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LETTER

And the beak shall inherit – evolution in response to invasion

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Abstract

The increased demographic performance of biological invaders may often depend on their escape from specifically adapted enemies. Here we report that native taxa in colonized regions may swiftly evolve to exploit such emancipated exotic species because of selection caused by invaders. A native Australian true bug has expanded its host range to include a vine imported from tropical America that has become a serious environmental weed. Based on field comparisons and historical museum specimens, we show that over the past 30–40 years, seed-feeding soapberry bugs have evolved 5–10% longer mouthparts, better suited to attack the forest-invading balloon vine, which has large fruits. Laboratory experiments show that these differences are genetically based, and result in a near-doubling of the rate at which seeds are attacked. Thus a native biota that initially permits invasion may rapidly respond in ways that ultimately facilitate control.

Keywords

Alectryon, Australia, biological control, *Cardiospermum*, conservation, evolution, invasive, *Leptocoris*, natural selection, soapberry bug.

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INTRODUCTION

Biologists have recently begun to explore in depth how their emerging understanding of evolution as a vital contemporary process (Hendry & Kinnison 1999) relates to established practices in ecology (Thompson 1998; Reznick & Ghalambor 2001), conservation biology (Lee 2002; Stockwell *et al.* 2003) and genetics (Carroll *et al.* 2003a). As human activities alter habitats worldwide, the global shuffling of organisms is a chief agent of selective change (Randall 1996). Consequently, we can view today's biological invasions as unplanned experiments in contemporary evolution (Cox 2004). Here we demonstrate the relevance of such evolution to conservation issues by showing that natives may evolve fast enough to influence the invasion process itself.

The predominant explanation for the rapid establishment and proliferation of non-indigenous species is that their geographical displacement has inadvertently granted them escape from their specialized predators and parasites, and thus an advantage over native species that are not 'released' from such enemies (Wolfe 2002; Reinhart *et al.* 2003;

Colautti *et al.* 2004; Torchin & Mitchell 2004). Nonetheless, selection is not necessarily relaxed in populations of successful invaders. Several studies show that exotics may rapidly evolve reductions in allocation to defence (e.g. Siemann & Rogers 2003; Wolfe *et al.* 2004) or enhanced abilities to exploit local resources (reviewed by Cox 2004).

In contrast, there has been less study of evolution in native taxa in response to biological invaders (Cox 2004), and similarly treatments of ecosystem 'resilience and adaptability' in the face of invasion lack explicit evolutionary content (e.g. Janssen 2001). The prospect is important for at least two reasons. First, to the extent that certain invasives become abundant as a result of enemy release, they may be more likely to create conditions for the evolution of new local enemies. The second is that rapid evolution in natives may reduce an invader's ability to spread.

Invasive plants are useful models for investigating these ideas because they often accumulate native herbivores (Frenzel & Brandl 2003; Graves & Shapiro 2003). Not surprisingly, many such herbivores are diet-generalists that are more damaging to the native flora than to the newcomers (Keane & Crawley 2002). Classic earlier studies

