



Evolutionary demography: the dynamic and broad intersection of ecology and evolution

The evolutionary impacts of conservation actions

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Received: 29 March 2017 / Accepted: 20 April 2018
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Abstract

Conservation management for environmental sustainability is now ubiquitous. The ecological effects of these actions are well-intentioned and well-known. Although conservation biologists and managers increasingly incorporate evolutionary considerations into management plans, the evolutionary consequences of management strategies have remained relatively unexplored and unconsidered. But what are the evolutionary consequences? Here, we advocate a new research agenda focused on identifying, predicting, and countering the evolutionary consequences of conservation management. We showcase the examples of park creation and invasive species management, and speculate further on five other major methods of management. Park creation may cause selection for altered dispersal and behavior that utilizes human foods and structures. Management of invasive species may favor the evolution of resistance to or tolerance of control methods. In these and other cases, evolution may cause deviations from the predicted consequences of management strategies optimized without considering evolution, particularly when management results in or coincides with major environmental change, if population size change strongly, or if life histories are short enough to allow more rapid evolution. We call for research focused on: (1) experimental predictions and tests of evolution under particular management strategies, (2) widespread monitoring of managed populations and communities, and (3) meta-analysis and theoretical study aimed at simplifying the process of evolutionary prediction, particularly at systematizing a means of identifying traits likely to evolve due to likely existing genetic variance or high mutation rates. Ultimately, conservation biologists should incorporate evolutionary prediction into management planning to prevent the evolutionary domestication of the species that they are trying to protect.

Keywords Anthropogenic impact · Evolutionary domestication · Invasive species · Parks · Restoration · Unintended consequence

This manuscript was submitted for the special feature based on a symposium in Jozekei, Japan, held on 4 November 2016.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10144-018-0614-9>) contains supplementary material, which is available to authorized users.

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Introduction

Humans have long affected the abundances of species. Hunting practices, agriculture, and land-use changes across the world over the last 2000 years have led to the extinction

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of many species, as well as to the dispersal and expansion of others (Dupouey et al. 2002; Hansen and Galetti 2009). Urbanization and development fragment populations, hamper dispersal and migration, and alter the community composition of nearby natural habitats (Epps et al. 2005; Rubbo and Kiesecker 2005). Trade moves species into new areas and expands their ranges, often at the expense of native species (Dobson 1998). While these impacts on the conservation status of plants and animals have long been acknowledged, the evolutionary impacts of human influences on the natural world only recently have become the subject of scientific study.

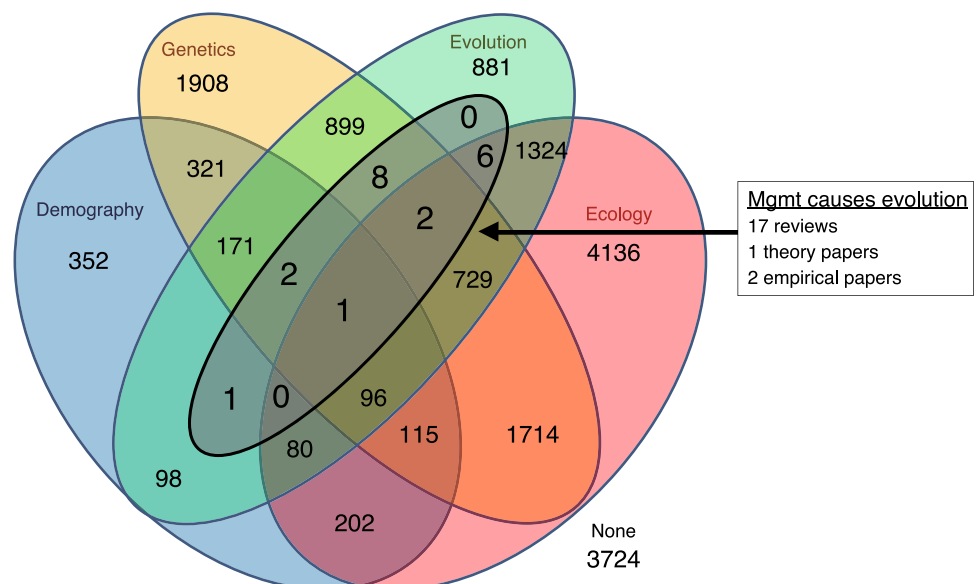
Organisms meet the challenges posed by changing environments by adapting to them at the individual or population level (Torres-Dowdall et al. 2012), or by moving away (dispersal). When the challenges experienced by species include anthropogenic factors, these species become of conservation concern. Such factors may lead to evolution, sometimes predictably (Stockwell et al. 2003; Shefferson et al. 2017). For example, widespread hunting and fishing have led to the evolution of smaller body size and cryptic behavior in many animals (Allendorf and Hard 2009; Palkovacs 2011), and widespread pesticide application has led to the evolution of pesticide resistance in many wild species, including dieldrin-resistance in insects and warfarin-resistance in rodents (Bishop et al. 1977; Mallet 1989; French-Constant et al. 2004). These considerations have sometimes led managers and conservation biologists to consider the evolutionary impacts of human influences on natural populations when developing conservation strategies (Ranker 1994; Stockwell et al. 2003). However, although some evolutionary biologists have raised the prospect of management influencing evolution (Baskett et al. 2007; Martínez-Abraín and Oro 2010; Smith et al.

