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Brave New World: the epistatic foundations of natives adapting to invaders

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Abstract Classical examples indicated rapid evolution to be both rare and largely anthropogenic. As the pace and scale of human disturbance increase, such evolution is becoming more the norm. Genetically based adaptation may underlie successful biological invasions, and may likewise characterize responses in natives to invasives. Recent published studies confirm that natives are adapting morphologically, behaviorally, physiologically and life historically to selection from invasive species. Some of the processes involved are evident in our studies of recent host shifts to invasive plants by native soapberry bugs in North America and Australia. On both continents populations have differentiated extensively in fitness traits. Genetic architecture of these adaptations involves a surprising degree of non-additive variation (epistasis, dominance), a result that in theory may reflect a history of colonization by a small number of individuals followed by population growth. Such ''founder-flush'' events may unleash extraordinary evolutionary potential, and their importance will be clarified as more studies take advantage of the accidental perturbation experiments that biotic invasions represent. From a conservation standpoint, rapid evolution in natives will present challenges for ecologically appropriate and sustainable management, but at the same time may enhance the capacity of the native community to act in the biological control of invasive species.

Keywords Adaptation · Epistasis · Genetic architecture · Founder-flush · Global change · Insect · Invasive species · *Jadera* · *Leptocoris* · Rapid evolution · Soapberry

Introduction

For evolutionary biologists, the changes engendered by biotic invasions are of both scientific and personal significance. The establishment of non-indigenous species threatens the structure of habitats that we regard as natural and as having inherent value and integrity; it also threatens biodiversity and as such tends to undermine the products of the evolutionary process itself. At the same time, biological invasions are unplanned experiments in ecology and evolution with clear historical information (Carroll and Boyd 1992; Cox 2004; Strauss et al. 2006). Invasions allow comparisons between taxa in the old versus new habitats, and may also permit the direct observation of evolution within new habitats. This is important because a limitation of the comparative method in evolutionary biology is the difficulty in determining which, if any, of the contemporary populations retains an ancestral state from which other populations evolved. As chronicled perturbations, invasions also offer unusual opportunities to test theories of population regulation (Colautti et al. 2004), the niche (Shea and Chesson 2002), ecological genetics (Lee 2002; Balanyà et al. 2003) and community assembly (Vermeij 1996; Yoshida et al. 2003; Cox 2004; Lambrinos 2004). It is my hope that the results of such scientific inquiries will support efforts to manage and ameliorate the ecological and evolutionary impacts of biological invasions.

The majority of in-depth studies of evolution during invasion treat change in the invasive species

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themselves. In her review of the evolutionary genetics of invasive species, Lee (2002) concluded that the success of invaders depends more on evolvability than on physiological tolerance or phenotypic plasticity. Moreover, she suggested that non-additive genetic architecture may play a role in rapid adaptation to the novel circumstances encountered during colonization of new habitats.

In contrast, there is comparatively little recognition of evolution in *native* residents in response to the activities of novel taxa within their environments. Nonetheless, Strauss et al. (2006) report 33 examples of native species that have evolved in response to the addition of novel species to their communities. Those responses include several classes of traits (morphological, physiological, behavioral and life history), and represent several types of ecological interactions (herbivory, competition, predation, and disease). The biggest group of instances involves phytophagous insects shifting onto introduced host plants.

Host shifts in phytophagous insects offer excellent study systems because the timing of plant introductions is often documented, and the colonizing insect populations may sometimes be directly compared with others that remain on native hosts. That combination of circumstances permits the testing of hypotheses about the rate and direction of evolution on ‘‘ecological’’ time scales (Carroll and Boyd 1992). For relative trophic specialists, the invasives create a sudden ecological shift in habitat state analogous to that encountered by invaders themselves. The ‘‘accidental experiment’’ metaphor thus cuts in both directions as natives colonic ‘‘islands’’ (sensu Janzen 1973; Southwood and Kennedy 1983) of previously unencountered habitat.

In this paper I focus on results for one such system, host shifts by soapberry bugs. In North America, colleagues and I have studied the ecology and the evolutionary quantitative genetics of evolution in the soapberry bug *Jadera haematoloma* as it has colonized and established on introduced Asian plants closely related to its indigenous hosts. We have recorded rapid adaptive change in morphology, physiology, behavior and life history. In addition, we are examining the evolutionary consequences of a similar ‘‘dual’’ colonization event, that of the Australian soapberry bug *Leptocoris tagalicus* adopting the rainforest-invading Neotropical balloon vine, *Cardiospermum grandiflorum*. The paper reviews and integrates some of those published findings and relates them to the genetic architecture of rapid adaptation and to the consequences of such evolution for the ecology and conservation of invaded communities. I first briefly treat relevant concepts concerning natural selection during invasions and the genetic architecture of adaptation.