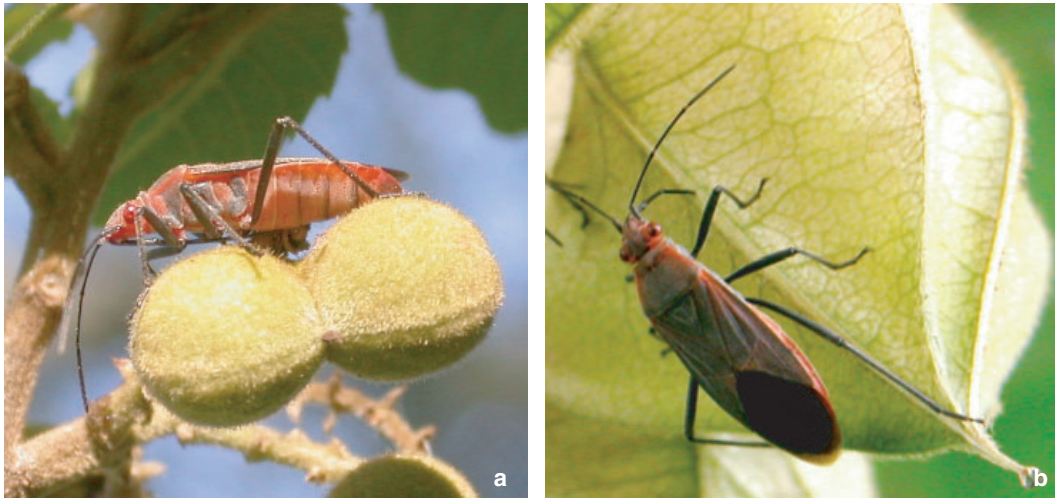


Figure 1 The Australian soapberry bug *Leptocoris tagalicus* on fruits of its native and introduced host plants. Note the difference between the two hosts in the size of the fruit relative to that of the seed predator. Insect body length is about 14 mm. (a) The native tree ‘woolly rambutan’ (*Alectryon tomentosus*) is common in rain forest fragments throughout much of subtropical eastern Australia. The beak is visible folded beneath the insect’s body. (b) The invasive balloon vine (*Cardiospermum grandiflorum*) has established in a large area of eastern Australia since the 1960s. The insect is probing a seam of the plant’s inflated fruit capsule with its elongated ‘beak’. Three seeds are held centrally, distant from all panels of the capsule wall. The bug may access the seeds of an intact capsule only if its beak is longer than the minimum distance between the capsule wall and the seeds.

explored the time dependence of this phenomenon (e.g. in the widely exported crop plant, cacao; Strong 1974), and suggested that community saturation could take place on a time scale of decades. Yet, little is known about the functional integration of exotics into complex natural communities, or about the extent to which they will cause evolutionary change, or the influence such evolution may exert on invading species themselves. The few available cases show that native insects shifting onto introduced plants may undergo rapid behavioural, morphological and life-history evolution (Singer *et al.* 1993; Filchak *et al.* 2000). In the American soapberry bug *Jadera haematoloma* (Hemiptera: Rhopalidae) we found that the length of the piercing-sucking mouthparts, or ‘beaks’, declined substantially after populations shifted from native *Cardiospermum corindum* (balloon vine) to introduced horticultural relatives with smaller fruit. Differences in host preference, physiology and life history evolved rapidly as well (Carroll & Boyd 1992, Carroll *et al.* 1997, 2001, 2003a).

Now, in eastern Australia, we are examining whether similar rapid evolution has occurred in a closely related insect that has shifted to invasive balloon vine, and whether this process may augment the native community’s capacity to regulate the invader. The soapberry bug *Leptocoris tagalicus* Hahn is the sole insect to have colonized the Neotropical balloon vine *Cardiospermum grandiflorum* Swartz (Sapindaceae, or soapberry family) in Australia (Carroll *et al.* in press a) (Fig. 1). Balloon vine has naturalized during the past

80 years (Carroll *et al.* in press b). Its geographical spread has accelerated since the 1960s (Carroll *et al.* in press b) and it was formally declared a pest in the past decade because it smothers subtropical riparian forests (Batianoff & Butler 2003). It propagates by seeds, which develop at the centre of large inflated balloon-like capsules (Vivian-Smith & Panetta 2002). Soapberry bugs are worldwide seed predators of Sapindaceae that depend on these hosts for growth and reproduction (Carroll & Loye 1987). In eastern Australia’s moist montane and coastal forests the insect’s principal native hosts are comparatively small-fruited trees of the genus *Alectryon* (wild rambutans) (Carroll *et al.* in press a) (Fig. 1).

