REVIEWS AND SYNTHESES

Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities?

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Abstract

Biological invasions dramatically affect the distribution, abundance and reproduction of many native species. Because of these ecological effects, exotic species can also influence the evolution of natives exposed to novel interactions with invaders. Evolutionary changes in natives in response to selection from exotics are usually overlooked, yet common responses include altered anti-predator defenses, changes in the spectrum of resources and habitats used, and other adaptations that allow native populations to persist in invaded areas. Whether a native population is capable of responding evolutionarily to selection from invaders will depend on the demographic impact of the invader, the genetic architecture and genetic variability of the native population and potentially the history of previous invasions. In some cases, natives will fail to evolve or otherwise adapt, and local or global extinction will result. In other cases, adaptive change in natives may diminish impacts of invaders and potentially promote coexistence between invaders and natives. Here, we review the evidence for evolutionary responses of native species to novel community members. We also discuss how the effects of introduced species may differ from those caused by natural range expansions of native species. Notably, introduced species may come from remote biotas with no previous evolutionary history with the native community. In addition, the rate of addition of introduced species into communities is much greater than all but the most extreme cases of historical biotic exchange. Understanding the evolutionary component of exotic/native species interactions is critical to recognizing the long-term impacts of biological invasions, and to understanding the role of evolutionary processes in the assembly and dynamics of natural communities.

Keywords

Anti-predator behavior, character displacement, community ecology, evolutionary ecology, natural selection, phylogenetics, plasticity, rapid evolution.

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INTRODUCTION

Human transport over the past five centuries has augmented rates of biotic exchange among the Earth's realms far beyond pre-industrial norms (Elton 1958; Perrings *et al.* 1992). Non-indigenous organisms may become invasive, meaning that they naturalize, i.e. become numerically and ecologically prominent, and are often capable of dominating native populations and communities (Crooks 2002). Owing to time-lags common in the establishment of non-native species, the impacts of many prior introductions are just now beginning to become manifest (Kowarik 1995). Invasive species participate in ecological webs as predators, pathogens or parasites of natives, as competitors with natives for space and other resources, and as mutualists or hosts (Schiffman 1994). The subdiscipline of invasion biology has developed to address our lack of knowledge regarding the capacity of invasives to alter native communities, as well as the attributes leading to vulnerability in native communities and the characteristics that make some invading species so successful. This review focuses on a relatively understudied effect of invasions: how and whether

native species can evolve in response to invaders, and the consequences of such evolution.

Evolutionary changes in both native and exotic taxa may play a role in the reconfiguration of communities that follows invasion (Vermeij 1996; Yoshida *et al.* 2003; Cox 2004; Lambrinos 2004). For example, declines in native populations may be ephemeral if natives are genetically variable in their susceptibility to the exotic and can evolve in response to invasion (e.g. Phillips & Shine 2004). Alternatively, lack of the ability to evolve in the face of strong selection from invaders can cause extinction (Case & Bolger 1991). In this review, we investigate the role of evolution of natives in the invasion process. Because other reviews have concentrated on evolutionary effects via introgression/ hybridization (Rhymer & Simberloff 1996), the evolution of invaders in novel habitats after colonization (Lee 2002), and macroevolutionary processes such as extinction and speciation (Mooney & Cleland 2001), we focus on the evidence for adaptive evolutionary responses of natives to exotics and on how such responses could influence community dynamics. We discuss evidence illustrating adaptive genetic responses of natives to invasion and the methods used to investigate such responses, and we speculate on the long-term consequences of evolutionary responses for native populations. We further address how interactions and selection imposed by exotic vs. native species might differ. We conclude that incorporating knowledge of evolutionary processes may facilitate prediction and analysis in invasion biology, and may provide insights into the way that natural communities function.

WHEN ADAPTIVE EVOLUTIONARY RESPONSES BY NATIVES TO BIOLOGICAL INVASIONS ARE EXPECTED

For natives to evolve in response to biological invasions, the criteria for Darwinian natural selection must be met: the exotic must affect native fitness, fitness effects of the exotic on the native must be non-random (i.e. some genotypes must be more fit than others), and the traits involved in the selective response must have a heritable component. The likelihood of an evolutionary response may be further influenced by the demographic effects of the invasion, form of genetic variation in the native, and consistency of selection.

The demography and population structure of the native species has important implications for whether an evolutionary response can occur. For example, if an invasive species reduces the population size of the native through attack or competition, then native populations that have been invaded may be demographic sinks relative to those that have not (Fox *et al.* 1997; Woodworth *et al.* 2005) If there is gene flow among invaded and uninvaded populations, the selective pressures and evolutionary responses in

the invaded regions may be swamped by the demographic vigour and greater population growth rates of genotypes from uninvaded populations. For example, Vermeij (1982) compares the shell phenotypes of two marine molluscs before and after invasion by the predatory green crab. One mollusc *Nucella lapillus* showed adaptive phenotypic change with shell thickness (an anti-predator defence) increasing after the crab invasion. A second mollusc *Littorina littorea* did not show a change in shell thickness over the past 100 years, despite evidence of increased predation rates. Vermeij speculates that evolutionary responses were observed in *N. lappilus* because of its low dispersal rates, and evolutionary responses were not observed for *L. littorea* because of high rates of gene flow among invaded and uninvaded geographical areas.

Interactions between native species and invaders will not necessarily result in evolutionary responses to invasion, at least initially, because natives may possess traits (i.e. pre-adaptations) that allow successful coexistence with the invader. For example, exotic plants attract native herbivores (Agrawal & Kotanen 2003) and may readily become integrated into their diets (Tabashnik 1983; Singer *et al.* 1993; Carroll *et al.* 1998; Solarz & Newman 2001). Similarly, introduced predators may emit cues sufficiently like those of native predators to stimulate defensive behaviour in their native targets (Pearl *et al.* 2003). Such exaptations (coincidental 'pre-adaptations') do not necessarily require genetic change and are perhaps more likely when exotics are relatively closely related to native counterparts, as evidenced by the rarity of host shifts by native enemies onto distantly related introduced plant taxa (Parker & Gilbert 2004). Similarly, plastic, non-genetic processes may underlie dramatic shifts in morph frequencies in polyphenic traits. When a morph is disfavoured after invasion, we may see a shift in morph frequency in invaded areas, but no appreciable evolutionary change in the native population, if the cues inducing plastic divergence in morphs are not under selection. Trophic polymorphisms are one such class of polyphenic characters that we consider in some detail later in this paper. Likewise, various behavioural and other plastic responses to the ecological influence of invasions may alter native phenotypes, without any genetic changes to the population.