2014), no empirical research that we are aware of has addressed the ways in which currently used conservation management actions themselves influence the evolutionary trajectory of target species (Fig. 1).

Why should we expect that conservation management strategies have evolutionary impacts? First, evolution due to natural selection often occurs at ecological timescales (Endler 1986; Ellner et al. 2011). Even across a large range, microgeographic variation in selection may combine with uneven dispersal to yield strong, local adaptive patterns (Richardson et al. 2014). Second, the smaller range sizes of rare species can still yield evolution via natural selection if sufficient genetic variation exists. Third, management strategies represent changes to a population's immediate environment, and such changes may lead to altered selection. Finally, management practices are often standardized and applied at large spatial scales. Widespread application may yield common selection, potentially yielding convergent evolution. This same mechanism has resulted in the proliferation of antibiotic-resistant bacteria species in modern hospitals via widespread use of antibiotics (Baquero and Blázquez 1997), and the evolutionary domestication and life history evolution of lab animals (Smith et al. 2014).

In this paper, we make a case for research on evolution in response to conservation management. First, we link conservation and evolution via the underlying ecology that is fundamental to both fields. Then, we showcase the theoretical and empirical evidence and expectations suggesting evolutionary effects to several specific management protocols, and discuss key situations in which the evolution occurring as a result of management may yield strong deviations from the predictions of ecologically optimized management strategies. Finally, we suggest three major research priorities for the near future.

Fig. 1 Venn diagram of sciences involved in conservation management papers, covering a total of 16,770 papers published from 1984 to 2017. Four categories of papers in 67 journals were identified (ecology, demography, genetics, and evolution), with numbers signifying numbers of papers dealing with those subjects. The subset in the middle quantifies the number of papers exploring the evolutionary impact of conservation actions



Conservation actions and their potential evolutionary impacts

Conservation actions may have evolutionary impacts via shifts in the ability of natural selection to cause evolution, direct or indirect shifts in the direction and intensity of selection on traits, or both. The first pathway includes factors that influence the response to natural selection, particularly via changes in genetic variation, population size, and heritability. Such factors include the size of the population and the degree of neutral and adaptive genetic variation (Ellstrand and Elam 1993), and they have often been the subject of study in evolutionary conservation biology, particularly with regards to genetic rescue strategies (Tallmon et al. 2004; Frankham 2005).

