When Policy Shapes Selection:
Anticipating Evolutionary Feedbacks in Conservation

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Abstract

Applied ecology and conservation increasingly operate in systems where ecological and evolutionary processes are tightly coupled and can unfold on management-relevant timescales, yet most policy still treats populations as evolutionarily static. As a result, interventions often generate unintended outcomes, from resistance evolution and harvest-induced trait shifts to hidden losses of adaptive capacity under apparently stable management. We argue that conservation should be reframed as an evolutionary decision problem and propose Stackelberg evolutionary games (SEGs) as a framework for doing so. In SEGs, managers act as leaders who shape selective environments through policy, while populations and stakeholders respond as adaptive followers through ecological, behavioral, and evolutionary change. This framing makes explicit that conservation is not simply ecological control, but a strategic interaction with evolving systems. Through simple examples, we demonstrate how evolutionary rescue, evolutionary suicide, or hidden eco-evolutionary tipping points may arise depending on how interventions reshape fitness landscapes and how conservation objectives are formulated. Policies that stabilize population size in the short term may erode evolutionary stability and adaptability, whereas objectives that explicitly account for traits and their diversity can steer systems toward more robust long-term outcomes. SEGs provide a tractable framework for anticipating evolutionary feedbacks and designing conservation policy that works with, rather than against, evolution.

Introduction

Evolutionary change in natural ecosystems is ubiquitous, rapid, and increasingly policy-relevant. A large body of work in evolutionary ecology and eco-evolutionary theory has shown that traits affecting growth, reproduction, behavior, and resource use can evolve on timescales comparable to ecological dynamics[1–6]. These insights have reshaped our understanding of population persistence, community structure, and responses to environmental change[7]. Recent work further demonstrates that when environmental change is driven by governance, markets, or management decisions, evolutionary responses are not merely background processes but endogenous reactions to policy itself[7,8]. In such contexts, adaptation becomes part of the policy response, affecting both ecological outcomes and the effectiveness of interventions.

Yet evolutionary processes remain only weakly integrated into conservation decision-making[7,9,10], partly because of the lack of workable frameworks and the complexity of ecological dynamics from theoretical and empirical views even in the absence of evolutionary considerations[7,9,11–14]. In practice, evolution is typically treated either as a background process or as a constraint, represented through indirect or retrospective indicators such as genetic diversity thresholds, inbreeding risk, or minimum viable population sizes[15–18]. Management targets, by contrast, focus primarily on ecological state variables: population abundance, recovery targets, harvest limits, or habitat extent[10], which is often driven by other relevant constraints[19–21]. Although rapid evolution under anthropogenic pressure is well documented[8,22–24], conservation policy and management continues to be designed with the implicit assumption of evolutionary stasis. This is consequential: when trait change feeds back into demographic rates, resource use, stakeholder behavior, or ecological dynamics, the policies we design may cause unintended evolutionary feedbacks that amplify, rather than mitigate, the pressures we seek to manage. As one example, it was recently suggested that calibrated ecosystem models fail to predict ecosystem reaction to a disruptive change[25]; this problem may be compounded by the propensity of ecosystems to undergo abrupt, potentially irreversible shifts between alternative stable states[26] - transitions that eco-evolutionary feedbacks may accelerate. When managing complex evolving ecosystems, the policies we adopt should aim to anticipate and steer eco-evolutionary dynamics in ways that mitigate or take advantage of our actions as a force of natural selection. For instance, we should ask, will evolution make it easier or harder to control and manage a particular species or ecosystem?

The consequences of ignoring rapid evolution in response to human activity and human-dominated landscapes are well documented[27,28]. Resistance to pesticides and herbicides[29–36], harvest-induced life-history changes in fisheries[22,24,37], and trait erosion under habitat degradation[3,23,38–40] are often framed as unintended side effects of management (**Fig. 1A**). Yet, these outcomes follow directly from evolutionary principles: by altering mortality, resource availability, predator-prey systems or competitive interactions, policies reshape selection gradients and fitness landscapes[41]. Populations respond to these incentives, adapting to the structure of management rather than to its stated objectives[42]. Conservation thus becomes a dynamic interaction between managers (leaders) and populations (followers): a feedback process in which policy modifies the selection pressure, and evolutionary responses modify conservation and policy outcomes.

Eco-evolutionary feedbacks are only part of the challenge. Conservation interventions rarely act directly on populations; instead, they are mediated through institutions, stakeholders, and management decisions that shape how ecological systems are used. Policymakers set constraints and incentives; end-users of the policy are often strategic and can anticipate management decisions[9,43,44]; and populations evolve in response to the resulting ecological conditions and selective pressures shaped by management decisions[12,24,45]. Hard experience has taught conservation decision-makers that these evolutionary changes can undermine, or even reverse, the expected benefits of a conservation investment[46–48]. From this perspective, conservation is not simply an ecological optimization problem but a dynamic decision problem in which evolutionary change should be included as an anticipated response[42,49,50]. In this sense, conservation is inherently hierarchical: policymakers shape incentives, stakeholders respond behaviorally, and populations respond adaptively (**Fig. 1B,C**). When adaptation is treated as endogenous rather than exogenous, policy evaluation must account for how interventions shift trait distributions, alter demographic feedbacks, and potentially generate eco-evolutionary tipping points.

Modern conservation has become increasingly effective at stabilizing and even restoring populations in the short term, but not necessarily at preserving their adaptive capacity[51–53], with a few exceptions of rescues informed by evolutionary theory[54–59]. Ecological stability can mask reduction in adaptation potential as management suppresses trait variation and lowers the ability of populations to respond to future perturbations[60–67]. The central challenge of conservation is not preventing evolution, but designing interventions that shape evolutionary feedbacks that foster long-term persistence. Although conservation genetics, adaptive management, and emerging eco-evolutionary applications have begun to incorporate evolutionary processes into decision-making (recently reviewed in [7]), these approaches remain only partially integrated and rarely provide predictive frameworks for anticipating evolutionary responses.

To illustrate this point, we consider a simple thought experiment in which managers control the amount of area allocated to the wild population of species[68–70] versus that directed towards humans, their crops or livestock[71]. By reducing the area allocated to the ecosystem, managers reshape selection pressures potentially driving rapid evolution whose direction depends on the underlying ecological feedbacks **Fig. 2**. As we show, this can produce qualitatively different outcomes: depending on the fitness landscape and structure of the evolutionary trade-off, evolution may rescue the population or push it towards extinction, generating management-induced eco-evolutionary tipping points. Small changes in policy structure can therefore determine whether species adaptation stabilizes or destabilizes the system. This example of how natural selection may act on populations or species subjected to habitat degradation underscore a broader message: conservation policies reshape evolutionary incentives. In doing so, they generate feedbacks that can stabilize, destabilize, or fundamentally reorganize ecological systems. **Fig. 1** provides a conceptual overview of this process, contrasting purely ecological management with approaches that explicitly anticipate adaptive responses, illustrating where intervention points lie within eco-evolutionary feedback loops.

We argue that conservation should therefore be framed explicitly as a decision process that includes both ecological and evolutionary consequences (**Fig. 1B**). Governments and agencies act as leaders who define the selective environment through regulation, subsidies, access rules, or habitat manipulation. Strategic end-users (stakeholders) anticipate and respond to these decisions. Evolving populations respond eco-evolutionarily as followers (**Fig. 1C**). Effective policy must anticipate evolutionary responses, embedding eco-evolutionary feedbacks directly into optimization and risk assessment frameworks. This hierarchical structure can be formalized, as we show in the present work, by a Stackelberg evolutionary game (SEG)[42,50], in which a leader chooses a strategy anticipating the response of followers.

By adopting this perspective, conservation moves beyond reacting to evolutionary "side effects" and toward designing interventions that shape evolutionary trajectories themselves. Doing so requires formal tools capable of (i) forecasting trait change under alternative policy regimes, (ii) identifying extinction boundaries and tipping points generated by eco-evolutionary feedback, and (iii) distinguishing interventions that enhance long-term evolutionary resilience from those that merely stabilize ecological states temporarily. Developing and operationalizing such tools is essential for managing adaptive systems in a rapidly changing world, and here we propose and demonstrate one such tool, a framework grounded in SEG, that provides a basis for addressing these challenges.

