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PERSPECTIVE

Conciliation biology: the eco-evolutionary management of permanently invaded biotic systems

Scott P. Carroll[1,2]

1 Institute for Contemporary Evolution, Davis, CA, USA
2 Department of Entomology, University of California, Davis, CA, USA

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Correspondence
Scott P. Carroll, Institute for Contemporary Evolution, Davis, California USA 95616.
Tel.: +1 530 902 8267;
Fax: +1 530 297 6080;
e-mail: spcarroll@ucdavis.edu

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Abstract

Biotic invaders and similar anthropogenic novelties such as domesticates, transgenics, and cancers can alter ecology and evolution in environmental, agricultural, natural resource, public health, and medical systems. The resulting biological changes may either hinder or serve management objectives. For example, biological control and eradication programs are often defeated by unanticipated resistance evolution and by irreversibility of invader impacts. Moreover, eradication may be ill-advised when nonnatives introduce beneficial functions. Thus, contexts that appear to call for eradication may instead demand managed coexistence of natives with nonnatives, and yet applied biologists have not generally considered the need to manage the eco-evolutionary dynamics that commonly result from interactions of natives with nonnatives. Here, I advocate a conciliatory approach to managing systems where novel organisms cannot or should not be eradicated. Conciliatory strategies incorporate benefits of nonnatives to address many practical needs including slowing rates of resistance evolution, promoting evolution of indigenous biological control, cultivating replacement services and novel functions, and managing native–nonnative coevolution. Evolutionary links across disciplines foster cohesion essential for managing the broad impacts of novel biotic systems. Rather than signaling defeat, conciliation biology thus utilizes the predictive power of evolutionary theory to offer diverse and flexible pathways to more sustainable outcomes.

Introduction

Anthropogenic invasions are classically defined as the human-mediated introduction, establishment, and spread of species outside of native geographic ranges (Prentis et al. 2008). Key challenges for workers in invasion biology are prevention, control, and eradication of invasive organisms. Efforts at prevention include identifying and controlling risky organisms before they can be introduced or spread in ecological landscapes (Mack et al. 2000; Novak 2007), human health systems (Ferguson et al. 2005), and agricultural settings (Pimentel et al. 2005; Waage and Mumford 2008). Eradication or decimation of nonnative organisms has been successful in cases such as in the global elimination of smallpox virus, *Orthopoxvirus variola* (Fenner 1983), and more commonly in the local ousting of certain weeds, invertebrates, and mammals introduced to islands (Ramsey et al. 2008; Simberloff 2008) – the same types of circumscribed habitats in which natives themselves are vulnerable to extinction from invasions (e.g., Sax and Gaines 2008). In noninsular habitats, while local eradications may permit re-colonization by natives (Hoffmann 2010), such outcomes will often be sustainable only through long-term vigilance and defense. Unfortunately, the associated costs of eradication programs are often prohibitive, and larger scale ambitions are often beyond our current abilities, regardless of budget (Rejmanek and Pitcairn 2002; Norton 2009; Panetta 2009).

Invasion management requires an understanding of organismal attributes that predict invasiveness, as well as those that make native populations and communities susceptible or resistant to invasion (Strauss et al. 2006a;

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Whitney and Gabler 2008; Gluckman et al. 2009, 2011; Simberloff 2009). While frameworks for predicting invasiveness and vulnerability have been difficult to develop in an environmental context (Theoharides and Dukes 2007; Crowl et al. 2008), new evolutionarily minded designs for controlling weed invasions in croplands, and tumor cell populations in human cancers, hint that more interdisciplinary approaches to invasions may be productive (Merlo et al. 2006; Gatenby et al. 2009a; Weiner et al. 2010; Thrall et al. 2011).

It is important to emphasize from the outset the potentially far-reaching biological and practical parallels and linkages in invasion-related phenomena among environmental, medical, and agricultural biology (Daszak et al. 2000; Altizer et al. 2003; Vandermeer and Perfecto 2007; Silbergeld et al. 2008; Gatenby et al. 2009a; REX Consortium 2010). Think for a moment of agricultural cereal grains as invaders that are subsidized by ongoing mutualisms with people. They not only replace native communities, but also alter the human nutritional environment. Epidemic type 2 diabetes is a maladaptive plastic response to novel grain-based high glycemic foods and macronutrient mixes (Gluckman et al. 2011). Nonetheless, recent rapid human evolution in response to cereal diets may ease this physiological risk (Hancock et al. 2010). Other interdisciplinary examples include new human influenzas for which geographic spread follows their evolution in novel livestock polycultures (Webster et al. 1992; Crowl et al. 2008), and incursions of genes from nonnative and engineered sources into wild populations (Sasua et al. 2009). While there are conceptual and practical liabilities in generalizing too broadly across systems, I will highlight parallels and practical interdependencies that show the value of a more inclusive approach to invasion biology.

Regardless of the objective – eradication, restoration, or subsidy of nonnatives of economic value – managers are confounded by the fact that biotic systems typically do not assemble in an additive, stepwise fashion, but rather are subject to steep, difficult to predict transitions among states (Suding and Hobbs 2009). Consequently, dismantling mixed communities by removing nonnatives can be far from straightforward. The ecological and evolutionary impacts of nonnative populations that are functionally integrated in new communities mean that incautious eradication risks unintended, counter-productive outcomes and that there will often be no straightforward way to restore native communities to a preinvasion state (e.g., Zavaleta et al. 2001; Bergstrom et al. 2009; Collins et al. 2009; Norton 2009; Wallach et al. 2010).