In contrast to the effects of conservation actions on population size and genetic diversity, the effects of specific actions on natural selection are largely unexplored (Fig. 1; Electronic Supplementary Material (ESM) S1). Evolution in response to conservation actions will depend on numerous factors, including the status and history of the population, the life history of the species, the selective agents responsible for the species' conservation status, and the conservation actions implemented. We define the status of the population in terms of population size, because populations are more likely to evolve via genetic drift as they get smaller (Frankham 2005), although natural selection will still operate (Koskinen et al. 2002). At the other extreme, large populations of invasive species may be more likely to evolve predictably in response to natural selection, with rapid adaptive evolution during range expansion potentially common (Prentis et al. 2008). Further, populations with longer histories at large sizes may generally have a greater amount of adaptive genetic diversity, leading to quicker adaptive evolution (Bowman et al. 2008).

Evolutionary response should also differ with life history. Patterns in age-specific mortality select for longer or shorter juvenile periods, as well as different lengths of reproductive periods (Reznick et al. 1990). The age-specific force of natural selection may also be altered by relationships between growth and fitness components. For example, an age-specific decline in the force of natural selection is generally predicted in unitary organisms (Hamilton 1966). However, if mortality is strongly elastic in response to growth, then the pace of this decline should change, and at least theoretically it is possible for a species to escape organismal senescence (Vaupel et al. 2004). Any actions that alter growth or mortality patterns across the lifespan may therefore change natural selection associated with life history traits, such as the age at maturity, developmental rate, and mean lifespan.

The specific selective agents that have caused species to become of conservation concern may also determine

evolutionary response to conservation actions. For example, selection associated with changing climate is likely to yield a different evolutionary pattern than selection imposed by species invasions. In the former case, growth rates and vital rates may evolve to optimize to different temperature norms (Huey and Kingsolver 1989; Shefferson et al. 2017), while competitiveness or tolerance mechanisms may be favored by selection to counter the greater competitiveness of invasive species in the latter (Callaway and Ridenour 2004).

Finally, the type of conservation action used should also strongly impact evolution via natural selection (Table 1). We suggest that conservation actions on rare populations may alter selection by (1) decreasing age-specific mortality at key times of life, (2) increasing it at others via the direct effects of conservation protections on the biotic community and abiotic environment, (3) altering selection for tolerance mechanisms to experienced stresses, and (4) changing levels of genetic variation in the population. However, other evolutionary responses are most certainly possible.

Management actions are a diverse body of techniques. Given the general pathways in which they might affect the course of evolution, we believe that there are certain specific scenarios in which they are particularly likely to do so. First, management plans that involve relatively large changes in population size should affect the ability of natural selection to operate. A management plan that includes a large influx of immigrants from another population or connects previously unconnected populations will likely increase the effectiveness of natural selection, and alter the genetic variance present. Second, management focused on species with short lifespans should be more likely to cause rapid evolution in response to management, simply because more generations will experience the ecological consequences of the management technique within a shorter time. Third, management involving strong shifts in the environment should yield novel natural selection that changes evolutionary trajectories. For example, the removal of a dominant species from a community, or the creation of an artificial wetland, may both result in unpredicted responses to conservation management. These are three general situations of concern under conservation management scenarios.

Below, we hypothesize possible evolutionary outcomes in response to the most common changes to the kind, direction, and/or intensity of selection that might be experienced by populations under two commonly implemented, specific conservation management strategies, park creation and invasive species removal. We chose these two examples because we believe that they are the most widespread management techniques currently utilized, and so their ecological impacts are likely to be well-known to ecologists. We also include other examples in ESM S2, and summarize some possible evolutionary outcomes in

Table 1. The examples utilized in this paper are in no way meant to be an exhaustive list, but rather to showcase possible evolutionary scenarios in relatively commonly used management techniques. We particularly do not address management methods involved in some of the newest conservation problems, such as the restoration of pollination services (Dixon 2009), but we see no reason to believe that management techniques involved in those scenarios are exempt from evolutionary effects.

Park systems

Large parks, reserves, and regional park systems are effective tools for the conservation of rare species and ecosystems. Although parks protect natural habitat within them, they also often attract development in their periphery focused on eco-tourism (Fig. 2a). This development can surround the area protected by the park with towns and other human-altered land use types, and so the frequency of interactions between humans, park-inhabiting species, and other species in human-associated landscapes should increase (Mules 2005; DeFries et al. 2007). Parks are also often subject to intensive management regimes, for example fire management, grazing, and culling (Parsons and DeBenedetti 1979; White et al. 2011) (Fig. 2), and such management shifts generally change the structure of natural communities (Baker 1994).