The likelihood that soapberry bugs in this region will evolve longer beaks in response to the large size of the invader’s fruit will be influenced by factors beyond the apparent advantage of gaining access to the seeds of the invasive plant. These include genetic variance, population structure, generation time and time since colonization. All may be in flux as a function of how behaviour and reproductive performance on the respective hosts affect gene flow. For example, the two plant species often occur within metres of one another, such that the probability of interchange that could negate the power of diversifying selection seems high. We have begun our assessment by measuring beak length as an indicator of whether the strength of selection for efficient performance on the invasive species has overcome the influences of the potentially limiting factors listed above.

METHODS

Study sites are in eastern Australia around Brisbane, Queensland, and adjacent northern New South Wales. This is an area with year-round moist and mild conditions that balloon vine colonized from horticultural escapes in the 1930s (Carroll *et al.* in press b). The Brisbane River watershed is heavily impacted by balloon vine, and the sale and propagation of the vine has been illegal in Queensland since 2002. In 2003 and 2004, we found that *Leptocoris tagalicus* occurred on all fruiting balloon vines at 34 sites sampled within a 140 km radius of the University of Queensland Brisbane campus (Carroll *et al.* in press a). Within this region the primary native host is the woolly rambutan tree, *Alectryon tomentosus* (F. Muell.) Radlk. (Carroll *et al.* in press a).

These insects access seed contents by penetrating the fruit wall and then the seed coat with their elongated mouthparts (beaks). During January to April 2004 we measured the beak (labial) length, body length and thorax (pronotum) width in a total of 857 live adults from 10 populations on the native woolly rambutan and 12 populations feeding on infestations of balloon vine. Sites were sampled as encountered, but within a host species, no sites within *c.* 10 km of another site were included. We used body length and thorax width as body size covariates of beak length. We measured fruit size as the distance between the outside of an intact fruit and the centre of the nearest seed ($n = 5$ plants from separate watersheds, 20 fruits per plant, for each species). We made all measurements with Mitutoyo handheld digital calipers (Model CD 6B, 0.01 mm measurement increment, Mitutoyo America Corporation, IL, USA).

We took two approaches to test the hypothesis that beak length differences between bugs on native and alien hosts are the result of evolution, one descriptive and the other experimental. First, we compared the same beak and body measures in 38 historical museum specimens from eastern Australian regions in which balloon vine was invading, in this case not by host species (as those data do not exist), but instead by epoch of collection. Specimens were from between the 1920s and 2000, and based on our associated research (Carroll *et al.* in press b), *a priori* we regarded those from before 1965 as representing the epoch before balloon vine became common, and those after 1965 as from the epoch when it began to become widespread and abundant. We measured eight specimens from five separate collection events prior to 1965, and 30 specimens from nine separate collection events thereafter. Measurements were made as for the contemporary live specimens. Specimens were from the Australian National Insect Collection, University of Queensland Insect Collection, the Queensland Museum, CSIRO-Long Pocket, and the US National Museum. (We located no

relevant specimens in other Australian museums, nor in the British or American Museums of Natural History.)

Second, to test for genetic, maternal or dietary effects underlying host-associated differences in beak length, we conducted reciprocal-rearing experiments in the laboratory (24 ± 2 °C, with approximately 14 : 10 L : D). Approximately 30 newly matured (virgin) 'grandparental' (G_1) bugs of each sex were collected from one population on each host in the Brisbane region (invader: Kholo Botanical Gardens; native: Sherwood Forest Park). Within each population each female was assigned a mate haphazardly, and the pair was isolated in a plastic Petri dish with dehisced seeds of their natal host and water. The ensuing hatchlings constituted the 'parental' generation (G_2). They were removed from the Petri dishes before they fed and reared to maturity in sibling broods of approximately 20 individuals, split evenly between two rearing containers ($10 \times 16 \times 6$ cm deep plastic boxes) per family, with *ad libitum* seeds of one host or the other. On maturing, one female (dam) from each host and each family was paired with a male from another family. In half of the pairings the two adults had been reared on the same host as their parents, and in the other half they were reared on the alternate host. Their hatchlings were the 'grandchildren' (G_3), and these were collected and reared in the same manner as G_2 . We measured beak length in five G_3 adults of each sex from both hosts for each family producing sufficient offspring ($n = 16$ per population). We conducted ANOVA of the fixed effects 'source host population' (defined as originating from native or exotic host), 'dam rearing host' and 'offspring rearing host', with family treated as a random variable within population. Within this analysis we used *t*-tests of least squares means to compare the treatments. This was performed with Proc Mixed of the Statistical Analysis System (SAS 2003).