Exhibited phenotypic plasticity may be maladaptive, buffering or opportunistic, and thus may either decrease or increase the ability of populations to evolve when faced with new selective pressures from invaders. For example, mistaken responses to cues from novel taxa may lure natives into suboptimal or lethal 'evolutionary traps' (Schlaepfer *et al.* 2005). In contrast, plasticity that helps maintain or increase population size, or that slows or prevents the culling of genetic variation, will increase the opportunity for populations to evolve in response to new threats. Finally,

adaptive buffering through plasticity may decrease selective impacts and thus reduce the probability of genetic change (Carroll & Corneli 1999; Huey *et al.* 2003). Even in this buffering role, plasticity may not completely eliminate the effects of selection on genetic variability; Losos *et al.* (2004) conclude that, despite behavioural responses that minimize predation rates on anoles by an introduced predator, predation is still high and a likely selective agent on anole behaviour and morphology. Moreover, plastic strategies themselves may differentiate genetically under diversifying selection (Carroll & Corneli 1999). For example, an invasive host plant of soapberry bugs in Florida differs from the native host in its temporal and spatial production of seeds on which the insects feed. Resulting selection has altered both flight/life-history morph frequencies and the genetic control of morph determination in less than 100 generations (Dingle & Winchell 1997; Carroll *et al.* 2003b). Such complex and labile interactions between native developmental systems and selection from invaders suggest that we should use caution in interpreting the processes underlying phenotypic change in invaded populations in the absence of genetic evidence.

Multiple invasions may complicate adaptation of natives to exotic species in a number of ways. For example, native populations frequently are depleted after the first wave of an invasion. In a case involving West Nile virus, 72%, including 82% of juveniles, of an Oklahoma population of American crows (*Corvus brachyrhynchos*) died in a single year (Caffrey *et al.* 2005). While such mortality may sometimes attend rapid adaptive evolution, resulting bottlenecks will likely deplete genetic variation available for responses to future episodes of selection. Such is the case in native white pines; white pine blister rust dramatically increases mortality, resulting in significantly lower levels of genetic variation following outbreaks (Kim *et al.* 2003). Additionally, selective pressures often depend on the particular combination of species present in a community (Benkman 1999; Thompson 1999; Benkman *et al.* 2001; Rudgers & Strauss 2004; Siepielski & Benkman 2004; Lau 2005, in press) and may shift rapidly with multiple invasions. For example, the native plant *Lotus wrangelianus* has evolved in response to invasion by the exotic plant *Medicago polymorpha* (Lau 2005, in press). However, this response is only observed in the absence of a shared exotic herbivore. When herbivores are abundant, there is no evidence of adaptation. Lau speculates that *Lotus* was able to adapt to the initial invasion by *Medicago*, but invasion by an exotic insect herbivore 80 years later may have negated this adaptive response.

Another mechanism that can influence the capacity for native species to evolve in response to exotic species involves the underlying genetic architecture of traits in the native species. Genetic correlations among traits can limit rates of evolution when they are not in accord with the direction of selection (e.g. Via & Lande 1985; Caruso *et al.* 2005). For example, if two traits are advantageous in the presence of an exotic, but are negatively correlated, the magnitude of selection acting on both traits will be reduced and the predicted evolutionary response reduced. Similarly, across-environments, negative genetic correlations can also constrain the potential for evolutionary responses, particularly when the environmental conditions fluctuate temporally or over small spatial scales. Both genetic correlations between traits in a single environment and between fitness in different environments have been shown to slow rates of evolution in response to novel ecological threats such as global climate change (Etterson & Shaw 2001; Etterson 2004). Genetic architecture may also facilitate rather than constrain rates of evolution. Rapid adaptive differentiation may involve genes of major effect (Merilä & Sheldon 1999), and significant non-additive (dominance, epistasis) genetic control is prominent in novel trait values of soapberry bugs coevolving on recently introduced host plants (Carroll *et al.* 2003a). Carroll (in press) suggests that such resource perturbations lead to 'founder-flush' demographic events that convert nonadditive to additive genetic variation. Such genetic change could increase the potential for adaptation even in temporarily reduced or fragmented populations.

EVIDENCE FOR EVOLUTIONARY RESPONSES OF NATIVES TO INVASIONS

For the sake of inclusivity, in writing this review, we have used rather broad (but still basically genetic) criteria in deciding what qualifies as evidence for evolution in natives. We require (1) some demonstration of change in allele frequency or genotype of native species in response to an exotic or (2) use of common garden/environment experiments that show genetically based differences in traits under selection from an exotic or (3) inference from a comparative phylogenetic approach. For example, when a native species is recorded as using a new, exotic resource, we do not consider this event sufficient evidence for evolution in natives. If, however, populations of natives that use the exotic novel resource are genetically differentiated from those that do not, then we construe this differentiation as an evolutionary response, i.e. a change in gene frequency associated with novel resource use.

Experimental manipulations of the presence of the exotic species are fundamental in determining whether the invader is the direct cause of any evolutionary response. Experimental removals separate the effects of the exotic *per se* from environmental factors correlated with invasion (e.g. many invasive plants thrive in wetter, nutrient-rich habitats). For example, if there has been adaptation to the presence of an exotic, one expects native genotypes from invaded source populations to outperform genotypes from uninvaded

source populations in the presence of the exotic species (i.e. control areas), but not in the absence of the exotic species (experimental removal areas). One caveat with this approach, however, is that the effects of exotic species may occur over longer time-scales than the time-scale of the experimental manipulations. Thus, negative results should be interpreted cautiously.

Relatively few studies have experimentally removed invaders to identify them as the elicitors of an evolutionary response from natives. We have therefore had to rely on strong correlative evidence, or on weaving together evidence from a combination of studies, to document what appears to be evolution of natives in response to introduced species. Accordingly, we accept as evidence for evolution in natives studies that use either time-series comparisons or comparisons of native populations in invaded and uninvaded areas, even though these broad strategies are correlative in nature. In such cases, evolution in response to exotic species cannot be formally differentiated from evolution in response to other ecological changes that occur over the same time period of the invasion, from pre-existing habitat differences that are associated with whether or not an area is invaded, or from genetic drift. However, these approaches, when replicated in multiple invaded and uninvaded populations, coupled with supplementary reciprocal transplant experiments demonstrating the adaptive nature of the phenotypic shift, or combined with supplementary information that eliminates concurrent environmental change as a source of selection on the trait, can provide a convincing case for evolution by natives in response to invaders. For example, McIntosh & Townsend (1994) suspected that predation from introduced trout altered foraging strategies of mayfly prey. They demonstrated that mayflies from streams invaded by introduced trout predators forage nocturnally and are quiescent during the day, whereas mayflies from streams lacking trout are active diurnally. These differences remain even in a laboratory setting, in the absence of predators or predatory cues, suggesting that the differences are genetic in nature rather than plastic responses. Active, diurnal mayflies are more susceptible to trout predation than nocturnal foragers; thus, the behavioural shift in mayflies is adaptive in the face of the introduced selective agent. *In toto*, these results make a strong case for evolution of mayfly anti-predator behaviour in response to introduced trout. A number of other studies have successfully used common environment/garden approaches to implicate evolutionary responses by natives (see Table 1). Similarly, time series comparisons of populations before and after invasion, coupled with evidence demonstrating the adaptive nature of the change in phenotype with respect to the invasion, and careful elimination of other environmental changes as a source of selection over the

same time period, also provide a convincing demonstration of evolution in native populations in response to invaders (e.g. Phillips & Shine 2004; Table 1).