Shaping evolution through resource management

Conservation and resource management often prioritize ecological stability, understood as low variability in population sizes or qualitative ecosystem states[10]. While desirable in the short term, such stability does not guarantee evolutionary resilience, i.e. the capacity of populations to adapt to future environmental change[42,50]. In eco-evolutionary systems, these properties may diverge: minimizing variance and enforcing a single attractor can suppress response diversity and adaptive capacity, the very processes that underpin resilience[72–74]. One mechanism underlying this mismatch is constraint on effective system capacity, such as reductions in energy, resource availability, or habitat extent. Declining capacity lowers carrying capacity and population sizes, often producing deceptively stable, low-variance dynamics while simultaneously tightening demographic and evolutionary constraints. Small populations experience stronger genetic drift and reduced ability to respond to selection, making them increasingly brittle precisely when adaptation is most needed[60,75]. Under such conditions, management can reshape fitness landscapes to produce evolutionarily stable states (ESSs; **Box 1**) that are locally robust but globally fragile, suppressing trait variation. A key early-warning signal is the collapse of invasion potential: an invasion window exists when a mutant with a different trait value has positive fitness in a resident population. As management actions progressively constrain the system, invasion windows shrink, reducing the range of viable strategies, signaling a contraction of the adaptive landscape and pushing systems toward eco-evolutionary tipping points beyond which recovery or evolutionary rescue becomes unlikely.

To formalize this mechanism, we consider a simple thought experiment. In many conservation and resource-management contexts, managers do not act directly on traits or demographic rates. Instead, they regulate effective system capacity through habitat, resource availability, harvesting pressure, or disturbance regimes. We capture these interventions using a single control parameter, E, representing the energetic conditions required for persistence. Population growth depends on whether E exceeds a critical threshold[71]. However, here we construct a thought experiment in which we assume that this critical threshold is trait-dependent so that management actions on the ecological environment simultaneously shape the fitness landscape, indirectly affecting both ecological and evolutionary dynamics.

The effect of energy availability on system adaptability can be captured through evolutionary trade-offs that give rise to either rescue or suicide (**Fig. 2**, **Box 1**). In rescue scenarios (**Fig. 2A**), adaptive trait change restores positive growth following environmental deterioration. In suicide scenarios (**Fig. 2B**), selection drives traits in directions that ultimately undermine persistence, leading to extinction despite ongoing adaptation. These outcomes arise from differences in fitness landscape structure (**Fig. 2C**), which determine whether adaptive trajectories guide populations toward viable regions of trait space or toward extinction boundaries. Viewed through the corresponding stability landscapes (**Fig. 2D**), evolution reshapes attractors and persistence basins, altering long-term viability. Crucially, adaptation does not necessarily enhance resilience; management interventions can determine which regime dominates. As a result, environmental change or management actions that alter underlying trade-offs may push systems toward extinction even when adaptive responses are present. Conversely, even when evolutionary rescue is possible, persistence depends on whether eco-evolutionary trajectories remain within viable regions of state space[76].

We illustrate this mechanism using a minimal eco-evolutionary model within the fitness-generating function framework (**Box 1**)[41]:

$$G(v,u,x) = r(u)\left(1-\frac{x}{K}\right)\left(\frac{E-E_c(v)}{E_c(v)}\right) - d\,\Big|_{v=u}, \tag{1}$$

with dynamics

$$\dot{x} = x\, G(v, u, x), \qquad \dot{u} = \sigma \frac{\partial G(v, u, x)}{\partial v} \Big|_{v=u}. \tag{2}$$

Here, $r(u)$ is the effective growth rate, K the carrying capacity, d the death rate, $E \in [0, 1]$ is the manager's control, $E_c(u)$ is the trait-dependent critical threshold, u is an evolving trait, and σ determines the speed of evolution. Here, we treat $E = 0$ as the poorest environmental conditions or zero area being allocated to the wild populations, while $E = 1$ is the highest quality environment with the pristine reserve area. Note that K is treated as a constant in this minimal model, with management acting exclusively through E. A more general formulation would allow K to depend on E directly.

We assume a simple trade-off,

$$r(u) = r_{\max} e^{-gu}, \qquad E_c(u) = \frac{a}{b + u}, \tag{3}$$

where $r_{\max}$ is the maximum growth rate, $g > 0$ determines the reproductive cost of the trait and $a > 0$ and $b > 0$ determine the rate at which the tolerance to energetic stress increases (lower E_c) with increasing trait value u. This trade-off can also be incorporated in the carrying capacity (which leads to evolutionary suicide) by making it a similar function of u, for example, $K(u) = K_{\max} e^{-gu}$.

This captures a general class of life-history trade-offs observed in managed systems, where adaptation to stress or exploitation comes at a cost to growth or reproduction. Whether this reshaping stabilizes or destabilizes the population (evolutionary rescue or suicide) depends on the combination of manager's choice of E and the structure of the trade-off, as illustrated in **Fig. 2**.

Biological interpretation of the energy constraint

To relate this abstract formulation to real systems, we interpret the control parameter E and trait u in biological terms. Here, E represents a measure of effective system capacity, capturing the ecological conditions required for persistence. In conservation contexts, reductions in E arise from habitat loss and fragmentation, declining resource availability, altered disturbance regimes, or direct anthropogenic mortality[71]. Similar abstractions have been used to study evolutionary responses to harvesting, pesticide application, and environmental degradation, where human actions modify the ecological conditions on which selection operates[32,77,78]. The evolving trait u represents a class of persistence-related adaptations that improve performance under deteriorating conditions (as E decreases), but incur demographic or competitive costs. Across systems, such traits take diverse biological forms, yet share a common functional role which we discuss below.

A first class of examples concerns dispersal and spatial strategies. Fragmentation and patchiness consistently select for increased dispersal ability, colonization capacity, or altered movement behavior. Experimental work demonstrates that plants such as *Arabidopsis thaliana* can evolve increased height and dispersal within a few generations under spatially heterogeneous environments[5], while fish populations subject to habitat fragmentation and altered connectivity exhibit rapid evolution in migration timing, morphology, and life-history traits[79]. While such traits enhance persistence across fragmented landscapes, they typically reduce competitive performance within local habitat patches.

A second class involves life-history and physiological adaptations to resource limitation. Under declining resource availability, selection may favor earlier maturation, greater investment in survival and maintenance, or broader niche breadth[80,81]. Such strategies enhance persistence under energetic stress but typically reduce maximum reproductive output. Similar trade-offs arise in resistance evolution, where tolerance to pesticides or antibiotics increases survival but often carries metabolic or demographic costs[32,78].

A third class of examples comes from systems that mimic reductions in effective habitat or resource base. Island systems provide a well-studied analogue: mammals such as *Mus musculus* evolve substantial changes in body size over relatively short timescales[82–84], while reptiles such as rattlesnakes exhibit coordinated shifts in body size and venom characteristics[85]. Urban environments show comparable, though mechanistically different, evolutionary responses, including changes in body size and life-history traits[86]. Across these systems, adaptation is driven by constrained resources and altered competitive environments.

Despite their biological diversity, these examples share a common structure: adaptation to constrained or degraded environments favors traits that improve persistence under stress while reducing reproductive output or competitive ability. This trade-off is captured in the model by the joint dependence of growth rate $r(u)$ and persistence threshold $E_c(u)$ on the evolving trait (Eq. 3).

Thus, as environmental conditions deteriorate (declining E), selection favors higher values of u, allowing populations to persist under lower effective resource availability. However, this adaptation comes at a demographic cost, reducing growth rates or competitive strength. Evolution can thus buffer the effects of environmental degradation, but only within limits set by the underlying trade-off structure. This interpretation highlights that the model is not tied to a specific trait or disturbance type, but captures a general class of eco-evolutionary responses to anthropogenic effect. Because adaptation modifies the conditions for persistence, it also alters the system's response to perturbations. This provides a direct link to resilience: if both ecological conditions and evolving traits determine persistence, then resilience must be understood as an emergent property of their interaction. This motivates a closer examination of how evolutionary processes modify classical notions of resilience.