Ecology of selection during invasion

Colonization of new environments is a main context in which contemporary adaptive evolution has been observed. Reznick and Ghalambor (2001) concluded that it is a ‘‘combination of directional selection with at least a short-term opportunity for population growth’’ that fosters rapid evolution. Whereas strong selection may often lead to population decline, environments susceptible to colonizers will provide the conditions for evolutionary change. In other words, populations of individuals that are sufficiently pre-adapted to a novel environment to survive and reproduce, but not so pre-adapted or homogeneous to be immune to selection, are those most likely to exhibit rapid evolution. It follows that many taxa categorized as ‘‘invasive species’’ will fit these descriptions and so offer rich information on evolution in response to selection.

‘‘Niche opportunity,’’ the biotic and abiotic factors that determine the suitability of a new habitat (Shea and Chesson 2002), may be increased by disruption of indigenous communities. Indeed many invasions appear to depend on advance physical disruption by humans or other agents (Rejmánek et al. 2004). Colonist populations in disrupted sites may experience reduced competition from natives and grow rapidly as a result. Strong initial population growth should also be important in creating a demographic buffer so that colonies may survive transient circumstances to which they are least pre-adapted (e.g., environmental episodes or life cycle vulnerabilities). It will also be important in multiplying beneficial alleles rare among the colonists, as well as generating novel gene–gene interactions and ultimately new genes that permit further evolution in response to such challenges.

Genetic architecture and adaptive evolution

Some of our best-documented instances of adaptation resulting from natural selection thus involve sudden shifts of habitat or geography, mainly influenced by people. Well-known examples include industrial melanism in peppered moths (Majerus 1998), host range expansion in the apple maggot (Feder et al. 2003) Edith’s Checkerspot butterfly (Singer et al. 1993) and soapberry bugs (Carroll et al. 2003a), novel habitats for introduced mosquito fish (Stearns 1983), and habitat shifts in salmon (Hendry et al. 2000; Quinn et al. 2001).

However, while these instances are well understood from an ecological perspective, little is known, empirically, from these cases or any others, about the genetic bases of adaptive evolution. In spite of the fact that the role of interactive versus non-interactive (additive) genetic effects in development and evolution has been a central debate throughout the modern synthesis (Coyne et al. 2000; Goodnight and Wade 2000; Merilä and Sheldon 1999), the role in genetic architecture in determining response to selection is still poorly understood (Brodie 2000).

Central to the question is how genetic variation is measured and how developmental systems contribute to phenotypic variation. Predictions and evidence of low additive genetic variation for fitness-associated traits (Blows and Hoffman 1996) have sharpened focus on other sources, including environmental variance (Kruuk et al. 2000) and non-additive (epistasis, dominance) genetic variance (Brodie 2000; Merilä and Sheldon 1999; Templeton 2000; Agrawal et al. 2001; Wade 2001). Environmental sources may be especially influential in traits that integrate many functions and events, such as those of the life history (Price and Schluter 1991; Kruuk et al. 2000). Moreover, Merilä and Sheldon (1999) suggest that non-additive control may be more potent in fitness traits due to their ostensibly more complex architecture.

Empirically, dominance and epistatic fitness differentiation among closely related but ecologically distinct populations and species have recently been reported (Armbruster et al. 1997; Hatfield 1997; Fenster and Galloway 2000). Genetic correlations are likewise important (e.g., Etterson 2004). Population bottlenecks that result from habitat loss or alteration (including, e.g., the exploitation by natives of invasive species) may cause genetic reorganization that increases additive genetic variation in spite of reduced effective population size (so-called ‘‘founder-flush’’ models of speciation, e.g., Goodnight 1988; Regan et al. 2003). A focus of our work with soapberry bugs has been to ask for the first time whether such non-additive control can play a role *very early* in the process of adaptive differentiation between populations, perhaps even in the presence of substantial additive genetic variation. Indeed, we have found surprising levels of non-additive, as well as maternal, control of evolution in fitness-associated traits distinguishing populations diverged for less than about 100 generations (Carroll et al. 2001, 2003a). These results are important because they indicate that the genetic variation necessary for rapid evolution into new niches is resident within ancestral populations, prior to the colonization event. Further, they show that the variation in some traits is strongly non-additive rather than simply additive. These are very intriguing findings that we treat in some detail in the next sections.

