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Dissecting the evolutionary impacts of plant invasions: bugs and beetles as native guides

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Abstract

The introduction of plants into new biogeographical realms is a main repercussion of human trade. The responses of native insects to alien plants may provide insight into how invaders influence ecological processes in their new communities. We illustrate this point with results from our field and lab studies of seed-feeding insects on alien plants. Soapberry bugs (*Jadera, Leptocoris*) have colonized several species of weedy invasive plants (sapindaceous trees and vines) in the United States and Australia. After initial reduction in physiological performance, they evolved behavioral, morphological, physiological and life history adaptations permitting more efficient exploitation of those hosts. Those changes occurred quickly, in fewer than 100 generations (ca. 30–50 years). The underlying genetic changes are surprisingly complex, and also involve loss of function on native hosts. Contrasting with this is the bruchine beetle (*Stator limbatus*) on seeds of leguminous trees. Large numbers of *S. limbatus* oviposit on an alien tree in Arizona, but few offspring survive. The main influence on larval survival is a maternal effect determined by the host the mother experiences as her eggs mature. Adaptive plasticity in egg size and composition may ultimately permit successful exploitation of novel resources. Together, these studies show that both complex genetic and developmental factors influence the integration of ecological and evolutionary processes in environments altered by anthropogenically initiated plant invasions. Tractable insect study systems may be valuable guides to understanding biotic dynamics in a changing world.

Keywords: egg size, invasive species, insect-plant interactions, *Jadera haematoloma*, maternal effects, phenotypic plasticity, preference, rapid evolution, *Stator limbatus*

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Introduction

The expansion of human trade has augmented interchange among Earth's environments far beyond pre-industrial norms (Elton, 1958; Perrings, 2002). In consequence, large numbers of organisms have expanded their geographic ranges and many are now living in novel habitats and becoming members of new biological communities (Vitousek *et al.*, 1996; Pitelka & Plant Migration Workshop Group, 1997; Simberloff, 2003). Many colonists become naturalized or even invasive (i.e., they produce self-sustaining populations that have the potential to become numerically and ecologically prominent; Richardson *et al.*, 2000). Such invasive species, acting as predators, parasites, competitors, or resources, may permanently alter native populations and communities, and are recognized as both a principal result and main agent of global change (Crooks, 2002). Studying the interactions of alien species within native communities is, therefore, fundamental to understanding, predicting and managing the impacts of biological invasions (Vermeij, 1996).

Plant invasions are environmentally prominent worldwide, and alien species develop a variety of relationships with native community members (reviewed by Cox, 2004). Among these novel relationships are host shifts of native insects onto alien plants (Agrawal & Kotanen, 2003; Graves & Shapiro, 2003) especially those with close relatives in the native flora (e.g. Duncan & Williams, 2002). Such colonization events have been treated as accidental experiments of

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ecological significance for several decades (e.g. Strong, 1974; Agrawal & Kotanen, 2003; Graves & Shapiro, 2003). In addition, studies of such host shifts have contributed to the recent understanding that adaptive evolution can take place over relatively short periods of time (Hendry & Kinnison, 1999). The conservation significance of such rapid evolution has recently begun to receive attention (Carroll & Dingle, 1996; Dingle *et al*., 1997; Rice & Emery, 2003; Stockwell *et al*., 2003; Cox, 2004; Carroll *et al*., 2005a–c; Strauss *et al*., 2006).

Alien plants that have native relatives already present in the community quickly accumulate insect associates (Strong, 1974; Agrawal & Kotanen, 2003); particularly diet generalists (Graves & Shapiro, 2003). If fitness is lower on alien than native hosts, the novel plants may function as 'evolutionary traps' that depress survival or reproduction. Such traps produce signals releasing normally adaptive behavioral responses in novel or significantly altered settings (Schlaepfer *et al*., 2005). Traps that are difficult to escape may exert strong selection on the disrupted species, driving the evolution of behavior, morphology and life history traits. Evolutionary traps can thus be of conservation significance.

The ecological and evolutionary interplay of plants and insects in novel contemporary relationships permits the direct study of such selective processes that otherwise could only be inferred (Carroll & Boyd, 1992; Sakai *et al*., 2001). Host shifts onto alien plants have been associated with genetically based adaptive change in life history, morphology, physiology, behavior and phenology (e.g. Tabashnik, 1983; Bowers *et al*., 1992; Fraser & Lawton, 1994; Leclaire & Brandl, 1994; Singer & Thomas, 1996; Gratton & Welter, 1998; Filchak *et al*., 2000; Fox & Savalli, 2000; Carroll *et al*., 2001, 2003a, b, 2005a; Malausa *et al*., 2005). In several of those studies the use of novel hosts appears to have led to the evolution of genetically distinct ecotypes, subspecies and even species. Yet these changes are taking place on what is commonly regarded as an ecological rather than an evolutionary time scale (Thompson, 1998). While it is still rare to consider evolutionary processes in conservation practice (Rice & Emery, 2003), such so-called 'rapid' changes in traits and population structure may serve as keys to understanding the integration of alien taxa into native communities (Strauss *et al*., 2006).

In this paper, we consider in detail two examples of adaptation during insect shifts onto alien host plants. We use these examples to explore both the complexities and the subtleties that ensue from the changing interactions of multiple species. We then consider whether these analyses may aid in understanding how communities assemble, as well as provide insight into controlling invasive species or mitigating their affects on native communities.

Rapid adaptation to new hosts in North American and Australian soapberry bugs

How rapidly can organisms evolve in response to habitat change, in what manner and to what degree, and with what outcome? The case of industrial melanism in English peppered moths (*Biston betularia*) is a classic that serves not only as a key example of evolution studied in process (Majerus, 1998) but also as a harbinger of the growing recognition that many other organisms are also evolving rapidly in response to anthropogenic changes in the environment. Colonization events are the chief settings in which evolution in response to altered selection regimes is taking place (Reznick & Ghalambor, 2001; Carroll *et al*., 2007); several of the most dramatic examples of contemporary evolution reviewed by Hendry & Kinnison (1999) involve biological invasions. One case that we have studied is the New World seed predator *Jadera haematoloma*. This insect is one of the soapberry bugs, specialists on plants of the soapberry family, Sapindaceae, for all development and reproduction. Called 'soapberries' or 'sapinds', these mainly tropical plants include the familiar litchi fruit, as well as the maples. The well known 'box elder bugs' (*Boisea trivittata* and *Boisea rubrolineata*) are soapberry bugs that feed on seeds of maples across North America.