Evolutionary adaptation as resilience

Ecological resilience has become a central concept in conservation, referring to the capacity of systems to absorb perturbations and recover without shifting to alternative states[26,87]. For example, the 2022 Kunming-Montreal Global Biodiversity Framework couples species-centric targets with actions to restore ecosystem stability, connectivity, and resilience[7,88]. This perspective is commonly framed in terms of stability landscapes, where ecosystem dynamics are visualized as movement within basins of attraction shaped by external conditions such as resource availability, disturbance, or management interventions.

In simple settings, such landscapes can be represented by a potential function $V(x, E)$, where x denotes population size and E external conditions[89,90]

$$V(x(t), E) = -\int_0^{x(t)} \dot{y}(y(t), E)\,\mathrm{d}y + C \tag{4}$$

where V is the potential energy in the stability landscape, y represents population size x in the integrand (for notational clarity), and C is an arbitrary constant (that may be set conveniently, e.g. to ensure that $V \geq 0$). Local minima of $V(x, E)$ with respect to x correspond to stable ecological states x^*, and the landscapes $V(x, E)$ versus x are often illustrated as "ball-in-cup" diagrams. However, changing the external conditions E changes the shape of the stability landscape, which in turn changes the location of the local minimum of V that the population size x stabilizes at[26,91].

Within this framework, management is typically understood to act by modifying external drivers and thereby reshaping the stability landscape. However, most resilience-based approaches implicitly assume that the landscape is determined by these external conditions and thus remains fixed if external conditions do not change. This assumption breaks down when traits evolve. In eco-evolutionary systems, populations do not simply move within a fixed landscape. They reshape it. As traits change over time, the stability landscape becomes a function of both environmental conditions E and evolving traits $u(t)$. For notational simplicity, we write population dynamics as $x(t)$, while noting that ecological trajectories are themselves coupled to and therefore implicitly determined by trait dynamics $u(t)$:

$$V(x(t), u(t), E) = -\int_0^{x(t)} \dot{y}(y(t), u(t), E)\,\mathrm{d}y + C \tag{5}$$

Evolution therefore alters not only the position of equilibria, but also the structure of the landscape itself, including the depth and location of attractors (see **Fig. 2D**). This perspective extends resilience thinking by recognizing that adaptive responses are not only responses to the landscape, but drivers of its transformation. As a result, resilience is not solely determined by external conditions, but emerges from the interaction between ecological dynamics, evolutionary change, and management actions. From a conservation perspective, this has important implications. Policies designed under the assumption of fixed system dynamics may fail if evolutionary responses alter the underlying landscape, as not accounting for evolution of systems may lead to suboptimal management decisions[92]. More importantly, management actions that shape resource availability also shape the evolutionary trajectories that determine future resilience. In this sense, conservation does not simply preserve resilience. Instead, it actively shapes it through its influence on evolution. This provides a mechanistic explanation for the mismatch between ecological stability and evolutionary resilience discussed above.

From density dependence to frequency dependence

An additional layer of complexity arises when selection is frequency dependent. The model above considered selection in a density-dependent setting, where population regulation acts through carrying capacity and trait evolution affects demographic properties directly. In that case, the ESS is described by a single optimal trait value whose location shifts with environmental conditions. Selection operates primarily through how trait change modifies growth, mortality, or persistence thresholds[93].

In many biological systems, however, selection is also *frequency dependent*[94]: the fitness of a focal phenotype depends not only on the environment and total abundance, but also on the trait distribution of its competitors. This introduces an additional feedback, because trait evolution changes the competitive environment, which in turn reshapes selection. As a result, eco-evolutionary equilibria need not correspond to a single dominant strategy; depending on the environment, multiple strategies may coexist, invasion windows may widen or collapse, and trait branching may occur[95–97].

To capture this effect, we extend the model by allowing the interaction to depend explicitly on trait differences:

$$G_i(v, \mathbf{u}, \mathbf{x}) = r(v)\left(1 - \frac{\sum_{j=1}^{n} x_j\,\alpha(v, u_j)}{K}\right)\left(\frac{E - E_c(v)}{E_c(v)}\right) - d\,\Big|_{v=u_i}, \tag{6}$$

where $\alpha(v, u_j)$ is an asymmetric Gaussian interaction kernel describing how strongly a focal trait v competes with trait u_j and $\alpha(v, v) = 1$[41]. As before, E denotes effective resource availability and $E_c(v)$ the trait-dependent persistence threshold. The trade-off remains the same: higher trait values reduce reproductive output but lower the minimum resource requirement for persistence.

Under frequency-dependent selection, the relationship between effective resource availability and eco-evolutionary equilibrium changes qualitatively. Under high effective resource availability (rich environment, high E), the fitness landscape becomes broader and more permissive, so that a wider range of traits can invade and persist. This supports multiple coexisting strategies or branching trait distributions (**Fig. 3E, 3G, 3I**). During the transient approach to each new ESS, invasion windows remain open

(**Fig. 3D, 3F, 3H**), allowing additional strategies to invade. These windows close only once a new species establishes and occupies the newly available peak in the adaptive landscape. In poorer environments (low E), by contrast, the landscape contracts - invasion windows narrow, coexistence becomes less likely, and the system is driven toward fewer viable strategies. This shift has direct conservation implications. Environments with higher effective resource availability can support not only larger populations, but also greater phenotypic or species diversity, because more of trait space remains viable. As resource availability declines, the loss of abundance is accompanied by a loss of adaptive options (**Fig. 3**). Frequency dependence therefore makes clear that management actions can reshape not only equilibrium population size, but also the breadth of evolutionary possibilities available to the system.

These observations complicate the interpretation of eco-evolutionary equilibria for conservation. Management actions do not only determine which traits are optimal, but also how many adaptive pathways remain viable. In the following section, we explore the implications of this dependence of evolutionary outcomes on management actions for conservation decision-making.

Implications for conservation in evolving systems

Building on the thought experiment described above, the dependence of invasion windows and coexistence on resource availability has direct implications for conservation management. When space, resource, or energy availability is high, fitness landscapes are relatively permissive: multiple trait values coexist, invasion windows are broad, and phenotypic and ecological diversity can be maintained (**Fig. 3**). In this regime, selection tends to be weakly directional and adaptive capacity is high.

As resource availability declines through habitat loss, harvesting, or disturbance, the fitness landscape contracts. Invasion windows narrow, selection becomes strongly directional, and the system eventually converges toward a single ESS. Although such systems may appear stable, with reduced variability and increasingly predictable dynamics, this apparent stability reflects the loss of alternative adaptive pathways rather than increased robustness. Populations become increasingly sensitive to further environmental change as alternative strategies disappear. From a conservation perspective, this creates a risk of *over-stabilization*. Policies that constrain resource availability may successfully reduce short-term variability while simultaneously eroding the evolutionary pathways available to populations. The result is a system that is ecologically stable but evolutionarily brittle.

Current conservation practice has begun to address these challenges, but only partially. Much of management remains organized around static targets. Yet ecological systems can shift among alternative regimes, exhibit hysteresis, and respond nonlinearly to disturbance, so that stability does not guarantee resilience[26,72,73]. Adaptive management[98–102] represents an important step forward by incorporating uncertainty and learning into decision-making. By iteratively updating decisions based on observed outcomes, it allows managers to respond to ecological changes and the consequences of their decisions on these changes, to potentially reduce unintended consequences. However, most adaptive frameworks remain focused on ecological state variables and short-term responses, rather than explicitly anticipating how management actions reshape selection pressures and evolutionary trajectories, with a few exceptions[103,104]. As a result, even adaptive policies may respond to evolutionary change only after it has occurred, rather than guiding it proactively.

A similar limitation arises in conservation genetics, which has rightly emphasized maintaining genetic variation, yet commonly used measures such as neutral genetic diversity may not be reliable indicators of adaptive capacity or extinction risk[60,75,105]. The assumption is that populations with low genetic diversity will suffer inbreeding and low capacities to evolve to changing circumstances. There are important examples of inbreeding depression threatening populations such as the Florida panther[106].