Contemporary adaptive radiation of North American soapberry bugs on invasive host plants

Soapberry bugs are brightly colored, aggregating seed predators. In three genera they comprise the Hemipteran sub-family Serinethinae (Rhopalidae), a worldwide group of about 70 species of medium-size bugs specialized on the plant family Sapindaceae. The Sapindaceae, or ‘‘Soapberry’’ family, is mainly tropical, including such fruits as lychee and longan. Temperate zone members include the soapberry tree (*Sapindus saponaria*) and the maples (*Acer*). In North America, the soapberry tree is one native host of the most-studied soapberry bug, *J. haematoloma*. In the same region, the well-known maple, box elder (*Acer negundo*) is host to a widely recognized Serinethine, the box elder bug (*Boisea trivitatta*) (Carroll and Loye 1987). Soapberry bugs are absent from Europe, but they are widespread in Africa, southern and southeastern Asia, Australia and Oceania.

Populations of *J. haematoloma* have been differentiating since their colonization of sapinds introduced into their North American range, mainly within the past 50 years (Carroll and Boyd 1992; Carroll et al. 1997). This fast moving adaptive radiation has resulted from populations on two native host species colonizing three introduced host species. Populations continue to use the native hosts as well (Table 1). The introduced hosts differ from the natives in fruit size (Carroll and Boyd 1992), phenology (Carroll et al. 2003b), seed nutritional quality (Carroll et al. 1998) and chemical defense (Siegler and Kawahara 1976). All of these traits have been the basis for adaptive diversification in the bugs. For example, Table 1 shows how beak length values vary with the size of the fruits upon which the bugs forage. These population differences have a clear genetic basis (Carroll et al. 1997).

Our experimental studies have focused on bugs within Florida, where the native host, balloon vine (*Cardiospermum corindum*) occurs in the far south of the state. The alien host, *Koelreuteria elegans* (ssp. *formosana*, goldenrain tree, also known as the Chinese rain or flamegold tree) was commonly planted in central Florida beginning five decades ago. This ornamental has naturalized across the southeastern US, and in Florida it is listed by the state as a potentially serious environmental weed. In addition to having smaller fruit, seeds of the introduced tree are higher fat, lower

Table 1 Native and introduced host plants of *Jadera haematoloma*: origin, geographic range and population age, with mean (± 1 sd) fruit radius and female beak length in mm (*N*)

Host species	Origin	Range	Age (years BP)[a]	Fruit radius[b]	Beak length
Florida					
Cardiospermum corundum	Native	Southern Florida	<10,000	11.92 ± 0.51 (20)	9.32 ± 0.86 (44)
Koelreuteria elegans	Introduced	Central Florida	30–60	2.82 ± 0.59 (21)	6.93 ± 0.48 (40)
Southcentral US					
Sapindus saponaria	Native	Throughout	<10,000	6.05 ± 0.34 (25)	6.68 ± 0.82 (64)
Koelreuteria paniculata	Introduced	Throughout	40–100	7.09 ± 0.84 (25)	7.23 ± 0.47 (37)
Cardiospermum halicacabum	Introduced	Throughout, principally Gulf Coast region	20–80	8.54 ± 0.65 (20)	7.80 ± 0.52 (27)

[a] Age for native host populations is a very general guess based on post-glacial climatic patterns in southern North America in the past 10,000 years

[b] "Fruit radius" is the minimum distance from the outer wall of the fruit to the center nearest of the seeds

protein, with an alternate cyanolipid seed-defense, and are produced in larger numbers over a much briefer annual period of seed production.

Current populations of bugs on the native balloon vine closely resemble museum specimens collected in Florida before the introduction of *K. elegans* (Carroll and Boyd 1992). We therefore regard those modern populations as an "ancestral-type" race, and infer that they have given rise to a "derived" race on *K. elegans* over a period of perhaps 100 generations. When reared on the new host versus the native host, derived bugs mature 25% more rapidly, are 20% more likely to survive, and lay almost twice as many eggs. Fecundity is twice as great as that of ancestral-type bugs reared on either host, while egg mass is 20% smaller; performance tradeoffs of similar magnitude have evolved for these traits as well (Carroll et al. 1997, 1998, 2001, 2003a, b), a fact that may contribute to selection underlying the considerable differences that have evolved in host preference as well (Carroll 2003a). The direction of evolution in each of these traits could enhance reproductive success in the more ephemeral, annually cycling habitat that the new host's seed crop represents (sensu Southwood 1977).

Genetic architecture of adaptive differentiation in soapberry bug host races

Finding such deep and diverse, evidently adaptive changes evolving on such a clear, brief timeline motivated our study of the genetic architecture underlying them. Accordingly, we conducted line cross experiments between the ancestral-type and the derived Florida races. We analyzed purebred, hybrid and backcrossed phenotypes of individuals reared in two common environments, namely on the seeds of the native or of the introduced host. We used joint-scaling statistical analysis (Mather and Jinks 1982), a weighted least squares test designed for comparing populations with contrasting variances (as expected when comparing additive traits between first- and second-generation hybrids, between which variance are expected to differ even though means will be similar). It is a goodness-of-fit test of scaled generation means and variances to assess models of additive, dominance, epistatic and maternal effects. Moreover, data from reciprocal backcrosses allow estimation of the components of digenic epistasis, including additive × additive, additive × dominance, dominance × dominance, maternal × additive and maternal × dominance (Hard et al. 1992; Lair et al. 1997).