In the United States, *J. haematoloma* has differentiated into host races on three native plant species: the soapberry tree (*Sapindus saponaria* v. *drummondii*), the balloon vine (*Cardiospermum corindum*), and the serjania vine (*Serjania brachycarpa*). Between ca. 1940 and 1970 some *J. haematoloma* populations adopted three naturalizing horticultural introductions as hosts (Carroll & Boyd, 1992; Hoffman & Steiner, 2005). The alien hosts differ variously from the native hosts in fruit size, seed nutritional and defensive chemistry, and phenology. In fewer than 100 generations, *J. haematoloma* populations have evolved contrasting morphology, life history, behavior and physiology on these alien species (Carroll *et al*., 2001, 2003a, b). Populations still on the native hosts appear to have maintained original phenotypes (inferred from museum specimens collected preintroduction of the horticultural species). We compared these 'ancestral-type' phenotypes with those of the 'derived' populations on their new host plants to measure the direction and rate of evolution in the colonists. Some of the differences observed in these ancestral-derived comparisons are greater than those observed among the original races on the native hosts. In addition, by comparing and hybridizing ancestral-like and derived

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populations we have examined the genetic architecture of the new phenotypes.

Beak length and host preference

Recognition of host-based differentiation in *J. haematoloma* began with the chance observation that beak length differed among bugs on alternate native host species in areas adjacent to the United States (Carroll & Loye, 1987). 'Beak' refers to the elongate mouthparts the insect uses to probe fruits for the seeds inside. Native fruits differ in size, a pattern reflected in the length of bugs' beaks (Table 1). Populations on hosts with small fruits have evolved short beaks, and vice versa. This is because bugs with short beaks are unable to reach seeds inside the largest fruits, and bugs with long beaks have difficulty feeding on small fruits.

Remarkably, a very similar pattern of beak length differentiation is evident in populations that recently adopted sapinds introduced from other parts of the world (Carroll & Boyd, 1992) (Table 1). In Florida, for instance, where beak length on the native host (which has an inflated fruit) is very long, beak length on the flat-fruited alien host is much shorter – bugs have evolved short beaks in response to the novel host. In the southcentral US, the opposite pattern has emerged from the same process, with beaks now longer on the two new alien hosts in, which have larger fruits than the native host (Table 1). Incremental changes in beak length since introduction of these new hosts are evident in time series of museum specimens (Carroll & Boyd, 1992). Through a series of cross-rearing experiments we determined that the host-associated differences in beak length are genetically based rather than developmentally induced by the juvenile or maternal environment (Carroll *et al.*, 1997). We treat these genetic findings in greater detail in the next section. Loss of performance on the ancestral host is evolving at the same rate (Carroll *et al.*, 2001, 2003a, b; Carroll, 2007). Among species for which evolutionary rate has been measured in nature (Hendry & Kinnison, 1999), the rate of evolution of beak length in Florida soapberry bugs is rapid, averaging about 0.025 standard deviations per generation, and comparable with values measured in studies involving intentional manipulations to induce evolution (e.g. predation regimes in Trinidadian guppies, Reznick *et al.*, 1997).

In Florida, the emerging host race is hundreds of kilometers from its ancestral population in the far south, so gene flow between them is probably minimal. In contrast, in the southcentral US, alien hosts interdigitate to varying degrees with the natives, and gene flow is likely greater as a result of greater proximity. Even where host plants are close, however, the 'preference' that individuals show for a host may be an important determinant of who mates with whom, and thus the rate and degree of differentiation that is possible (Craig *et al.*, 2001). Hence, the relationship between preference for a host and the evolution of other traits involved in exploiting that host is of broad interest in evolutionary ecology.

We measured whether the nascent 'races' in each region are evolving differences in host preference. To control for environmental influences, parents of trial

Table 1 The native and introduced plants of *Jadera haematoloma* in and adjacent to the United States: origin, geographic range, population age, fruit radius, and beak length of associated bug populations*

Area and host species	Origin	Range	Date host became common†	Fruit radius (mm)	Beak length (mm)
Florida					
Cardiospermum corindum	Native	Southern	–	11.9 ± 0.5	9.3 ± 0.9
Koelreuteria elegans	Taiwan	Central	~1950	2.8 ± 0.6	6.9 ± 0.5
Bahamas					
Cardiospermum microcarpum	Native	N. Providence	–	1.2 ± 0.1	5.8 ± 0.5
Southcentral US					
Sapindus saponaria	Native	Throughout	–	6.1 ± 0.3	6.7 ± 0.8
Koelreuteria paniculata	E. Asia	Throughout	~ 1940	7.1 ± 0.8	7.2 ± 0.5
Cardiospermum halicacabum	World	Coastal plain	~ 1960	8.5 ± 0.7	7.8 ± 0.5
Southern Texas					
Serjania brachycarpa	Native	Far south	–	1.3 ± 0.1	6.1 ± 0.6

*Fruit radius is the minimum distance from the outer wall of a fruit to the center of the nearest seed. Fruit radius and beak length means of adult females (±SD) are given for specimens in nature. Host 'age' is an approximation based on herbarium records and other data described by Carroll & Boyd (1992).

†An approximation of when a plant species became common enough to be biologically significant to the insect. Rare plantings of each alien plant preceded the dates listed.