An extreme case involves the Australian shrub *Muehlenbeckia tuggeranong* where just a handful of individuals exist in the wild and in a botanic garden[107]. In this case coddling each individual and carefully assessing and managing their breeding becomes essential. Yet there is more to evolutionarily informed management than maintaining genetic diversity. Many small populations thrive despite low genetic diversity[108]. Furthermore, the rapid adaptive evolution of invasive species, urban invaders[109], and island populations[110] shows that natural selection happens and can be expected even in species having experienced bottlenecks[111]. Anolis lizard introductions and recent invasions on Caribbean islands show the extent to which a small inoculum of individuals leads to rapid behavioral and morphological evolution often leading to species coexistence[112].

Taken together, these limitations reveal a common blind spot: conventional conservation frameworks tend to monitor ecological state, update policy reactively, and use static genetic proxies, yet rarely evaluate how management actions reshape the selective processes that determine future adaptive capacity. What matters for long-term persistence is not only where a system is, but how it responds to current and future change. This motivates a shift toward decision frameworks that explicitly account for eco-evolutionary feedbacks and the dependence of evolutionary outcomes on management actions. In the following section, we introduce such a framework by treating conservation as a strategic interaction between managers and evolving populations.

Evolutionary management as a strategic interaction

Management actions do not act on populations in isolation: they reshape the selective environment to which species respond. As a result, conservation operates as a strategic interaction between managers and evolving populations. This interaction can be formalized using Stackelberg evolutionary games (SEGs, see **Box 2**), in which a leader (a policymaker) anticipates the eco-evolutionary responses of species when choosing interventions[31,49].

Within this framework, the manager selects control variables $\mathbf{m}$ to optimize an objective function

$$\max_{\mathbf{m}} Q(\mathbf{m}, \mathbf{u}, \mathbf{x}), \tag{7}$$

where $\mathbf{x}$ denotes population size and $\mathbf{u}$ evolving traits. Crucially, the leader's decisions reshape selection pressures, while species respond by adopting fitness-maximizing traits. This interaction distinguishes three qualitatively different management regimes: naive strategies that ignore both ecology and evolution and employ a fixed control (**Fig. 1B(i)**), ecologically informed strategies that account for population dynamics but neglect evolutionary consequences (**Fig. 1B(ii)**), and evolutionarily informed strategies that explicitly account for eco-evolutionary feedbacks (**Fig. 1B(iii)**). In hierarchical settings, evolutionarily informed strategies weakly dominate the others in terms of long-term system performance[31].

SEG-based approaches have been applied to a limited number of systems, including cancer therapy, resistance management in agriculture, and fisheries management[49,113,114]. These studies demonstrate that anticipating evolutionary responses can fundamentally alter optimal policies, often favoring moderate or heterogeneous interventions over aggressive control. However, existing theory remains restricted to highly simplified settings, typically involving scalar traits, single control variables, or steady-state analysis[42]. More generally, eco-evolutionary models suitable for evolutionarily informed management, particularly those capturing trait distributions, multiple feedbacks, and transient dynamics, remain underdeveloped.

Objectives as a design problem. As a concrete continuation of the land-use example developed above, we consider the same stylized SEG setting in which the manager controls the fraction of habitat conserved, $E \in [0, 1]$. For each choice of E, the eco-evolutionary system settles into an equilibrium defined by a corresponding ecological and eco-evolutionary state. The manager does not select these states directly, but instead influences which equilibrium emerges by shaping the policy environment under which populations respond.

This makes the objective function a design problem rather than a purely technical one. In conservation settings, managers rarely optimize a single quantity. Instead, objectives are typically composed of several components reflecting competing priorities: the economic value of converted land, the ecological value of biomass or abundance, the persistence of species at viable densities, and the maintenance of traits or strategies that support future adaptation. Which of these components are included, and how strongly they are weighted, determines which eco-evolutionary states are treated as desirable and which are effectively ignored.

For notational simplicity, we write the management objective as a function of the control alone, with the dependence of each component on ecological and eco-evolutionary state variables left implicit through their equilibrium responses to $\mathbf{m}$

$$Q(\mathbf{m}) = \sum_i c_i \, q_i(\mathbf{m}), \tag{8}$$

where each q_i captures a distinct management priority and each weight c_i reflects its relative importance. Here, each component q_i may depend on different subsets of ecological and evolutionary variables, but all are evaluated through the eco-evolutionary state induced by $\mathbf{m}$. This formulation emphasizes that conservation objectives are not neutral descriptions of system performance, but explicit statements of preference over ecological and evolutionary outcomes.

From biomass-based to biodiversity-aware objectives. The simplest objectives prioritize aggregate biomass or abundance while balancing these against the economic value of land conversion (for example, see[115]). Such objectives are common in resource management and implicitly assume that ecological value is well approximated by total biomass. Under this view, populations with similar biomass are treated as functionally equivalent, even if they differ substantially in species composition, trait structure, or long-term adaptive potential.

This property has important consequences. In particular, biomass-based objectives cannot distinguish between eco-evolutionary states that maintain similar aggregate biomass but differ markedly in the diversity of strategies they support (**Fig. 3A**). As a result, systems with comparable biomass may be treated as equally desirable even when one retains multiple adaptive pathways and the other has already collapsed onto a narrower and more fragile subset of strategies (**Fig. 3I vs 3H** for example). In effect, biomass-based objectives flatten managerial preferences across ecologically distinct states, creating a structural mismatch between management incentives and biodiversity conservation. This mismatch is most apparent in the frequency-dependent case, where communities with similar biomass can differ in the number of coexisting strategies and therefore in their long-term adaptive potential (**Fig. 4C, 4F**).

A biodiversity-aware objective alters the tradeoff faced by the manager by assigning explicit value to dimensions of the system that biomass alone cannot capture. These may include the number and relative abundance of species, the persistence of species above viability thresholds, and the maintenance of functional or life-history diversity. Once these components enter the objective, ecological states that were previously indistinguishable become differentiated, and policies become sensitive not only to how much biomass is maintained, but to how that biomass is distributed across species and strategies. In the frequency-dependent setting, this allows the manager to distinguish between otherwise similar biomass outcomes that differ in coexistence structure and abundance of evolutionary pathways (**Fig. 4C, 4F**).

Accounting for evolutionary structure. Even biodiversity-aware objectives may remain evolutionarily incomplete if they account only for ecological properties of the system (see **Box 2**). When evolutionary responses are expected, managers must also account for the traits under selection. This can be done by incorporating explicit measures of trait structure into the objective, such as the mean trait value, the spread of trait values, or the diversity of coexisting strategies.

The choice of trait component depends on the management context. In some systems, managers may wish to avoid extreme trait values associated with maladaptive or risky strategies, as in the density-dependent case where trait values shift toward the viability boundary. Particularly, as E declines, selection favors traits that improve energetic stress tolerance (lower E_c), which comes at the cost of a lower reproductive rate due to the trade-off (**Eq. 3**), allowing the population to persist at lower E than it otherwise could. However, this lowered growth rate lurks dangerously close to the viability boundary and if E is reduced even slightly, the population may be pushed to extinction (**Fig. 4A**, **4D**). In others, the goal may be to preserve trait variation because it sustains alternative adaptive pathways and increases resilience to future change, as in the branching regimes generated by frequency-dependent selection (**Fig. 3**) and the multi-trait equilibria shown in **Fig. 4C** and **Fig. 4F**. More generally, incorporating trait structure into the objective allows the manager to distinguish between ecological states that are similar in abundance but differ markedly in their evolutionary richness.

Selection mechanism. The consequences of objective design depend critically on the selection mechanism through which populations respond. The same objective can induce very different outcomes depending on whether selection is primarily density dependent or frequency dependent.

Under density-dependent selection, trait change is driven largely by how environmental conditions alter demographic trade-offs. In this setting, incorporating trait information into the objective can steer management away from equilibria that are ecologically attractive but evolutionarily brittle. In our example, an evolutionarily informed (evo-aware) Stackelberg leader is less likely than an ecology-focused (eco-aware) manager to select policies that maximize profits while pushing the population toward the edge of viability (**Fig. 4A, 4D**). Here, anticipating trait responses acts as a safeguard against over-stabilizing the system in ways that reduce adaptive capacity.