Figure 1 shows how the five traits responded to genetic and environmental manipulation. Beak length was larger in the ancestral-type than in the derived race, as anticipated from previous observations (Fig. 1a). It was comparatively unaffected by rearing host, especially in the purebred lines. Hybrid values were large, resulting from epistasis, maternal effects and their interaction, as well as dominance effects in those offspring reared on the native (but not on the introduced) host (Table 1). Averaged across the two hosts, additive effects accounted for about 60% of the between population variance, and non-additive effects accounted for the remaining 40%.

Within each rearing host, mean thorax width (our measure of body size) varied less than 2% during the first experimental generation (Fig. 1b), substantially less than interracial variation in beak length. Nonetheless, as for beak length, genetic effects were substantial: hybrid lines were larger than purebreds, but little differentiated as a function of rearing host. In contrast to beak length, additive control of body size was weak, with only 9 and 7% of the variance explained on the native and introduced hosts, respectively (Table 2). Like beak length, maternal effects and

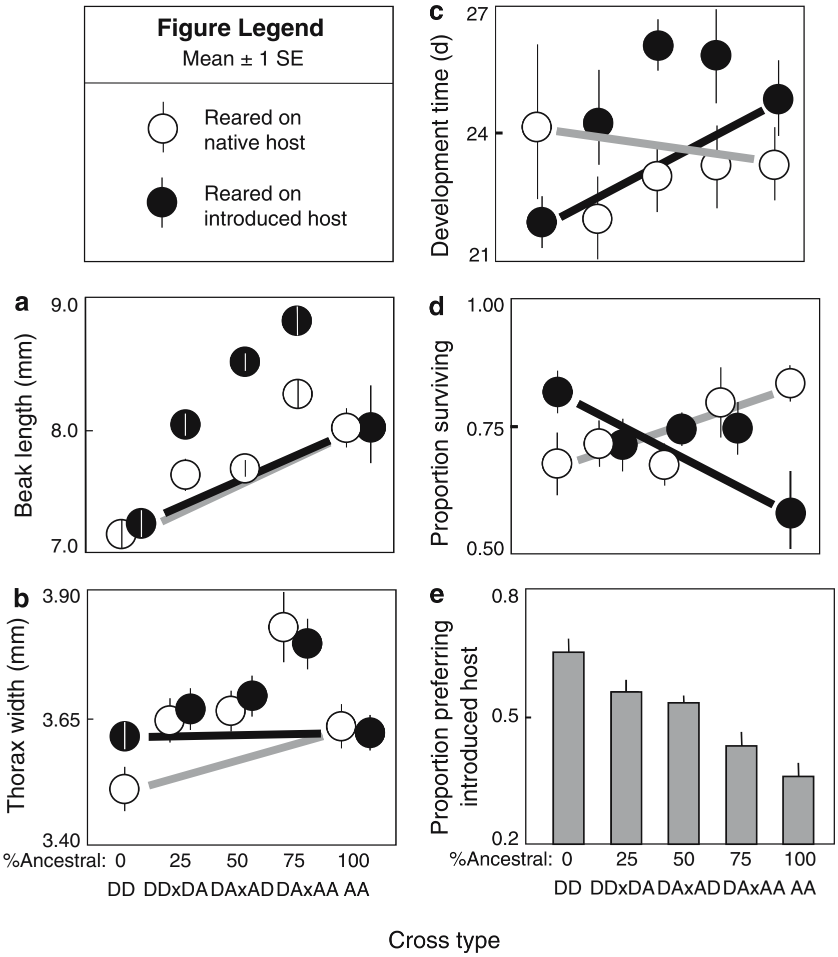

Fig. 1 Trait means from second-generation line cross experiments for adult female soapberry bugs (*Jadera haematoloma*) from an ancestral-type race (Plantation Key) and a derived race (Lake Wales) in Florida. Bugs were reared either on seeds of the native host (*Cardiospermum corindum*) or introduced host (*Koelreuteria elegans*) (see legend). *A* denotes the ancestral-type race, and *D* denotes the derived race; their combinations along the abscissa denote hybrid and backcross lines. *Large lines* connect the grand means for the purebred lines (*DD* and *AA*) reared on the two hosts (additivity hypothesis, see text). %*A* indicates the proportion of ancestral-type genome in each line. Modified from Carroll et al. (2001) and Carroll et al. (2003a)

especially epistasis were strong. Unlike beak length, these effects were significant in likelihood ratio tests when bugs were reared on either native or introduced host seeds (Table 3).

