in a behavioural trait, host preference (which we measured in direct-choice tests of dehisced seeds), was nonadditive control absent. For this character, means of the purebred, hybrid and backcross lines were arrayed in a clear cline determined by their pro-portion of ancestral vs. derived genes. Beak length also showed a high degree of additive control (*c*. 60%), but differed in that the remaining variance was strongly

comprised of significant inter-gene interactions, especially epistasis and dominance. In thorax width (our measure of body size), such additive effects were, in contrast, trivial (< 10% on both rearing hosts). Instead, the modelled interaction of the three nonadditive factors explained the bulk of the remaining variance (as high as 88%). For both development time and juvenile survivorship, non-additive effects were also significant, and they were especially prominent when rearing was on the native host rather than on the novel host (Carroll *et al.* 2001, 2003, 2007).

Nonadditive architecture of fitness differentiation among ecotypes has been reported in similar comparisons with other species, but only in cases in which thousands of generations are likely to have passed (Armbruster *et al.* 1997; Hatfield 1997; Fenster & Galloway 2000). The Florida results suggest that such substantial changes in genetic architecture may evolve more rapidly than previously expected. The deeper the developmental–genetic differentiation between populations, the more likely it is that reproductive isolation will evolve, and also perhaps the more likely it is that interpopulation hybrids will produce novel phenotypes; some of which may, by chance, be particularly adaptive (e.g. super-sized beaks in certain bug backcrosses, Carroll *et al.* 2001).

The course of adaptation in North American bug populations gives several reasons to be optimistic that similar processes will follow suit in Australia. First, both phenotypic plasticity and evolution appear to have played a role. Second, the rapid evolutionary responses indicate that the genetic variation necessary to take advantage of the niche opportunity was already present within the ancestral population before colonization of the new host. Third, the early appearance of novel gene–gene interactions suggests that underappreciated, nonadditive sources of genetic variation (Naciri-Graven & Goudet 2003) may contribute to rapid adaptive evolution in highly disrupted, human-altered environments.

Yet in order for invasive balloon vine to cause a repeat of such adaptation in the native community in Australia, several conditions must be met. The invader must have substantial ecological impact, but at the same time must not cause rapid extinction (e.g. as an evolutionary trap, Schlaepfer *et al.* 2005). In addition, the native bug, which is similar but in a different genus, must have the phenotypic or evolutionary potential for adaptation (Carroll & Watters in press), and the interaction of the invasive and native must induce adaptive phenotypic expression or impact native genotypes differentially (Strauss *et al.* 2006a). If bugs in the greater clade have retained at least one of the adaptive pathways toward host adaptation and share any of the developmental and genetic potential observed in the related *J. haematoloma*, they may respond similarly to the altered conditions in Australia.

Note further that, while colonization of introduced plants by native insects is common (e.g. Agrawal & Kotanen 2003), it is far from certain. For example, Bahamian populations of *J. haematoloma* offshore from Florida ignore the flamegold tree (Carroll, unpublished), with large seed crops remaining untouched. Invasive *Opuntia* cactus, historically one of Australia's worst environmental weeds and the antagonist in one of invasion biology's seminal dramas (e.g. Elton 1958), has yet to attract any native insect herbivores 150 years after its naturalization (Moran 1980). Thus the detection and use of introduced balloon vine by one of the Australian *Leptocoris* soapberry bugs represents a significant first step. That interaction, and the plant's abundance, have the potential to generate a selectively significant ecological impact on the insect. Thus the stage is set for the development or evolution of indigenous, adaptive biological control of balloon vine via seed predation by the native community.

Initial results from Australia show that fruiting balloon vine consistently attracts *Leptocoris tagalicus*, the most polyphagous Australian soapberry bug (Carroll *et al.* 2005a), and bugs measured on balloon vines have longer beaks than those on adjacent native host (Carroll *et al.* 2005c). That apparently adaptive pattern could reflect one or more processes at work. First, bugs may colonize balloon vines randomly with respect to beak length, but shorter-beaked individuals may then show adaptive behavioural plasticity and abandon that host when they are not able to feed on the seeds, moving instead to abundant, smaller-fruited natives. Second, feeding on the balloon-vine seeds during development (juveniles, with inherently small beaks, must always rely on seeds in dehiscent fruit) induces beaks to grow longer. The third possibility is that a subpopulation of *L. tagalicus* has evolved that consists of longer-beaked bugs that preferentially colonize balloon vine.