Evolution in a community context

Evolution has been studied in native multi-species communities in several contexts such as character displacement from competition, predator/prey behaviour and cues, disease resistance and host shifts for herbivores and parasites, mutualisms and other multi-species interactions. The same kinds of (co)evolutionary interactions occur over short time scales in response to invasion (Table 1). In addition, we suspect that indirect effects of invasions may also impose selection (and possible concomitant evolutionary change) on natives (e.g. Smith *et al.* 1995). Table 1 provides examples of native species that have evolved in response to the addition of novel species in communities. Thirty-three well-documented examples representing several different types of ecological interactions (herbivory, competition, predation, and disease) are listed, including 21 examples of morphological or physiological change, 11 examples of behavioural change, and 3 examples of change in life-history traits. We discuss these examples in detail, and organize them by the type of interspecific interaction involved.

Evolution to novel resources and hosts

Perhaps the largest and best body of evidence for the evolution of natives in response to novel species comes from the literature on phytophagous insects. Host shifts onto exotic host plants are associated with genetically based adaptive change in life history, morphology, physiology, behaviour and phenology (e.g. Hsiao 1982; Tabashnik 1983; Thomas 1987; Filchak *et al.* 2000; Carroll *et al.* 2001, 2003b; Malausa *et al.* 2005). The use of novel hosts has been associated with genetically distinct ecotypes, sub-species and even species. For example, use of alfalfa introduced to California *c.* 200 years ago has been reported for at least seven native lepidopteran species (Graves & Shapiro 2003). There is evidence that use of novel hosts has resulted in genetic differentiation in these native herbivores. For example, naturalized alfalfa is used by a genetically distinct ecotype of *Lycaeides melissa* (Nice *et al.* 2002).

Some of the best examples of evolution in native phytophagous insects as a result of sympatric host-shifts onto introduced species come from the *Rhagoletis pomonella* species complex. Shifts onto novel host apple from hawthorn have resulted in genetically distinct ecotypes with different phenology (Smith 1988; Filchak *et al.* 2000). Additionally, a new speciation event via hybridization of two species in the same *Rhagoletis* complex is associated with a host-shift onto an introduced, invasive honeysuckle,

Table 1 Summary of studies documenting evolutionary responses of native species to biological invasions. Studies are grouped by type of ecological interaction. Here we list the native species, the exotic species responsible for the altered selection pressure, the evolutionary response (i.e. the native trait evolving in response to invasion), whether available evidence suggests that this change is adaptive, the time since invasion, and the method used to detect the evolutionary response. 'X' indicates whether the example meets the criteria that evolutionary divergence has occurred [modified from the criteria for character displacement suggested by Schluter & McPhail (1992) and Dayan & Simberloff (2005)]. These criteria include whether the change is not likely due to chance, has a genetic basis, represents an evolutionary shift in phenotype, is due to the invader altering patterns of natural selection, is directly associated with invasion and not other correlated environmental variables, and whether there is independent evidence for the ecological effects responsible for the altered selection pressures. The last three studies demonstrate differences in natural selection as a result of biological invasions, but trait evolution was not addressed

Native species/ exotic species	Evolving trait	Adaptive?	Time since invasion	Method*	Change not due to chance	Genetic basis	Evolutionary shift	Invader alters selection	Not due to corr. env. var.	Evidence of ecol. effect	Reference
Herbivory (novel host)											
Studies showing trait evolution in response to biological invasions											
Jadera haematoloma *Leptocoris tagalicus* Sapindaceous host spp.	Morphology, development, behavior	Yes	20–50 years 40–150 gens.	T, RT, C	X	X	X	X	n/a	X	Carroll & Boyd (1992), Carroll *et al.* (1997, 1998, 2003b, 2005)
Pieris napi *Alliaria petiolata*	Performance			T		X	X		n/a	X	Courant *et al.* (1994)
Rhagoletis pomonella *Malus pumila*	Development, physiology, phenology	Yes	*c.* 150 years	C	X	X	X	X	n/a	X	Smith (1988), Filchak *et al.* (2000)
Prodoxus quinquepunctellus *Yucca aloifolia*	Phenology, reproductive morphology			C	X	X	X	X	n/a	X	Groman & Pellmyr (2000)
Ostrinia nubilalis *Zea mays*	Divergence b/t populations		*c.* 500 years	C		X	X	X			Malausa *et al.* (2005)
Lycaeides melissa *Medicago sativa*	Genetic divergence b/t populations		*c.* 150 years	C		X	X	X			Nice *et al.* (2002)
Rhagoletis sp. *Lonicera* spp.	Speciation via hybridization		*c.* 250 years	C	X	X	X	X	X		Schwarz *et al.* (2005)
Papilio zelicaon *Ammi visnaga*	Performance	Yes?		T		X	X	X	X		Shapiro (personal communication), Graves (1997)
Euphydryas editha *Plantago lanceolata*	Host preference, performance	Yes?	100 years	C, T	X		X	X	X		Thomas *et al.* (1988), Singer *et al.* (1993)
Colias philodice *Medicago sativa*	Performance		*c.* 90 years	C	X	X	X	X	X		Tabashnik (1983)
Herbivory (novel herbivore)											
Thuja plicata *Odocoileus hemionus*	Plant resistance		100 years	C, T	X	X	X	X	X	X	Vourc'h *et al.* (2001)
Gentianella campestris Introduced livestock	Plant tolerance	Yes	> 100 years	C	X	X	X	X	X	X	Lennartsson *et al.* (1997)

Table 1 continued

Native species/exotic species	Evolving trait	Adaptive?	Time since invasion	Method*	Change not due to chance	Genetic basis	Evolutionary shift	Invader alters selection	Not due to corr. env. var.	Evidence of ecol. effect	Reference
Plant/animal interaction, indirect effect											
Vestiaria coccinea / Feral ungulates	Feeding morphology		c. 100 years	T	X		X	X		X	Smith *et al.* (1995)
Predation											
Pseudacris regilla / *Lepomis macrochirus*	Prey morphology (induced)	Yes	c. 100 years	C	X	X	X	X	X	X	Benard (2005, unpublished manuscript)
Pseudacris regilla / *Rana catesbeiana*	Anti-predator behaviour		c. 70 years	C	X			X	X	X	Chivers *et al.* (2001)
Daphnia magna / Various fish spp.	Anti-predator behaviour		c. 7–10 years	T	X	X	X	X	X	X	Cousyn *et al.* (2001)
Triturus spp. / Various fish spp.	Extinction of paedomorphs		< 90 years	C	X	X		X		X	Denoel *et al.* (2005)
Abytes muletensis / *Natrix maura*	Anti-predator behaviour		2000 years	†	X			X	X	X	Griffiths *et al.* (1998)
Rana aurora / *Rana catesbeiana*	Anti-predator behaviour	Yes	60 years	C	X	X	X	X	X	X	Kiesecker & Blaustein (1997)
Nesameletus ornatus / *Salmo trutta*	Foraging behaviour	Yes	120 years	C(E)	X		X	X	X	X	McIntosh & Townsend (1994)
Littorina obtusata / *Carcinus maenas*	Anti-predator behaviour	Yes	15–100 years	T, RT						X	Seeley (1986), Trussell & Smith (2000)
Nucella lapillus / *Carcinus maenas*	Prey morphology	Yes	> 7 years	T				X		X	Vermeij (1982)
Daphnia retrocurva / *Alosa pseudoharengus*	Size		c. 12 years	T	X			X	X	X	Wells (1970)
Toxic prey											
Two snake spp. / *Bufo marinus*	Predator morphology	Yes?	< 65 years, 20 gens.	T	X		X	X	X	X	Phillips & Shine (2004)
Brood parasitism											
Poliaptila californica / *Molobhrus ater*	Breeding biology		80 years	T				X		X	Patten & Campbell (1998)
Five native species pairs / *Molobhrus ater*	Rejection behaviour	Yes?		‡				X		X	Peer & Sealy (2004)
Disease											
Onychomys leucogaster / *Yersinia pestis*	Survival from infection	Yes?	c. 50 years	C	X	X	X	X		X	Thomas *et al.* (1988)

