

## SYNTHESIS

# Invasive species as drivers of evolutionary change: cane toads in tropical Australia

Richard Shine

Biological Sciences A08, University of Sydney, Sydney, NSW, Australia

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**Correspondence**

Richard Shine, Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia.

Tel.: +612-9351-3772;

fax: +612-9351-5609;

e-mail: rick.shine@sydney.edu.au

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**Abstract**

The arrival of an invasive species can have wide-ranging ecological impacts on native taxa, inducing rapid evolutionary responses in ways that either reduce the invader's impact or exploit the novel opportunity that it provides. The invasion process itself can cause substantial evolutionary shifts in traits that influence the invader's dispersal rate (via both adaptive and non-adaptive mechanisms) and its ability to establish new populations. I briefly review the nature of evolutionary changes likely to be set in train by a biological invasion, with special emphasis on recent results from my own research group on the invasion of cane toads (*Rhinella marina*) through tropical Australia. The toads' invasion has caused evolutionary changes both in the toads and in native taxa. Many of those changes are adaptive, but others may result from non-adaptive evolutionary processes: for example, the evolved acceleration in toad dispersal rates may be due to spatial sorting of dispersal-enhancing genes, rather than fitness advantages to faster-dispersing individuals. Managers need to incorporate evolutionary dynamics into their conservation planning, because biological invasions can affect both the rates and the trajectories of evolutionary change.

**Introduction**

As an introduced species spreads outside its native range, it initiates a complex array of evolutionary processes that can produce clear effects over a timeframe of years or decades. The opportunity to measure not only selection, but also its results, has motivated many biologists to explore this intersection of ecology, evolution, and population biology (Cox 2004; Huey et al. 2005). The consequent explosion of information on evolutionary aspects of biological invasions has attracted several excellent reviews (e.g., Thompson 1998; Mooney and Cleland 2001; Cox 2004; Lambrinos 2004; Strauss et al. 2006b; Sax et al. 2007; Vellend et al. 2007; Buswell et al. 2011; Westley 2011). It is clear that evolutionary change can occur rapidly (Reznick and Ghalambor 2001; Hairston et al. 2005; Carroll et al. 2007; Hendry et al. 2008) and can modify traits both in invaders and in the taxa with which they interact. Thus, the proposition that invasion can drive evolutionary change is well supported, and researchers are now asking more detailed questions such as how

frequently such changes occur (Buswell et al. 2011) and what genetic mechanisms and adaptive processes underlie them (Lee and Bell 1999; Carroll et al. 1998, 2005; Carroll 2007a,b, 2008). Understanding such topics may provide a basis for novel approaches to controlling the invader, or mitigating its impact, for example, we may be able to identify and exploit adaptive trade-offs and evolutionary traps to curtail invader numbers (Ward-Fear et al. 2010; Lankau and Strauss 2011). In this review, I will examine ideas and evidence on the evolutionary consequences of biological invasions, with a strong focus on one study system – the invasion of cane toads through tropical Australia.

**Impacts of biological invasion on the rate and trajectory of evolution**

In many cases, the most rapid changes in trait values may occur early in the process of adaptation, as soon as the novel selective challenge is encountered. Fitness differentials are high initially, but reduce through time until the

most common genotypes are those that confer highest fitness. The arrival of an invasive species thus can elicit a rapid shift in genotype frequencies until the challenge exerted by the interloper has been blunted by adaptation (e.g., Vermeij 1996; Stockwell et al. 2003; Buswell et al. 2011). Because many invader populations are increasing ( $r_0 > 1$ ) whereas those of many native taxa are not, and rapid population growth enhances the opportunities for rapid evolution (Reznick and Ghalambor 2001), invaders may evolve more rapidly than the native taxa they affect.