Carroll *et al.* (2005c) showed that beak length has evolved. First, although only 38 museum specimens from the proper times and places were located, they indicate that there has been a significant increase in beak length since balloon vine first became widespread in the 1960s, over which time body size has, in contrast, remained stable. Further, cross-rearing of bugs on seeds of the common native host and those of balloon vine indicated that the beak-length increment was not a simple result of induction in the ancestral-type population. Both host-associated populations perform better, and mature with larger beaks, on their natal hosts. In addition, we found that, compared to bugs from native hosts, bugs from balloon vine damaged more than twice as many balloon vine seeds per unit time in laboratory experiments. If that observed increase in the rate of damage translates into nature, the capacity for the native bug to control the spread of invasive balloon vine in Australia may be growing as beak length evolves.

## Conservation in the midst of evolution

The title of this gathering, 'Evolutionary Change in Human-altered Environments' acknowledges the over-arching power of adaptation in defining and determining the fates of populations and communities. Strong selection can cause extinction even as a population adapts (Gomulkiewicz & Holt 1995), and it is the *failure* to adapt or survive the adaptive process, that is at the heart of the anthropogenic collapse of biodiversity. Adaptation is key to the success of the refugee taxa that persist, and it will only become more important as local and global change accelerate and ramify, and as many nonhuman populations diminish further, in coming decades (e.g. Carroll 2007b).

Overharvesting and habitat degradation are both major evolutionary forces operating on a near global scale (Stockwell *et al*. 2003; Heino & Dieckmann in press). Due to ecological release, species that benefit from human activities, such as invaders, may often evolve and diversify even more rapidly because in those instances, selection takes place in growing rather than in decimated populations (Reznick & Ghalambor 2001). In addition, like humans, other successful invaders may often show unusually great adaptive plasticity, taking great advantage of even small inequalities or opportunities, with devastating results. By decimating the community of key native animals, for example, crazy ants (*Anoplolepis gracilipes*) invading Christmas Island have greatly altered the ecological dynamics of the native forest in just a few years. Among their multifarious nefarious activities, the tending of tree-attacking scale insects has resulted in an island-wide canopy dieback (White *et al*. 2006). As anthropogenic becomes 'ant-o-genic', both direct and indirect effects will ramify broadly into the native community, favouring adaptation to the altered conditions. That a significant proportion of all species is now undoubtedly in the process of changing substantially is a fact that conservation managers now face and which they should plan for.

Case studies of ongoing adaptation in insect populations are relevant to noninsect taxa as well. Insects are important to community structure and function, and so their evolution will often impact many species directly and indirectly. Moreover, while insects are sometimes construed as almost freakishly adaptive due to their tendency toward larger population sizes and briefer generation times than bigger organisms, there are numerous instances, involving species from fish to trees, of significant adaptive evolution occurring in tens of generations or fewer (e.g. Hendry & Kinnison 1999; Strauss *et al*. 2006a). Thus, the seemingly unusually great rate of adaptive evolution of soapberry bugs will likely typify other, more commonly regarded species as well.

Our findings also underline the importance of phenotypic plasticity as an adaptive process. How plasticity interacts with selection is a complex issue (Ghalambor *et al*. 2007), and whether plasticity facilitates or slows adaptive evolution in a trait will depend strongly on the genetic and environmental context. Yet population persistence will always depend on the phenotypic potential in each generation to express the behavioural plasticity and homeostatic capacity needed to survive and reproduce in altered conditions. Organisms that persist in these ways constitute the stock of phenotypes among which selection favours any of the more phenotypically successful genetic variants. Many of the organisms that continue to populate altered environments are the descendants of such resilient individuals, and the evolving history of soapberry bugs over the last half century shows some of the complexity of the evolutionary changes that can ensue in even brief time frames. To the extent that many organisms rely heavily on phenotypic plasticity for adaptation within generations, human influences may promote both the contemporary evolution of pertinent reaction norms (e.g. Carroll & Corneli 1999), as well as the catalysis of evolution by plastic responses to changing conditions (Ghalambor *et al*. 2007).

Until the recent advent of concepts of 'evolutionarily enlightened management' (Ashley *et al*. 2003), applied evolutionary work in conservation biology had focused on the basics of (i) preserving genetic variation in the face of drift and inbreeding in small populations; (ii) guarding genetic identity in restored populations; and (iii) managing adaptation to captive conditions. With the recognition that evolutionary change will inevitably characterize many taxa of concern for the foreseeable future, it will be important to develop and deploy the other tools of evolutionary biology to assist in the maintenance of populations and their sustainable management. This will be challenging at several levels. Most fundamental is the question of how deeply we wish to manipulate the taxa whose habitats and populations we are already monopolizing. In addition, models of the community-level impacts of eco-evolutionary change are still in their infancy (e.g. Urban 2006; Kinnison & Hairston 2007).