The creation of a large park may alter selection in at least three ways (Table 1). First, for some species, parks may impose selection on dispersal at different scales. The imposition of political boundaries around a large wilderness area inevitably brings development that leads to an “island ecosystem” (Murphy 1983; Bultjens et al. 2005), and such development restricts dispersal via the elimination of suitable habitat, increased fragmentation, and reduced gene flow. Such changes may be expected to alter both the structure of the “habitable” environment across scales in ways that alter dispersal and hence community composition (Hubbell 2001; Rosindell et al. 2011), and in so doing also alter the fitness value of dispersal at particular scales (Baskett et al. 2007; Edelaar and Bolnick 2012). The disconnect between the spatial scales of dispersal and habitat protection, and the geographic range of the focal species, may favor altered dispersal rate or distance (Gandon and Rousset 1999). Landscapes with a mix of different suitability of habitats, as would be expected along an urban–rural gradient, are particularly expected to favor the evolution of dispersal to the regional scale (Henriques-Silva et al. 2015). If shorter-range dispersal becomes favored, selection may favor those genotypes more tolerant of more localized environmental stresses and variability (Blondel et al. 2006), and of intraspecific competition. Studies of populations of weedy plants dispersing onto islands support this hypothesis,

showing that older populations have evolved lower dispersal ability compared with younger populations (Cody and Overton 1996). The documented evolution of dispersal in fragmented landscapes also supports the importance of this phenomenon. For example, the bog fritillary butterfly has evolved altered dispersal behavior to yield straighter, faster flight paths in response to fragmentation within its range (Baguette and Schtickzelle 2006). And although dispersal is still possible for many species through urban zones (Lundberg et al. 2008), the spatial configuration of urban habitat and quality differences between urban and wild habitat still suggest different adaptive landscapes.

Eco-tourism may also select for more human-tolerant behaviors. Parks result in higher levels of interaction between wild organisms and people than would occur without both protection and development. When these interactions include hunting and foraging, then the removal of large adults will undoubtedly lead to the evolution of smaller size (Allendorf and Hard 2009). When these interactions exclude harvest, then the primary influence of humans on selection may come from proximity to lands exploited by humans, such as farms and towns. In the latter case, selection may favor novel behavior to exploit human foods and structures. Black bears (*Ursus americanus*) in northeastern Minnesota, USA, provide an example, as bears that eat human garbage as a food source reach first reproduction on average at half the age of those that do not (Rogers 1987). Such a strong shift in age at maturity may yield higher fitness associated with this behavior, leading to its spread. Although the behavioral change associated with this ecological shift is most likely due to learning and behavioral plasticity, nonetheless such plasticity may be evolutionarily reinforced and even canalized if the condition persists (Scheiner 2014).

Parks may also impose new selection related to more intensive management practices. Fire suppression for much of the history of the United States’ western parks has led to dense forests unlike those that preceded formal protection, and along with them decreased fire frequency and increased fire intensity (Parsons and DeBenedetti 1979). Such altered fire cycles have likely favored genotypes with a greater resistance to catastrophic fire, and with greater competitive ability at high densities (Bond and Midgley 1995). Prescribed fire may then lead to altogether different selection (Fig. 2c), for genotypes that respond more easily to low-intensity fires and have less competitive ability at higher densities.