In contrast to morphology, development time was strongly influenced by host (Fig. 1c). As in previous experiments (Carroll et al. 1998) the derived race developed more quickly, with the juvenile period between 8 and 15% briefer in the first generation. In the second generation, both hybrids and backcrosses to the ancestral-type race took longer to develop than did the purebred lines. These slower lines were those with larger morphological values. Like the phenotypes, genetic architecture too was strongly related to rearing host. Additive control was substantial only on the introduced host (Table 2). On the native host, dominance, epistasis and maternal effects all contributed to the model's accuracy. All factors are required for substantial power, however, explaining 78% of the variance (Table 2).

Survivorship was likewise influenced by host, showing distinct reciprocal interaction (Fig. 1d). The evolved increment on the introduced host (approximately 25%) mirrors a simultaneously evolved loss on the native host (16%). Hybrids were intermediate in each rearing host treatment, but sufficiently irregular as to indicate substantial non-additivity, in this case dominance and probably epistasis (Table 2). In addition, on the introduced host, the full model (ADME) was significantly more explanatory than ADE ($p < 0.05$), and also differed from AD and ADM ($0.05 < ps < 0.10$). In terms of gene flow, this result suggests that natural hybrid matings would tend to produce fewer offspring than would purebred matings on a local host.

The final trait, host preference, is potentially important in the transition from one host to another as well as to gene flow. Figure 1e shows the mean (± 1 se) preference values, measured as feeding frequencies for groups of siblings given a choice between seeds of the two host species. Preference for the introduced host was far greater in the purebred descendants of the derived race than in the ancestral-type race. Genetically intermediate lines tended to be phenotypically intermediate in a pattern proportional to respective contributions of the parental genotypes.

Table 2 Percentage of the total variance explained by the models when fit to the character means, with bugs reared on dehisced seeds of either the native or the introduced host plant

Trait/host	Percentage variance explained beyond that explained by additivity				
	Additivity	Dominance	D × E	D × M	D × M × E
Beak length					
Native	65	20**	31**	22*	35**
Introduced	54	1	43***	23***	46***
Thorax width[a]					
Native	9	4	53***	58***	73***
Introduced	7	10	81***	36**	88***
Development time					
Native	13	15	17	32**	78***
Introduced	46	3	19	14	28*
Juvenile survivorship					
Native	40	25*	49†	25	53
Introduced	37	4	16	14	55
Host preference	64	2	25	14	34

Each of the four analyses per trait (by host) includes additivity as a parameter. Compiled from Carroll et al. (2001) and Carroll et al. (2003a)

D dominance, *M* maternal effects, *E* epistasis, and × denotes interaction

† $p \leq 0.10$

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

[a] Width of the pronotum, which covers the thorax dorsally

Table 3 Contrast of goodness-of-fit statistics (χ^2 values) for models of additivity (A), dominance (D), epistasis (E) and maternal (M) effects, with bugs reared on seeds of either the native or the introduced host plant

Trait/host	Model				
	D–A	ADM–AD	ADE–AD	ADME–ADM	ADME–ADE
Beak length					
Native	9.7**	0.9	5.3	6.3†	1.9
Introduced	2.5	32.4***	60.2***	32.1***	4.4
Thorax width					
Native	1.8	23.7***	21.4***	6.2†	8.4*
Introduced	4.8*	13.0**	35.6***	26.0***	3.4
Development time					
Native	5.6*	10.4**	1.0	13.6**	23.1***
Introduced	1.3	5.4†	7.5†	6.6†	4.5
Juvenile survivorship					
Native	4.4*	0.1	4.3	4.8	0.6
Introduced	0.8	1.73	2.1	7.3†	6.9*
Host preference	0.5	2.4	4.5	3.9	1.8

Values are differences between chi-square statistics of each model comparison. Compiled from Carroll et al. (2001) and Carroll et al. (2003a)

† $p \leq 0.10$

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Almost two-thirds of phenotypic variation was attributable to additive factors, there was no indication of dominance, and the effects of other non-additive factors, including those of epistasis, were not statistically significant (Table 2).

Higher order contrasts among the models showed that dominance, epistasis and maternal effects remained significant in several comparisons (Table 3). Note, for example in the first column that the addition of dominance significantly improved the additivity model on one rearing host (usually the native host) for each trait. For beak length, maternal effects and especially epistasis were influential on the introduced host; addition of epistasis to ''additivity × dominance'' and to ''additivity × dominance × maternal effects'' substantially improved fit. For thorax width, in which the influence of non-additive processes was much greater (Table 2), results were qualitatively similar on the introduced host, but the impact extends to the native host as well.