Adaptation is not inevitable. The potential for evolutionary change can be reduced by low genetic diversity within the invader, as a result of founder effects (Lee et al. 2007; but see Kolbe et al. 2007). Likewise, intense selection exerted by an invader may depress population sizes of the native taxa so greatly that extinction is more likely than adaptation. Other selective forces may oppose the changes favored by the invaders' presence. Phenotypically, plastic responses to invader cues may generate sub-optimal phenotypes, curtailing effective selection (Richards et al. 2006) but potentially serving as a bridge to ultimate adaptive evolution (Ghalambor et al. 2007). Attributing a lack of evolutionary response to such mechanistic constraints is a formidable logistical challenge, requiring sophisticated experimental work to tease apart the genetic underpinnings of adaptive responses, or the lack thereof (Carroll et al. 2005).

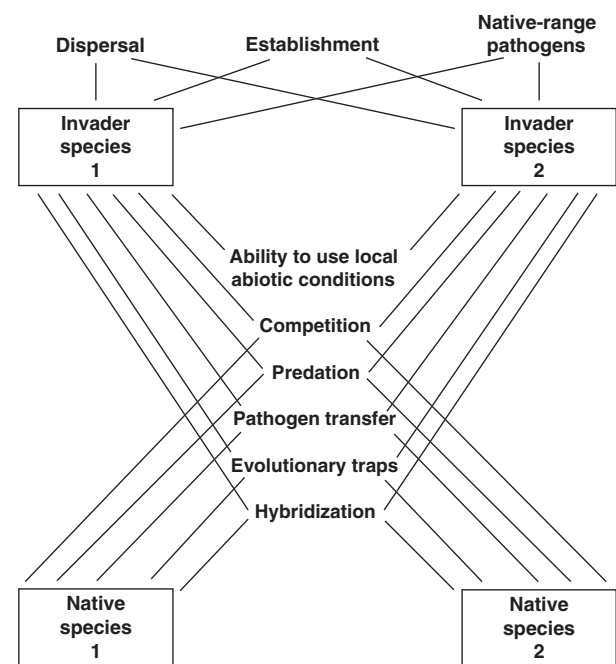
Thus, invasive species have the potential to cause rapid evolutionary change, but may not always do so. Proliferating empirical studies on evolutionary shifts associated with biological invasions (Thompson 1998; Westley 2011) mean that it may soon be possible to quantitatively compare rates of evolutionary change between invasive species in their ancestral range versus the newly occupied area, or invasive species in sites that have been colonized for differing lengths of time, or native taxa in areas that have or have not been invaded, or invasive versus native taxa. Such comparisons will clarify the effects of biological invasion on rates of evolution.

Natural ecosystems contain complex webs of interactions among species, and the arrival of an invasive species can reverberate via many pathways. We may see evolutionary changes in the invader, in native species directly impacted by it, and in species influenced indirectly via their interactions with affected native taxa. Many systems are under simultaneous challenge from multiple invaders, adding to the complexity of response. The traits affected also are diverse, ranging through morphology, ecology, life history, physiology, and behavior. The interspecific interactions may involve relationships such as predation, herbivory, pathogen transfer, interference or exploitative competition, evolutionary traps (such as consuming a lethally toxic invader that resembles a

harmless native prey species), and hybridization. In total, then, a biological invasion – even by a single species into a relatively species-poor natural system – can impose novel ecological and evolutionary pressures on a vast array of biological traits, via a vast array of direct and indirect pathways (see Schlaepfer et al. 2002; Cox 2004; Strauss et al. 2006a). I review such processes below.

### Evolution driven by the process of range expansion

Some of the selective challenges experienced by invaders result from the invasion process *per se* whereas others involve system-specific interactions with abiotic challenges, with the native biota or with other invaders (Fig. 1).



