IDEAS AND PERSPECTIVES

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Introduced species as evolutionary traps

Abstract

Invasive species can alter environments in such a way that normal behavioural decisionmaking rules of native species are no longer adaptive. The evolutionary trap concept provides a useful framework for predicting and managing the impact of harmful invasive species. We discuss how native species can respond to changes in their selective regime via evolution or learning. We also propose novel management strategies to promote the long-term co-existence of native and introduced species in cases where the eradication of the latter is either economically or biologically unrealistic.

Keywords

Conservation, contemporary evolution, ecological trap, exotic, invasive, management.

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INTRODUCTION

Our track record in dealing with invasive species has not been particularly impressive: species are being increasingly transported by humans and establishing themselves outside their historic ranges (Mooney & Hobbs 2000). Invasive species cause environmental damage that costs on the order of \$137 billion per year to control (Pimentel *et al.* 2000) and can, in some cases, displace or extirpate native organisms (Gurevitch & Padilla 2004). Preventing the importation of non-indigenous species in the first place is an important tool to invasive species management, but we also need a strategy to effectively contain harmful non-indigenous species once they have become firmly established.

One approach that has been tried – and that has generally failed – is intensive management with intent to eradicate invasive species. Unless successful biological controls are developed, any management practice that relies upon perpetual intervention (e.g. annual mowing, application of pesticides, removal of animals) is likely to falter at some point in the future because of limitation of resources, person power or changing priorities, essentially rendering all past efforts and investments moot. Even in cases where the complete eradication of an invasive species at a given location is possible, re-colonization from adjacent areas will inevitably occur unless the entire range of the invasive species is treated simultaneously. Intensive management with intent to eradicate invaders is also likely to fail unless it precludes re-invasions by addressing the ecological conditions or vectors that made the invasion of the nonindigenous species possible in the first place (Byers 2002).

Here we explore the possibility that native species, under the right circumstances, may either evolve or learn mechanisms to cope with the invaders (e.g. through chemical defences, improved competitive abilities, predator-avoidance behaviour) and ultimately persist on their own (Ancel Meyers & Bull 2002). Behavioural and evolutionary processes are too rarely integrated into conservation and management strategies explicitly (e.g. Watters et al. 2003), perhaps because of the implicit assumption that these processes operate on a spatial and temporal scale that exceeds most human efforts (Ashley et al. 2003). However, many examples of rapid behavioural responses to environmental changes (e.g. Griffin 2004) and several examples of 'contemporary evolution' (i.e. on the order of years and decades) in response to human activities have recently been described (Ashley et al. 2003; Rice & Emery 2003; Stockwell et al. 2003). These examples offer the exciting possibility of managing the behavioural landscapes and selective regimes of native species to meet the conservation goal of long-term persistence, so-called 'evolutionary enlightened management' (Ashley *et al.* 2003). A management plan of finite duration that subsidizes the survival of native species long enough to allow a transition to their novel selective regime is likely to be more costeffective and successful in the long-term than attempts at eradication.

THE EVOLUTIONARY TRAP

Organisms can be viewed as assemblages of morphological traits, life-history characteristics and behavioural decisionmaking rules that were moulded by natural selection to match a set of local abiotic and biotic conditions. Decisionmaking rules or 'Darwinian algorithms' (Cosmides & Tooby 1987) are expected to be adaptive, because they rely on cues that, over evolutionary time, reliably correlated with survival and reproductive success (Williams & Nichols 1984). However, Darwinian algorithms are only as complex as necessary to promote survival and reproductive success in the environment in which species evolved, and not so complex as to cover all suddenly introduced contingencies (Schlaepfer et al. 2002). In environments that have been rapidly altered, formerly reliable cues might no longer be associated with adaptive outcomes. In such cases, organisms can become 'trapped' by their evolutionary responses to the cues and experience reduced survival or reproduction (Schlaepfer et al. 2002).