Adding terms to the model likewise tended to improve the prediction of development time, most notably on the native host, where maternal effects and epistasis were influential. Such parsing provided little additional insight into survivorship, however, or host preference. This is not surprising in the latter case, where control was largely additive (Tables 2, 3).

In summary, the genetics underlying adaptive divergence differed substantially among the five traits. In spite the recency of the novel host's introduction, non-additive control was prominent in four of the five traits.

Looking forward: Australia—a parallel case with conservation potential

Serendipitously, a Neotropical balloon vine has invaded the eastern seaboard of Australia and is recognized as a serious environmental weed (Batianoff and Butler 2002; Carroll et al., 2005c). A horticultural escape, over the past 80 years *C. grandiflorum* has colonized riparian and disturbed forest habitats, and is now extending its range inland and into intact moist forests. The native sapindaceous flora of Australia is speciose, and there are five species of *Leptocoris* soapberry bugs on that continent (Carroll et al. 2005b). The prominence of the balloon vine as destroyer of native flora, the speed of its spread and the relative inattention to environmental (versus agricultural) weeds in general has motivated our work there. Our goals are to determine whether native soapberry bugs are colonizing the plant, whether they are evolving to better exploit it, and whether such adaptation might in consequence contribute to control efforts.

One of the bug species, *L. tagalicus* occupies the invader more reliably than it does its principal native host in the region of the invasion, the woolly rambutan tree (*Alectryon tomentosus*; Carroll et al. 2005a). Woolly rambutan has small fruits, while those of the balloon vine are inflated so that a much longer beak is required to reach the seeds inside of an average capsule. In 2004 we measured the beak length and thorax width (a measure of overall body size) of 857 adults in 22 populations. In both sexes, the grand mean beak length of the 12 populations on balloon vine were greater than the means for all 10 populations on native rambutan [e.g., females (± sd) 7.43 ± 0.15 mm versus 7.11 ± 0.11 mm; $p < 0.002$ in Wilcoxon rank-sum test of population means; respective thorax widths (3.42 ± 0.06 versus 3.36 ± 0.07) did not differ significantly; Carroll et al. 2005a]. Average female beak lengths in 10 of the 12 populations on balloon vine were greater than in all 10 populations on the native host. Developmental data from cross-rearing experiments indicate that these host-associated differences in beak length are genetic (Carroll et al. 2005a).

To probe the history of change further, we compared the beak and body measures of museum specimens collected between the 1920s and 2000. Based on our analysis of the invasion history (Carroll et al. 2005c), a priori we regarded those from before 1965 as from the period before balloon vine became common, and those after 1965 as from the period when it became widespread and abundant (and therefore capable of exerting selective force on associated insects). No host data accompany these museum specimens, and later collections may include bugs from either host. Nonetheless, *L. tagalicus* prior to 1965 were similar to those now on the native woolly rambutan, while those collected after are on average more similar to those collected from the invading balloon vine. In females, beak length of the 16 individuals collected after 1965 averages almost half a millimeter longer than that of 6 comparable individual collected prior to that date (7.41 ± 0.35 mm versus 6.81 ± 0.35 mm, $p < 0.003$ in Wilcoxon rank-sum test; Carroll et al. 2005a). Thorax width has not changed (3.41 ± 0.10 mm versus 3.39 ± 0.15 mm, respectively), indicating that the morphological difference is substantive and may have required substantial developmental reorganization. Results for males are similar.

Lastly, we exposed undamaged balloon vine seed capsules either to females reared from that plant or reared from the native. Both types attempted to feed with equal frequency, but the balloon vine bugs (with their longer beaks) successfully fed on 75% more of the seeds over a 1-week period in the lab (Carroll et al. 2005a). Because of the importance of propagules in recruitment for an expanding population, and for the establishment of new subpopulations in new habitats in particular, the ability of *L. tagalicus* to serve as a biological control agent appears to be increasing as it evolves adaptations to the invasive species.

Discussion

A central thesis of this paper is that members of native communities will not be evolutionarily passive in the face of biological invasions. Yet comparatively little attention has been paid to this prospect. Possibly this can be explained by insufficient recognition of the phenomenon of evolution on ecological time scales outside of evolutionary biology, and also incomplete appreciation for the fact that ecologically significant anthropogenic invasions have been taking place for centuries. Darwin (1962) remarked on the great demographic success and great capacity of invaders to alter their new environments, citing many striking examples across the globe in the 1830s (still early in the modern period of accelerated long-distance travel). The depth and frequency of “global change” events today indicates that such evolution must be increasingly commonplace (Strauss et al. 2006). Examples are not limited to rapidly cycling organisms, but include vertebrates (e.g., Kiesecker and Blaustein 1997; Phillips and Shine 2004) and even trees (Vourc’h et al. 2001; Kinloch et al. 2003).