Lastly we tested the hypothesis that the derived population on the alien balloon vine has evolved the ability to better reach the plant's seeds, and thus kill propagules that might otherwise contribute to the ongoing invasion. Groups of 20 adult females (all collected as young nymphs) from three populations per host (woolly rambutan or balloon vine) were placed separately into laboratory population cages containing balloon vine fruits. Each group was replicated, so that there were two groups of females for each of the three populations from each host, for a total of 12 groups. Each cage contained 20 newly ripened fruits collected and distributed haphazardly from a local site. These fruits were free of insect damage. After 1 week the fruits were removed and the presence/absence of feeding scars on the seeds was scored and compared (Wilcoxon rank sum test). To measure feeding frequencies we counted the number of individuals feeding with scan samples twice daily for each cage.

RESULTS

The fruit of the invasive balloon vine is substantially larger than that of the native host, and so the distance over which beaks must extend to feed on seeds is much greater in balloon vine (see Fig. 1). Grand mean \pm SD of the distance from the fruit exterior to the centre of the seed (fruit radius) were woolly rambutan 4.26 ± 0.23 mm and balloon vine 10.70 ± 1.61 mm ($n = 5$ plants per species).

The first prediction of the evolutionary hypothesis was that beaks of adults occupying the alien host would be longer than those of bugs on the native host. This is the case for both sexes. In females (the sex in which adult-stage feeding is more critical for reproduction; Carroll 1991), grand mean beak length of the 12 populations on balloon vine was greater than the means for all 10 populations on native rambutan (Table 1; Fig. 2). Average female beak lengths in 10 of the 12 populations on balloon vine were greater than in all 10 populations on the native host. The result in males is similar but with more overlap among the means and less difference in average length. Beak length has increased proportionately more than thorax width or body length in females, and done so in the absence of body size changes in males (Table 1). Host effect on beak length was independent of body size measures, and comparatively little variation in beak length was attributable to differences among populations within each host species (ANCOVA, e.g. in females, with thorax width as covariate, F and P -values were ‘Host’, 96.81, $P < 0.001$; ‘Thorax width within host’, 84.50, $P < 0.001$; ‘Population within host’, 2.02, $P < 0.01$. Similarly, with body length as covariate, F -values were ‘Host’, 93.84, $P < 0.001$; ‘Thorax width within host’, 81.79, $P < 0.001$; ‘Population within host’, 2.12, $P < 0.01$).

The pattern in historical specimens was congruent with what we observed in the 2004 field populations. In

Table 1 Grand means (\pm SD) of beak length and body size measures (in mm) of soapberry bugs in 12 populations from the alien host and 10 from the native host

Trait	Host	
	Alien	Native
Females		
Beak length	7.43 \pm 0.15	7.11 \pm 0.11***
Thorax width	3.42 \pm 0.06	3.36 \pm 0.07
Body length	13.71 \pm 0.31	13.39 \pm 0.21*
Males		
Beak length	6.53 \pm 0.93	6.39 \pm 0.07***
Thorax width	2.94 \pm 0.05	2.96 \pm 0.06
Body length	12.07 \pm 0.25	11.98 \pm 0.22

* $P < 0.05$, *** $P < 0.002$ in Wilcoxon rank-sum tests of population means.