**Figure 1** A schematic view of evolutionary processes at work during biological invasions. Lines linking two taxa show potential pathways by which selective forces may be exerted by one species upon the other. Invaders may be subject to selection or sorting for more rapid dispersal and also for traits that facilitate population establishment and minimize dispersal-reducing effects of pathogens. Invaders also interact with each other, and with native species, via a network of processes that include competition, predation, pathogen transfer, toxic ingestion, and hybridization. Each species can interact with others either directly or via indirect effects (mediated by perturbations to other links). The end result is that invasion can unleash a complex array of ecological and evolutionary pressures, even in relatively simple (stable, species-poor) systems.

### Establishment success

The ability of a few founders to set up a population depends on the mating system, but generalities may be elusive. Colonizing populations of smooth cordgrass show high rates of self-fertilization, allowing a small number of individuals to found a new population (Brown and Marshall 1981; see also Lavergne and Molofsky 2007 for similar results on vegetative reproduction), but the reverse situation also occurs (outcrossing increases genetic diversity in newly founded populations: Brown and Marshall 1981). The mating system also may be under divergent selection in invasion-front populations compared to those in long-colonized areas, reflecting spatial differences in variables such as population density. Mating systems and patterns of genetic diversity within populations may interact in complex ways with the determinants of dispersal rate. For example, highly dispersive organisms often have multiple introductions to the same site, increasing genetic variation (Kolbe et al. 2007).

High levels of phenotypic plasticity may enhance colonization success, by allowing invaders to adopt the phenotypes best-suited to local conditions (Brown et al. 2011a), but environmentally induced flexibility sometimes may reduce rather than enhance fitness (Price et al. 2003; Yeh and Price 2004; Richards et al. 2006; Ghalambor et al. 2007; Thibert-Plante and Hendry 2011). Some traits may benefit from flexibility whereas others do not. Because colonization success is enhanced by larger relative brain size (in mammals, birds, reptiles, and amphibians: Amiel et al. 2011), we might expect the evolution of larger brain size during colonization of some but not all environments (e.g., smaller brains may be optimal in Australia, reflecting resource constraints: Amiel et al. 2011). Plausibly, the selective advantages of behavioral flexibility (and thus, larger brain size) may shift in complex ways during a biological invasion, with initial benefits reducing through time since colonization, as the challenges to the invader cease to be novel. Trade-off models suggest that invaders will be under selection (and also spatial sorting; Shine et al. 2011) to reduce investment into any processes that constrain dispersal rate. Thus, for example, we might expect lower investment into immune defense in invaders (Lee and Klasing 2004).

Cane toads (*Rhinella marina*) are large toxic anurans native to Central and South America, but introduced to northeastern Australia in 1935 in a futile attempt at bio-control (Shine 2010). They have since spread across the Australian tropics. Behavioral plasticity has allowed toads to colonize climatic zones well outside those experienced in the native range (Brown et al. 2011a). Analyses of progeny from adult toads collected at various points across the toads' invasion history reveal significant evolutionary

changes in growth rates, consistent with the hypothesis that selective targets at the invasion front may differ from those in long-colonized areas (Phillips 2009; Phillips et al. 2010c). The prediction of reduced immunocompetence in toads at the invasion front accords with a high incidence of bacterially influenced arthritis in these animals (Brown et al. 2007), as well as weaker responses to subcutaneous injection of phytohemagglutinin (G. P. Brown and R. Shine, unpublished data), and lower metabolic investment in response to a standardized immune challenge (Llewellyn 2009).

### Dispersal rate

In a range-expanding population, natural selection can favor the evolution of enhanced rates of dispersal, whereby individuals that disperse most rapidly benefit because their access to resources is not constrained by high densities of conspecifics (Travis and Dytham 2002). Selection for rapid dispersal also can occur at the level of families (variance in dispersal reduces among-progeny competition: Hamilton and May 1977), or groups (if rates of population extinction are high, and all new populations are founded by dispersers, then population-level selection can maintain high frequencies of dispersing individuals: Van Valen 1973). Intriguingly, rapid dispersal also can evolve non-adaptively, by spatial sorting of genes within the invading species (Shine et al. 2011). Any alleles that code for faster dispersal will tend to accumulate at the expanding range edge, whereas alleles that code for slower dispersal will be confined to long-colonized areas (Travis and Dytham 2002). Because slow-dispersing individuals cannot reach the invasion front, accelerated rates of dispersal will evolve even if this trait does not enhance lifetime reproductive success (Shine et al. 2011). It is evolution through space not time and does not depend upon differential fitness.