Control of invasive populations

Invasive species are a primary cause of the decline and extinction of species, particularly on islands (Simberloff et al. 2013). Although there are numerous ways in which invasive species may contribute to extinction, it is likely

Table 1 Influence of 7 commonly used conservation actions on species ecology and evolution

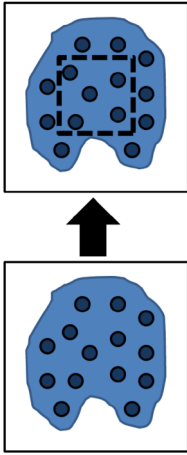
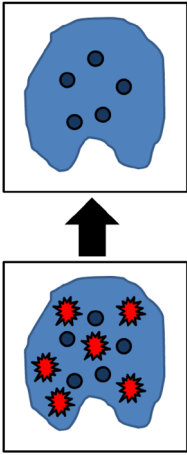
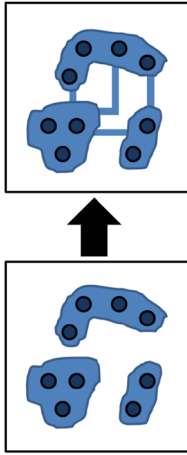
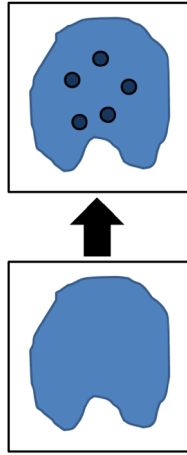
Conservation action	Goals	Potential unintended ecological effects	Potential evolutionary effects
<p>Park creation</p> 	<p>Preserve habitat Maintain population size</p>	<p>Altered dispersal Increased interaction with humans Increased management Altered succession and community assemblage</p>	<p>Reduced gene flow Selection for reduced dispersal capability Selection for human-tolerant behaviors in animals Novel selection due to community changes</p>
<p>Control of invasives</p> 	<p>Reduce impact of invasives on natives Restore habitat to pre-invasion conditions</p>	<p>Altered succession and community assemblage Altered predator-prey dynamics Increased management</p>	<p>Strong selection on invasives for resistance or escape from control efforts Selection on natives that have adapted to invasives Novel adaptive landscapes for natives post-eradication</p>
<p>Biological corridors</p> 	<p>Reduce effects of habitat fragmentation Increase dispersal and migration</p>	<p>Increased density of individuals in corridors Increased interaction with humans Altered predator-prey dynamics Increased disease spread</p>	<p>Increased gene flow Outbreeding depression Selection for altered behavior Selection for reduced dispersal Changes to disease tolerance or avoidance</p>
<p>Reintroduction of extirpated species</p> 	<ul style="list-style-type: none"> • Restore ecosystem function • Increase biodiversity 	<p>Altered succession and community assemblage Altered species interactions Altered abiotic environment</p>	<p>Novel selection on reintroduced species due to changes since extirpation Selection on other species due to changing conditions Impacts on the evolution of plant-microbe relationships Life history evolution resulting from altered mortality patterns</p>

Table 1 (continued)

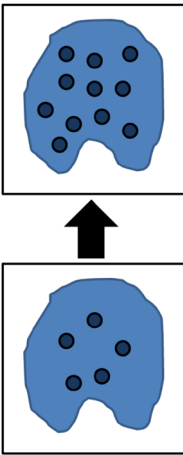
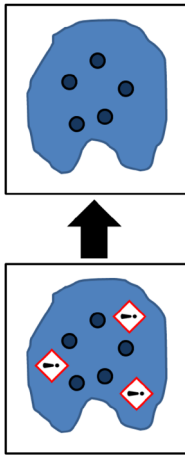

Conservation action	Goals	Potential unintended ecological effects	Potential evolutionary effects
<p>Reintroductions to existing populations</p> 	<p>Increase population census size Increase genetic diversity Reduce inbreeding depression</p>	<p>Increased intraspecific competition Increased density-dependent disease and predation</p>	<p>Reduced inbreeding depression Decreased chance of demographic collapse Increased diversity upon which selection can act Outbreeding depression</p>
<p>Bioremediation</p> 	<p>Reduce quantities and impacts of toxic substances in the environment</p>	<p>Altered succession and community assemblage Increased competition from non-natives Increased predation and herbivory on natives Altered ecosystem functioning</p>	<p>Selection against specialized tolerant natives Selection for loss of tolerance in natives Eco-evolutionary feedbacks due to loss of toxic substance Novel coevolution</p>
<p>Artificial wetlands</p> 	<p>Mitigate wetland loss Reduce impact of toxic substance on humans or environment Increase wetland habitat</p>	<p>Altered succession and community assemblage Increased competition from non-natives Concentrated toxicity Altered ecosystem functioning</p>	<p>Selection for tolerance to toxicity Selection for increased competitiveness under eutrophic conditions Eco-evolutionary feedbacks due to novel community structure and ecosystem function</p>