Because most nonnative organisms will not be eradicated in the foreseeable future, and many native populations will persist alongside them (e.g., Sax and Gaines 2008), it is imperative to anticipate the dynamic eco-evolutionary character of these new communities (e.g., Carroll and Dingle 1996; Lambrinos 2004; Kilpatrick 2006; Strauss et al. 2006b; Strayer et al. 2006; Carroll 2007a; Seastedt et al. 2008; Baucom and Holt 2009; Davis 2009; Gatenby 2009; Hobbs et al. 2009; Neve et al. 2009; Goodenough 2010). The more closely evolution is monitored in real time, the more incisive and useful will be the process and the results, both for organizing observations and for forecasting developments and outcomes of practical significance (e.g., Fenner 1983; Yoshida et al. 2003; Merlo et al. 2006; Bell and Gonzalez 2009).

Recent recognition of widespread rapid evolution in nonnatives is fueling a surge of investigation (e.g., Maron et al. 2004; Phillips et al. 2006; Novak 2007; Dlugosch and Parker 2008; Keller and Taylor 2008; Latta 2008; Prentis et al. 2008; Whitney and Gabler 2008; Lankau et al. 2009; Colautti et al. 2010; Marisco et al. 2010; Ridley and Ellstrand 2010). As nonnatives become established as resources, predators, parasites, or competitors, natives adapt in response (e.g., Strauss et al. 2006b; Fisk et al. 2007; Lau 2008; Atkinson and LaPoint 2009). Not surprisingly, nonnatives also alter selective interactions among natives within communities (Strauss et al. 2006b), and similar dynamics exist among interacting nonnatives as well (Simberloff and Von Holle 1999; Zangerl and Berenbaum 2005; Downes et al. 2010). The diversity of evolutionary factors that influence the ecological outcomes of introductions is impressive and includes phylogenetic history, population structure, and genetic constraint and facilitation under altered selection (Box 1). Understanding these processes is relevant to managing both short-term and long-term dynamics in native–nonnative systems.

The evident permanence, and rapid dynamics of mixed communities, automatically draws particular attention to longer-term issues in the management of nonnative taxa. Moreover, the implications of contemporary evolution extend well beyond explaining the spread of introduced organisms (Strauss et al. 2006b; Strayer et al. 2006; Vellend et al. 2007; Carroll and Fox 2008). The capacity for new biological interactions, with outcomes such as enhanced indigenous biological control value and nonnative–native coexistence rather than replacement, can evolve rapidly in many different circumstances ranging from plants and insects to birds and pathogens (e.g., Carroll et al. 2005; Foster et al. 2007; Mealor and Hild 2007). Developing the tools to predict and manage interactions and their outcomes in both predominantly natural communities and in constructed communities of mixed nativity is a clear new challenge for applied evolutionary biology (Carroll 2007a; Mealor and Hild 2007; Sax and Gaines 2008; Whitney and Gabler 2008; Gatenby 2009; Gilbert and Parker 2010; Leger and Espeland 2010).

Box 1. Many evolutionary roads to adaptation in novel biotic associations.

A. Preadaptation interacts with susceptibility to invasion

Prior to an introduction, phylogenetic history will influence whether new forms have novel ways to use resources, outcompete natives, or escape potential threats (Dietz and Edwards 2006), including beneficial or harmful plasticity (Ghalambor et al. 2007; Schlaepfer et al. 2010). Phylogenetic relatedness is ecologically informative for predicting outcomes of novel interactions (Strauss et al. 2006a).

1. Introduced predators decimate naïve prey (Darwin 1860; Fritts and Rodda 1998).
2. Introduced plants with allelopathic capacities selected in their ancestral environments suppress native plants that lack a counter response (e.g., He et al. 2009).
3. Invasive cane toad *Bufo marinus* toxins decimate Australian snakes, but the colubrid *Tropidonophis mairii* is resistant, apparently because of its toad-rich Southeast Asian ancestry, a heritage absent in other Australian snakes (Llewelyn et al. 2010a).
4. Introduced grasses less closely related to native community members are more likely to be invasive (Strauss et al. 2006a).

B. Circumstances of introduction determine genetic composition

Small founding populations are genetically depauperate, poorly buffered against inbreeding and drift, and thus have reduced potential for adaptive evolution. However, demographic and developmental processes may enhance their evolutionary potential.

1. Multiple introductions, gene hybridization, and gene flow.
   a. Propagules of serial introductions or multiple populations (e.g., crops or pests) create regional genetic diversity rivaling ancestral diversity (Taylor and Keller 2007; Simberloff 2009).
   b. Hybridization of introduced populations amplifies local genetic diversity, facilitating adaptation and invasion (Kolbe et al. 2004; Lavergne and Molofsky 2007; Taylor and Keller 2007; Dlugosch and Parker 2008; Olivieri 2009; Wilson et al. 2009).
   c. Hybridization with relatives reduces genetic constraints to adaptation (Ellstrand and Schierenbeck 2000; Hails and Timms-Wilson 2007; Arnaud et al. 2010).
   d. Flow of transgenes from engineered crops to wild relatives enhances performance and leads to ecologically significant adaptive evolution (Snow et al. 2003; Sasua et al. 2009).
2. Novel gene frequencies and genotype-by-environment interactions.
   a. Founder-flush. Gene frequencies in small founder populations differ from the parental, creating new genotype-by-environment interactions that convert dominance and epistatic variance to additive variance (Templeton 2008). The resulting phenotypic diversity may fuel adaptive evolution, particularly in growing ('flushing') founder populations under relaxed or novel selection (Carson 1968). Such epistatic systems may involve only a few loci (Narciri-Graven and Goudet 2003; Templeton 2008), and adaptations coded by fewer genes may evolve more quickly (Gomulkiewicz et al. 2010). In one example, adaptive differentiation of native insects flushing on invasive plants arose from rapid epistatic divergence of novel, major genetic effects (Carroll et al. 2003).
   b. Gene surfing. Genomes in local evolutionary equilibrium before invasion accumulate neutral, unexpressed genetic variation (e.g., Barrett and Schluter 2008). In new environments, rare alleles may be favored (Price et al. 2003; Ghalambor et al. 2007), and available to selection as drift in low-density propagules at the invasion edge change allele frequencies (gene surfing; Excoffier and Ray 2008). For example, invasion by Brazilian water hyacinth (*Eichornia paniculata*) on Caribbean Islands lacking adequate pollinators has been facilitated by formerly rare recessive alleles for self-pollination, a mating system unsuspected in the native range (Barrett et al. 2008).