A wide range of traits that influence rates of dispersal might evolve at an expanding range edge. For plants, traits such as small seed size, short generation time, high fecundity, and reliance on abiotic dispersal mechanisms may enhance dispersal rate (Daehler 1998; Grotkopp et al. 2002; Ridley and Ellstrand 2009). For animals, range expansion may be accelerated by better locomotor ability, high fecundity, rapid growth, and habitat breadth (Lodge 1993; Thomas et al. 2001; Cassey 2002). The traits that enhance dispersal rate are system specific – the features that enable a seed to drift through the air are very different from those that enable it to cling to a mobile bird or mammal, and from the ones enabling that host organism to move further than its conspecifics. One interesting set of traits involves host–pathogen interactions; if pathogens vary in the degree to which they impede host dispersal, we expect to see the evolution of lower-impact pathogens

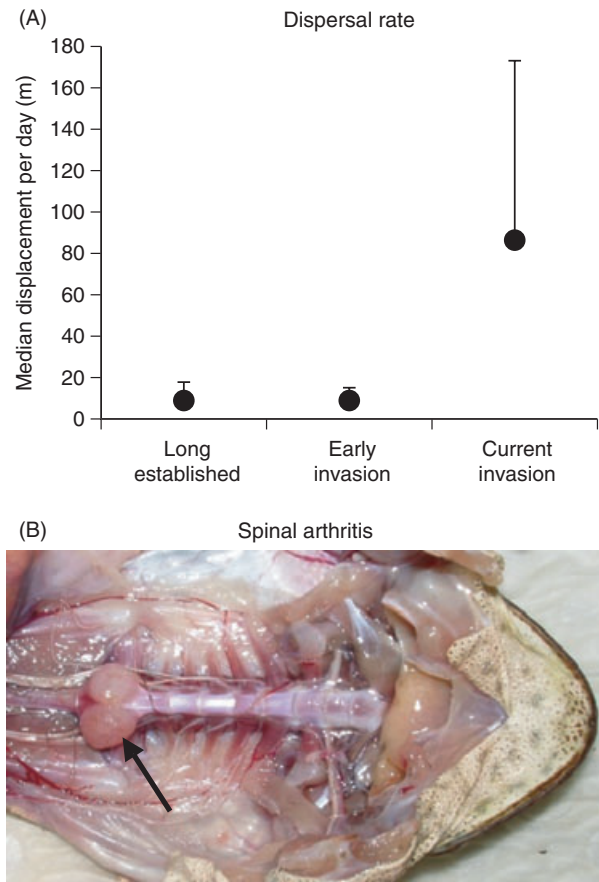
in invasion-front populations of the host (Phillips et al. 2010a).

A growing literature provides examples of dispersal-facilitating traits accumulating at expanding range edges. For example, seed mass of lodgepole pine was lowest at the range edge (Cwynar and Macdonald 1987). Speckled wood butterflies in colonizing populations were larger and had longer thoraxes (where the flight muscles are located) and broader wings than conspecifics in more central parts of the species' range (Hill et al. 1999). Two species of bush crickets showed more of the long-winged morph than the short-winged morph in range-expanding populations (Simmons and Thomas 2004). Similar trends occur in populations of ground beetles colonizing northwards in southern Canada (Niemala and Spence 1991). Work on allozyme variants in the flight abilities of butterflies has shown how the genetic underpinnings of differential dispersal rates can influence extinction and colonization rates in metapopulations (Hanski and Saccheri 2006; Saccheri and Hanski 2006; Zheng et al. 2009). In some cases at least, selection imposed during the process of dispersal may create a distinctive subset of traits that facilitate colonization: for example, the individuals surviving a long and rigorous migration episode to a new habitat patch are likely to exhibit above-average migratory efficiency and/or energy utilization (Kinnison and Hairston's 2007 'favored-founder' hypothesis).