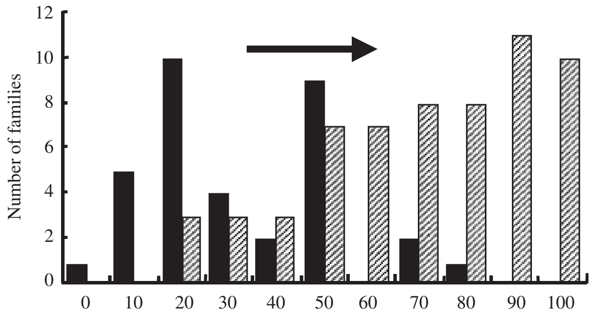

Fig. 1 Evolution of host preference in Florida soapberry bugs, *Jadera haematoloma*. Data are from the early 1990s, approximately 30 years after the likely colonization of the introduced host (hatched bars, Leesburg Florida). Values for the ancestral-type population (dark bars), on the native host, are from Key Largo Florida. The arrow indicates the direction of evolutionary change. Each family consisted of about 20 full sibling hatchlings. Preference was summed for each family from 10 observations taken over 3 days.

bugs were reared on either one or the other regional host and preference was assessed in naive, captive hatchlings that were given a choice between similar quantities of seeds from either regional host. In Florida, the derived bugs have evolved preference for the alien host at a rate that exceeds even that of beak length evolution (Carroll *et al*., 2001) (Fig. 1). In ancestral-type bugs, the average preference for the alien plant averaged 44 ± 11%. Derived bugs, in contrast, preferred it at a frequency of 71 ± 12%. There was no effect of maternal diet (S. P. Carroll *et al*., unpublished data). This dramatic change has probably evolved not because it favored breeding within the race, given allopatric hosts, but for other, undetermined reasons perhaps related to developmental or reproductive performance.

In Oklahoma, the relative frequency of the alien host varies geographically. We sampled six populations across a cline of host frequency and proximity (Table 2). Regardless of locale or relative host frequency, however, preference for the alien host was significantly higher in the three populations sampled from that host. Preference for the novel host was lowest where that host is absent, and greatest where it is predominant. Again, we found no substantial influence of parental rearing host on the preferences of their offspring at hatching.

It is notable that locales as close as 1 km showed considerable differentiation in preference. Such microgeographic differences have been treated as evidence of sympatric divergence and ecological speciation (e.g. Feder *et al*., 1988; Funk *et al*., 2002). However, as in other study systems, we cannot distinguish whether the race differences are evolving locally, or are simple local representatives of subpopulations that tend to exhibit fidelity to one host or the other as they move about the landscape. Likely there is a mosaic of spatial and temporal proximity in the events underlying the patterns we observe in nature. Suffice it to say that substantial and most likely adaptive differences in host preference have evolved in a brief period of no more than about 100 generations.

Table 2 Differences in preference of *Jadera haematoloma* for the introduced host in Oklahoma populations as a function of host association and host frequency

Host-association	Locale	Proximity to adjacent host (km)	% preference for new host
1. *Native host only*	Watonga	ca. 20	15.2 ± 2.7
2. *Native host common, introduced host rare*			
Native	Woodward 1	7	16.8 ± 2.8
Introduced	Woodward 2	7	28.8 ± 3.9
3. *Native host rare, introduced host common*			
Native	Norman 1	1	20.0 ± 2.5
Introduced	Norman 2	1	37.0 ± 3.4
4. *Introduced host only*	Oklahoma City	ca. 20	44.5 ± 3.6

The native host is the soapberry tree, *Sapindus saponaria*, and the introduced host is the goldenrain tree, *Koelreuteria paniculata*. Preference was measured as in Florida, and presented as means ± SE.

Evolutionary path of soapberry bugs on alien hosts

Whether introductions of alien taxa to natural communities will exert selective pressure on natives will depend on their degree of establishment (Carroll *et al*., 2005a; Strauss *et al*., 2006). Many alien plants become invasive and often abundant and so may influence evolution through a variety of ecological interactions (e.g. Crooks, 2002). Phytophagous insects that adopt abundant alien species as hosts may be especially sensitive gauges of consequent evolution. Soapberry bugs offer the opportunity to examine how different traits within a species respond to plant invasions. We have used cross-rearing and hybridization experiments to examine the phenotypic and genetic architecture of adaptations in the Florida races.

In cross-rearing experiments, we split broods of full-siblings into two groups, one raised on the seeds of the native host and the other on the alien host. From these we take a variety of body size, developmental and reproductive measures. In interpreting the results for evolutionary analysis, we infer and assume that the performance of populations from the native host, when reared on the alien host, represents the ancestral condition (i.e., the phenotype that would have been expressed by the first bug colonists to use the new host plant). To measure the direction and amount of evolutionary change, we compare such values to those of the derived populations now resident on the new host. The alternative comparison, in which each population is measured when reared on the seeds of its current host in nature, is inferior because host effects on development can largely obscure any evolved differences, as shown in the example below. Comparing each population on seeds of the new host, then, should better reveal the actual scope of the 'evolutionary path' taken by the phenotypes as they adapted from the ancestral to the derived state (Carroll *et al*., 2001). Evolving concurrently with that adaptation is the loss of performance in the ancestral environment, evolution that is likely developmentally intertwined with adaptation to the new host. We measure it by rearing both the derived and ancestral-type bug populations on the native host.

The degree to which bug populations have differentiated in their response to hosts varies substantially among a broad set of morphological, physiological and life-history traits. Interestingly, rearing host is often a much more critical determinant of phenotype in derived than ancestral races. In ancestral-type bug populations from the Florida Keys, for example, beak length and fecundity are the traits least affected by rearing host. In contrast, in the derived race, beak length was greater and fecundity nearly double when reared on alien host (Carroll *et al*., 1997, 1998). Both body size and egg size showed similar patterns; bugs of both populations were larger and laid larger eggs when reared on their natal host. Some of these evolved differences result in entirely new phenotypic values, including unprecedented beak length and fecundity. Others reveal an evolutionary path toward the reestablishment of ancestral values in the derived race. For example, we see very substantial host affects on development time and juvenile survivorship that are reciprocal and symmetrical between the races. Those differences are essentially invisible when bugs are reared on the host their population uses in nature (Carroll *et al*., 1997, 1998). Thus, the cross-rearing experiment allows us to infer that survivorship was poor, and development protracted, in the early bug colonists of the alien host. Rapid evolution in response to such strong, countergradient selection would be cryptic and undetected in the absence of experimentation (Carroll *et al*., 2001).

When we infer that performance was initially poor on the alien host, note that these measures are strictly physiological. Such pioneering colonists were in one sense making the best of a bad situation. In Florida, for example, reproducing on new host once it was encountered was probably a tactic superior to continued searching for distant native hosts. Moreover, uncontested seed crops probably provided much higher per capita food availability for developing families, even if the high-fat, low-protein seeds of the alien tree were nutritionally inferior (Carroll *et al*., 1998). As a result, while the novel environment was a physiological 'evolutionary trap' for the dispersing bugs, it also served as an oasis. Owing to geographic isolation, the subsequent adaptation probably took place in the absence selection by the native host. The initially small fitness opportunity on the alien host (compared with the native) nonetheless was sufficient to provide a bridge for evolving offspring that soon turned the novel resource into a boon.