Such invasions may often drive competitors or prey to local extinction. At the same time, as some natives adapt to resulting changes in their own niche structure, new forms of biological integration, including coevolution, will appear. At present we know little about how common this will be, how rapidly such associations will evolve, and how they may influence community structure, biodiversity and biological control in the long term (Vermeij 1996). For the many invaders that will become permanently established, this is the process from which some of the most interesting, surprising and potentially useful patterns will emerge. As such non-indigenous species themselves evolve in their new environments, they may further complicate local selective environments. This will happen as they adapt to new habitat, and as the relaxation of selective pressures in their natal environments yields new genetic cohorts as well. Accordingly, complementary studies of evolution within interacting native and invasive species will be the next step toward a more holistic examination of these multispecies processes.

In our case, at the genetic level, we have found unexpected impacts of non-additive genetic architecture underlying rapid adaptation to a new host plant. As a practical extension, we are also discovering how such evolution may augment the “biological control” potential of the native community to limit invasion.

Quantitative genetics of rapid adaptation

In the hybridization experiments summarized here (Carroll et al. 2001, 2003a) we analyzed the architecture of genetic differences that have evolved between the ancestral and derived phenotypes over about 100 generations. Four traits—beak length, thorax width, development time and survivorship—have evolved under various combinations of additive and non-additive control. In some cases non-additive control appears paramount. The fifth trait, host preference, is under additive control.

Combined, those findings reveal complex, perhaps unpredictable genetic organization underlying adaptive population differentiation. Differences in the relative contributions of additive and non-additive effects are somewhat ambiguous, at least in part because the strengths of the effects are environment (host) dependent. The traits are undoubtedly developmentally and functionally interrelated, yet we find intriguingly dissimilar architecture among them. This is the case even in comparing beak length and body size (thorax width): the phenotypic values are closely correlated, yet how the developmental genetics interacted with the developmental host differed sharply between them. In order to assess the relation between epistasis or dominance and fitness in the soapberry bug, we would need both to evaluate more traits and more closely consider the impact of host on development.

The functional interaction should be considered both in terms of selection and gene flow. With strong host effects on juvenile survival, for example, the sampling of individuals that comprised the cohorts we analyzed for development time, body size and beak length were likely a non-random subset of the original hatchling genotypes entered into the experiment. Thus, our results for these traits may not exactly describe the form of differentiation between the populations. The results for survivorship itself may therefore give a more direct picture.

Likewise, preference may determine the hosts on which adults aggregate and mate. Beak length, however, may influence the efficiency with which individuals can feed, and thus their residence time on particular hosts. An untested possibility is that individuals with inappropriate beaks are prone to leaving even an otherwise preferred host. The evolution of linkage between preference and beak length is an obvious prediction. At the same time, tradeoffs in juvenile development time and survivorship render hybrids less suitable on either host, further favoring genotypes expressing coadapted trait values and perhaps ultimately favoring positive assortative mating by race. We have not documented mating discrimination to date, however (unpublished data).

The importance of epistasis and other non-additive genetic effects in adaptive evolution has received increased attention in recent years (e.g., papers in Wolf et al. 2000). Our findings are not unique in demonstrating major non-additive genetic influence in the divergence between populations. What *is* very notable in our results is the prominence of non-additive control as a basis of diversification. In classical theory epistatic differentiation, based on mutation, should take thousands of generations to evolve (Roff 1998). Comparable differences have been found in hybrid analyses of more distantly related taxa (Orr and Coyne 1992; Bradshaw and Holzapfel 2000). We have found that adaptive gene differences may evolve in approximately 100 generations, and the theoretical dependence of adaptation on additive genetic variation sensu strictu should be reconsidered in light of this.

Increasingly, theoretical treatments are investigating the contexts in which epistasis may be surprisingly important (e.g., Crnokrak and Roff 1995; Merilä and Sheldon 1999; Agrawal et al. 2001; Wade 2002). Particularly relevant to the scenario we have studied may be models of founder-flush “speciation.” Founder-flush models suggest that population bottlenecks, as may occur in colonization events, cause inadvertent genetic reorganization that can enhance (rather than reduce) additive genetic variation and thus promote evolutionary response to selection (e.g., Goodnight 1988; Willis and Orr 1993). These models examine changes in the frequencies of alleles (and allelic combinations) for that subset of bottlenecked loci at which genetic variation is not lost. In spite of the loss of some alleles rare in the parental population due to bottlenecking, relatively slight increases in the frequencies of surviving rare alleles will overcompensate for that loss (Falconer and MacKay 1996). Increases in the frequencies of surviving rare alleles due to inbreeding will increase additive genetic variation by making frequencies more equitable in the derived population (Willis and Orr 1993). In spite of the costs of inbreeding depression (Charlesworth 1998), quantitative traits structured by epistatic interactions, in particular, may experience an increased variance in adaptive allelic combinations, and in consequence, in additive genetic variation available for response to selection in the new environment (Cheverud and Routman 1996).