As predicted from the ideas mentioned earlier, cane toads in Australia have evolved faster dispersal during their invasion. Annual rates of spread have increased about five-fold within 75 years (from 10–15 to 55–60 km per annum: Urban et al. 2008), driven by evolved changes in behavior, morphology, and physiology (activity levels, relative leg length, stamina: Phillips et al. 2006; Llewelyn et al. 2010). Mean daily dispersal distances are about 10-fold higher for invasion-front toads than for conspecifics from long-colonized areas (Alford et al. 2009; Fig. 2A). Raising offspring in common-garden conditions has confirmed significant heritability for dispersal rates (Phillips et al. 2010b). We do not yet know whether faster dispersal has evolved because it enhances individual fitness (i.e., via natural selection) or because of spatial sorting. In keeping with the latter hypothesis, the fastest-dispersing toads are the most likely to be killed by predators (Phillips et al. 2010c), invasion-front toads rarely reproduce (Crossland et al. 2008), and long-legged (fast-dispersing) toads at the invasion front often develop spinal arthritis (Brown et al. 2007; Fig. 2B).

### Evolution driven by interactions between invaders and native species

A range-expanding species is likely to encounter novel conditions as it spreads outside its previous geographic



**Figure 2** In Australia, cane toads at the invasion front now travel much further per night than was the case early in the toad's invasion process (A); this high dispersal rate puts substantial pressure on the toads' locomotor apparatus, resulting in spinal arthritis (large bony swellings on posterior spine, indicated by arrow (B)). Modified from Alford et al. (2009) and Brown et al. (2007).

distribution. If the optimal phenotype to deal with those novel conditions differs from that favored under ancestral conditions, selection likely will result in adjustments that enhance the invader's ability to exploit these novel opportunities.

At first sight, it would seem that local abiotic conditions pose a challenge to the invader (for which they are novel) but not the local taxa (which have evolved in those circumstances). However, the effects of competition can be mediated via shifts in abiotic factors. For example, an invasive woody shrub can alter thermal and light levels on the ground beneath it, as well as reducing nutrient availability and salinity in the soil (Cox 2004; Benkman et al. 2008; Gonzalez et al. 2008). In marine benthic and terrestrial plant communities, invaders may take up open space, thus restricting settlement opportunities. Any such shift in resource availability might impose selection on habitat selection and use by native species.

The parallel effects on invaders and natives of biotic interactions are more clear-cut and may influence establishment success (Strauss et al. 2006b; Tingley et al. 2011) as well as subsequent adaptive shifts (Langkilde 2009). Either or both the invader and the native may be affected by competition, predation, herbivory, toxic ingestion, pathogen transfer, or hybridization between taxa (Fig. 1). The nature of a native taxon's ecological relationship with the invader will necessarily modify the nature of impact. As Carroll (2008, p. 361) notes, 'both opportunity and catastrophe generate adaptive responses'.

Catastrophes induced by invasive species have attracted extensive research. In the case of invasive predators that consume native prey, selection may favor rapid adaptive responses in the endemic fauna to detect and avoid the unwelcome new arrival. For example, the arrival of mammalian predators (rats, stoats, cats, possums, etc.) may have exerted intense selection on New Zealand lizards. The absence of mammalian predators on these islands over evolutionary time presumably fashioned lizard biology in ways that reduced their vulnerability to visually hunting birds, but were ineffective against mammalian predators that use chemosensory cues for hunting (Hoare et al. 2007). The arrival of predatory mammals thus may have imposed selection on a suite of lizard attributes, with a sudden selective advantage to reducing the production and dissemination of scent cues detectable by such predators, to using retreat sites inaccessible to such predators, and to responding behaviorally to predator cues in ways that enhance lizard survival (e.g., Hoare et al. 2007). Similarly, the arrival of foxes in Australia may have imposed strong selection for arboreal rather than terrestrial nesting in birds and for avoidance of fox cues by edible-sized mammals.