Humans are altering virtually every environment at an unprecedented rate and extent (Vitousek et al. 1997), and humans may now represent the earth's most important biotic selective force (Palumbi 2001). As a result, evolutionary traps are important mechanistic explanations for the declines of populations and species in anthropogenically altered environments (Schlaepfer et al. 2002; Sherman & Runge 2002). A common by-product of human activities is the introduction of species outside their historical ranges. Furthermore, anthropogenic disturbances can create novel environments that benefit exotic species (Byers 2002). The evolutionary trap concept is useful in understanding the interactions between native and introduced species because the latter can create novel ecological contexts to which the responses of indigenous organisms may not be adaptive (Callaway & Aschehoug 2000; Shea & Chesson 2002).

Previous researchers have considered the ecological impacts of non-indigenous species (e.g. Mack *et al.* 2000; Townsend 2003), the behavioural properties associated with successful invaders (Sol *et al.* 2002; Schöpf Rehage *et al.* 2005), and how non-indigenous species adapt to the novel habitat (Blossey & Nötzold 1995; Sakai *et al.* 2001; Lee 2002). Recently several studies have also described how native

species change in behaviour and morphology as a result of interactions with non-indigenous species (Reznick & Endler 1982; Singer *et al.* 1993; Singer & Thomas 1996; Carroll *et al.* 1997, 1998; Magurran 1999). New understanding of the interactions between native and introduced species may be achieved if we consider the former evolutionarily adaptive environments of each species (Williams 1966; Symons 1990), and how these contrast with their current situation.

For example, (i) Bufo marinus (Cane Toad) was introduced to Australia in 1935. All life stages of B. marinus contain a toxin that is unique to toads and that serves as a chemical defence. There are no toad species native to Australia (Tyler 1994). As a result, B. marinus toads are both evolutionarily novel and toxic to native Australian predators (Crossland & Azevedo-Ramos 1999; Phillips et al. 2003). Naïve Australian predators will attack the toads, presumably because of their superficial morphological resemblance to Australian frogs, and the predators will sicken or die as a result of ingesting the toxic chemicals. Declines in native snakes, lizards and marsupials following the invasion of B. marinus probably result, at least in part, from this evolutionary trap (Phillips et al. 2003). Interestingly, recent evidence also suggests that certain Australian snakes may be evolving (by reducing their gape width to body length ratio) in response to this novel selective agent (Phillips & Shine 2004). (ii) Females of native pierid butterflies (Pieris virginiensis, P. napi marginata and P. napi oleracea) will readily oviposit on the introduced plant Alliaria petiolata (garlic mustard). The butterfly larvae, however, are unable to complete development on these novel host plants (Chew 1980; Courant et al. 1994; Porter 1994). Similarly, female Danaus plexippus (monarch butterflies), when given a choice between their native host plant Asclepias syriaca and the introduced Vincetoxicum nigrum (black swallowwort), lay about 25% of their eggs on the latter species (Tewksbury et al. 2002) although their larvae are unable to develop on V. nigrum. In all these cases, native lepidopterans oviposit on an introduced plant that is toxic or lethal to their offspring because they do not distinguish it from their native host plant. The introduced plant is an evolutionary trap, as opposed to a population sink, because some pierid butterflies exhibit a preference for the poor quality plant in choice experiments (Battin 2004).

Of course, the interaction between two species that do not share an evolutionary history could result, by chance, in a positive outcome for one or both species. Such situations, which represent the converse to an evolutionary trap, could be termed 'evolutionary releases'. For example, the native *Jadera haematoloma* (soapberry bug) has successfully shifted to evolutionarily novel host plants (Carroll *et al.* 1997, 1998). Introduced species may also benefit from evolutionary releases. For example, in the Western United States introduced *Rana catesbeiana* (American Bullfrog) prey upon native anuran tadpoles and metamorphs (Lawler *et al.* 1999; Kiesecker *et al.* 2001; Rosen & Schwalbe 2002). Naïve prey cannot recognize *R. catesbeiana* as potential predators. As a result, *R. catesbeiana* has been 'released' from some of the difficulties of finding prey (Kiesecker & Blaustein 1997; but see Baber & Babbitt 2003). The advantage of an evolutionary release may explain the paradox of why invasive species sometimes enjoy a competitive advantage over locally adapted species (Blossey & Nötzold 1995; Shea & Chesson 2002; Allendorf & Lundquist 2003). Future investigations into such situations may reveal why certain species are more likely to successfully invade than others, and why certain native species increase in abundance in conjunction with human-related alterations to the landscape.