The forces promoting contemporary adaptation will often be the same as those causing population declines, and so the basic task of predicting phenotypic responses to change will be most tractable in highly specialized species because their domain of viable alternative states is comparatively narrow. Yet even in the oligophagous soapberry-bug example, the interaction of plasticity and evolution differed in replicate host-shifting populations. Successful conservation will continue to depend on a knowledge of the natural history of species and communities, but ongoing adaptive changes in those organisms is likely to make the task of having accurate contemporary data more difficult. For species in which predicting responses is difficult, frequent monitoring, structured to be sensitive to detecting

change, may be required. To be clear, measurable selection does not always result in measurable evolution, for reasons ranging from constraints of developmental genetics to population structure (e.g. Merilä *et al*. 2001). However, the magnitude of ongoing alteration of the environment puts a premium on designing ways to detect and quantify both phenotypic and genetic shifts. Such monitoring will also be helpful for detecting when populations are threatened by evolutionary trapping.

One long-term outcome of such monitoring will likely be the confirmation that species already recognized as threatened are not only the most persecuted or assaulted, but also often the least likely to adapt. In some cases, the strong selection required for adaptive evolution might simply be part of an extinction process (Stockwell *et al*. 2003). Moreover, adaptation to environmental challenges will not always promote long-term population persistence, particularly in cases where intrapecific competition or frequency-dependent selection are strong (Ferrière *et al*. 2004). Even relatively great capacities for learning-based adjustments and forming cooperative networks may become liabilities in the face of change. For example, following the loss of social structure through decimation by humans, juvenile male savannah elephants (*Loxodonta africana*) have become hyperviolent, both intra- and interspecifically, and female Asian elephants (*Elephas maximus*) are exhibiting poor maternal skills (Bradshaw *et al*. 2005). Dependence on social webs that were once information-rich and buffering has become a vulnerability in the present.

So while all phenotypic responses to change are obviously not adaptive (Box 1), contemporary adaptation will often have the conservation value of reducing risk and increasing opportunities of for population of concern. Clearly many more taxa would now be at risk if they performed poorly outside of narrow, unchanging circumstances. Predicting the longer-term conservation implications of local adaptation is much more difficult. However, in the ecologically simplified cases of invasion by exotic species, plasticity may be the key that permits them to colonize and establish; with subsequent evolution being the next key that ultimately makes them invasive and generally deleterious to indigenous biodiversity (McKinney & Lockwood 1999; García-Ramos & Rodríguez 2002). Adaptation in invasive species includes the evolution of resistance to control measures. Management of resistance by varying the control measures and the regimens by which they are employed uses basic evolutionary theory about response to selection. Likewise, the preservation of untreated refuges for nonresistant genotypes keeps those vulnerable genes in the population, so that gene flow into resistant groups may compromise their adaptability (Barrett 2000).

As in colonizing species, the biotic 'rescue' of a small or declining native population depends on a panoply of demographic and evolutionary factors (e.g. Heino & Hanski 2001; Garant *et al*. 2007; Kinnison & Hairston 2007). The common tendency of phylogenetic lineages *not* to shift their niches over substantial periods of evolutionary history ('niche conservatism') results in part from the population-dynamic consequences of selection being stronger in the parts of the environment to which most individuals are better adapted (e.g. stabilizing selection in the core of the geographical range trumps directional selection at the periphery because much more reproduction takes place away from the niche margins, Holt & Gaines 1992). An extension of that 'source–sink' perspective is that adaptive evolution is less likely to proceed in populations that are in decline than those that are growing (Gomulkiewicz & Holt 1995; Reznick & Ghalambor 2001). In other words, demographic processes tend to dampen response to selection, and the adaptability of declining populations may often be too low to prevent extinction. In addition, the link between adaptation, persistence and community-level processes, including those governing biodiversity, are just beginning to be explored. Improved adaptation in any one population may or may not promote biodiversity at the community level (e.g. Urban 2006). These considerations indicate the importance of identifying and protecting source populations, because they are the ones in which adaptation is most likely. This is a huge challenge, but one that must be emphasized.