Native taxa with other types of ecological relationships to the invader will be affected in other (and sometimes multiple) ways. For example, an invasive species may consume juveniles of a native species, compete with subadults of the same species, and be consumed by adults of that taxon. The complexity of such interactions will generate equally complex evolutionary routes to impact mitigation. Rather than trying to review this extensive field in detail (see Cox 2004 for examples), I simply note that some invaders will compete with native taxa for resources (potentially favoring adaptive shifts in niche parameters for one or both parties), some will hybridize with native taxa (potentially exerting selection on mating systems and especially, mate choice), and some will exchange pathogens with native taxa (imposing selection on the ability of the novel host to recognize and suppress the newly encountered pathogen: Cox 2004; Pizzatto and Shine 2011a,b). In some cases, the invader may evolve in ways that reduce rather than increase the severity of its impact

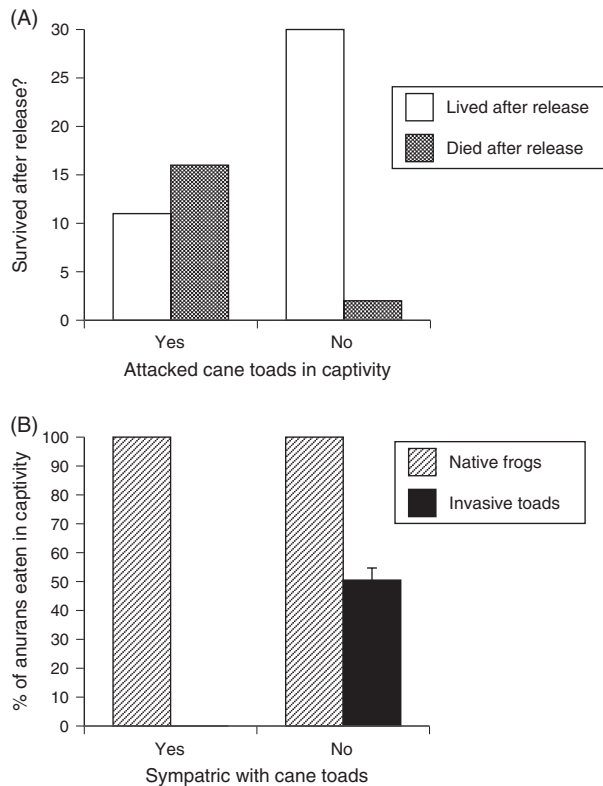
on native taxa (e.g., reduced allelopathy: Lankau et al. 2009).

The importance of invader-driven catastrophe for conservation issues has distracted attention from the possibility that invasion benefits a subset of native taxa (King et al. 2006; Hagman and Shine 2007). For example, the invader may provide an additional food source for predators and additional hosts for parasites. The net effect of an invasive species on any given native taxon will be the sum total of negative and positive effects. For example, beneficial effects of novel food may outweigh deleterious habitat modifications. If the morphology, physiology, or behavior that allows effective exploitation of this novel resource differs from that exhibited by the native taxon at the time of invasion, then we may see rapid shifts in traits that allow more successful exploitation of the new opportunity. Carroll's work on soapberry bugs provides elegant experimental evidence of the evolutionary processes that have enabled native insects to exploit invading plants (Carroll et al. 1998, 2005; Carroll 2007a,b, 2008). The actual changes likely will be complex and spatially heterogeneous and reflect adaptation in the invader (in ways that reduce its vulnerability to the native taxon) as well as adaptive responses of the endemic biota to the invader.