The genetic architecture of rapid adaptation

The genetic basis of adaptive evolution in nature has been debated for decades (e.g. Coyne *et al*., 2000; Goodnight & Wade, 2000; Merilä & Sheldon, 2000) but largely in the absence of empirical data. Understanding the process is important to predicting the responses of populations threatened by global change. As humans alter environments and reduce populations, they also eliminate genetic diversity, disintegrating the historical mapping of genotype to phenotype. In theory, the relative frequencies of remnant genes in depleted or 'bottlenecked' populations may differ substantially from their ancestral state, giving rise to new, nonadditive gene interactions (epistasis, dominance) that theoretically may produce novel phenotypes (Goodnight & Wade, 2000; Templeton, 2000; Wade, 2001). However, whether extreme environmental changes actually do alter the genetics of development in disturbed populations is little explored. Organisms adapting to global change are thus involuntary participants in a cosmopolitan unplanned experiment that may illuminate the genetic basis of such fundamental processes as those that lead to specialization and speciation.

To examine the genetic architecture of adaptive differences we hybridized the Florida host races. Hybrid broods were split for rearing on one or the other host. Rearing host strongly influenced developmental-genetic architecture (perhaps portended by the phenotypic asymmetries described above). Beyond that generalization, however, a complex pattern emerged. At one extreme, beak length and host preference differences among the races primarily involved additive genetic effects (i.e., multiple genes, each of small effect with minimal dominance and epistasis), following the classical, 'Fisherian' model of how adaptive evolution proceeds. In contrast, fewer genes with major effects such as dominance (within-gene allelic interactions) and epistasis (gene – gene interactions), *plus* maternal effects, influenced thorax width. Development time differences between the races were largely under epistatic control on the native host, but additive on the alien host. Lastly, juvenile survivorship was balanced between additive and nonadditive genetic control (Carroll *et al*., 2001, 2003a, b). These complex results offered three lessons. First, in species that survive rapid environmental change, novel genotype-by-environment interactions may generate new ways of being fit, with striking evolutionary consequences. Second, multiple forms of genetic variation, including epistasis, may interact to quickly put forth new phenotypes in a manner that is somewhat unanticipated by classical theory. Third, again probably due in part to nonadditive effects, loss of function in the ancestral environment may evolve even more quickly than adaptation to the new environment. As a result, the 'choices' made by natural selection in crafting a rapidly evolving population to fit an unprecedented environment may not permit ready reversion to the ancestral condition should the environment oscillate. Accordingly, the disturbances that invasions represent may have long-term consequences for the evolutionary potential and resilience of native species that respond to them.

Lastly, on a more positive note, novel specializations to alien plants have the potential to integrate newcomers into communities and reduce their ecological (and economic) impact. Among the naturalizing sapinds, that with the greatest current impact is probably the large Neotropical balloon vine, *Cardiospermum grandiflorum*, which is a serious environmental weed in mesic habitats in eastern Australia (Carroll *et al*., 2005c). An Australian soapberry bug, *Leptocoris tagalicus*, has adopted the plant as a new host, probably mainly since the 1960s (Carroll *et al*., 2005a, b). The balloon vine has fruit much larger than those of neighboring native hosts (this is the inverse of the situation in Florida), and beak length is correspondingly longer in bug populations on the alien host. As in the case of *J. haematoloma*, the history of beak length evolution is visible in temporal series in museum collections. Balloon vine is a deleterious invader because of its capacity to overtop and collapse trees in rainforest fragments, particularly riparian corridors. Captive adult female bugs, collected from balloon vines in nature, attack balloon vine seeds inside intact fruits at nearly twice the rate of females collected from the native host. In this case, then, rapid evolution by the herbivore (the bugs) may buffer the ecological, and ultimately the evolutionary, impact of this invasive species (Carroll *et al*., 2005a). While the adaptive responses of the bugs have been predictable in the short-term, how these interactions progress, as soapberry bugs respond to global change with increased diversity, population size, and geographic range (Carroll *et al*., 2005b), remains to be seen.

Maternal effects and diet expansion in the seed beetle, *Stator limbatus*

The studies of evolution and adaptation in soapberry bugs illustrate the rapidity with which adaptation to novel hosts may occur, and the genetic complexity underlying that evolution. Here, we explore an example in which our initial plan to study the genetic adaptation of an insect to alien host species became instead an intriguing study of phenotypic plasticity, maternal effects and community ecology.

Since 1993, we (C. Fox and colleagues) have been studying host use in the seed beetle, *S. limbatus* (e.g. Fox *et al*., 1997b, 2001). Seed beetles (Coleoptera: Chrysomelidae: Bruchinae), like soapberry bugs, have life cycles that evolve around the fruits and seeds of their hosts – females glue their eggs to host seeds and larvae develop inside those seeds, restricted to the seed chosen by their mother. Relative to most seed beetles, *S. limbatus* is a generalist. It uses about 50 native species of plants as hosts throughout its broad geographic range (northern South America to the southwestern US), most of which are mimosoid or caesalpinioid legumes (Johnson & Kingsolver, 1976; Mitchell, 1977; Janzen, 1980; Johnson *et al*., 1989; Morse, 2003; Morse & Farrell, 2005a, b). The beetle also uses seeds of more than 20 alien species, some of which are so widely planted or invasive (e.g. mimosa, *Albizia julibrissin*, a mimosoid legume) that the beetle has expanded its natural geographic range. Texas ebony, *Ebenopsis ebano* (previously *Chloroleucon ebano* and the junior synonym *Pithecellobium flexicaule*) has been widely colonized by beetles where it is planted as an ornamental in central Arizona, USA (Fox *et al*., 1997a). Females of *S. limbatus* readily oviposit on Texas ebony and larval densities are very high, but larval survival is very low. This expansion onto Texas ebony by *S. limbatus* is interesting because this tree is not used as a host by *S. limbatus* in locations where the beetle and plant are naturally co-occur (southern Texas and the gulf coast of Mexico); it is used by *S. limbatus* only where the tree is nonnative. However, the daughter species to *S. limbatus* (*S. beali*) is a specialist on Texas ebony in the tree's natural range. Indeed, the speciation event that split *S. limbatus* and *S. beali* was associated with beetle colonization of Texas ebony ~1.2 Mya (Morse, 2003; Morse & Farrell, 2005a, b). *S. beali* has since diverged from *S. limbatus* in a variety of life history traits directly related to the large size of Texas

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ebony seeds (e.g. larger body size and larger clutch size; Nilsson & Johnson, 1993; Fox & Mousseau, 1995; Fox *et al.*, 1996). The current expansion of *S. limbatus* onto Texas ebony in Arizona may thus provide insights into the ecological and evolutionary processes that occurred before the speciation of *S. beali*.