Fig. 2 Examples of commonly used conservation management practices. **a** Protection of the Mendenhall Glacier in the Tongass National Forest, Alaska, USA, has also resulted in some tourist development, including the creation of walking paths and roads (photo courtesy of Dr. Chase Mason). **b** Grazing maintains meadow communities in central Europe, such as this alvar meadow on Muhu Island, Estonia (photo courtesy of Dr. Kadri Tali). **c** Prescribed fire is a common technique used to maintain many kinds of communities in North America, such as this pine flatwoods at Archbold Biological Station, Lake Placid, Florida, USA (photo courtesy of Dr. Eric Menges). **d** Management for biodiversity commonly involves mechanical removal. Here, an intern uses a chainsaw to reduce canopy height of overgrown oaks in fire-suppressed Florida scrub at Archbold Biological Station, Lake Placid, Florida, USA (photo courtesy of Dr. Eric Menges)



that they have their most profound impacts via interspecific interactions with native species, and at least in some cases via large-scale modifications to habitat that make persistence more difficult for natives (Didham et al. 2005). Invasive species may impose selection on co-occurring populations of native species favoring changes in morphology or life history via increased competition (Mooney and Cleland 2001), or select for anti-predator behaviors if the invasive species represents a new source of mortality for the native (Strauss et al. 2006).

The management of invasive species is generally aimed at their eradication, with the hope of preserving populations of native species and restoring pre-invasion communities. Examples of techniques used in invasive species management include the use of pesticides to kill agricultural and silvicultural insect pests (Carrière et al. 1994), the use of herbicides and fire against invasive plants (Usher et al. 1986; Simmons et al. 2007), and the direct removal of animals and plants via hunting, trapping, and weeding (Usher et al. 1986; Aguirre-Muñoz et al. 2008) (Fig. 2). Such management strategies may be performed in conjunction with a restoration strategy aimed at altering the local community to a state more in line with what is deemed to be locally native, although restoration plans more and more reflect the

dynamic natures of the protected ecosystems (Hobbs and Harris 2001). Invasive species removal often has very positive impacts on native communities, but the success of this strategy is most likely when an invasion is still in its early stages and the ecological community has not been substantially altered by human activity (Jackson and Hobbs 2009). Communities with a long history of invasion or strong infiltration by invasive species may have unpredictable responses to management, because the invasive populations have already strongly altered the local community and even the abiotic environment (Zavaleta et al. 2001). Therefore, restoration efforts may actually result in novel communities, rather than the reconstruction of pre-invasion communities. Difficulty in predicting the course of community change in response to restoration means that managers need to sustain management efforts in the long-term, especially since the structure of the model community that managers seek to re-create may not be equilibrium.

Invasive management may have dramatic evolutionary impacts on native communities. Removal of invasive species is generally attempted in landscapes with large invasions, and the result can be a novel environment for the native species left remaining (Zavaleta et al. 2001). In such cases, rare species may encounter different selection after the

invasive harvest than occurred prior to invasion. For example, the removal of large stands of invasive shrubs or trees may result in the greater exposure of native plant species to herbivores, predators, and stressful conditions, leading to increased mortality. In this case, increased herbivory or predation may select for tolerance or escape mechanisms, and increased mortality across the lifespan may yield the evolution of a greater age at maturity if the force of natural selection declines with age, and if fecundity is strongly elastic in response to growth.