Here, I argue that a productive approach will be to pursue a conciliatory strategy of managing the eco-evolutionary dynamics of native community members with permanently established novel organisms found in agricultural, medical, or environmental contexts. I begin by outlining the meaning and domain of conciliation biology. We already know that native–nonnative communities are evolutionarily dynamic in the present, and thus, a conciliatory approach must emphasize community dynamics over longer time frames, a scale that has received relatively little attention in invasion biology (Strayer et al. 2006; Willis and Birks 2006). To substantiate the importance of this evolutionary perspective, I expand on the role of eco-evolutionary processes in invading populations, as well as in the responses of natives within invaded communities. I then develop examples in which conciliatory tactics will be especially valuable and make suggestions regarding the further development of conciliation biology, including prescriptive evolution and management for sustainable outcomes in fast-changing, novel communities.

What is conciliation biology?

Conciliation biology is that part of invasion biology that focuses not on prevention or eradication of invasive species, but instead predicts and manages outcomes of longer-term native–nonnative interactions at the levels of individual, population, species, community, and ecosystem. Conciliation biology recognizes that many nonnative species are permanent, that outcomes of native–nonnative interactions will vary depending on the scale of assessment and the values assigned to the biotic system, and that many nonnative species will perform positive functions in one or more contexts. Managing such mixed and novel systems will require integrated schemes responsive to change. Compared to invader-free communities, invader-perturbed communities are more likely to require monitoring and management of evolutionary processes. Indeed, these same communities may also be more susceptible to proactive eco-evolutionary manipulation than in the more integrated and redundant structures of deeply coevolved native communities.

The proposition that nonnatives offer services, that their eradication is not a simple fix, and that rapid evolution generated by native–nonnative mixing offers solutions are not all original insights. Yet together, these points show the value of formalizing the constructive management of native–nonnative coexistence. Strong philosophical emphases on prevention, eradication, and restoration may lead to discounting or discrediting of practices that accept nonnatives as ineradicable or in some cases desirable (Ewel and Putz 2003; Goodenough 2010). Nonetheless, compromises in this regard are commonplace. To address human needs, for example, nonnative crops are exported worldwide with detrimental consequences for native communities. Similarly, nonnative organisms and genes are widely deployed to protect food resources and public health. Many introductions of this nature will not be reversed, but may be managed in various ways to balance their costs and benefits. Similarly, eradicating established nonnatives on large scales is in many cases impossible, or expensive and potentially counterproductive.

The deleterious consequences of invasive species, from extinctions of natives (Simberloff 2008) and precipitous shifts in community structure to ecosystem 'meltdown' (Simberloff and Von Holle 1999; O'Dowd et al. 2003), are now widely appreciated. At the same time, however, there are diverse risks and complications associated with eradication attempts (e.g., Zavaleta et al. 2001, Suding and Hobbs 2009). In many contexts, such efforts may leave invader damage intact, impede restoration, threaten natives that depend on nonnatives, risk pest outbreaks, and promote the evolution of resistance to control measures (Table 1). Invasive entities are best considered in a whole-ecosystem context, and in light of ongoing, invasion-influenced evolution. Conciliatory approaches to native–nonnative coexistence that incorporate eco-evolutionary dynamics into management practices may be a solution to many enduring problems of invasion biology.

Table 1. Potential risks from management for eradication or nativism versus the conciliatory management of native–nonnative coexistence.

Risk	Examples
Failure to resolve problems associated with nonnatives	Soil salinization caused by nonnatives persists after eradication, hampers natives (Zavaleta et al. 2001)
Disruption of community/ecosystem function	Loss of native vegetation when removal of nonnative predator releases nonnative herbivores (Bergstrom et al. 2009) Predator control reduces productivity and diversity (Wallach et al. 2010) Nonnatives facilitate restoration of natives (Lugo 2004; Sullivan et al. 2007; Berens et al. 2008; Griffiths and Harris 2010)
Loss of 'replacement' functions on which natives depend	Habitat (Bajema et al. 2009; Stromberg et al. 2009) Herbivory (Hoare et al. 2007; Thomas et al. 2009; Griffiths and Harris 2010) Pollination (Cox and Elmqvist 2000; Olesen et al. 2002) Prey (Tablado et al. 2010), including buffering phenological disruption of native food sources in response to climate change (Hobbs et al. 2009) Seed dispersal (Foster et al. 2007)
Loss of novel functions	Nonnatives control nonnative pests (Fenner 1983; MacFadyen 1998; Wilson et al. 2007) Nonnative tree shelters sea turtle hatchlings from disorienting urban light (Salmon et al. 1995)
Evolution of resistance	Drug resistance in tumors (see Box 2; Gatenby 2009; Gatenby et al. 2009a,b) Antimicrobial resistance in industrial livestock production (Silbergeld et al. 2008) Pesticide resistance (Thrall et al. 2011)
Loss of invasion-based diversification of natives	Ecological diversification and speciation in insects (James and Abbott 2005; Schwarz et al. 2005; Carroll 2007b; Vellend et al. 2007)
Loss of augmentation of total local biodiversity	Local-scale and island plant diversity increases with invasion (Sax and Gaines 2003, 2008, respectively)
High effort and financial costs of eradication	Rejmanek and Pitcairn 2002; Panetta 2009

Eco-evolutionary dynamics and management in native–nonnative communities

Contemporary anthropogenic selection is commonplace, and as a practical matter, it is important to consider ongoing ecological and evolutionary processes together (e.g., Kinnison and Hairston 2007; Carroll et al. 2007). In the subsections that follow, I use examples to illustrate core aspects of managing the productive coexistence of natives and nonnatives. These aspects include the influence and management of rapid evolution, predicting the dynamics of invaded communities, the practical advantages of evolutionary management, the benefits of nonnatives, and unforeseen problems associated with control and eradication.