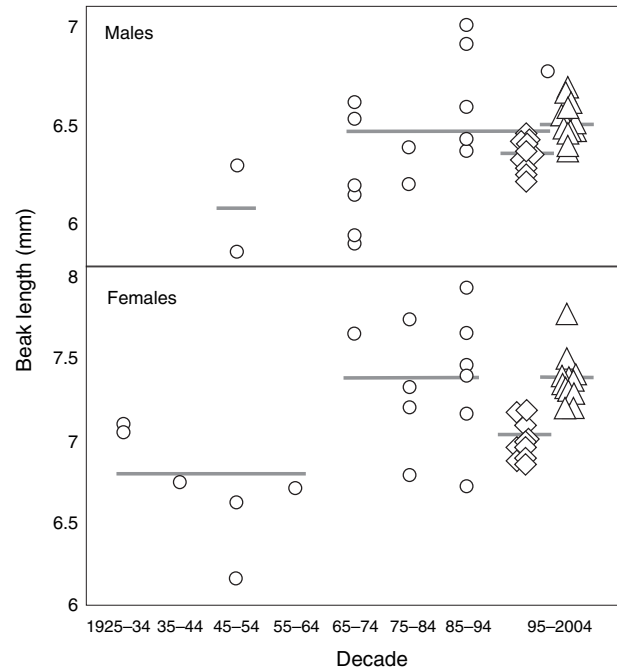


Figure 2 Beak length in historic museum specimens (circles) plus their means (grey bars) by invasion epoch (top panel: males, bottom panel: females). The two epochs are before and after the period during which invading balloon vine became a common plant in eastern Australia (1960s). Also shown are population means by host (diamonds: native host, triangles: alien host) plus grand means (grey bars) of those population means. All host population values are from 2004.

females, beak length after 1965 averaged almost 10% longer, while the body size measures were static (Fig. 2; Table 2). Again the trend in males was similar, but note

Table 2 Mean (\pm SD) beak length and body size measures (in mm) of soapberry bugs collected in eastern coastal Australia after versus before the invader became widespread

Trait	Invasion epoch	
	Post-1965	Pre-1965
Females		
Beak length	7.41 \pm 0.35	6.81 \pm 0.35**
Thorax width	3.41 \pm 0.10	3.39 \pm 0.15
Body length	13.24 \pm 0.60	13.65 \pm 0.68
n	16	6
Males		
Beak length	6.48 \pm 0.34	6.08 \pm 0.32
Thorax width	2.99 \pm 0.22	2.97 \pm 0.26
Body length	11.92 \pm 0.66	11.63 \pm 0.27
n	14	2

** $P < 0.003$ in Wilcoxon rank-sum tests of population means.

Table 3 Analysis of variance for beak length of historical specimens of soapberry bugs in relation to the invasion history of the alien host

Source	d.f.	Type I SS	F-value
Sex	1	6.87	73.47****
Invasion epoch†	1	1.54	16.41***
Sex × epoch	1	0.01	0.04
Body length	1	0.04	0.43
Thorax width	1	0.29	3.09

*** $P < 0.001$, **** $P < 0.0001$.

†Before or after 1965, by which time collection records indicate that the plant had become widespread in far eastern Australia.

that we only had two male specimens before 1965. We pooled the sexes for greater power in analysing the results for beak length (Table 3). Clearly invasion epoch had a major effect on beak length in both sexes, while the values of body size appear tangential to adaptation to modern conditions.

The cross-rearing experiments indicate that host-associated differences in beak length are genetically based rather than principally caused by developing on one host or the other (Table 4). In both sexes, beak length was consistently greater in the bugs collected from balloon vine than from the native host ($F = 38.6$, $P < 0.0001$). For each population, values were greatest for those reared on the natal host in each generation. Maternal host effects varied significantly between the populations ($F = 38.1$, $P < 0.0001$), as did rearing host effects ($F = 93.5$, $P < 0.0001$), in which host species had opposite effects on beak length.