Invasive species may also respond evolutionarily to management against them. Invasive species generally begin with a bottlenecked population, but multiple introductions create great genetic diversity that increases the potential for adaptation in invasive populations (Kolbe et al. 2004). A standardized, commonly deployed eradication or harvest strategy against a uniquely large population would only result in more consistent selection for traits tolerant of the management strategy, just as wide application of antibiotics in hospitals and pesticides in agricultural landscapes has led to the evolution of antibiotic-resistant bacteria and pesticide-resistant insect pests (Baquero and Blázquez 1997) (Table 1). For example, the obliquebanded leafroller (*Choristoneura rosaceana*) initially evolved increased diapause fraction in response to the use of a suite of pesticides, and this diapause fraction has been predicted to decrease as biochemical mechanisms of pesticide resistance spread throughout the population (Carrière et al. 1995). Invasive species may similarly evolve tolerance to the management regimes imposed against them.

Research priorities and future directions

We believe that the challenge of understanding conservation-driven evolution can best be met if scientists and managers develop and coordinate research along three lines: (1) experimental tests of evolution under conservation, (2) management-oriented monitoring of ecological and evolutionary change, and (3) theoretical studies and empirical meta-studies designed to simplify the process of cataloging and predicting evolutionary change.

Experimental tests of evolution

Managers already commonly monitor the demography of populations, and these studies allow the life histories and population trajectories of populations of concern to be studied for management planning purposes (Beissinger 2002). However, monitoring protocols are generally not enough to infer that evolution has occurred, or will occur. Initial research needs to focus on the development of predictions of evolutionary change due to management, and experimental

tests of such predictions. Evolutionary ecologists and conservation biologists should first identify the target traits, kinds, direction, and intensity of natural selection caused by major management actions. This can be done via studies combining selection analyses and the estimation of genetic variance and heritability. Selection analyses generally measure it as selection differentials or gradients, where the former measure all selection on a trait as the shift in phenotype across generations, and the latter measure only direct selection on a trait as partial regression coefficients of relative fitness while accounting for indirect selection due to linkage with other traits (Brodie III et al. 1995). Selection differentials and gradients may be measured even with basic demographic data, yielding potentially powerful analyses of the potential for life histories to evolve (Shaw and Geyer 2010; Caswell and Shyu 2017), and path analysis allows the testing of competing causal models of selection (Brodie III et al. 1995). In the absence of genetic data, predictions may be based solely on selection analyses and established evolutionary modeling protocols, such as game theory (Shefferson et al. 2017).

In some cases, breeding studies may be conducted to address the genetic basis for variability in traits and the extent of plasticity, which can mimic evolutionary change across generations without any real heritable change. By measuring the heritability and norms of reaction of traits, breeding studies combined with selection analyses grant the potential to predict actual evolutionary change (Rodd et al. 1997; Reznick and Ghalambor 2005). In cases where breeding studies are not logistically feasible, heritability and other genetic parameters may be estimated from field-collected monitoring data if pedigrees are known and the number of monitored individuals is sufficiently high (Kruuk 2004). It is also possible that rapid advances in the analysis of genomic data may make the estimation of these parameters possible without breeding studies themselves, although substantial logistical and theoretical problems currently exist for broad applicability (Stanton-Geddes et al. 2013). Once predictions have been made and tested, then further experimental research may even explore the potential to counter, if possible, these artificial patterns in selection.

Management-oriented monitoring

The previous line of research is most likely to be conducted only on a small scale by practicing evolutionary biologists. Ultimately, evolutionary predictions will need to be compared to large-scale data from monitoring programs overseen by the agencies managing species and ecosystems of conservation concern. Currently, monitoring efforts generally focus on counts of individuals of species, and sometimes include proxy metrics for environmental quality. Longitudinal

monitoring of individuals is also sometimes conducted, particularly on rare species (Bowles et al. 2001; Alexander et al. 2012). We believe that the latter should be incorporated into all management-oriented monitoring programs, because particularly for species with long lifespans or overlapping generations, fitness cannot be properly estimated without accounting for individual history (Shaw and Geyer 2010). These efforts need to be applied consistently, to avoid errors in inference due to an incomplete understanding of temporal trends (Magurran et al. 2010).