The main ecological impact of cane toads on the Australian native fauna is via lethal toxic ingestion by predators (and not, for example, by competition, predation, or pathogen transfer), and only a few predator species are affected at the population level (mostly large species: Shine 2010). Rapid aversion learning reduces mortality levels for most predator species and thus reduces the intensity of selection on toad-smart traits (Shine 2010; Somaweera et al. 2011). Nonetheless, at least one species of frog-eating snake (the death adder, *Acanthopis praelongus*) experiences strong selection on behavior (avoidance of toads as prey) and morphology (reduced head size relative to body size, a trait influencing the snake's ability to consume a toad large enough to kill it: Phillips et al. 2010d; Fig. 3A). In another toad-vulnerable species (the red-bellied blacksnake, *Pseudechis porphyriacus*), snakes from toad-colonized areas are less likely to eat a toad (Fig. 3B), and more tolerant to the toads' toxin, than are conspecifics from toad-free areas. Blacksnakes also show a reduction in relative head size as a function of the duration of sympatry with cane toads (Phillips and Shine 2006).

### Evolution driven by the invader's impact on interactions among native species

An invader's arrival may affect not only ecological (and thus evolutionary) interactions between an invader and a native species but also interactions between native species.



**Figure 3** Radio-tracking of death adders (*Acanthophis praelongus*) after cane toad invasion showed that a snake's fate in the wild could be predicted from its behavioral responses to cane toads (*Rhinella marina*) in laboratory tests: snakes that attempted to eat toads in the laboratory also did so in the field after release and were killed by the toads' toxins (A). This selective force has resulted in adaptive shifts in prey choice in snake species exposed to cane toads. (B) Geographic comparisons in blacksnakes, *Pseudechis porphyriacus*, show that snakes from toad-infested areas refuse to consume toads when offered them in captivity, whereas toad-naïve snakes readily attack toads (and thus are likely to be fatally poisoned). Modified from Phillips et al. (2010d) and Phillips and Shine (2006).

Adaptive shifts can be driven by changes in the abundance, behavior, ecology, morphology, or physiology of key species. For example, reduced abundance of some native taxon may force its main predator to shift in dietary habits, or a change in habitat use by that prey taxon may force the predator to forage elsewhere. Reduced abundance of a predator may allow a native prey taxon to expand its ecological niche. It is easy to envisage long and complex chains of causation ramifying through trophic levels, but documenting such changes poses a formidable logistical challenge. Examples include increased hatching success of turtle eggs because of invasive-toad-induced mortality of natural predators (varanid lizards: Doody et al. 2006), and an introduced leafhopper causing a population expansion in a parasitoid wasp, thereby

increasing rates of predation on a native leafhopper (Settle and Wilson 1990). The invader also may act as a bridge to connect two native taxa, for example, through gene flow (if native taxa can interbreed with the invader but not with each other) or pathogen transfer (if the invader can take parasites from native taxa into situations where they can infect other native taxa). Any such changes could enforce selection on the native species. The myriad ecological connections within natural food webs mean that the potential complexities of indirect effects of invasion are enormous.

The destabilizing effects of biological invasions on host–parasite relationships remain a substantial challenge for future research. Some parasites of native species may virtually disappear after an invader arrives, for example, a tapeworm of Australian pythons has declined since arrival of cane toads, apparently because the (virtually inedible) toad provides a terminal host within which adult tapeworms can develop, but are never passed on to snake predators (Freeland et al. 1986). Other parasites may benefit from the invader's arrival, for example, myxosporidians that occupy anuran bladders have increased in frequency among Australian frogs since the cane toad's arrival (Hartigan et al. 2010). Parasites that accompany an invader may host-switch to native taxa, sometimes with devastating results, and the reverse may occur also (transfer of parasites from native taxa to the invader). Such disruptions of existing host–parasite systems may impose selection both on the novel hosts (to better recognize and destroy the parasite) and on the parasite (to evade the novel host's immune responses). Invasive species allow us to explore the initial stages of parasite–host coevolution, before adaptive shifts obscure interactions (Pizzatto et al. 2010; Pizzatto and Shine 2011a,b).