Lastly, our experiment indicated that longer mouthparts increase the ability of these insects to feed on seeds within

the inflated capsule of balloon vine. Adult females collected and reared from the three balloon vine sites fed on an average (\pm SD) of $42 \pm 8\%$ of the seeds over a 1-week period (range, 29–51%), while those from three woolly rambutan sites fed on only $24 \pm 10\%$ of such seeds (range 10–41%, Wilcoxon $z = 2.32$, $P < 0.02$). The frequencies with which these insects probed the fruit over this period averaged no greater in the groups derived from balloon vine than in those from the native host ($11 \pm 4\%$ vs. $12 \pm 5\%$ respectively).

DISCUSSION

Our results portray a little-explored response of natural communities to biological invasion. An Australian soapberry bug has expanded its host range from a native host tree to include a phylogenetically related, forest-invading Neotropical vine. In doing so, it has evolved a genetically distinct beak length morph during the past several decades, as evidenced by field observations (2004) and historical specimens (1927–1997). Based on morphological capacity alone, these recently evolved, longer-beaked insects are more effective at attacking the invader's seeds, in laboratory experiments, than are those exhibiting the ancestral form.

Accordingly, this rapid evolution in a native organism has the potential to aid efforts to control the exotic plant. In cases in which seedling density is inversely related to survival, seed predation may not reduce weed population growth (e.g. Myers & Risley 2000), but, in general, seed-attacking agents may be underestimated as a tactic to control alien plants (Neser & Kluge 1986). In the case of balloon vine, the insect's evolving ability has geographically structured implications for control. Populations of the plant are

Table 4 Cross-rearing experiment comparing mean beak length between the two host-associated populations in relation to maternal and developmental diet (seeds of the native vs. seeds of the invasive host)

Source host	<i>n</i> families	Dam host			
		Native		Invasive	
		Offspring host		Offspring host	
		Native	Invasive	Native	Invasive
Females					
Native	16	7.02 \pm 0.25 a	6.93 \pm 0.26 a	6.97 \pm 0.25 a	6.87 \pm 0.27 a
Invasive	16	7.32 \pm 0.21 b	7.45 \pm 0.24 b,c	7.36 \pm 0.18 b,c	7.50 \pm 0.24 c
Males					
Native	16	6.38 \pm 0.17 a	6.30 \pm 0.21 a	6.27 \pm 0.20 a	6.20 \pm 0.21 a
Invasive	16	6.56 \pm 0.16 b	6.64 \pm 0.21 b,c	6.59 \pm 0.18 b,c	6.68 \pm 0.19 c

The sexes are treated separately, and within each sex values lacking common letters are significantly different at $P < 0.05$ (t -test comparisons of least squares means). Note that in both sexes bugs from the line collected on the invasive host had longer beaks irrespective of the rearing host.

Values are grand means of family mean beak length \pm SD (mm).

patchily distributed among the watersheds that drain the Great Dividing Range. For example, in northern New South Wales, watersheds in which it is abundant border those in which it is rare or absent (Carroll *et al.* in press b). While dispersal within catchments results in part from flood transport of floating capsules (Vivian-Smith & Panetta 2002), colonization of new watersheds depends on air transport. By killing more seeds before they can dehisce, long-beaked soapberry bugs may reduce the frequency with which new areas are invaded.

Based on the incidence of feeding scars, over a 1-week period, captive bugs derived from balloon vine attacked 1.8 times the number of balloon vine seeds than did those from the native host. This was in spite of the fact that both races attempted to reach seeds at similar rates. This difference in feeding success might be greater in nature, where inflated capsules may remain pendant for weeks on fruiting plants. Soapberry bugs were present at all field sites with fruiting balloon vines ($n = 34$ sites; Carroll *et al.* in press a), and such consistent attendance suggests that they have substantial potential to reduce seed populations. Moreover, given that the average radius of balloon vine fruits exceeds average beak length, selection may still be operating. We observed occasional asymmetrical capsules that had seeds nearer to capsule walls, and these may provide the initial selective environment favouring longer beaks.