Under frequency-dependent selection, however, fitness depends on interactions among individuals, trait values respond not only to environmental change but also to the trait composition of the population itself. As a result, the direction of selection can differ qualitatively from the density-dependent case (compare **Fig. 4A, 4D** with **Fig. 4B, 4E**), and management strategies that appear evolutionarily effective under one mechanism may become counterproductive under another. This makes the value of evolutionary information conditional on correctly identifying the process generating selection.

Frequency dependence also creates a further complication: it can generate branching and coexistence among multiple strategies, opening several distinct evolutionary pathways (**Fig. 3**). In such cases, managing for a particular trait value may be less informative than managing for the diversity of traits itself. Objectives that reward trait diversity can therefore preserve a broader adaptive portfolio, maintaining multiple evolutionary options and reducing the risk that management channels the system toward a narrow and fragile eco-evolutionary state (**Fig. 4C, 4F**).

Implication of SEG predictions for conservation policy. The key implication is that conservation outcomes depend fundamentally on how the manager's objective values different eco-evolutionary states. Biomass-based objectives generate profit profiles that are largely insensitive to biodiversity loss, allowing communities to erode toward low-diversity equilibria without altering the perceived value of management outcomes. By contrast, biodiversity-aware objectives reshape the manager's preferences, rewarding states that maintain multiple species and diverse life-history strategies.

In a SEG, the objective function is not merely a tool for evaluating outcomes, but a mechanism for shaping them. By specifying how ecological and eco-evolutionary states are valued, managers can influence the selective pressures acting on populations and thereby steer evolutionary trajectories. Decisions that appear optimal under biomass-based objectives may become suboptimal once biodiversity and evolutionary structure are explicitly incorporated. More broadly, this perspective reframes conservation as a problem of designing objectives that induce desirable eco-evolutionary responses. Rather than reacting to evolutionary change after it occurs, managers who use evolutionarily informed objectives can actively guide adaptation toward states that support long-term resilience, coexistence, and functional diversity.

Beyond conservation: controlling invasive species

In many conservation settings, the objective is not just to preserve but to eliminate invasive species. Invasive species management provides a useful counter-example to the previous conservation settings as it highlights the broader applicability of the SEG framework. When controlling invasive species, managers face a trade-off between eradication and stabilization[116,117]. In principle, complete eradication is desirable, but in practice it is only achievable in geographically bounded systems such as islands, where reinvasion risk is low and abundance data is of high quality[118,119]. Here, fast intensive interventions can drive invasive populations to extinction before substantial evolutionary responses occur (see for example[120]). Even when successful, these efforts can be expensive, time consuming and intrusive. For example, in the Channel island deer mice case, native individuals were collected and maintained in captivity until rodenticide applications had cleared islands of invasive rodents[121], an intervention feasible only under the relatively small spatial conditions that made eradication possible.

In contrast, at continental scales, complete eradication is rarely feasible due to spatial heterogeneity, poor detection data, and repeated reinvasion[122]. Here, high-intensity control strategies can induce rapid evolutionary responses, including resistance to pesticides or other control measures, increased reproductive rates, or altered dispersal behavior, as was documented before[32,78,123]. Such responses can lock management into an evolutionary arms race, increasing long-term costs and reducing overall effectiveness of the intervention.

This tension has been widely recognized in resistance management, where aggressive control often accelerates the evolution of resistance, while more moderate or heterogeneous strategies can delay it[36,124]. Similar principles have emerged in evolutionary medicine, where adaptive therapy in cancer aims to stabilize tumor populations rather than eliminate them, thereby slowing down the evolution of drug resistance[125,126]. From an eco-evolutionary perspective, these systems share a common structure: when eradication seems infeasible, management objectives shift from elimination to containment and stabilization. Rather than maximizing short-term mortality, managers aim to maintain the invasive population at acceptably low densities (or “safe” population sizes) while limiting the strength of selection for undesired adaptation.

Analogous dynamics may occur in biological invasions, where selection can favor reduced ecological impact over time. Just as pathogens in novel hosts may evolve lower virulence[127,128], invasive species may evolve to become less harmful to recipient communities. One example is *Alliaria petiolata*, a Eurasian understory plant that invaded North American forests and initially suppressed native competitors through the production of toxic phytochemicals. Over roughly 50 years, natural selection favored reduced phytochemical production, diminishing its negative effects on native species[129].

Within the SEG framework, invasive species control corresponds to a leader (manager) anticipating evolutionary responses and selecting control strategies that exploit ecological interactions such as competition or predation. Moderate or spatially heterogeneous interventions may reduce selective pressure thus allowing for ecological timescale to support the effect of control measures over longer timescales. Here, the key implication is that optimal invasive species management depends not only on ecological feasibility and economic cost, but also on the evolutionary responses induced by control. When eradication is unlikely, policies based on maximal suppression may be counterproductive, whereas strategies that shape evolutionary trajectories and anticipate adaptive feedbacks can stabilize populations and reduce long-term impact.

Discussion and outlook

Rapid evolution in response to anthropogenic pressures is now well established[23,24,27,28,39], challenging the traditional view that evolutionary processes are too slow to influence management outcomes[13,14]. Yet, evolutionary feedbacks remain only weakly integrated into conservation decision-making, in part because ecological optimization is already demanding and incorporating evolutionary dynamics adds further complexity. Here, we argue that Stackelberg evolutionary games (SEGs) provide a well-suited framework for addressing this gap because management actions precede and shape the environment that gives rise to eco-evolutionary responses. The hierarchical leader-follower structure of Stackelberg games mirrors the structure of conservation interventions..

Conservation outcomes depend critically on the specification of the manager's objective function Q. Stein et al.[130] proved that ecologically and evolutionarily enlightened strategies diverge unless either the leader's action does not affect trait evolution, or the manager's objective Q excludes the evolving trait *and* interactions among followers are purely density-dependent. Here, we extend this insight in two directions specific to conservation. First, we show that the structure of Q, not only trait-inclusion but also how diversity and viability are weighted, shapes evolutionary trajectories and the breadth of viable adaptive strategies. Second, we demonstrate that biomass-based objectives systematically fail to detect biodiversity loss, creating a structural misalignment between management incentives and conservation goals. This framing suggests that management can be interpreted as maintaining the system within a "safe operating space", avoiding undesirable ecological states or maladaptive trait configurations.

This perspective is particularly relevant in invasive species management. As we have shown, eradication and dynamic control strategies induce qualitatively different eco-evolutionary responses. While eradication may be optimal in spatially contained systems, aggressive suppression in large, open systems can favor resistant or highly dispersive phenotypes[27]. SEGs provide a framework for anticipating these feedbacks by embedding eco-evolutionary dynamics directly into the optimization problem, allowing policies to account for both ecological feasibility and evolutionary response.

More broadly, incorporating eco-evolutionary feedbacks requires a shift from static optimization toward dynamic, feedback-aware decision-making. We outline below six priorities for developing an evolutionary perspective on conservation management:

1. Management levers that reshape selection gradients must be identified. Policies rarely act on traits directly, yet interventions that modify space, habitats, resource availability, mortality, disturbance regimes, or interaction structure can profoundly alter evolutionary selection gradients.

2. Management should be evaluated in terms of its effects on fitness landscape structure, not only on the location or existence of evolutionarily stable states: transient dynamics, invasion windows, and landscape curvature determine whether populations retain adaptive capacity.

3. Early-warning signals of evolutionary bottlenecks need to be developed. The loss of invasion windows, compression of trait variance, or collapse of alternative strategies may precede demographic decline and provide actionable indicators of impending eco-evolutionary tipping points.

4. Decision tools are needed that explicitly trade short-term ecological stability for long-term evolutionary resilience. Policies that minimize variance or enforce single equilibria may appear successful while eroding the capacity for future adaptation.

5. Conservation planning should embed Stackelberg-style reasoning by accounting for multiple stakeholders whose actions jointly shape selection pressures. Evolutionarily informed management requires anticipating these strategic interactions and their impact on evolution rather than reacting to their outcomes only.

6. Human-induced perturbations should be treated as an optimal control problem. Managers must decide when to allow evolution to proceed autonomously and when to actively steer it. Importantly, in eco-evolutionary systems, inaction is itself an intervention that commits the system to a particular eco-evolutionary trajectory.