Competition

Category / Species	Trait studied		Duration	Study type[*]						Reference
Salvelinus fontinalis / *Catostomus commersoni*	Feeding morphology and behaviour	Yes		C	X		X		X	Bourke *et al.* (1999)
Five native grass spp. / *Centaurea maculosa*	Tolerance to allelopathy	Yes?	20–30 years	C (E)	X	X	X	X	X	Callaway *et al.* (2005)
Coregonus hoyi / *Alosa pseudoharengus*	Feeding morphology and behaviour		19 years	T	X	X	X	X	X	Crowder (1986)
Four native grasses / Two exotic forbs	Neutral marker divergence		> 25 years	C	X	X	X			Mealor *et al.* (2004)
Lotus wrangelianus / *Medicago polymorpha*	Local adaptation to competitor	Yes	*c.* 120 years	RT (E)	X	X	X		X	Lau (2005, in press)

Studies showing differences in natural selection in response to biological invasions

Herbivory

Category / Species	Trait studied		Duration	Study type[*]						Reference
Cirsium canescens / *Rhinocyllus conicus*	Flowering size	n/a	*c.* 10 years		X		X		X	Rose *et al.* (2005)

Herbivory and competition

Category / Species	Trait studied		Duration	Study type[*]						Reference
Lotus wrangelianus / *Medicago polymorpha* / *Hypera brunneipennis*	Anti-herbivore defences	n/a	50–120 years	C (E)	X	X	X	X	X	Lau (2005)

Predation

Category / Species	Trait studied		Duration	Study type[*]						Reference
Anolis sagrei / *Leiocephalus carinatus*	Prey morphology	n/a	*c.* 6 month	C (E)	X	X	X	X	X	Losos *et al.* (2004)

*T = time series, RT = reciprocal transplant, C = comparison between genotypes collected from invaded vs. uninvaded populations. (E) indicates that the presence of the exotic species was experimentally manipulated or manually removed.

†Compared responses to predatory snakes from introduced vs. native range.

‡Phylogenetically controlled comparison of species pairs with different durations of exposure to brood parasite.

Lonicera sp. (the hostplant itself a hybrid between introduced Asian *Lonicera* species) (Schwarz *et al.* 2005).

Soapberry bugs, which are seed predators of Sapindaceae, have adopted several introduced hosts in recent decades in both North America and Australia, where species of non-indigenous *Koelreuteria* and *Cardiospermum* are environmental and agricultural weeds. Over *c.* 100 generations, genetically based adaptive differences have evolved in behaviour, physiology, morphology and life history. For example, in the best studied populations, lifetime fecundity has doubled, the juvenile period is 20% briefer, with one-third higher survivorship, and the mouthparts have evolved from an average of 9.3–6.9 mm long in response to the smaller fruit of the invasive, which is now strongly preferred in choice tests. The population frequencies of flying and flightless morphs have changed a great deal, as has the genetic control underlying the flight polymorphism. Morphological trans-formations are evidenced by historical series of museum specimens (Carroll & Boyd 1992; Carroll *et al.* 1997, 1998, 2003a,b, 2005; Winchell *et al.* 2000). At the same time, loss of performance on native hosts has evolved with similar speed (Carroll *et al.* 2001). Much of the adaptive change is based on genes of major effect and novel gene–gene interactions (epistasis) (Carroll *et al.* 2003a) rather than additive genes alone. Yet there is no evidence of reproductive isolation to date (S.P. Carroll, unpublished data).

There have also been several instances in which native insects have adapted to use introduced host plants that were initially toxic. At least some populations of *Pieris napi oleracea* oviposit on and can now complete development on garlic mustard, even though previous attempts at rearing North American pierids on garlic mustard had failed in the first or second instar (Courant *et al.* 1994). Populations of native *Papilio zelicaon* exhibit different levels of tolerance to a toxic introduced apiacious host plant, *Ammi visnaga* (Graves & Shapiro 2003). While no individuals were initially able to survive on this host, larvae from some populations were recently successfully reared to adulthood on this host plant species (A.M. Shapiro, personal communication).

Introduced host plant species may also have more subtle effects on the evolution of native insects. For example, introduced host plants have extended the geographical range, increased the overall abundance, and increased the number of generations per year of several native lepidopteran species (reviewed in Graves & Shapiro 2003). *Papilio zelicaon*, the anise swallowtail, typically has one to two generations in the mountains and foothills of California where it feeds on native umbellifers. However, in habitats where introduced sweet fennel *Foeniculum vulgare* is abundant, *P. zelicaon* produces four to six additional generations each year using this novel host plant. Similar examples come from naturalized crop systems. Less than 50 years after the introduction of alfalfa, native legume-feeding *Colias eurytheme*

(Pieridae) experienced a population explosion throughout California as it began to use alfalfa as a host [Essig (1915) as cited in Graves & Shapiro 2003)]. The combination of these effects may increase the evolutionary potential of native lepidoptera by generating genetic variability on which selection may act and may increase the 'evolvability' of native populations. Indeed, alien fennel-based populations of *P. zelicaon* have evolved a preference for that host, a behaviour that may protect that trait from dilution by gene flow from native host-based populations (Thompson 1988).

Evolution to novel competitors

Probably the quintessential form of evolutionary response to species additions in natural systems comes from the literature on character displacement. A recent review of character displacement by Dayan & Simberloff (2005) lists scores of studies that have documented character displacement in a wide variety of taxa, although the genetic basis of trait shifts have not been documented in all of these cases. There is evidence that character displacement also occurs when introduced species establish in native communities.