INTEGRATING EVOLUTIONARY CONCEPTS INTO MANAGEMENT AND CONSERVATION EFFORTS

Native species that are 'trapped' by invasive species are not necessarily doomed. Natural selection will favour native individuals that can create a novel association between a set of cues (using multiple sensory modalities, if necessary) that uniquely identify the introduced species and a corresponding adaptive response (e.g. avoidance of the introduced species) to those cues. A successful transition to the novel selective regime will likely occur if the negative effects of the trap are not too severe, if there is some genetic variation or behavioural plasticity within the native population in its responses to the novel cues of the introduced species, or if the native population is large enough and can persist long enough for adaptive shifts in its behaviour to occur (Schlaepfer *et al.* 2002).

There are a few documented cases of native prey that, given enough time, learn or evolve the ability to escape the evolutionary trap caused by an invasive species. For example, Rana aurora (Red-legged Frog) individuals that have never encountered introduced R. catesbeiana (American Bullfrog) do not exhibit predator avoidance behaviour. Given as little as 70 years, however, R. aurora has acquired the ability to detect the chemical cues of their new predators and exhibit predator avoidance (Kiesecker & Blaustein 1997). Whether this occurs because of genetic changes in the prey or learning from observing the outcomes of conspecific interactions with predators is unknown. The important question for conservation biology now is whether we can manage the selective regimes of native species so that they have sufficient time and opportunities to adapt to the new challenges posed by non-indigenous species.

NOVEL MANAGEMENT STRATEGIES

Trapped species require novel management strategies. In cases where invasive species cannot be eradicated, management efforts should not pursue futile attempts to restore 'pristine' or 'ancestral' conditions. Instead, we suggest a novel approach where the survival of native species is subsidized until they have adapted to their novel environmental circumstances and evolved the ability to persist on their own. We can envision two ways in which this could be accomplished.

First, we might create conditions in which native species are exposed to sufficient selective pressure to drive an evolutionary change in behaviour or Darwinian algorithms, but not so strong as to extirpate a local population. For example, this might be accomplished by creating temporal or spatial refugia. In the case of naïve anuran larvae, a dense lattice work of aquatic roots and stems could offer spatial refugia from predation by evolutionarily novel predators such as R. catesbeiana or introduced fishes. In areas with a mix of refugium and non-refugium habitat, natural selection will favour the emergence within the prey population of traits that are likely to facilitate their long-term co-existence with the novel predator (e.g. increased escape speed, increased predator detection ability). This approach will be particularly useful for species with small ranges, where all populations can be provided with refugia, if necessary. Alternatively, or in addition to the creation of refugia, management efforts could focus on temporarily reducing the abundance, but not necessarily eradicating, an evolutionarily novel predator. Again, the goal is to maintain sufficient selective pressure to favour the emergence and spread within the prey population of traits that are likely to facilitate their long-term co-existence with the novel predator. Care should be taken, however, to ensure that the directional selection for predator avoidance does not itself cause population declines and increase the likelihood of local extinction. One way to guard against this possibility is to combine the novel selection with short-term population growth (Reznick & Ghalambor 2001). Once this has been achieved, management efforts geared towards suppressing the abundance of the introduced predator would no longer be necessary. The important difference between this approach and traditional management efforts is the inclusion of population genetics with an eye towards aiding native populations to successfully transition to their new selective environment (Rice & Emery 2003).