To test whether *S. limbatus* is adapting to the novel host, we compared survival of beetles on Texas ebony between a population that colonized Texas ebony trees at the Phoenix Zoo and Phoenix Botanical Garden in central Arizona (planted post-1972, Botanical Garden records) and those that have no exposure to Texas ebony from two nearby locations in Arizona (Apache Junction and Scottsdale), and from one location >1000 miles away (van Horn in northern Texas). Contrary to expectation, beetles using Texas ebony showed no evidence of adaptation to this alien host: egg-to-adult survivorship did not differ between populations. However, our most intriguing result was that larval survivorship on Texas ebony was lower in the lab (<5%) for all four populations, including the Phoenix populations, than we observed in the field (10% at the Botanical Garden and 14% at the Phoenix Zoo). Normally these beetles survive much better in the laboratory in the absence of egg parasitoids and other hazards.

Our previous studies of *S. limbatus* suggested an explanation – the host species on which the mother develops has large nongenetic effects on offspring (a maternal effect; e.g. Fox *et al.*, 1995). If beetles are indeed cycling through multiple generations on Texas ebony in nature, parents of field collected offspring would be reared on seeds of Texas ebony whereas we raised all parents in our first experiment on seeds of the Arizona native *Acacia greggii* (cat-claw acacia), our standard laboratory beetle diet. To test whether a host-associated maternal effect could influence larval survival on seeds of Texas ebony we manipulated maternal rearing host before measuring offspring survival on Texas ebony. Mothers were reared on seeds of *A. greggii*, Texas ebony, or blue paloverde (*Parkinsonia florida*, formerly *Cercidium floridum*) and their offspring were reared on seeds of Texas ebony. *P. florida* is a caesalpinoid legume that is the most common indigenous host for *S. limbatus* in Phoenix and field sampling has demonstrated that most eggs laid on seeds of Texas ebony at the Botanical Garden are laid by females that come from *P. florida* plants in the surrounding community (Fox, 2006). As observed in our previous experiment, egg-to-adult survivorship of offspring on Texas ebony was very low when their mothers had been reared on *A. greggii* (<3.0%). Survivorship of offspring was higher, but only slightly, when mothers had been reared on Texas ebony (4–8%), and highest when mothers were reared *P. florida* (>11%; Fig. 2). A one-generation experiment is not adequate to disentangle a maternal effect from an evolutionary response to selection (from nonrandom mortality in the parental generation) but subsequent work demonstrated that the increase in survivorship of larvae caused by maternal rearing on blue paloverde was nongenetic (Fox *et al.*, 1997b; Fox, 2006). In a similar selection experiment to test for adaptation to Texas ebony, all selected lines went extinct, suggesting that populations in the field would likewise go extinct without repeated recolonization.

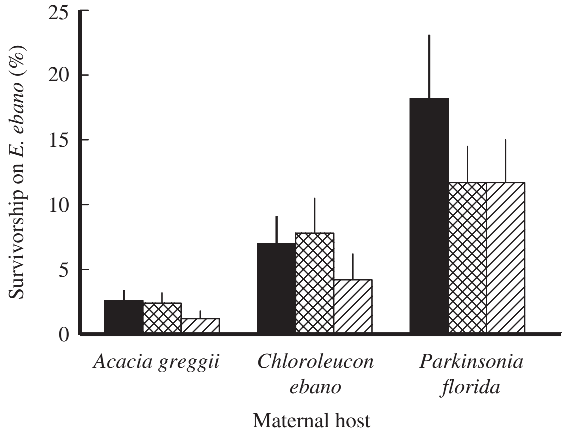

Fig. 2 The effect of maternal rearing host on *Stator limbatus* larval survivorship when larvae are raised on seeds of Texas ebony, *Ebenopsis ebano*. The three bars represent three separate replicates of the experiment. Data from Fox *et al.* (1997a).

These results demonstrate that seed beetle survival on an alien plant is influenced by a host-associated maternal effect – females that are reared on seeds of *P. florida* produce offspring that are capable of surviving on seeds of Texas ebony, whereas females reared directly from Texas ebony, or on seeds of *A. greggii*, are not. Thus, while Texas ebony is an evolutionary trap, maternal experience may inadvertently influence just how deleterious this host is for offspring. What is the mechanism of this maternal effect?

Egg size plasticity and larval survival on Texas ebony

To explain the maternal effect we must briefly cover the beetle's use of native hosts in the southwestern USA. In central Arizona and southern California *S. limbatus* primarily uses seeds of three natives, *A. greggii*, *P. florida* and *P. microphylla* (small-leaf paloverde; formerly *C. microphyllum*). Seeds of these species vary substantially in their suitability for larvae. Seeds of *P. florida* are largely resistant to penetration by *S. limbatus* larvae – first instars die while burrowing into the seed, generally with their abdomens visibly protruding from the seed; Fox *et al.*, 1995, 2001). This resistance may be largely