Some of the most interesting examples of character displacement come from fish. At least 34 fish species exhibit trophic polymorphisms in behaviour, gill raker and jaw structure, and body shape (Robinson & Parsons 2002). These conspecific forms diverge in both diet and habitat use which, in turn, is often determined by the presence of competitors. When benthic-feeding white suckers were introduced to lakes, native brook charr were excluded in all but pelagic habitats. The proportion of brook charr benthic morphs decreased markedly in invaded lakes where introduced competitors were benthic feeders (from a mean of 41.3% in allopatry to 9.9% in sympatry with white sucker) (Bourke *et al.* 1999). Recent studies of brook charr show that the basis of this trophic polymorphism is both genetic and environmental (Proulx & Magnan 2004). In addition, while the expression of different morphs is a plastic trait exhibited by many fish species, in every case where it has been examined a genetic basis to these plastic responses has been found (Robinson & Parsons 2002). The degree to which these adaptations have costs, and the impact of these adaptations on long-term population size (a critical part of long-term persistence), have yet to be documented.

Changes in life history may also serve to reduce the impact of introduced competitors. For example, in the 20 years following the invasion of Lake Michigan by alewife (*Alosa pseudoharengus*), native bloaters (*Coregonus hoyi*) dramatically abbreviated the juvenile stage during which they compete for zooplankton with the introduced fish (Crowder 1986).

While most of the evidence for evolutionary response to competition comes from animals, there are a few examples

from the plant literature. Invasive spotted knapweed, *Centaurea maculosa*, introduced from Eurasia, has come to dominate many rangelands of the West. Callaway and colleagues have shown that the success of this species can be attributed in part to an allelochemical produced in the roots (Callaway & Aschehoug 2000; Callaway & Ridenour 2004; Callaway *et al.* 2004a,b). Despite the large effects of knapweed via interference competition, there are native species that can coexist with knapweed and that may have adapted to its presence (Callaway *et al.* 2005). Seeds from five native North American grass species were selected from replicated invaded and uninvaded habitats. Uninvaded habitats were areas in which active measures had been taken to remove or prevent the spread of knapweed. The choice of sites with active removal programmes minimizes environmental correlates associated with naturally invaded and uninvaded sites. Native grasses collected from areas with a 20- to 30-year history of invasion by *C. maculosa* have higher tolerance to *C. maculosa*, and to its alleochemical, than do individuals from communities that have not experienced invasion. These results suggest that adaptation to tolerate the presence of *Centaurea* has occurred. Similarly, populations of the native California annual *Lotus wrangelianus* are also locally adapted to the presence of an exotic competitor. Genotypes collected from replicated populations invaded by the annual plant *Medicago polymorpha* outperform genotypes collected from similar uninvaded areas when transplanted into heavily invaded destination habitats (Lau 2005, in press). While the evolution of natives to neighbouring plants has received relatively little attention, several studies support the idea that (co)evolution occurs among neighbours in both invaded and natural plant communities (Turkington 1979; Ehlers & Thompson 2004).

Evolution of natives in response to novel predators/herbivores

There are many examples of native prey (*sensu lato*) that have plastic behavioural and morphological responses to the presence of introduced predators (e.g. Trussell & Smith 2000; Pearl *et al.* 2003; Moore *et al.* 2004). The degree to which the plastic response itself is under selection from novel predators, is rarely addressed (but see Langerhans *et al.* 2004; Arendt & Reznick 2005 for examples from native systems). *Evolutionary* responses in plasticity are probably a critical, but relatively undocumented, impact of introduced predators on native prey. Below, we describe examples in which there is a demonstrated genetic component to anti-predator responses.

Kiesecker & Blaustein (1997) show that *Rana aurora* frogs in ponds invaded by bullfrogs respond to chemical cues. When presented with chemical cues from bullfrogs, frogs from invaded ponds reduce their foraging activity and increase refuge use. In contrast, frogs from uninvaded ponds do not change their behaviour when in the presence of bullfrogs. The authors show that this plastic response is adaptive; in the presence of bullfrogs, genotypes from invaded regions experience less predation than genotypes from uninvaded ponds.

In an example of evolution in response to novel sources of leaf damage, plants from populations of *Gentianella campestris* with a history of grazing by introduced livestock or mowing produce more seeds than plants from populations that have been historically protected from grazers, when artificially clipped (Lennartsson *et al.* 1997); these common garden experiments indicate that plants have adapted to a novel grazing regime. Similarly, after deer were introduced to islands in Canada 100 years ago, red cedar (*Thuja plicata*) populations changed in their palatability to deer (Vourc'h *et al.* 2001). Old, island trees are more palatable to deer than are equal-aged old mainland trees. However, young island saplings that grew up in the presence of deer are not significantly different in palatability from mainland saplings. Palatability is influenced by terpene composition, a heritable trait in red cedar (Vourc'h *et al.* 2002). Thus, this population of red cedars has evolved greater resistance to browsing by deer during the 100 years post-invasion.

The evolution of increased resistance to predators is also documented in marine ecosystems. Several native molluscs have evolved thicker shell morphologies that decrease the success rate of introduced crab predators (Vermeij 1982; Seeley 1986). In these examples, the increasing incidence of scars on shells from survived crab attacks indicates a change in the strength of the ecological interaction, and the benefit of increased shell thickness post crab invasion. A concomitant warming trend in seawater has, however, also been implicated as favouring shell thickening (plastic) in some snails (Trussell & Smith 2000).

Shifts in aquatic vs. terrestrial morph frequencies in *Triturus* spp. newts offer another likely example of evolution to introduced predators. Surveys across Europe show that introduced fish are eliminating paedomorphic (aquatic) forms in two species of native newts (Denoel *et al.* 2005). Paedomorphic newts retain larval traits in adulthood and are more efficient at aquatic prey capture than conspecific metamorphic (more terrestrial) forms. Exotic fishes have been introduced to 44% of the 39 sites in across Europe in which paedomorphic forms of the alpine (*Triturus alpestris*) and palmate (*T. helveticus*) newts have been recorded. At all sites where exotic fish were introduced, paedomorphs have been selectively eliminated. Only the presence of fish explained these population changes across a continental scale; alternative factors associated with loss of paedomorphs, such as pond drying, were not significant. While plastic, the strong major-gene genetic basis of paedomorphosis has been well-documented in a related salamander

clade, *Ambystoma* (e.g. Voss & Smith 2005); unfortunately, no genetic information exists for *Triturus*. However, assuming paedomorphosis is at least under some genetic control, introduced fish predators are likely causing evolutionary shifts in the life histories of European newts.

On the flipside, in Australia, there appears to have been evolution in native snake predators to invasive, toxic cane toad prey over the past several decades (Phillips & Shine 2004). Two snake species that consume toads (*Pseudechis porphyriacus* and *Dendrelaphis punctulatus*) show a reduction in gape size and an increase in body length with time since exposure to toxic toad prey. A shift to smaller relative head size reduces the likelihood that a snake will consume a large toad with a lethal dose of toxin. In addition, two species of snakes that had tolerance to toxin or that did not typically feed on toads show no consistent change during this period. Together, these results imply that snake populations are adapting to toxic toad prey.