A second general management approach within our framework is to actively manipulate the genetic composition of native populations to increase their rate of evolution. This could be carried out by inoculating 'naïve' populations with individuals from 'experienced' populations that contain morphological or behavioural traits that are potentially useful. For example, 'experienced' populations of West Coast anurans that have somehow survived and learned to recognize *R. catesbeiana* as potential predators might be used to inoculate naïve populations before the front of the expanding *R. catesbeiana* invasion reaches them (Fig. 1).



Figure 1 Schematic of moving front of invasive species, and inoculation of 'naïve' native population with individuals from 'experienced' population. Translocated individuals carry genes or behaviours that increase the population's probability of survival once contact is made with the evolutionarily novel predator.

Another example might include using individuals that are resistant to a novel disease (e.g. chestnut trees that are resistant to the chestnut blight Cryphonectria parasitica) to either re-populate decimated areas or protect populations that have not yet been exposed to the disease. Provided there is a genetic basis to the desirable trait (e.g. predator avoidance behaviour, disease resistance), the hybridization of 'naïve' and 'experienced' individuals will increase the likelihood that at least some endemic individuals (and their genotypes) will survive. Even if there is no genetic basis for the predator-avoidance behaviour, the naïve populations may learn by observing and imitating the behaviour of 'savvy' individuals (Griffin 2004).

Some conservationists and managers may object to the 'tainting' of the naïve population gene pool and the more general risk of unintended consequences. All management options, including doing nothing, should be carefully considered within a formal decision-making framework (Shea et al. 2000). Our proposed strategies should be particularly relevant in situations where a native population is believed to be imminently vulnerable to extirpation and where, as a result, the consequences of no action are unacceptable.

Conservation biologists and wildlife managers also should consider the possibility of using learning techniques to help their target organisms survive in their novel environments (Griffin 2004). Learning has already been used to facilitate the re-introduction of endemic mammals from small predator-free islands to mainland Australia where they are likely to face a suite of novel predators (Griffin et al. 2000). Certain species of fish, birds, mammals, amphibians and reptiles can rapidly learn to associate chemical, visual and auditory cues with a novel predator or prey (Crossland 2001; Griffin 2004). For example, predator-avoidance behaviour

propagated through a naïve population of fish in less than

2 weeks after the introduction of an evolutionarily novel predator (Chivers & Smith 1995).

Two lines of enquiry will help in the success of microevolutionary management. First, there is an urgent need to understand what rate of change different species and populations can tolerate. Ashley et al. (2003) predict that populations exposed to long periods of stabilizing selection may not have the underlying genetic variation to adapt to a novel optimum. Battin (2004) suggests that small population size, low learning ability, and slow rate of evolution will make an organism vulnerable to an evolutionary trap. These gaps in our knowledge reflect the lack of emphasis on intraspecific variation in behaviour and genetic variation in past ecological studies that we now seek to redress (Rice & Emery 2003). Second, we need to better understand the relative roles of genetic vs. phenotypic responses to environmental change. For example, it would be useful to determine the heritability of morphological and behavioural responses to introduced species because this will help determine what management approach will most likely succeed. In addition, the possibility that phenotypic plasticity and learning may provide a short-term response to change, but a hindrance to long-term adaptation (Papaj 1994) needs to be rigorously evaluated.

By incorporating the evolutionary history and behavioural ecology of native and introduced species, biologists and wildlife managers will be better able to predict which species are likely to successfully invade a novel territory, and the effects these invasions will have on different native organisms (Shea & Chesson 2002). A view that acknowledges that species interactions may change over short time scales (weeks, months or years) as a result of learning and evolutionary forces (Ashley *et al.* 2003; Stockwell *et al.* 2003; Yoshida *et al.* 2003) will also promote new management schemes geared toward moulding behaviour and natural selection in desirable ways, rather than continually attempting to restore 'ancestral' conditions. The use of evolutionarily enlightened management represents a unique and fruitful way to potentially ensure the co-existence and long-term survival of all native and non-native species.

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