Rapid evolution

Ecologically significant ancestral traits of introduced organisms are often evolutionarily labile. In addition to the rapid evolution of the capacity to invade, adaptation proceeds as invading populations create and encounter new circumstances. This is evident in the dramatically re-evolving herbivore defense of invasive wild parsnip (*Pastinaca sativa*) in eastern North America. Carried as a food plant from Europe by human colonists to New England in about 1609 and quickly naturalized thereafter, this plant lived without specialized herbivores until 1869, when the European parsnip webworm (*Depressaria pastinacella*) was accidentally introduced (Zangerl and Berenbaum 2005). Wild parsnips synthesize furanocoumarins as specific defenses against webworm herbivory, and herbarium specimens collected before the webworm introduction showed very low levels of furanocoumarins when compared to contemporaneous European collections. Modest furanocoumarin production by introduced populations suggests that these metabolically expensive defenses declined under postinvasion selection in North America. After 1869, however, furanocoumarin concentrations quickly increased to near-European levels and have continued to increase ever since (Zangerl and Berenbaum 2005).

Investigating another accidental experiment, Lankau et al. (2009) showed how substantial eco-evolutionary lability of species interactions may generate practical management solutions. Garlic mustard (*Aliaria petiolata*) is a shade-tolerant Eurasian biennial with a powerful chemical arsenal that includes severe phytotoxic affects on both native tree germination and mycorrhizal fungi growth in the forests of eastern North America (Rodgers et al. 2008). Lankau and his colleagues sampled along a geographic transect of allelopathic activity that compared eastern *A. petiolata* populations established for 50 or more years with western populations established for as few as 10 years. A marked, genetically based decline in average invader root toxin production with population tenure has led to a rebound of native tree seedling performance in the eastern sample sites. The proximate factor that explains the change in germination success is diminished suppression of germination-enhancing symbiotic mycorrhizal fungi by eastern *A. petiolata*. Concomitantly, total area of *A. petiolata* ground cover is declining in older populations while native woody cover is increasing, a pattern that is opposite to observed trends in the more recently invaded forests to the west.

What is interesting about this result is that even though garlic mustard appears to have strong phenotypic effects in the early stages of invasion, over slightly longer time periods, apparent resolutions to ecological problems of invasion have begun to evolve. The mechanisms behind this change deserve further investigation. Equally important insights into the eco-evolutionary interplay of invader and native populations should be expected from considering extensive time frames in other systems.

Evolution during invasion may dramatically alter both the fitness and impacts of nonnative populations (e.g., Kinnison et al. 2007), resulting in selection favoring altered and novel phenotypes in the natives they affect (e.g., Phillips et al. 2004; Carroll et al. 2005; Strauss et al. 2006b; Gilbert and Parker 2010; Leger and Espeland 2010). In some cases, evolutionary change in invaded communities may have practical importance. For example, morphological and life-history evolution in native soapberry bugs on invasive trees in Florida has likely increased soapberry bug fitness several fold over the past few decades (Carroll et al. 1997, 1998). Similarly, the rate of successful attack on related invasive vine seeds by native soapberry bugs in Australia has more than doubled during the same period (Carroll et al. 2005). These findings suggest that useful new indigenous biological control tools are rapidly evolving in response to invasion on both continents. There are likely many cases in which natives may be actively selected for biocontrol efficacy as an alternative to introducing nonnative agents. The potential for incorporating rapidly evolving traits into applied management challenges some current conservation practices (Box 2).

Practical dynamics of invaded communities

There is growing evidence from both experimental and natural settings that rapid evolution impacts community and ecosystem function (Harmon et al. 2009; Jones et al. 2009). Moreover, higher-order impacts of ongoing adaptation reflect complex and indirect consequences of evolving species interactions. Effects of nonnative organisms are modulated over time by changes in the invader, changes in the invaded community, changes in their interactions, and changes in their abiotic impacts. Invasive plants, for example, may quickly alter ecosystem processes such as carbon and nitrogen cycling, fire frequency and intensity, and soil attributes including structure, topography, weathering, water content, and salinity (Strayer et al. 2006). Many nonnative taxa 'engineer' environments in ways that influence their own further expansion and the suitability of the environment for natives (Cuddington and Hastings 2004). Eco-evolutionary accommodation in native communities will be an inevitable result of such developments.

Under environmental change, models that incorporate contemporary evolution may improve the prediction of community dynamics (Fussmann et al. 2007). Indeed, rapid evolution in invasive species, and native–nonnative coevolution, may have stronger ecological impacts than

Box 2. Conciliatory implications of recent eco-evolutionary findings: examples in environment, food, and health.

Three recent studies in different areas of applied evolutionary invasion biology indicate how conciliation concepts can be applied in strategic management. For each, I present the problem, current eco-evolutionary findings, conciliatory approaches, and similar findings.

Environment: Evolution of indigenous biological control and the preservation of invader nurseries of beneficial evolution in natives

Problem	Among the rampant invasive plants in eastern Australia is a tree-smothering, Neotropical vine that is spreading rapidly, but few human resources are available to control it (Carroll et al. 2005).
Eco-evolutionary finding	Native Australian insects attacking the plant's seeds have evolved longer mouthparts that more than double the numbers of seeds killed (Carroll et al. 2005). On a related but less invasive vine present in northern Australia for much longer (at least 200 years), the insects show 5 × greater increase in relative mouthpart length. Allopatric northern and eastern insect populations are interfertile (S. P. Carroll unpublished).
Conciliatory strategy	Introducing or hybridizing long-mouthpart populations with those on the destructive eastern invader may speed evolution to achieve better control. However, northern plants are prone to manual eradication, which threatens adapted insect populations. The conciliatory approach is to preserve populations of the earlier, more benign invasive plant while the biocontrol value of its adaptively hypertrophied native enemy populations is more thoroughly assessed.
Similar dynamics	Mealor and Hild (2007) and Leger (2008) found that a history of cohabitation between native and invasive grasses increased native tolerance to the invaders. Further, Ferrero-Serrano et al. (2009) showed that such adaptation improved tolerance to yet another, novel invader. Managing for coexistence to retain native genes selected by competition with exotics may promote the evolution of traits that improve restoration capacity.