It is also worth mentioning that there are many examples of failure to adapt to introduced predators, especially from island systems (Case & Bolger 1991; Fritts & Rodda 1998). Small population sizes and small habitat areas coupled with low genetic variation often prevent island populations from responding quickly enough to preclude extinction from predators that have almost immediate large impacts on population size or fitness. Lack of an evolutionary history with predators has meant the loss of basic anti-predator responses that could allow for some degree of escape, even in the absence of more specific responses to particular introduced predators.

Parasitism and disease

Brood parasites like cuckoos and cowbirds lay their eggs in nests of other species. The range of the brown-headed cowbird expanded in North America soon after forested landscapes were cleared and large domesticated mammals like cattle were introduced (Rothstein 1994). Five closely related North American species pairs exist such that members of the pair differ in the length of contact with cowbirds. In each case, the species with the longer period of contact showed greater egg rejection behaviour (Peer & Sealy 2004). In addition, the degree to which host bird species reject eggs of brood parasites has a strong phylogenetic signal (Peer & Sealy 2004); 90% of rejecter species were related to other rejecters, whereas only 39% of accepters were related to rejecters. The systematic differences in rejection behaviour that vary with length of exposure to cowbirds and the fact that rejection behaviour has a genetic basis in some hosts (Soler *et al.* 1999) suggests the evolution of egg rejection behaviour in response to the cowbird range expansion.

Disease introductions may devastate native populations (e.g. Chesnut Blight and Dutch Elm Disease in North America), and it is likely that resulting selection will cause evolution evident in populations of survivors (Altizer *et al.* 2003). Within native communities, well-defined spatial heterogeneity in virulence-resistance genotypes provides evidence of ongoing evolution (Thrall & Burdon 2003). Yet there have been surprisingly few studies of resistance evolution in natives faced with introduced diseases, so evidence for evolution in native hosts is largely circumstantial.

Kinloch *et al.* (2003) describe the impacts of white pine blister rust (*Cronartia ribicola*), introduced to western North America *c.* 100 years ago, on native western white pine (*Pinus monticola*). Successive waves of epidemic rust since *c.* 1940 caused nearly complete mortality over extensive regions, altering succession and other ecological processes. A small population that appeared to be naturally resistant to the blister rust was discovered in Oregon. A gene, called Cr2, was estimated to be several hundred times more frequent in the resistant population than it was in the species at large. Notably, in 1994 a Cr2-adapted scion of the rust destroyed that population of white pine, suggesting coevolutionary counter-play between the native and the invader.

Results of another study suggest that mortality from introduced plague (*Yersinia pestis*) has caused resistance evolution in a western North American rodent. Plague is thought to have been introduced from eastern Asia via the port of San Francisco in *c.* 1900, and by 1940 it had reached its eastern limit in the state of Colorado. Thomas *et al.* (1988) reported that three-quarters of grasshopper mice (*Onychomys leucogaster*) from Colorado survived experimental infection with plague, while only about one-quarter of a population from Oklahoma (outside the range of plague) did so.

Lastly, avian malaria (*Plasmodium relictum*) in Hawaii, which was brought to the archipelago by the introduction of alien birds along with vector mosquitoes around 1825, may have selected for resistance evolution in two native honeycreeper species. The disease likely contributed to rampant extinctions within the Hawaiian honeycreeper clade and is thought to be the principal factor limiting the distribution and abundance of the remaining taxa today (Jarvi *et al.* 2004). Most native birds no long occur at lower elevations to which the mosquito and parasite are largely restricted, but two *Hemignathus* species have colonized lower elevations. There the O'ahu Amakihi (*H. flavus*) remains uninfected, while the incidence in local alien birds is *c.* 10% (Jarvi *et al.* 2001). Those workers speculate that the resistance is a derived condition that has evolved over 125–170 generations. A similar pattern may be developing in a congener on another island in the archipelago, Hawaii. The Hawaii Amakihi (*H. virens*) exhibits acquired immunity when it survives infection (Atkinson *et al.* 2001), and it has been colonizing

lower elevations in large numbers over the past decade (Woodworth *et al.* 2005).

In summary, while these studies suggest that evolution of resistance in naïve host species after exposure to a novel pathogen may be both ecologically and evolutionarily important, surprisingly little evidence has been collected to show the degree to which such invaders are important selective agents in native populations. Another key aspect is that introduced pathogens may be coevolving with natives, complicating the assignment of causation when host susceptibility changes (Parker & Gilbert 2004).

(CO)EVOLUTION IN COMMUNITIES: WHAT CAN INVASIVE SPECIES TELL US?

In native systems, selection on traits and subsequent evolution are known to change with the gain or loss of community members. The geographical mosaic model espoused by Thompson (1999), in which traits of species reflect shifting community composition across regions or areas, has been supported in a variety of natural systems. For example, seed-feeding insects, crossbills and squirrels each select for different trait combinations in lodgepole pine cones (Benkman *et al.* 2001, 2003). Other native communities have also shown locally varying evolution in response to component species (Rudgers & Strauss 2004; Galen 2001). Coevolutionary interactions among community members may ramify and alter basic ecological outcomes like trophic cascades (Loeuille & Loreau 2004). As invasive species interact with residents, networks of new direct and indirect effects that result in novel coevolutionary relationships between natives and invasives are likely to result. These processes provide insights into how natural communities assemble.

The ecological impact and consequent selective environment when an invader integrates into a native community depends on both its traits and those possessed by species in the native community. Predators or parasites against which natives are poorly defended may quickly eliminate their food sources. In this case, the invaders may become rare or absent after an initial 'epidemic' phase (Simberloff & Gibbons 2004) or they may shift to using a different food source (Fritts & Rodda 1998). In contrast, invaders such as plants whose primary impact is to compete with natives may remain at high population densities after the elimination of natives. In both of these examples, additional community interactions will also occur: introduced predators and parasites will not only affect native prey, but will also *compete* with native counterparts; a diminished native prey base will affect native competitors of prey, possibly increasing their abundance, etc. We expect ecological effects of introduced species to ramify throughout native webs.

Real world examples reveal some of these complexities. In Guam, for example, the brown treesnake (*Boiga regularis*), introduced *c.* 1950, has systematically eliminated almost all native bird and bat species (Fritts & Rodda 1998). Case & Bolger (1991) hypothesize that its huge impact stems from the island biota lacking an evolutionary history with snake predators, and thus all appropriate anti-predator defence. Despite the elimination of native endothermic prey, the snakes remain at high density (*c.* 500/square km), mainly feeding on introduced, diurnal lizards. This change in diet has resulted in a reduction in body size, and the snakes have also became significantly more diurnal and more terrestrial since the 1980s (Fritts & Rodda 1998). Thus, brown treesnakes are perhaps evolving on Guam following the extinction of native endothermic prey. The trophic cascades present in this community are likely also changing with these shifts. Ultimately, evolutionary responses of both native and exotic species may more fully integrate the exotic species into the native community (Vermeij 1996; Cox 2004).