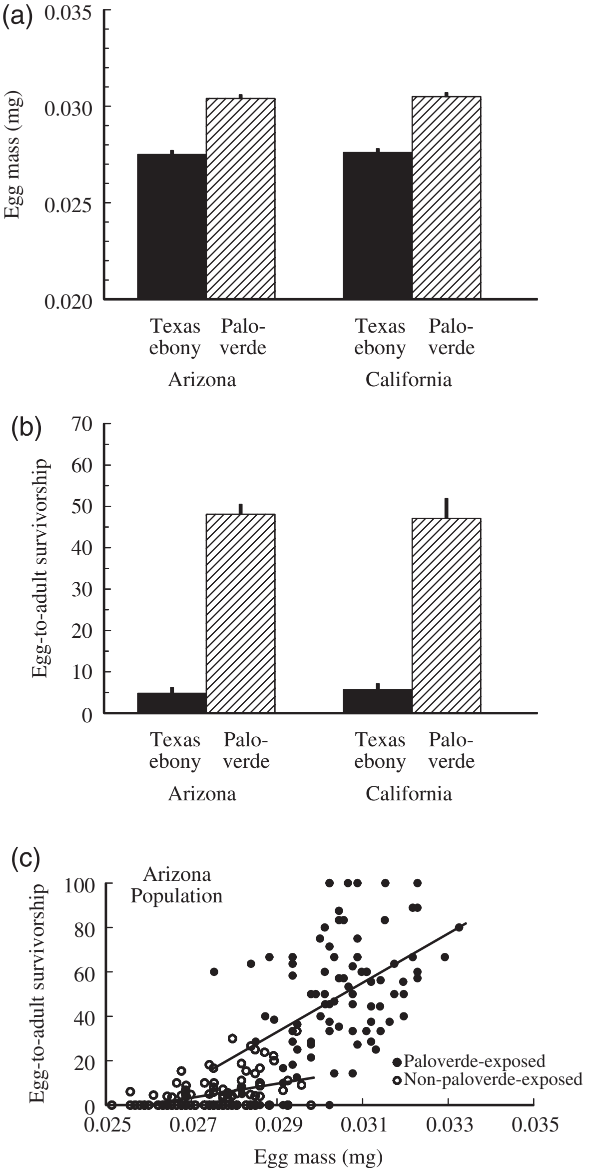

Fig. 3 The effect of maternal experience during egg maturation on (a) the size of eggs laid by females on Texas ebony seeds, and (b) the survivorship of their offspring on Texas ebony (*Ebenopsis ebano*) seeds. (c) The relationship between egg size and larval survival for the Arizona populations. Note that females encountering seeds of blue paloverde (*Parkinsonia florida*) during egg maturation produce larger eggs, and offspring hatching from those eggs have 10-fold higher survivorship than do offspring hatching from eggs laid by females that migrate straight to Texas ebony seeds without encountering paloverde seeds. The experiment was replicated with two populations of *Stator limbatus*, one from southern California and one from central Arizona (details in Fox & Savalli, 2000).

chemical (A. Amarillo & C. Fox, unpublished results) but also partly mechanical (e.g. seed hardness; Siemens *et al.*, 1992, 1994; once inside the seed, larval survival is much higher). The effectiveness of seed coat resistance varies with beetle egg size – larvae hatching from large eggs have larger heads and are more likely to penetrate. Beetles from small eggs experience especially high mortality at this stage. This imposes substantial directional selection favoring large eggs when larvae develop on seeds of *P. florida* (Fox & Mousseau, 1995; Fox *et al.*, 2001).

In contrast, seeds of both cat-claw acacia and the small-leafed paloverde, which are frequently sympatric with *P. florida*, do not appear to have any seed-coat resistance mechanism and larval survival is very high regardless of size of the egg from which they hatch (Fox *et al.*, 2001). Selection favors females that lay small eggs on these hosts, allowing these females to have high fecundity. Interestingly, populations of *S. limbatus* adapted to these three natives show relatively little difference in mean egg size. The major source of variation is within populations – females that encounter seeds of blue paloverde (*P. florida*) during egg maturation increase the size of their eggs relative to the size of eggs they lay on seeds of either *A. greggii* or *P. microphylla* (Fox *et al.*, 1997b; Savalli & Fox, 2002). This plasticity is clearly adaptive – females that lay small eggs on seeds of *P. florida* have almost zero fitness because all of their offspring die, whereas females that lay large eggs on seeds of *A. greggii* have low fecundity relative to what they would have had if they laid small eggs.

This egg size plasticity affects larval survival on seeds of Texas ebony. In a laboratory experiment, we simulated host shift scenarios in which all females were reared on *A. greggii* and then were either (a) allowed to oviposit on seeds of Texas ebony or (b) confined with seeds of blue paloverde during egg maturation, then transferred to seeds of Texas ebony. As observed in previous experiments, females laid much larger eggs on Texas ebony if they had experienced paloverde seeds during egg maturation (Fig. 3a). Most striking, however, was that larvae hatching from eggs laid by paloverde-exposed mothers had 10-fold higher survival on seeds of Texas ebony relative to offspring hatching from eggs laid by mothers that 'dispersed' directly to Texas ebony (Fig. 3b) (Savalli & Fox, 2002). Thus, females need not be reared from paloverde seeds to produce offspring that survive well on Texas ebony; they must only encounter seeds of blue paloverde during egg maturation.

This improved survival on seeds of Texas ebony is partly due to the effect of maternal experience on the size of eggs that she lays (Fig. 3c). There is a significantly positive relationship between egg size and larval survival in both treatments. To explore this further, we compared survival in lines of beetles artificially selected for large vs. small eggs (Czesak & Fox, 2003). Although

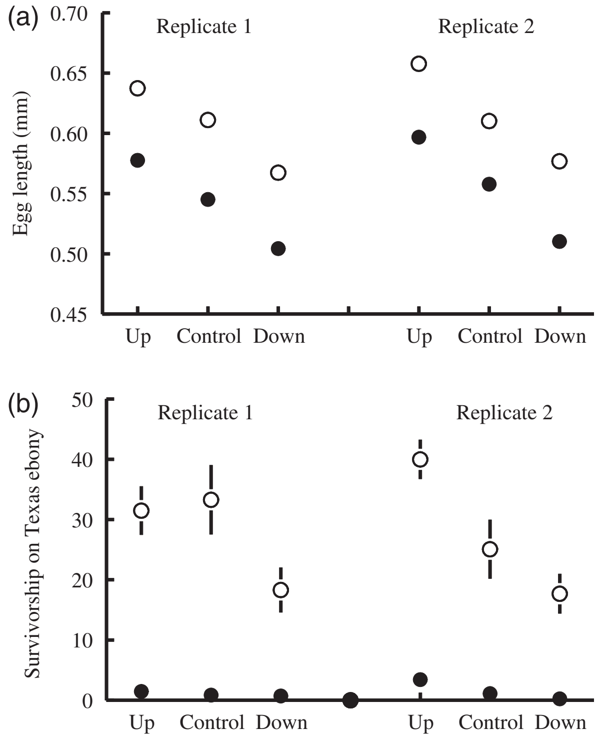

Fig. 4 The size of eggs laid by females (a) and the survival of their larvae (b) on seeds of nonnative Texas ebony for lines of *Stator limbatus* selected for large vs. small eggs. Note that larval survival varies among lines (indicating that egg size affects larval survival) but that the majority of the variance in larval survival depends on maternal experiences during egg maturation (open vs. closed circles). (a) Standard errors are smaller than the points. Data from Fox (2006).