How, specifically, can populations best be managed to promote persistence, and perhaps increase adaptability at the same time? Conservation efforts tend to proceed from the standpoint that more is better. Increasing the quantity of available habitat, for example, may increase population sizes of vulnerable taxa and promote community and evolutionary processes that sustain diversity. A complementary evolutionary approach is to manage populations more qualitatively. Alternative tactics (polyphenisms and polymorphisms), for example, are distinct phenotypic classes within species that exploit or pursue resources very differently. Such intrapopulation 'niche partitioning' may lead to increased population stability (Bolnick *et al*. 2003) and thus persistence. It may be productive to manipulate the frequencies of such phenotypes in order to reduce intrapopulation competition for remnant resources (Watters *et al*. 2003). For example, coho salmon (*Oncorhynchus kisutch*) express two conditional male life histories that differ in time to maturity and mating tactics. Juveniles that acquire feeding territories in stream riffles grow and mature more quickly than males relegated to swifter stream flow sites, and the former ultimately return from the sea a year earlier as small, nonterritorial breeders ('jacks'). Less successful juveniles of a cohort return a year later as much larger, aggressive 'hooknoses'. The two morphs spread risk and resource access by living different fractions of their lives in marine and freshwater habitats, and likely

compete less directly for food after the juvenile period, permitting larger local populations (Watters *et al.* 2003). In addition, the differences between the types in development time means that genes mix between generations, so that the breeding population size is less likely to drop to zero (Nunney 1993). Such frequency-dependent, 'bet hedging' life histories may be favoured over monomorphic strategies in variable environments, both reducing perennial variation and increasing annual productivity.

Thousands of examples of alternative morphs, syndromes and personalities are known, and ecological differences among the phenotypes, though not regularly investigated, may be quite common. Because such variation should promote population persistence in the face of change, Watters *et al.* (2003) recommend that restoration focus on supplying a diversity of habitats so that individuals may develop along more than one environmentally determined trajectory. Managing phenotypic frequencies by manipulating key habitat elements and cues may be the best way to enhance carrying-capacity and population stability in cases in which protecting additional habitat is not feasible, and in cases in which artificial communities are created specifically for conservation purposes. Targeted management for heterogeneity may favour plastic, adaptable phenotypes as well.

Such management is about phenotypic diversity and functional potential, akin to notions about genetic diversity and evolutionary potential, and it may be employed via a variety of means and in a variety of circumstances (Carroll & Watters in press). For example, habitat degradation especially threatens specialized populations if their narrow niches collapse. In some cases, disturbance may erode population differentiation (e.g. Hendry *et al.* 2006). So while one key to maintaining diversity is to protect and restore locally adapted natives by inhibiting outbreeding to other ecotypes (e.g. Rice & Emery 2003; Stockwell *et al.* 2003), it also follows that a means of conserving functionality in habitats rendered more generic, or more mosaic, may be to interbreed populations of specialists, if a reasonable proportion of less specialized, more broadly functional phenotype is the result.

Lastly, taxa may be genetically designed — through hybridization, artificial selection or genetic modification — to meet certain challenges or fulfil certain community needs or roles. For example, introduced pathogens have decimated tree species worldwide, and one of the most devastating human impacts in North American in recent centuries was the introduction of Asian chestnut blight fungus, *Cryphonectria parasitica*. The invasion quickly drove the American chestnut tree, *Castanea dentata*, estimated to comprise 25% of all trees in the central Appalachian region (Saucier 1973), to a point of near-extinction from which it has not recovered. No significant resistance was present in the tree's population at the time of the invasion, nor has it appeared since (there is no reproduction, and the species persists as declining stump sprouts (Huang *et al.* 1998). However, substantial captive breeding efforts have been made to reconstitute a near-American Chestnut that, via hybridization and backcrossing, contains Eurasian resistance genes (Hebard 1996). That process has been difficult and very slow, and it suggests that genetic engineering of resistance should be considered. Recognition of the ecological importance of trees in many natural communities raises the possibility that environmentalists with otherwise conservative perspectives on the use of genetic engineering, would support its use for situations in which the potential ecological benefit is perceived to be great relative to the risks.

Non-molecular methods of genetic modification, however, still have great potential relevance for conservation. For example, we have proposed artificial selection on beak length in Australian soapberry bugs, in the context of mass rearing for release into invasive balloon-vine populations. The goal is to create bugs that are better adapted to control the vine's reproduction by destroying more seeds before they can colonize new areas. That would permit hands-on control efforts to concentrate on areas already colonized.

In conclusion, the largely unforeseen fact of contemporary evolution in human-altered environments presents conservationists with both challenging dilemmas and opportunities yet to be explored. Historically, the protection and restoration of habitats and populations has been paramount and practiced largely in isolation from evolutionary concerns. Now, as more populations no longer phenotypically 'match' their habitats, adaptation to permanently altered ecological conditions will result in permanently altered species. The best conservation practices for evolving species will often not then be those based on historical analyses under different or more stable conditions (Schlaepfer *et al.* 2005). Beyond simply being aware of evolutionary change, we may apply a diversity of means to promote, channel, direct and alter their adaptive processes. Managing evolution in complex systems will be very challenging, but the limits have yet to be well explored. The ultimate answers may arise as much from philosophy as science, as we debate the extent to which we wish to bring evolutionary processes under human control, along with other elements of the biosphere.

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