Agriculture – Eco-evolutionary agronomics for sustainability in the face of rapidly evolving pests

Problem	Transgenic Bt crops are partial alternatives to insecticide applications for controlling insect pests of major global crops. As a constitutive rather than facultative defense system, transgenic Bt is relatively likely to select for resistance, which has evolved in five lepidopteran crop pests in 15 years since its commercialization (Carriere et al. 2010).
Eco-evolutionary finding	Resistance evolution is influenced by the relative frequencies and performance of resistant versus sensitive genotypes in the crop environment. Strategies that maximize local productivity of Bt crops also favor resistance evolution. Accommodating the certainty of resistance evolution requires regional rather than local management (Downes et al. 2010).
Conciliatory strategy	Sustaining the efficacy of Bt crops requires, first, conciliatory recognition that pests are unlikely to be eliminated and that resistance will evolve. Fitness advantages of resistance mutations can be reduced by agronomic practices including increasing plantings of non-Bt varieties (which are refuges for nonresistant pest genotypes), and managing refuges to increase fitness costs to resident resistant genotypes by manipulating additional factors such as host quality, natural enemies, sterile male release or pathogens (Crowder and Carriere 2009, Tabashnik et al. 2010). Coupling with other evolutionarily informed tactics such as 'pyramiding' two or more pest-control genes that reduce the probability of resistance evolution may cut cropping-related costs of regionally coordinated resistance management.
Similar dynamics	Chronic use of antimicrobials in uninfected livestock promotes the evolution of resistant pathogen populations (Silbergeld et al. 2008), perhaps because no untreated refuges are provided for treatment-sensitive strains that are fitter in those environments. Very low risk strategies of resistance management may be required where maintaining treatment-free refuges is judged too costly or unethical.

Health: Noneradication strategies for tumors may protect patients by maintaining refuges for therapy-sensitive cells that outcompete resistant mutants

Problem	Promising systemic cytotoxic cancer therapies often fail in application.
Eco-evolutionary finding	By hastening the evolution of resistance, therapies to eliminate cancers potentially hasten tumor reoccurrence (Gatenby 2009). Managing for coexistence of cell types may control resistance evolution and improve patient survival. Spatial and temporal heterogeneity in tumor microenvironments of most cancers undergoing cytotoxic control reduces the probability of eradication and so contributes to the evolution of toxin resistance by tumor cells (Gatenby 2009; Silva and Gatenby 2010).
Conciliatory strategy	Models predict that for micro-environmentally dynamic tumors, treatment for stability rather than for cure may improve host survival by managing for the controlled survival of chemosensitive tumor cell subpopulations that, in turn, suppress proliferation of otherwise less fit but chemoresistant subpopulations. Conciliatory therapies may further manage mutant chemoresistant subpopulations with manipulations that accentuate their pleiotropic metabolic shortcomings (Silva and Gatenby 2010).
Similar dynamics	In infectious disease, susceptible and vulnerable hosts may select for lower virulence. Interventions that reduce the contribution of these hosts to pathogen transmission favor increased virulence (Williams and Day 2008). Likewise, vaccines neutralizing pathogenicity rather than blocking infection may select for greater virulence (Gandon et al. 2003). However, by directing antipathogenic vaccines specifically to the most vulnerable subsets of populations, the intervention may simultaneously protect patients and favor reduced virulence (Williams 2010).

other modeled drivers of ecosystem function (Yonekura et al. 2007; Palkovacs et al. 2009). A pertinent concern in invasion management is the risk that constraints inferred from a source population's phenotypic performance profile, geographic distribution, or gene expression (i.e., the 'realized niche') may poorly predict the niche realized in new conditions.

As a case in point, the invasion wave of the cane toad in Australia is not only passing beyond the range limits predicted by bioclimatic models, but accelerating as it does so. The key to this enigma lies in one or more aspects of the population-by-environment interaction (Urban et al. 2007, 2008). Do cane toads better tolerate the thermal extremes of interior Australia owing to more rewarding prey, to lower intraspecific competition at the invading front, or to loss of biotic limiters (e.g., specialized parasites), or to all of these factors? At the same time, are the enormous populations of cane toads evolving better means of coping with the regional and local scale environmental exigencies of interior Australia? Recent increases in locomotory speed (Phillips et al. 2006), travel distance (Alford et al. 2009) and endurance (Llewelyn et al. 2010b), for example, may increase the probability of locating suitable but patchily distributed microhabitats. The likely combination of induced developmental and performance enhancement, as well as adaptive evolution for dispersal ability and physiological tolerance, may promote colonization and establishment in habitats that would otherwise have been unavailable. This research suggests that models for predicting invasive species ranges will often need dynamic updating to incorporate the broadening of realized niches and evolution in response to changing habitats.

Evolutionary principles and management practice

Opportunities to apply evolutionary principles to management practices are widely available in many areas of immediate human interest. Indeed, the exchange of biotic invaders between agricultural and biomedical contexts demonstrates in striking terms the importance of evolutionary principles in applied management schemes. For example, antimicrobial-resistant bacterial infections now account for many emerging infectious diseases worldwide (Okeke et al. 2005; Erb et al. 2007). Agriculture employs the majority of antimicrobials worldwide, including all classes of antimicrobials important for human medicine. Many agricultural applications of pharmaceuticals employ subtherapeutic doses that incidentally favor drug resistance evolution in pathogenic microbes. This situation in turn promotes microbe invasion of formerly defendable human and livestock populations. For public health, the most serious consequence of agricultural antimicrobial use/misuse is the expansion of reservoirs of resistance wherein resistance genes transfer widely among microbial communities (Silbergeld et al. 2008). Even after the cessation of subtherapeutic dosing, resistance has been observed to persist in microbes of industrial chicken populations (Price et al. 2005). Further, resistance evolution has been linked to increased microbial production of toxins (Stevens et al. 2007).