The profound impacts of some invasives on natives suggests that the processes involved in these range expansions may differ from those involved with range shifts by native species. Examples of invasives profoundly altering the biotic and physical environment and having strong ecological impacts on native species may be most common on islands (e.g. brown treesnake), but they occur continentally as well (e.g. knapweed, tamarisk). Such ecosystem dominance develops even though the exotics are unremarkable members of their indigenous communities (e.g. Ridenour & Callaway 2001). While release-from-enemies is one common hypothesis to explain the explosive behaviour of some exotic species in novel habitats, it is not supported in all cases (reviewed in Agrawal & Kotanen 2003) and other historical and constitutional factors may distinguish the rapidly dominating range expansions of invasive species from range expansions of natives.

To begin with a null hypothesis, consider the historical perspective that native species with dominant effects have already expanded their ranges and caused similar extinctions to those caused by high impact invaders; those native species that were unable to coexist are no longer present. In this non-anthropogenic scenario, such expansions are expected to be rare, given the limited number of high-impact natural range expansions that we have witnessed. Where native range shifts have been recorded, they have often been in response to human-caused changes in environment (e.g. Parmesan & Yohe 2003); even in these cases, few of these expanding native species exhibit ecologically dominant behaviours. Under this null hypothesis, the processes underlying the success of exotic species do not fundamentally differ from those involved in native range expansions.

Contrasting with this hypothesis is the alternative that the large ecological impacts of invasion by exotics is symptomatic of novel forces at work. For example, gene flow from populations that coexist with expanding natives may buffer other native species from the effects of native range expansions; in contrast, lack of prior history with an invader in any native population may underlie the disproportionate effect of exotics on native communities. To elaborate, gene flow connecting native communities of differing composition may maintain genetic diversity on which selection acts in the context of shifting interactions. If the range of a competitor A is larger than the range of an expanding native species B, gene flow from populations of A where there has been coexistence between A and B may provide genes adaptive to naïve A populations that are faced with expanding species B. That gene flow could buffer a population that would otherwise not persist in the face of a strong interactor until a new mutation or recombination event occurs that is favourable (as in the case with a completely novel invader). No such buffering would exist for an interaction with a novel invader because no native population will have experienced prior selection from that invader. Lack of genetic variation in island species may be one reason why they are so vulnerable to extirpation from invaders – these species may lack enough genetic variation to accommodate a novel interaction and do not have enough time to accumulate favourable mutations that would ameliorate the negative effects of invaders. Furthermore, even in mainland communities, the strong, rapid ecological impact of invaders may limit the spread of adaptive alleles among heavily invaded native communities (e.g. Vermeij 1982) and may decrease native population sizes to levels that cannot support the necessary genetic variation for rapid evolutionary responses (Kim *et al.* 2003).

A third point worth considering is whether human transportation creates species combinations that are otherwise almost infinitely unlikely. Human introductions, in this case, would not be analogous to phenomena like natural range expansions. If the source areas from which introduced species originate do not coincide with, for example, any past history of vicariance, then bizarre species combinations may generate pathological behaviour owing to a lack of evolutionary history (*sensu* Elton 1958). In California alone, considering just the geographical origins of 167 introduced grasses, there are species from Africa, Asia, Australia, Europe/Eurasia and India (Hickman 1993; S.Y. Strauss *et al.*, unpubl. data). The resulting unlikely combinations of introduced and native species could underlie some proposed mechanisms for the dominance of invasives. The pathological effects of some exotic species may result from naïve native species that are exposed to novel interactions and traits with which there has been no previous evolutionary history (Elton 1958). For example, introduced brood parasites like cowbirds have low impacts on birds belonging to clades with a history of brood parasitism, even when the species being tested has itself never been exposed to parasites (Peer & Sealy 2004; Underwood *et al.* 2004). In contrast, species belonging to clades with no past history of parasitism are much more severely affected by brood parasites. Similarly, evolutionary naïveté of the native plant and microbial community is suggested by Callaway *et al.* (2005) for why Eurasian knapweed has such large effects on North American plant communities.

One approach related to that third hypothesis is to ask whether introduced species with large impacts are less related to native species than are introduced species with small impacts on native communities. If phylogenetic relatedness is associated with ecological similarity – as shown in recent phylogenetic analyses of ecological communities (Harvey & Pagel 1991; Webb *et al.* 2002; Cavender-Bares *et al.* 2004) and as suggested by Darwin in his Naturalization hypothesis – then we might expect more distantly related invaders to be ecologically more 'novel' to native communities. In fact, Ricciardi *et al.* (2004) found that high impact invaders in aquatic systems are more likely to come from novel genera not represented in the native fauna than are invaders with low impacts. Lockwood *et al.* (2001) found the same patterns with respect to invasive congeners for introduced plants in three states. Similarly, S.Y. Strauss *et al.* (unpubl. data), using a supertree of all grasses in California, show that invasive pest grass species have a greater mean phylogenetic distance, on average, from native grasses than do introduced, non-pest grass species. All these cases support the idea that the match between the evolutionary history of invader and native species might determine the impact that exotic species have on native communities.

CONCLUSIONS

While the ecological effects of invasions have been well studied (reviewed in Lodge 1993; Levine *et al.* 2003), few investigators have examined the likely evolutionary consequences of invasions for natives. It is now understood that micro- and even macroevolution commonly takes place over very short time-scales (Thompson 1998; Carroll & Boyd 1992; Hendry & Kinnison 2001; Reznick & Ghalambor 2001), and examples include rapid evolution by natives in the face of other novel ecological threats such as pollution and climate change (Ward *et al.* 2000; Reale *et al.* 2003), as well as rapid evolutionary changes in introduced species in response to their novel habitats (Lee 2002; Cox 2004). It follows that evolution and coevolution between natives and exotics after colonization may be important in the species dynamics and ecological impacts of biological invasions.

We identified a variety of ecological contexts for the evolution of natives in response to invasive species. These

contexts include invasives acting as new hosts and resources for natives, as competitors, predators, parasites or pathogens. Accordingly, short-term ecological effects on natives extend from increasing their population size and geographical range to their near or total extinction. Short-term evolutionary responses can augment the ability of natives to exploit novel resources, or reduce fitness costs of new antagonistic interactions. Adaptations that reduce the immediate impact of invaders may include specialization on a subset of the original niche (Boyd & Barbour 1993; Vogel *et al.* 2002), and the evolution of evasion or resistance. However, failure to adapt sufficiently, either facultatively (plastically) or genetically, to the ecological consequences of invasion may ultimately result in long-term attrition and declines in population size.