A further consideration concerns the transient nature of eco-evolutionary dynamics. Even when adaptive trait values exist that would allow long-term persistence, populations may fail to reach them. If environmental change drives population size below critical thresholds before adaptation can occur, extinction becomes unavoidable despite the presence of a viable evolutionary solution. Conservation outcomes therefore depend not only on equilibrium states, but on whether those states are reachable and whether eco-evolutionary trajectories remain within safe bounds. Persistence is ultimately determined by the balance between adaptation and decline. In this sense, conservation is not only about preserving ecosystems, but about designing evolutionary futures they will follow. Hence, preserving a desired evolutionary context, whether pristine or not, becomes a key consideration[131].

Addressing these priorities requires building on the foundations that conservation science has already established. Indeed, important progress has already been made toward incorporating evolutionary processes into management. Conservation genetics has long emphasized the importance of maintaining genetic diversity and avoiding inbreeding depression, while adaptive management frameworks explicitly account for uncertainty by updating decisions based on observed system responses. In parallel, a growing body of work in eco-evolutionary dynamics has demonstrated that evolution can occur on management-relevant timescales and influence conservation outcomes, with successful applications in systems where assisted evolution and trait-based interventions have been explored[103,104].

However, these approaches remain only partially integrated. Conservation genetics often relies on static indicators that do not capture the direction or speed of adaptation. Adaptive management typically focuses on ecological state variables, assessing evolutionary change only after it has already happened. Existing eco-evolutionary applications, while powerful, are often system-specific and do not provide a general framework for decision-making under adaptive feedbacks.

Our approach builds on these foundations by linking them within a unified decision framework. By treating measurable traits as proxies for evolutionary processes and embedding them into a Stackelberg game structure, we explicitly connect management actions to selection pressures and evolutionary responses. This allows conservation to move from reactive adjustment toward proactive design of evolutionary trajectories, where policies are evaluated not only by their ecological outcomes but also by concomitant evolutionary changes they induce. The result is a framework in which policy does not merely respond to evolution, but participates in directing it toward outcomes compatible with the success and persistence of long-term goals.

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Competing Interests

The authors declare no competing interests.

Data and Code Availability

All data and computer codes are available upon request.

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Box 1 – Evolutionary rescue vs evolutionary suicide

Eco-evolutionary dynamics. Populations are shaped by interacting ecological and evolutionary processes: population sizes respond to environmental and competitive pressures, while traits evolve in response to selection generated by these dynamics. Eco-evolutionary models capture this feedback by allowing population dynamics and trait evolution to unfold simultaneously. Let $\mathbf{x} = (x_1, \ldots, x_n)$ denote the abundances of n evolving entities and let $\mathbf{u} = (u_1, \ldots, u_n)$ denote their associated trait values. Depending on the level of biological organization, these entities may correspond to traits within a population, species within a community, or strategies occupying distinct ecological niches. The coupled eco-evolutionary dynamics are

$$\dot{x}_i = x_i\, G(v, \mathbf{u}, \mathbf{x})\big|_{v=u_i}, \qquad \dot{u}_i = \sigma_i \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v}\Big|_{v=u_i},$$

where σ_i controls the speed of evolution and v denotes a focal trait. The function $G(v, \mathbf{u}, \mathbf{x})$ is the *fitness-generating function*, defining the per-capita growth rate of a focal entity as a function of its own trait, the trait distribution of others, and the current ecological state[132–134]. Depending on model structure, G may be defined at the level of traits, species, or niches, and selection may be primarily density dependent (through absolute abundance or resource limitation) or frequency dependent (through relative trait composition and competitive interactions)[135]. Note that $\mathbf{x}^*$ and $\mathbf{u}^*$ denote the abundances (populations) and trait values at equilibrium, that is, for $\dot{\mathbf{x}} = \dot{\mathbf{u}} = 0$.

Fitness landscapes. The G-function defines a fitness landscape whose shape changes endogenously with population densities, trait distributions, and environmental conditions. In density-dependent settings, this landscape is shaped primarily by demographic constraints such as crowding or resource limitation. In frequency-dependent settings, its shape also depends on the relative abundance and traits of competitors, such that the fitness of a focal strategy depends on who else is present. Trait evolution corresponds to movement on this continuously shifting landscape, with selection gradients given by partial derivatives of G with respect to traits.

Eco-evolutionary equilibrium and ESS. An eco-evolutionary equilibrium $(\mathbf{u}^*, \mathbf{x}^*)$ is an *evolutionarily stable state* (ESS) if it cannot be invaded by a rare mutant. At an ESS, each evolving entity maximizes its fitness at ecological equilibrium,

$$u_i^* \in \arg\max_v G(v, \mathbf{u}^*, \mathbf{x}^*)\Big|_{v=u_i}. \tag{9}$$

ESS conditions are necessary but not sufficient for convergence to a fitness maximum; eco-evolutionary dynamics may instead converge to stable fitness minima, which can act as branching points leading to trait diversification[136–139].

Evolutionary rescue. Evolutionary rescue occurs when rapid trait evolution restores positive growth following environmental deterioration, preventing extinction[76,140–144]. The interaction between the rate of adaptation and demographic feedbacks can produce non-trivial rescue dynamics[145], and evolutionary rescue has recently been observed in managed koala populations in Victoria[146]. As an illustration, consider a system in which higher trait values improve competitive performance or reduce minimum energetic requirements, but do so at a reproductive cost. Following environmental deterioration, selection may then favor higher trait values, allowing populations to adapt rapidly enough to avoid extinction (see **Fig. 2A, 2C**).

Evolutionary suicide. In contrast, shifting the cost of trait expression from reproductive output to ecological capacity fundamentally alters the evolutionary outcome (for example, by setting r as a fixed parameter and letting $K(u) = K_{\max} e^{-gu}$). When the same adaptive response reduces the carrying capacity of the environment, selection may continue to favor higher trait values under environmental deterioration, but the associated decline in ecological capacity progressively undermines persistence. As a result, the population can be driven across an extinction boundary despite continued adaptation. This mechanism leads to evolutionary suicide, as illustrated in **Fig. 2B, 2C**.

Box 2 – Stackelberg evolutionary games: linking decision-making and evolution

Stackelberg evolutionary games (SEGs). SEG is an emerging branch of game theory that allows to build a policy with eco-evolutionary feedbacks[50]. The theory was successfully applied to a handful of systems where human actions act as a selective force on the evolution of other species, such as the treatment of metastatic cancers[113,114,147], the control of insect pests[31], and management of commercially valuable fish populations[49]. With this new selective force, the species evolve by natural selection towards new eco-evolutionary states[41]. The policymaker can either just react to the current state of the system, or take the lead by anticipating the ecological and/or evolutionary consequences of their actions and act accordingly. Thus, the leader's interactions with evolutionary followers can be framed as a special form of a Stackelberg (leader-follower) game[148] (**Fig. 1B**).

Evolutionary followers. As now the fitness landscape depends on the leader's action profile $\mathbf{m}$, the evolutionary dynamics from **Box 1** will need to be adjusted. A compact representation of the evolutionary process can be written as

$$\dot{x}_i = x_i \, G(\mathbf{m}, v, \mathbf{u}, \mathbf{x})\big|_{v=u_i}, \qquad \dot{u}_i = \sigma_i \frac{\partial G(\mathbf{m}, v, \mathbf{u}, \mathbf{x})}{\partial v}\Big|_{v=u_i},$$

where σ_i controls the speed of evolution for each species.

Eco-evolutionary equilibrium and ESS. For a fixed leader action $\mathbf{m}$, followers may converge to an ESS $(\mathbf{x}^*(\mathbf{m}), \mathbf{u}^*(\mathbf{m}))$, where $\mathbf{x}^*(\mathbf{m})$ is defined by $G\left(\mathbf{m}, v, \mathbf{u}, \mathbf{x})\right)\big|_{v=u_i} = 0$ when $\mathbf{x}^*(\mathbf{m})$ is positive and the the followers' evolutionarily stable strategy in response to the leader's strategy $\mathbf{m}$ maximizes G:

$$u_i^*(\mathbf{m}) \in \arg\max_v G(\mathbf{m}, v, \mathbf{u}^*(\mathbf{m}), \mathbf{x}^*(\mathbf{m}))\big|_{v=u_i}. \tag{10}$$

Leader's objectives and equilibrium concepts. The leader maximizes an objective $Q(\mathbf{m}, \mathbf{u}, \mathbf{x})$ (e.g., yield, profit, or quality of life), but differs in how followers' responses are anticipated.