Implementing restricted and strategic use of antimicrobials in agriculture will curb resistance evolution, but at the same time, possibly introduce undesirable risks to production for individual growers. Design and experimentation informed by evolutionary biology may best succeed in practice if the needs of growers are accommodated in a manner similar to the approach taken with growers of Bt cotton in Australia (Downes et al. 2010).

Several other examples from the agricultural/medical milieu illustrate the need for an evolutionarily informed approach to sustainable control of agricultural and human pests. Integrated pest management (IPM) in agriculture, an ecological approach that recognizes the permanence of pests in the landscape, has long been employed to defend nonnative crops (Kogan 1998). IPM uses biological knowledge of pest vulnerabilities to gain leverage within agricultural systems. One relatively recent approach in IPM is genetic 'pyramiding', i.e., the engineering of individual cultivars with multiple pest-resistance genes to reduce the probability that pests will evolve the capacity to overcome them (Downes et al. 2010). Similarly, antibiotic resistance evolution and spread may be slowed by the simultaneous application of multiple antibiotics (called 'mixing' in the medical literature; Bergstrom et al. 2004). Another eco-evolutionarily integrated pathway in public health may be to engineer biocontrol pathogens of pests. For example, viral and microsporidian pests of *Anopheles* mosquitoes may reduce malaria transmission in a manner relatively immune to resistance evolution in the host even though these control agents reduce both adult mosquito longevity and biting rate. Resistance to host counter-evolution occurs because these particular pests of mosquitoes select strongly on juvenile survival, a life-history feature that exhibits a developmental trade-off with the adult traits (Koella et al. 2009). Engineered mosquito viruses might similarly target disease transmission through delayed killing of mosquitoes until after reproduction begins but before adults have become efficient malaria vectors. Thus, disease control is promoted without generating strong countervailing selection for resistance in the mosquito.

Benefits of nonnatives

In managing mixed communities of native and nonnative taxa, conciliation biologists must also consider short- and long-term benefits that accrue from invasive taxa, and how these balance against negative impacts. The intentional spread of endemic European cowpox virus (*Orthopoxvirus* sp.) around the globe was implemented more than two centuries ago as a means to inoculate people against the closely related but more virulent smallpox virus. In this instance, the introduction was regarded as a net benefit despite the serious and scarring illness caused by cowpox virus in both humans and cattle (Fenner 1983; Rusnock 2009).

The potential benefits of intentionally introduced organisms have been more widely considered in agriculture than in medicine (e.g., Roderick and Navajas 2003), and increasingly so in environmental biology with respect to both accidental and intentional introductions (Ewel and Putz 2003; Griffiths and Harris 2010). Practitioners in each of these fields may miss opportunities by attempting to eradicate, contain, or control nonnatives that might be benign players or allies (Table 1). For example, invasive species may perform functions lost after extinctions (resuming lost pollination services, for example; Cox and Elmqvist 2000), and species may be intentionally introduced to resurrect lost roles (Griffiths and Harris 2010). In addition, nonnative taxa may be superior to native taxa in providing certain ecosystem services in the face of climate change (Hershner and Havens 2008). Intentional introduction of biological control agents is a striking example of how such ecosystem services can be provided. For example, Eurasian tamarisk trees (*Tamarix spp.*) were promoted in some regions of North America as a public health measure to reduce standing water available for mosquito breeding. Now, broadly invasive in the west of the continent, eradication programs are ongoing. Those efforts are complicated by the fact that tamarisk has become important to the reproduction of endangered bird species (Bajema et al. 2009; Stromberg et al. 2009).

Introduced organisms also augment local biological diversity in the short term through their presence and in addition may promote evolutionary diversification. This may occur because of founder effects and adaptive divergence of invaders in new environments, the creation of new ecological opportunities for natives, and the generation of new phenotypes or new species from novel hybridization (e.g., Carroll and Boyd 1992; Schwarz et al. 2005; Vellend et al. 2007). New taxa may play positive new roles while greater diversity may improve structural values such as resilience to perturbation. Vellend et al. (2007) regard such biodiversity-based processes as part of a suite of factors relevant to a balanced assessment of nonnative impacts.

Similarly, the multifarious benefits of nonnatives (Table 1) are likely to be context-dependent and be subject to change over time. One possibility is an increase in invasiveness or impacts that reduce net benefits, or conversely, rapid disappearance (Simberloff and Gibbons 2004). As time passes after introductions, we should anticipate increasing interdependence and coevolution between natives and nonnatives (Gilbert and Parker 2010). Once native natural enemies are selected to specialize on deleterious invaders, invasions may decline or reverse. Although this state of affairs may seem propitious, reductions or eradications of invaders, whether through human intervention or independent eco-evolutionary change, may have complex and potentially deleterious unforeseen consequences.