### Applications of an evolutionary perspective

How does an evolutionary perspective help us to manage invasion biology systems (see also Ashley et al. 2003; Stockwell et al. 2003; Carroll 2011)? My own group's research on invasive cane toads has suggested the following practical applications of evolutionary thinking:

1 *Predicting the rate of invader spread* – Both selection and sorting can favor rapid acceleration of the invasion front's spread, as well as potentially favoring broader habitat use. Managers in advance of the invasion front thus are likely to overestimate the time lag before invaders arrive. The magnitude of this increase in cane toad invasion rate (10-fold shift in mean daily displacement within 70 years: Alford et al. 2009; see Fig. 2A) suggests that such effects often may be substantial.

2 *Predicting the attributes of invaders* – Rapid adaptive or non-adaptive shifts associated with the invasion process

may change many attributes of the invader, such that information and approaches developed from long-colonized areas may provide an unreliable basis from which to predict the attributes, impacts, and interactions of the invasion vanguard.

**3 Novel control approaches based on evolved traits of invaders** – If selection or sorting for accelerated dispersal results in lower investment in dispersal-constraining traits (such as immunocompetence: Lee and Klasing 2004), or lower investment into defensive compounds (Siemann and Rogers 2003), we might be able to target control at such evolved vulnerabilities (Brown et al. 2007).

**4 Novel control approaches based on phylogenetic conservatism** – If the invader belongs to a phylogenetic lineage not present in the invaded region, it may differ from native taxa in basic facets of biology. Such divergences provide opportunities for species-selective control. For example, the tadpoles of invasive cane toads use pheromones to communicate alarm and food location, and we might be able to utilize such species-specific communication systems to control toads without influencing native anurans (Hagman and Shine 2009; Crossland and Shine 2011).

**5 Novel control approaches based on evolutionary mismatches** – A species that evolves in one part of the world is unlikely to be perfectly suited to conditions within some other area that it invades. Identifying and exacerbating those mismatches may provide opportunities for target-specific control (Stockwell et al. 2003; Hendry et al. 2011). For example, cane toads in Australia do not recognize large predatory local ants as dangerous and are more vulnerable to ant attack than are native frogs; thus, we might be able to exploit the ants' selective predation to help control toad numbers (Ward-Fear et al. 2010). Traits with strong phylogenetic conservatism likely will respond less rapidly to selection than less conservative traits, enhancing the feasibility of exploiting such traits for biocontrol.

**6 Prioritizing vulnerable native taxa for active management** – The traits determining a native species' vulnerability to an invader, and the mechanisms by which it eventually adapts to the invader's presence, likely will show strong phylogenetic conservatism. Thus, we can predict which native taxa are most vulnerable and allocate management to those species for which the magnitude of impact will be greatest. We can also predict the duration of impact, based on the mechanisms by which native taxa adjust to invader presence. In the case of cane toad impacts, a capacity for taste aversion learning enables a rapid recovery from initial toad impact; a capacity for adaptive (genetically based) shifts allows recovery over a much longer timescale; and an inability to modify responses by either mechanism results in persistent high vulnerability to the invader (Shine 2010).

## Summary

Understanding the powerful evolutionary forces unleashed by biological invasions can assist managers to predict and mitigate undesirable impacts of the invasion process. Although the study of invasion biology reveals many catastrophes, the emerging evidence of dynamic responses to invasion provides a glimmer of encouragement. Given the opportunity, many native taxa may prove surprisingly capable of dealing with – or even exploiting – the arrival of invaders. If we understand those evolutionary adjustments, we may be able to assist vulnerable taxa to withstand the challenges that we have imposed upon them by translocating so many organisms around the globe.

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