these selected lines differed in offspring survival on Texas ebony (demonstrating both that survival on Texas ebony is genetically variable within populations and that egg size affects survival on Texas ebony) egg size explained very little of the variation in survival (both among and within lines) relative to the effects of maternal experience during egg maturation after removing egg size effects (Fig. 4; Fox, 2006). Clearly, females are manipulating egg content (protein, mRNA, or nutritional content of eggs) in response to paloverde seeds, and these changes in egg composition are allowing offspring to survive on Texas ebony seeds. We have recently isolated proteins that are up-regulated in females that encounter seeds of *P. florida* (E. Demoll & C. Fox, unpublished data) but the function of these proteins is not yet known.

This plasticity in egg size and composition likewise affects the ability of *S. limbatus* to use other alien legumes. For example, Mexican paloverde (*Parkinsonia aculeata*, a caesalpinoid legume) is native from Mexico south through central America but invasive throughout the southwestern US (and other arid regions of the world). Like Texas ebony, Mexican paloverde is not used as a normal host of *S. limbatus* in regions where the plant is native but it has been incorporated into the diet of *S. limbatus* in regions where it is alien. Also, like Texas ebony, larval survival on *P. aculeata* is very low in the field, and while we detect genetic variation in larval survival, the factor having by far the largest effect on larval survival is maternal experience with seeds of *P. florida* during egg maturation (a four- to fivefold increment; Fox *et al*., 2006).

Phenotypic plasticity and the evolution of diet in S. limbatus

The ability of *S. limbatus* to adjust egg size and egg composition in response to maternal experience (maternally mediated phenotypic plasticity) is a fascinating response that directly influences the ability of offspring to survive on at least two alien host species. The role of phenotypic plasticity in the ability of plants and animals to colonize new habitats is a current topic of extensive research and conjecture (Ghalambor *et al.*, 2007). Phenotypic plasticity likely facilitates invasiveness by increasing environmental tolerances (Baker, 1974) and by allowing nongenetic 'acclimation' to the novel environment to occur in a single generation rather than the many generations needed for genetically based adaptation (Sultan, 2005). Experimental results of studies quantifying the effect of plasticity on invasiveness, however, have been mixed (Lee, 2002; Brock *et al*., 2005; Dybdahl & Kane, 2005). It is likely that the importance of plasticity in colonizing new environments, and the relationship between plasticity and invasiveness, will vary substantially among taxa and the ecological conditions in which colonization occurs.

Plasticity in egg size has likely been an important factor in the evolutionary history of *S. limbatus* diet breadth. Most species in the genus *Stator* are extreme specialists, using seeds of just one species or genus (Morse & Farrell, 2005a); only four *Stator* use hosts from more than one genus. *S. limbatus* uses >50 native species, in 18 genera, plus a large number of alien species (>20), as hosts. Is this extreme generalization in part due to egg size plasticity? Egg size plasticity appears to be an ancestral trait in *S. limbatus*. Populations from South America (Colombia) are phylogenetically deeply divergent from populations in the southwestern United States (Morse & Farrell, 2005b) but exhibit egg size plasticity in response to at least one native host (e.g. *Pseudosamanea guachapele* in Colombia and *P. florida* in the Sonoran desert; Amarillo-Suárez & Fox, 2006). Hence, egg size plasticity probably appeared early in the evolutionary history of *S. limbatus*.

We propose that plasticity facilitates diet expansion by increasing larval survival on otherwise low-quality hosts, reducing selection against use of those hosts and providing populations time to respond evolutionarily to their new host before going extinct. Continued study of *S. limbatus* populations that have incorporated alien species into their diet should allow us to test this hypothesis and develop a better understanding of the role of plasticity in facilitating diet evolution in insects and, more generally, expansion of organisms into novel anthropogenically modified environments.

It has been suggested that plasticity may not only facilitate expansion of organisms into new environments, it may actually facilitate adaptation to those new environments and possibly speciation (e.g. West-Eberhard, 1989; Agrawal, 2001; Ghalambor *et al*., 2007). For example, in *Rhagoletis* flies, host plant effects on oviposition behavior (plasticity in behavior) reduce gene flow between fly populations on native and alien hosts, facilitating divergence between populations (Feder *et al*., 1994). Even in organisms where plasticity does not directly affect gene flow, natural selection may favor canalization of the traits that were originally plastic (Pfennig & Murphy, 2002). Thus, the phenotypic plasticity that originally provided a mechanism for colonizing a new environment may also provide the underlying variation for canalization of development and adaptation to the new environment. We suspect that this latter process occurred to give rise to *S. beali*, the sibling species that diverged from *S. limbatus* ~1.2 Mya and specialized on Texas ebony. We propose that plasticity in egg size and composition in response to a native host initially facilitated use of Texas ebony seeds. *S. limbatus* females do not recognize Texas ebony seeds as a host on which to induce plasticity (the traits of seeds that stimulate egg size plasticity are not the same traits that cause larval mortality; Fox *et al*., 1997c). This 'mistake' in recognition should impose intense selection for females that are less plastic (i.e., canalized) and always produce the egg phenotype that has high survival on seeds of Texas ebony. Populations evolving canalized responses would suffer substantial fitness costs on alternate hosts and likely be selected for more specialized host use. Although hypothetical, this scenario would account for the shift from generalist to specialist feeder and predicts that phenotypic plasticity in egg size and composition has been lost in this derived species (a prediction that still needs to be tested).