Complex and unforeseen consequences of eradication efforts

The evolutionary dynamic that resulted from the well-known 1950 introduction of South American myxoma *Leporipoxvirus* populations to control invasive Iberian rabbits (*Oryctolagus cuniculus*) in mainland Australia has been replayed at multiple locations around the world with diverse and significant practical consequences at each location. For example, coevolution ensued in Great Britain when the rabbit, which was introduced nearly a millennium earlier as semi-domesticated livestock (Ferrand and Branco 2007), was exposed to the same virus in 1952 as part of a program that sought to emulate the Australian undertaking that was already underway (Fenner 1983). With nearly complete rabbit mortality during the first epizootic in each region, reciprocal avirulence in the virus and resistance in the host evolved within a year in both Australia and Great Britain (Fenner 1983). Over subsequent decades, these traits have cycled around intermediate virulence and resistance values in the two regions, and during this period, rabbit populations have remained depressed by around 90%, a level of control that largely satisfies the goals of the biocontrol initiative. Unfortunately, *Myxoma* has spread and now threatens rabbits in the native Iberian range. A vaccination program for rabbit kits is being considered to restore Iberian rabbit populations and to support endangered rabbit predators such as the Imperial eagle (*Aquila adalberti*) and the Iberian Lynx (*Lynx pardinus*) (Ferrer and Negro 2004).

In addition to strong direct eco-evolutionary affects of eradication efforts, indirect effects may also perturb community states and shift them precipitously to favor or disfavor natives. This is strikingly illustrated by the extinction of the visually stunning Large Blue butterfly (*Maculinea arion*) in England, perhaps the world's most intensively studied and expensively conserved butterfly (Thomas et al. 2009). Large Blues and other Lycaenid butterflies commonly show taxonomically narrow host specialization (Fiedler 1996). Importantly, it was the discovery of the arcane developmental requirements of the Large Blue that eventually permitted restoration through the introduction of a European replacement population. After fifty years of failed efforts, the Large Blue was declared extinct in England in 1979. The butterfly's dependence on *Thymus*-dominated grassy hillsides was known, but the discovery that butterfly larvae feed exclusively on immature individuals of the ant *Myrmica sabuleti* came too late to make a difference in conservation planning. The ant itself has narrow habitat requirements and is found in warm soil conditions located under diminutive vegetation. As vegetation became rank following reduced livestock grazing in the mid-1800s, ant populations declined concomitantly and in turn reduced the success of the Large Blue. In a darkly fascinating turn of events, the hillsides to which the ant was confined were later grazed primarily by Iberian rabbits, but with the introduction of myxoma virus to England, sites with the Large Blue became too overgrown for the primary host.

Postextinction analyses pinpointed larval butterfly dependence on the ant, and intensive management for ant populations in turn fostered successful re-introductions of Large Blues from Sweden beginning in 1983. Today, the Large Blue is common across many sites in southern England, and insights from its study have provided short-cuts to the conservation of other *Maculinea* species across Europe (Thomas et al. 2009).

The case of the Large Blue highlights the point that invader removal will not simply reverse changes in community structure and function. The pathway of degradation differs from that of recovery (Suding and Hobbs 2009; see also Tompkins and Veltman 2006), so that eradication may enhance or create rather than solve problems (Courchamp et al. 2003; Wallach et al. 2010). In particular, the order in which species are removed may matter critically (Collins et al. 2009). Feral domestic cats (*Felis catus*) introduced in 1818 to Macquarie Island, south of Australia, provide another striking example. The cats apparently caused the extinction of an endemic flightless parakeet (*Cyanoramphus novaezelandiae erythrotis*) and rail (*Rallus philippensis macquariensis*), and subsequent cat eradication in 2001 was intended to protect nesting seabirds. However, the major result of cat eradication has been the release of population growth in Iberian rabbits that were first introduced in 1878. A growing rabbit population had drastic island-wide consequences for native vegetation and functions that the plants support, including effects on native herbivores and soil protection (Bergstrom et al. 2009). Troubles for plants arose despite prior effectiveness of integrated rabbit control started in 1968 that later included the 1978 introduction of myxoma virus.

The unexpected trophic cascade in this comparatively well-known island system reversed the gains of almost 35 years of invasive species management in only 6 years. Top-down control by the cats was assumed to be redundant to that provided by myxoma. Not as well considered was the possibility that selection for avirulence was reinforced by cat predation, such that even with annual re-supply with virulent strains, local adaptation to the cat-thinned rabbit population favored reproduction by less lethal virus genotypes. The risk of rabbit resurgence after cat eradication was predictable on evolutionary grounds; moreover, the virus is not reliably perennial in the habitat (Bergstrom et al. 2009), so re-evolution of high virulence without continuing virus management is uncertain. Similar precipitous shifts in community structure have been observed in other cases of nonnative predator removal. Wallach et al. (2010) compared trophic analyses of communities with and without nonnative dingoes (*Canis lupus dingo*) and suggested that native biodiversity is better protected with dingoes present, because of how trophic relations in contemporary Australian communities with mixed nativity now function.

Discussion

A conciliatory approach to introduced organisms complements prevention and eradication efforts. It is well appreciated that eradication can indeed restore former functionalities in environmental, health, and agricultural contexts (e.g., Fenner 1983; Panetta and Lawes 2005; Hoffmann 2010, respectively). In addition, many permanently established nonnatives are effectively managed at low densities (Simberloff 2008). However, the global mixing of life by humans is not amenable to control, and we are many centuries into the translocation and modification of taxa with indelible ecological and evolutionary results (see, e.g., Darwin 1860, p. 120). Human actions combined with natural processes will not generally restore ecosystems to their preindustrial states, and we are left with the uneasy task of managing key biotic functions in the attempt to recoup losses and avert problems even greater than those we have already set in motion.

Along with the other agents of global change, biotic invasions raise the possibility that adaptive evolution emerging from the deep changes experienced by novel and native taxa will substantially alter the form and structure of biota and biotic systems. A principal challenge for conciliation biologists will be to predict and manage future systems that have unprecedented assemblages of rapidly evolving organisms (Carroll 2007a). A conciliation approach can support this goal in at least five ways.

First, understanding the ecological and evolutionary processes that govern the influences of invasive species over time will require a shift from the current focus on the 'acute' ecological, economic, agricultural, and health aspects of invasions to a longer-term focus on 'chronic' affects (*sensu* Strayer et al. 2006). Accomplishing this change in emphasis will require expanding eco-evolutionary theories of communities (Fussmann et al. 2007), fashioning models that link individual traits to community outcomes (Butterfield and Briggs 2009), and initiating longer-term monitoring of new and existing variables to dynamically update community and niche-based invasion models (Urban et al. 2008).