- *Nash equilibrium:* The leader optimizes assuming traits are fixed, while followers evolve given the leader's action. A Nash equilibrium $(\mathbf{m}^N, \mathbf{u}^N)$ satisfies $\mathbf{m}^N \in \arg\max_{\mathbf{m}} Q(\mathbf{m}, \mathbf{u}^N, \mathbf{x}^*)$ and $\mathbf{u}^N = \mathbf{u}^*(\mathbf{m}^N)$, given by (10).
- *Stackelberg equilibrium:* In a Stackelberg equilibrium $(\mathbf{m}^S, \mathbf{u}^S)$, the leader anticipates the followers' eco-evolutionary response and chooses

  $$\mathbf{m}^S \in \arg\max_{\mathbf{m}} Q(\mathbf{m}, \mathbf{u}^*(\mathbf{m}), \mathbf{x}^*(\mathbf{m})),$$

  and $\mathbf{u}^S = \mathbf{u}^*(\mathbf{m}^S)$.

Importance of accounting for the evolving trait. By explicitly anticipating evolution, Stackelberg strategies can avoid undesirable evolutionary outcomes. Under broad conditions, the Stackelberg outcome weakly dominates the Nash outcome for the leader, though the two may coincide[50]. More specifically, Stein et al. (2023) prove that Nash and Stackelberg equilibria are equivalent under two conditions: either the leader's action does not affect trait evolution at all, or the leader's objective excludes the evolving trait *and* interactions among followers are purely density-dependent[130]. This implies that a conservation manager who is trying to prevent the species of interest from extinction has to understand how they adapt AND directly include this adaptation into their decision-making process, as management actions that leave trait evolution unaffected are unlikely in most real conservation contexts.

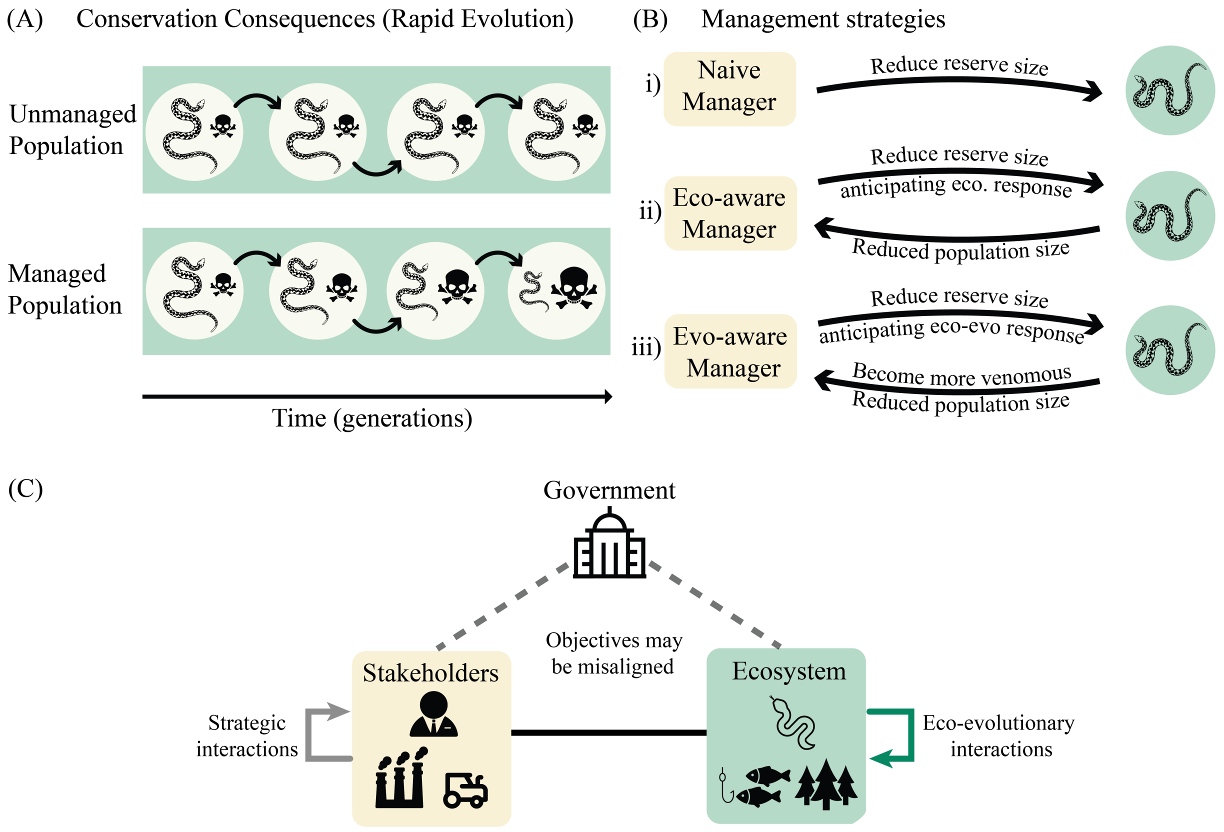

Figure 1: Overview of evolutionary management in conservation. (A) Comparison of trait evolution over time (in generations) between managed and unmanaged populations - management-induced selection can drive rapid evolutionary change, here illustrated as the population (represented by the snake) becoming more venomous over time. (B) Three different management approaches: i) the naive manager who acts unilaterally to reduce reserve size without concern of ecological or evolutionary responses, ii) the ecological manager anticipates ecological feedback (change in population size) while adjusting reserve size but does not account for evolutionary responses, iii) the evolutionary manager who anticipates both ecological and evolutionary feedback while making reserve size decisions. Managers therefore act as leaders who influence the ecological and evolutionary environment of the followers who then respond to these changes. (C) Hierarchical structure of conservation policy making and its consequences. While governments and policy makers determine broad constraints and incentives, end-users (stakeholders) interact strategically and can anticipate management decisions. The ecosystem consists of followers who respond eco-evolutionarily to management actions.