The effect of community structure on colonization of new hosts

Numerous researchers have examined the ecological variables that influence the expansion of insects onto alien species (e.g. Cornell & Hawkins, 1993). Our experiments with *S. limbatus* illustrate that the ability to survive on new plant species (both Texas ebony and Mexican paloverde) depends on the composition of the local community. The affect of local community composition on patch colonization dynamics has been recognized in studies of butterfly metapopulations. For example, in *Melitaea cinxia*, colonization of suitable hosts in empty patches is affected by species composition of nearby patches (Kuussaari *et al*., 2000; Hanski & Singer, 2001). This is because species composition of adjacent patches affects oviposition behavior of moving females and, thus, affects their likelihood of colonizing suitable hosts in the empty patches. Similarly, female oviposition preference, which is influenced by local community composition, affects colonization dynamics in *Euphydryas editha* (Singer & Thomas, 1996; reviewed in Hanski & Singer, 2001). In these butterfly studies the effects on female behavior are likely due to evolved responses. However, numerous studies have shown that early adult *experience* also affects host finding behavior and oviposition preference in insects (e.g. Barron, 2001). It is likely that such nongenetic effects commonly influence the responses of insects to novel hosts and, thus, the likelihood that females colonize these species.

Ecological and evolutionary lessons from bugs and beetles

Taken together, the lesson that emerges from these two study systems is that unexpected, surprisingly complex genetic and developmental factors influence the integration of ecological and evolutionary processes in environments altered by anthropogenic plant invasions. The soapberry bug and seed beetle examples have strong parallels, and even more interesting differences. Both involve the colonization of alien plants sufficiently related to the native flora to attract the insects, and the host taxon experienced during prereproductive development strongly affects the performance of individuals at multiple points in the life cycle. But in the beetle, the most important effects are nongenetic effects of maternal experience, whereas in the bug substantial genetic change has evolved.

The results for *S. limbatus* indicate that even in organisms with relatively narrow niches, the impacts of plant invasions may be strongly dependent on the composition of the community. In that example, however, it is the nongenetic, plant-induced phenotypic plasticity in egg size, which evolved in another context, which makes the community context important. By permitting some survival of offspring on the alien Texas ebony in Arizona, egg size plasticity sustains the

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evolutionary potential of the interaction. It does so by continually recreating the phenomenon until a future time when chance genetic combinations may allow adaptive evolution to the new host. Such a view suggests that the factors determining the outcome of seemingly straightforward biotic scenarios may, on further inspection, prove to come from unexpected interactions. The case of the soapberry bugs also reveals unexpected features. Foremost of these is that evolution may occur very rapidly, on an ecological time scale, and that the genetic change underlying rapidly evolved adaptations can include a surprising degree of epistasis and dominance. Such nonadditive genetic differentiation is typically associated with thousands of generations of isolation during which mutations occasionally appear in one population but not the other. Further speculation about the abrupt origin of nonadditive control is beyond the scope of this paper, but it is intriguing to consider that such interactions may be more likely to produce nonincremental steps along adaptive evolutionary pathways, and therefore, to contribute disproportionately to ongoing adaptation that is based also on additive factors. Regardless of the source, genetically dependent changes in soapberry bug phenotypes mean that the plant invasions have made the bugs substantially different organisms over the past few decades. As the results for the Australian species indicate, shifts in the ecological and evolutionary potential of soapberry bugs may include the ability to exert some control over reproduction by their adopted, recently introduced hosts.

Alien plants with local relatives are more likely to elicit feeding or oviposition responses in native insects due to shared chemical or structural attributes. Nonetheless, from a functional standpoint such events may be regarded as cases of 'mistaken identity' (Fox & Lalonde, 1993) and plant introductions may therefore serve as evolutionary traps (Schlaepfer *et al*., 2005) in the sense that response to cues that led to positive outcomes in the past may lead to deleterious outcomes in the altered environment. In the case of *S. limbatus* on introduced Texas ebony, the great majority of females appear to be wasting their reproductive effort on a host upon which their offspring cannot survive. Likewise, we infer from the cross-rearing experiments that soapberry bugs were initially physiologically much less able to use the seeds of the alien than the native hosts.

The phenotypic and evolutionary responses of native insects that ensue after their colonization of alien hosts may strongly determine the impacts that the aliens have on the insects. If large numbers of individuals are attracted to hosts on which their performance is poor, population decline is a possible outcome. Phenotypic plasticity, including behavioral responses or, for example, the fortuitous egg size plasticity of *S. limbatus*, may modulate such deleterious effects in the short term. At the other extreme, alien plants that naturalize and become invasive may represent substantial resources for natives that can use them. To the extent that alien plants become invasive through release from their former natural enemies, native insects able to colonize aliens may experience exceptionally strong selection favoring the exploitation the new, uncontested resource (Carroll *et al*., 2005a). Our results for soapberry bugs implicate this latter scenario. By revealing the realm of possible responses in a meaningful ecological and evolutionary context, systems like the beetles and bugs are models for exploring how organisms, including species more difficult to study (e.g. threatened vertebrates and long-lived plants) may react to global change. Maternal effects and phenotypic plasticity are important throughout the biological world (Ghalambor *et al.*, 2007; Räsänen & Kruuk, 2007). Few generations were required for the bugs to develop into substantially different organisms in morphology, physiology, behavior, and life history. Such 'sudden' adaptations are likely acting to sustain or retard the decline of a great many organisms faced with altered environments (Cox, 2004; Strauss *et al*., 2006). Other developments of global scope, including climate change, are likewise inducing adaptive plasticity *and* causing sustained directional evolution (Bradshaw & Holzapfel, 2001; Réale *et al*., 2003; Umina *et al*., 2005). Conservationists should be alert for adaptive changes in organisms that can be used to address environmental issues, such as the control of invasive pests/weeds, as in our example of the rapidly evolving capacity of Australian soapberry bugs to attack a rainforest-invading vine. At the same time, however, experience and prudence dicate that we not rely on rapid adaptation as a ready solution for the biotic problems of global change. Instead, the adaptive lability of many populations should be recognized for what it is: a factor contributing to the complex realities of managing and sustaining natural communities and ecosystem functions in anthropogenically altered landscapes.

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