Second, conciliation biologists will work to design and employ proactive, experimental, and process-oriented evolutionary considerations in invasion biology practice. Latta (2008) suggests three means of implementing this vision: making greater use of existing evolutionary theory; testing management alternatives with experimental evolution; and conducting field trials under an adaptive management framework. Similarly, Possingham and Kinnison (2010) argue that conservation biology is 'too conservative,' being constrained by often-futile efforts to restore historical communities, and not appreciating the unavoidable and dynamic contributions of ongoing adaptive evolution. Their eco-evolutionary suggestions include re-initiating extinct adaptive radiations with introduced taxa. This is a radical approach to biodiversity 'conservation,' but the millennia of domestication of plants and animals in fact attest to a human capacity to pursue the rewards of enduring evolutionary management.

Combining phenotype-centered, experimental, and process-oriented approaches such as those treated in Box 2 may yield reliable predictors of dynamics within invaded communities (Carroll 2008; Latta 2008). Even in such long-lived and logistically challenging study targets as trees, phenotypic analyses have successfully predicted the rapid evolution of defensive phytochemical allocation as a conservation solution to introduced herbivores (Vourc'h et al. 2001). Detailing the eco-evolutionary impacts of introduced organisms in their native ranges, for example, may not only permit more confident and refined predictions about their impacts in the invaded community but also assist managers in promoting invasion-tolerant or invasion-resistant phenotypes in natives (O'Reilly-Wapstra and Cowan 2010).

Third, working more effectively with adaptation will require modification of current first-order approaches. For example, management schemes that aim to preserve genetic variation as the basis for future adaptation to an uncertain future should not come at a cost to adaptive evolution to the tangible present (Kinnison et al. 2007). Conservation measures that shield populations from selection, for example, will generate increasingly management-dependent organisms, and management aimed at preserving stasis that shifts mortality schedules will cause life-history evolution. Conciliation biologists must devise the means to balance longer-term adaptive capacity with the demographic and genetic diversity costs of fostering ongoing adaptation. Predicting and managing limits to adaptation will be a part of this undertaking (Colautti et al. 2010).

Fourth, identifying and supporting community mechanisms that provide resilience in the face of change should not be overlooked in favor of controlling the agents of that change. Biotic communities form and exist not just in ecosystems but also in evosystems (Faith et al. 2010). As observed in the evolution of indigenous biological control, ongoing evolution is providing 'solutions' as environmental circumstances change (Carroll et al. 2005; Carlsson et al. 2009). Invaded communities may prove to be particularly dynamic in this way, as novel juxtapositions of taxa create new eco-evolutionary dynamics (see also Jackson and Sax 2010). New services and benefits, including ecosystem services, may arise from novel species assemblages. Just as there may be a premium on preserving natural communities that are 'engines of evolution' (Smith and Grether 2008), it will be profitable to manage evolutionarily dynamic communities of natives and nonnatives to generate beneficial outcomes.

Some of those benefits will manifest through the acceptance of nonnatives as valuable community members. In managed coastal ecosystems, for example, anthropogenic stress on native flora has dramatically reduced plant capacity to physically stabilize shoreline. The comparative vigor of invasive plants that we are struggling to eradicate indicates that most especially under conditions of extreme or rapid change, risk management should weigh beneficial attributes of nonnative taxa (Hershner and Havens 2008) against those of waiting for needed potential recovery in natives, which may itself require evolution.

Fifth, conciliation biology can make the study of invasions more productive by emphasizing interdisciplinary connections. As is evident in many of the examples treated above, from tumor cells and viruses to rabbits, butterflies, and transgenics, the fascinating networks forged by novel and nonnative organisms reach across disciplinary boundaries with manifold influences on our food, health, and environment. The differences in the contexts and constraints faced by practitioners – whether in agriculture, natural resources management, medicine, public health, invasion biology, conservation biology, or biodiversity science – generate complementary perspectives that lend strengths, across fields. The resulting insights have the potential to radically alter practice (e.g., Gatenby 2009). Moreover, cutting edge developments and successes in one discipline, such as the recent progress in medical epigenetics (Gluckman et al. 2011), may support and inspire practice in analogous and homologous evolutionary applications (M. Kinnison, *Evolution Island* http://www.instituteforcontemporaryevolution.org). Building greater commonality and precision in meaning and terminology is an important next step to improving communication across disciplines.

Regardless of personal or professional tolerance levels for novel organisms (e.g. cancer cells, transgenic crops) or nonnative species (introduced taxa), judging and assigning values of various types are inherent in how we define living systems and in the decisions we make regarding whether and how to manage them. Anthropogenic influence on ecology and evolution is as old as humanity, and traditional goals of restoring 'pristine' ecosystems or inventing 'magic bullet' solutions for agricultural pests and medical pathogens cannot be implemented under conditions of indelible human impacts, untold generations of response in natural communities, and ongoing as well as future evolution. While it will often be a defensible convenience to advocate that nonnatives should be regarded as 'guilty until proven innocent' (e.g. Ricciardi and Simberloff 2009), we will nevertheless be unable to eradicate most nonnatives, and so in many cases, we will be better off judging them with analyses that acknowledge and exploit their potential benefits. At the same time, novel communities in changing environments will probably generate many more cases of 'self-introductions' that will inevitably soften the distinctions practitioners make between invasives and natives. Problems and opportunities in food, health, and the environment are deeply and permanently intertwined. Regardless of how we segregate them culturally or linguistically, the organisms involved will, being the invaders that they are, find means of crossing our interposed boundaries. Long-term solutions to the problems of invasive species will therefore be better served by a more nuanced and inclusive approach.

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