Monitoring programs should also be expanded to include the measurement of traits likely to evolve, and to include other species in the community that are likely to experience management-induced selection. Target traits may include dispersal-related traits, feeding and mating behaviors, etc., and target species should include rare, common, and even invasive taxa. Trait monitoring would allow managers to make process-based evolutionary predictions, and to account for phenotypic and potentially genetic variation within populations and communities (Brodersen and Seehausen 2014). If such monitoring efforts are conducted widely enough and on enough different taxa, then even the hypothesis of convergent evolution in response to standardized management practices can be tested, and all traits might be included in analytical frameworks that can account for genetic correlations, trait linkage, and other potential constraints.

Theoretical and meta-analytical studies

Ultimately, the prediction of management-induced evolutionary change will need to be conducted on a broad scale, and this fact will require the development of a toolkit for managers to make such predictions. The development of such a toolkit requires not only experimental tests of evolutionary predictions and long-term monitoring programs, but also theoretical and meta-analytical study aimed at simplifying the process of evolutionary prediction in conservation systems. Theoretical research may also be conducted to develop workable models of evolutionary change (e.g., Carrière et al. 1995), and software or statistical packages may be developed to make complicated analyses more accessible (e.g., Stubben and Milligan 2007). Meta-analyses can focus on developing robust metrics that can be used as proxies for parameters that are difficult to estimate, such as heritability, and on assessment of evolutionary change in cases of management of applied at different spatial scales, such as nationwide vs. regional vs. local invasive species removal programs. Some of this literature is already available (e.g., Endler 1986; Riska et al. 1989), as are studies predicting evolution in conservation scenarios (e.g., Norberg et al. 2012; Williams et al. 2015; Shefferson et al. 2017; Bay et al. 2017), but not for conservation-specific management plans.

Conclusions

Over a century ago, the debate over the future of conservation was framed by the arguments of American conservationists Gifford Pinchot and John Muir, among others. Pinchot argued that nature should be conserved, and in so doing used by multiple interests in a sustainable manner (Meyer 1997). Muir argued that human influence on nature was generally harmful, and so nature should be protected. Increasing human density and its inevitable impacts on the natural world have led to a practical approach to conservation management similar to Pinchot's philosophy, as even wilderness areas show the impacts of human activity (Jackson and Hobbs 2009; Zalasiewicz et al. 2011). Indeed, it is difficult to imagine a corner of the Earth in which a species exists untouched by some human action. It is equally difficult to imagine that there is a species not influenced evolutionarily by humanity. Given the large area occupied and influenced by people, it is very likely that we are evolutionarily taming nature, whether we are aware of it or not. Darwin was aware of the strong evolutionary impact that people had on domestic plants and animals, and often framed his description of natural selection as an evolutionary mechanism by comparing it to artificial selection (Darwin 1859). It is therefore surprising that so little research has been focused on the evolutionary impact of conservation management.

We argue in this piece that conservation actions likely do have potentially strong and important evolutionary impacts and that they may not necessarily be in line with the goals of conservation plans. While we do not argue against conservation action in this paper, we do argue that more attention to the potential for evolutionary change is warranted in all actions that humans take on the environment, even when those actions are overall positive. It will take a great deal of effort on the part of evolutionary conservation ecologists and managers to work out the exact, practical methods to accomplish the goal of incorporating evolutionary considerations into conservation management, but we believe that empirical, quantitative research on evolutionary impacts of management is the most important, immediate first step to take.

We believe that tools are readily available to study altered selection. Monitoring of rare populations subject to management is commonplace. Analytical methods such as population matrix sensitivity and elasticity analysis, meta-population modeling, game theoretical simulations, individual-based evolutionary modeling, and selection analysis are well-developed and have been used to understand the evolution of countless traits of importance to conservation management. All that is missing now is the research.

Acknowledgements We would like to thank J. Byers, J. Drake, M.J. Hutchings, and three anonymous reviewers for providing constructive

critiques of this manuscript, and S. Lance for contributing to the discussion. We also thank E. Menges and K. Tali for providing photographs of management practices. The authors wish to report no conflicts of interest.

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