Accordingly, even minor differences in beak length may affect the number of seeds that are killed. For comparison, beaks in North American soapberry bugs on native balloon vine average around 9 mm in length (Carroll & Boyd 1992), and these bugs kill up to 90% of mature seeds (Carroll *et al.* 2003b). We estimate that Australian bugs are similar to their American relatives in producing about three generations per year (Carroll *et al.* 2003b). Balloon vine in Australia has become much more abundant since 1965 (Carroll *et al.* in press b), and the museum data analysed here suggest that much of the observed evolution has taken place since then, during the past *c.* 100 generations. Any evolution of even longer beaks would likely increase mortality in invasive balloon vine seeds.

Our findings imply that preference for the invader is evolving as well. At several sites, native and alien hosts were within a few hundred metres of one another. The bugs are capable of flight and such proximity may result in gene flow, yet we consistently observed significant differences in beak length between such proximate hosts, suggesting population genetic predispositions to colonize either one or the other plant species in a manner that may limit gene flow between the nascent races (*sensu* Filchak *et al.* 2000). We found only limited evidence of maternal and juvenile rearing host effects on beak length in our cross-rearing experiment, but a very strong indication of host-associated genetic differentiation. In the North American soapberry bug *Jadera*

haematoloma, maternal effects on host-associated performance traits also tend to be comparatively weak. In that species, preference evolution stems mainly from changes at additive genetic loci, but beak length and other traits are strongly influenced by epistatic and dominance interactions of major effect (Carroll *et al.* 2003a). Such substantial genetic rearrangements may underlie the rapid evolution of considerably altered, newly adaptive phenotypes. Notably, in one case, second generation backcrosses between a long-beaked race and a long-short hybrid produced bugs with even longer beaks (Carroll *et al.* 2001). This type of unexpected interaction could facilitate swift adaptive change.

A variety of factors may influence the time course by which natives begin to use and adapt to invasive exotics. For example, in cases where aliens are phylogenetically distant from the native community, they may be colonized only slowly (Mack 1996; Duncan & Williams 2002). In contrast, experimental work by Agrawal & Kotanen (2003) showed that herbivore damage was frequently greater on exotic plants than on their native congeners, contrary to predictions of the enemy release hypothesis. However, in the absence of information about any temporal dynamism or evolutionary history that may predate the contemporary pattern they report, rejecting that hypothesis is premature. Note that invading plants have been reported to lose herbivore resistance, likely in response to correlated selection for increases in other performance traits (Siemann & Rogers 2003, Wolfe *et al.* 2004). Such losses could be ephemeral in the face of evolving herbivory from natives. Certainly, rapid evolution in response to alien organisms is not extraordinary: many agricultural pests, for example, are natives specifically adapted to highly abundant introduced plants and animals (e.g. Malausa *et al.* 2005).

The natural process we describe will not prevent biological invasions because a non-indigenous species must normally establish before it will exert substantial selective force on the native community. Nonetheless, our findings for a natural system are relevant to conservation in two ways. First, biologists should be alert to the possibility that evolution may swiftly render natives as allies in efforts to control some invasions. Likewise, natives threatened by invaders may quickly evolve resistance. For example, in an analysis of historical data much like our own, Phillips & Shine (2004) indicate that Australian snakes are evolving morphologically in response to the threat of introduced cane toads (*Bufo marinus*). Second, strategic management may foster or enhance such evolution within native communities (e.g. Schlaepfer *et al.* 2005). Indeed, the development of coevolving relationships between invaders and natives may accelerate rates of change (Thompson 1998). Evolution in native communities may complement, or in some cases obviate, the need for 'classical biological control', in which pests of established aliens are imported from the invaders'

natal regions. Classical biological control is successful in perhaps 15% of attempts, but its great value is sometimes balanced by the serious unforeseen environmental consequences of multiplying invasions (Roderick & Navajas 2003). Such difficulties are probably less likely with newly evolving, native control agents.

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