Founder-flush speciation models are typically studied experimentally with captive populations (e.g., Regan et al. 2003), and so our data from wild populations may be particularly interesting. We believe that these adaptations in soapberry bugs have evolved from mass selection on latent extant genetic variation (and on any favorable mutations that have appeared as well). Whether our evidence of statistical non-additivity reflects the influence of physiological epistasis is uncertain, and the presence of any relevant latent variation would have reduced the number of mutations required at interacting loci, if selection acted to rearrange loci already present (Carroll et al. 2003a). The unexpected rate and extent of the phenotypic change may reflect the depth of genetic change. The large seed crops from the new host likely created strong selection for variant individuals within an expanding population (sensu Reznick and Ghalambor 2001). The result is a complex of genetic differentiation showing varying degrees of non-additive and additive control.

Conservation consequences of rapid evolution

The findings from our ongoing work with Australian soapberry bugs indicate that the North American results are not a special case. Moreover, they point out one form of conservation significance for rapid evolution. The time frame over which the evolution has taken place in Australia is similar to that in the US, and some of the same plant genera and species are involved, with the native versus invasive status partially reversed. We have sampled more populations in Australia than in the US, and our results show that the pattern of differentiation in beak length in nature is robust. In addition, we have recently gathered evidence that beak length is smaller in populations of soapberry bugs that have colonized invasive *K. elegans*, with its small fruits as in Florida, in the same region of eastern Australia. That finding is consistent with further instances of host race differentiation on various native sapindaceous hosts in Australia (S.P. Carroll et al., unpublished data).

At a less basic, more applied level, we are also interested in whether “biocontrol” value is evolving in these insects. The preliminary results point in this direction, and seed predation could slow expansion of balloon vine populations (Carroll et al. 2005a). It is important for conservation biologists to recognize that demographic changes are not the only consequences of human-induced environmental change. Evolution is ongoing and anthropogenic change likely increases both its frequency and rate, whether in threatened taxa, invading species or in native taxa whose niches are modified by novel populations of non-indigenous colonists.

Conclusions

Part of the drama of biological invasions is the scope and depth of change they may generate in resident ecosystems. Yet while the perspicacious Elton (1958) elaborated the ecological risks of conveying organisms across Wallace's biogeographic provinces, he perhaps did not suspect that invasiveness is often a consequence of rapid evolution in colonists. We now know that evolutionary processes may be consequential from the time of arrival in invading populations. In contrast, such non-indigenous taxa must achieve a degree of establishment before they exert selective force on natives. Nonetheless, even recent biological invasion are now known to be causing rapid evolution in impacted native species.

Ecological effects of invasions are direct (e.g., predation, competition, novel resources) and indirect (e.g., alteration of resources of natives that depend on directly impacted species, Smith et al. 1995), and the evolutionary responses observed are predictable from the same principles used to explain patterns in more natural circumstances (e.g., Endler 1986). Yet these accidental experiments, in which perturbations can be dated, measured and mapped, offer greater resolution and precision for predicting and quantifying the rate and direction of evolution than standard comparative and phylogenetic comparisons. They are useful hybrids of natural comparisons and premeditated experimentation, and for better or worse, lack the direct legal and personal ethical constraints that would encumber many intentional experimental releases.

From what we recognize today about the ecological seriousness of threats from invasive species, it is not surprising that the classic, best-known examples of evolution in action, once thought to be rare exceptions to a general pattern of much more gradual change, depended on anthropogenic influences (industrial melanism, host shift in apple maggot flies, plants on mine tailings). Relating to those three examples, we now live in a world reconditioned by polluted air, introduced species, and toxic waste, respectively. In heavily impacted populations and species that successfully adapt to these changes, rapid evolution may become the norm rather than the exception. Lee (2002) suggested that the adaptation of invasives to new habitats may depend on non-additive genetic variation, and we have growing evidence that similar complex sources of variation underlie evolution in adapting natives that have colonized new resources (e.g., Carroll et al. 2003a, Feder et al. 2003). Perhaps the importance of non-additive variation to rapid adaptation will differ between cases in which perturbed populations are expanding rather than suffering the hard mortality that results from many human activities. Biologists should be alert to the possibility of such unprecedented evolutionary change in their study systems, particularly those in which trait functions are clear, demography and selection can be measured, and genetic control can be identified and accounted.

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