While these examples and inferences paint a general picture, we have little idea of either the proportion of invasions that exert significant selection on natives, or the proportion of selected native populations that respond evolutionarily. However, basic knowledge of evolutionary processes in general can lead to predictions regarding when evolutionary responses to invasion are especially likely to occur (Fig. 1). We have only just begun to document the kinds of evolutionary responses that native species might exhibit in response to selection from invasive species. To
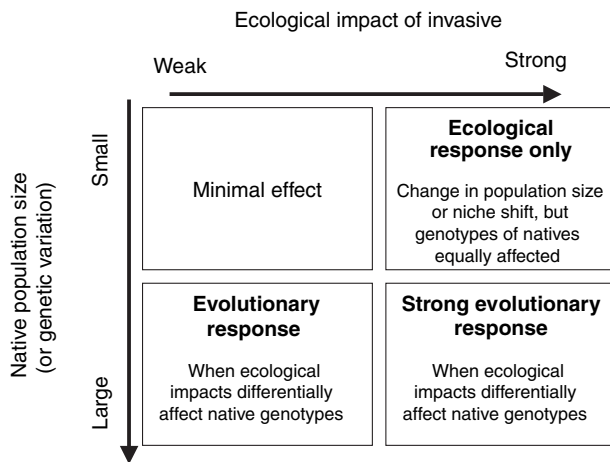

Figure 1 The likelihood of an evolutionary response depends on characteristics of both the invader and the affected native(s). If the invader's impact is very weak, it may not be an important selective agent and will have minimal ecological and evolutionary effects on natives. If the invader's impact is strong and if impacts do not differentially affect genotypes, then natives may experience population declines or exhibit plastic changes in habitat or resource use, but have no evolutionary response. When an invader has strong ecological effects, when these effects affect genotypes differentially, and when the native has a large enough population size to withstand these ecological impacts and to provide the genetic variability on which selection can act, then we expect an significant evolutionary response to occur.

the extent that exotic invasions may differ from range shifts of natives, and may exert stronger selection, can we predict the types of evolutionary responses that are likely to occur first, or be most evident? A number of the examples we cite involve changes in behaviour (e.g. the avoidance of a novel predator, the adoption of a novel host, or tracking changes in prey community composition). Evolution in other traits, including life history, physiology and morphology, also appears in several cases to have resulted from, or coevolved with, initial changes in behaviour. Such plastic responses, including non-genetic variation in avoidance or exploitation behaviour, may result in natives' exposure to novel environmental conditions beyond the direct physical impacts of the invasives themselves, setting the stage for rapid evolution in many traits, and perhaps coevolutionary relations between natives and exotics. The accidental experiments created by invasions should be productive settings for testing microevolutionary hypotheses in complex communities. In particular, biological invasions are exceptional natural experiments for investigating the role evolution plays in community assembly.

Clearly, exotics pose many kinds of selective pressures; in documenting the kinds of evolutionary responses exhibited by natives to exotics, we are limited only by our imaginations in where to search for these responses. For example, an underexplored area involves sexually selected traits that may come under selection from new predators or competitors. Rapid changes in sources of risk, or in environmental effects on signal transmission and reception, could influence, the ability of individuals to choose or get access to the most desirable mates. One documented instance is the introduction of native predators into historically predator-free environments inhabited by guppies. These predators cause evolution of decreased gonopodium length in male guppies (Langerhans *et al.* 2005). Introduced predators are likely to evoke similar evolutionary responses in sexually selected traits. One might imagine that other kinds of impacts on signalling traits could also occur. For example, does the deafening mating chorus of introduced coqui frogs (*Eleutherodactylus coqui*) pollute the acoustic environments of night-calling natives?

The vast majority of the cases of evolutionary responses to invaders have focused on the direct effects of exotic species on natives; how native species are affected by cascading indirect effects of exotics has received little attention. Even in cases where some natives appear to benefit, as in the bolstering of a native insect herbivore population in response to an introduced host plant, another native in the web, like an indigenous host, may subsequently suffer as a result of increased attack. Other complications can occur by such developments as the specialization of threatened natives on invaders, like the endangered willow flycatcher that nests particularly well in highly invasive tamarisk (e.g. Malakoff

Table 2 Evolutionary processes and invasions

1. Exotic species can exert strong selection

Novel selective agents that are exceptionally strong may rapidly decrease population size of natives, and may reduce genetic variability to levels too low to allow adaptive or compensatory evolutionary responses

Strong selection associated with introductions provides a number of our best examples of contemporary evolution – both in native and introduced species

Native species may evolve to minimize negative impacts of invaders; long-term data on demographic impacts of these evolutionary responses are needed to assess the long-term effects of exotics on native species persistence

2. Native population structure may influence the likelihood of evolutionary responses

Gene flow among native populations may impede responses to invasion waves, if invaded populations are demographic sinks relative to uninvaded populations

Gene flow among native populations may promote adaptive evolutionary responses, if gene flow promotes population persistence until novel mutations that are advantageous in the face of invasions occur, or if gene flow facilitates the spread of advantageous alleles from adapted populations in other parts of the native range

3. Plasticity can provide important means of responding to novel selection

Plasticity may buffer natives from reductions in genetic variability

Plasticity, itself, can be under selection from invaders

4. Shared evolutionary history, or lack thereof, may influence impacts of invaders

Past selection by phylogenetically or functionally similar species can facilitate appropriate responses in natives

Invaders less related to natives may have larger ecological impacts because they pose completely novel threats

1999). In many cases, however, a slow population death by attrition, caused directly by interactions with invaders, or indirectly from the costs associated with adaptations to them, may be the ultimate fate of many native species. Such slow declines are difficult to detect in short-term studies. Long-term demographic data coupled with experimental removals of invaders are necessary to address the more subtle potential effects of introduced species. These effects may be occurring at continental scales and over long time periods. Another likely consequence of invasion is the culling of genetic variation from native populations. Such loss of genetic variation may compromise native species ability to respond to shifting selection pressures from other, new invaders or other selective forces (habitat destruction, climate change, natural disaster, etc.). Table 2 summarizes some of the ways in which evolutionary processes may provide insights into the impacts of invaders and the functioning of natural communities.

Human conveyance has resulted in the redistribution of thousands of species over short periods of time; this fact makes human-mediated range expansions different from all but the most extreme cases of historical biotic exchange. In addition, previous large biotic exchanges have occurred between land masses that may have been in more recent contact in geological and evolutionary time. The importance of shared history is unknown, but the mélange of species introduced by humans from all corners of the globe, and from areas with no history of vicariance, creates communities with little shared evolutionary history. As the unique taxonomies and adaptive attributes of Wallace's biotic provinces are eroded, we have intimations that such history may be important in determining the impact of at least some introduced species on naïve native communities.

Finally, while much attention is paid to the effects of introduced species with apparently large ecological impacts, far fewer studies address the effects of species that appear to seamlessly slot into native communities; however, even these less conspicuous species may evoke evolutionary responses in natives that coexist with them (e.g. Lau 2005). Moreover, species with traits that appear unaffected by invaders may in fact have evolved rapidly to restore former functionality, phenotypically masking substantial genetic change that affects evolutionary potential (Carroll *et al.* 1997). The importance of such evolutionary changes to species persistence, and what it tells us about the assembly and degree of coevolution in natural communities, is some of the most valuable information we can attain from the study of invasions. Understanding the extent to which, and how human-caused introductions and natural range expansions differ, will also provide key insights into the structure and functioning of diverse ecological communities.

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