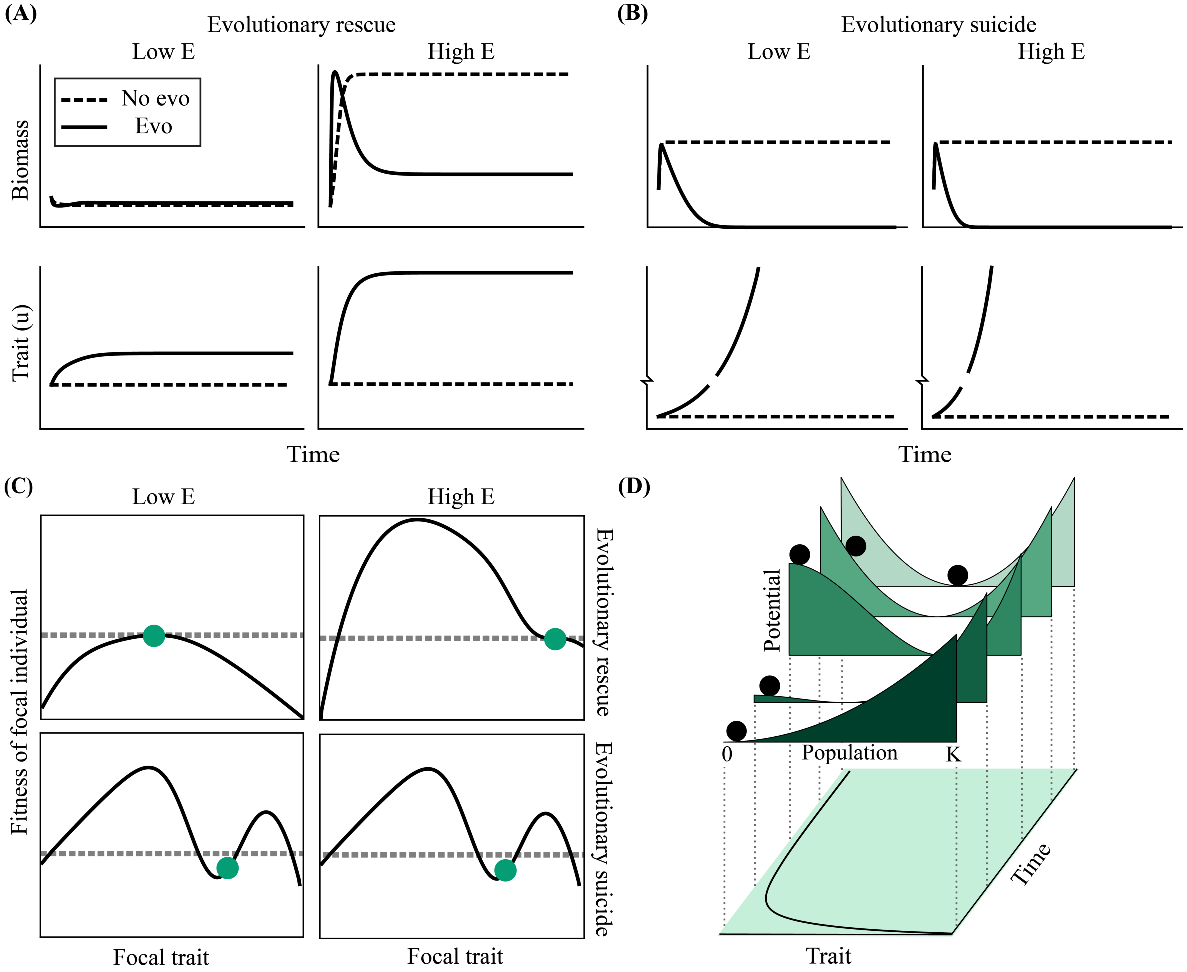

Figure 2: Eco-evolutionary dynamics when selection is density- and frequency-dependent. The different outcomes of eco-evolutionary dynamics under low and high E, the manager's control parameter when both density- and frequency-dependence influence selection. (A) Evolutionary rescue: Following environmental deterioration (low E), positive growth is restored due to rapid trait evolution (solid line), while populations that do not evolve (dashed line) go extinct. Under high E, both populations are able to survive. (B) Evolutionary suicide: when the cost of trait expression is in the carrying capacity, evolution drives traits in a direction that ultimately results in extinction under both high and low E scenarios. Only the non-evolving population (dashed line) survives. (C) Fitness landscapes illustrate the mechanism underlying these outcomes. The vertical axis is the per capita growth rate (fitness) of a focal individual across trait values (horizontal axis). The horizontal dotted line 0 fitness. The solid green circle represents the trait value of the evolutionary species from (A) at equilibrium and (B) just before extinction. In rescue scenarios (top row), under low E (top left), the extant species' trait (solid circle) sits on the global maximum of the fitness landscape. Under high E (top right), the species sits on a local maximum with a valley separating it from a region of trait space with positive fitness (invasion window). In suicide scenarios (bottom row), under both low and high E, selection drives the trait towards a value where persistence is no longer possible – the population goes extinct despite adaptation. (D) The stability landscape (potential $V(x(t), u(t), E)$ versus population x, as time t changes and trait $u(t)$ evolves) is dynamic even for a fixed environmental condition – the evolving trait continuously reshapes it, altering the position of the equilibria (minimum of V). The black circles (balls) in the stability landscapes (ball-in-cup diagrams) mark the positions of the system at each time point.

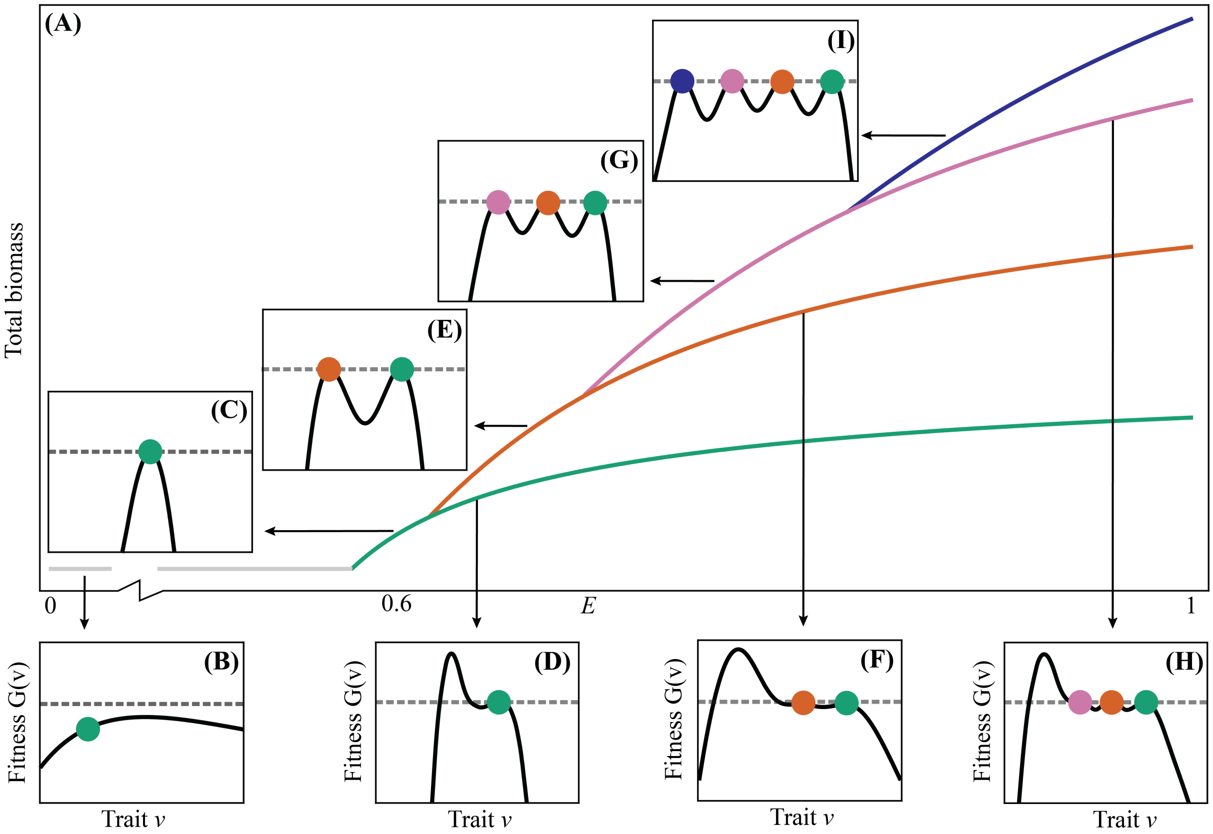

Figure 3: Eco-evolutionary equilibria when selection is density- and frequency-dependent. The total population (or biomass) increases with E. The number of distinct species (or traits) that can coexist also increases with E. (A) shows the total population against E for five distinct eco-evolutionary regimes, with zero (gray), one (green), two (orange), three (pink) or four (blue) coexisting species. Note that the for a given total biomass, there can be different number of coexisting traits. (B-I) show fitness landscapes for all possible outcomes for different values of E, and colored circles indicate the equilibrium trait values of surviving species. Note that (C, E, G, I) have the same axes as (B), with labels omitted. (B) For very low E (gray, roughly $E < 0.6$), no species survive since the peak of the fitness landscape lies below the 0 line (horizontal dashed line). (C) As E increases past a threshold ≈ 0.6, a single species sits on the peak of the fitness landscape with no invasion window, also a single species ESS. (E-I) As E increases further, the fitness landscape broadens and permits coexistence of additional species. (D), (F), and (H) show fitness landscapes of 'under-saturated' communities in which resident species sit below the global fitness maximum and an invasion window remains open allowing a mutant with a different trait value to invade. (E), (G), and (I) show stable two-, three-, and four-species ESSes respectively, where each species sits on top of a peak and no invasion window remains. The four species ESS (I) supports the highest total population. This highlights that management actions decreasing the resource availability contracts invasion windows and trait diversity.

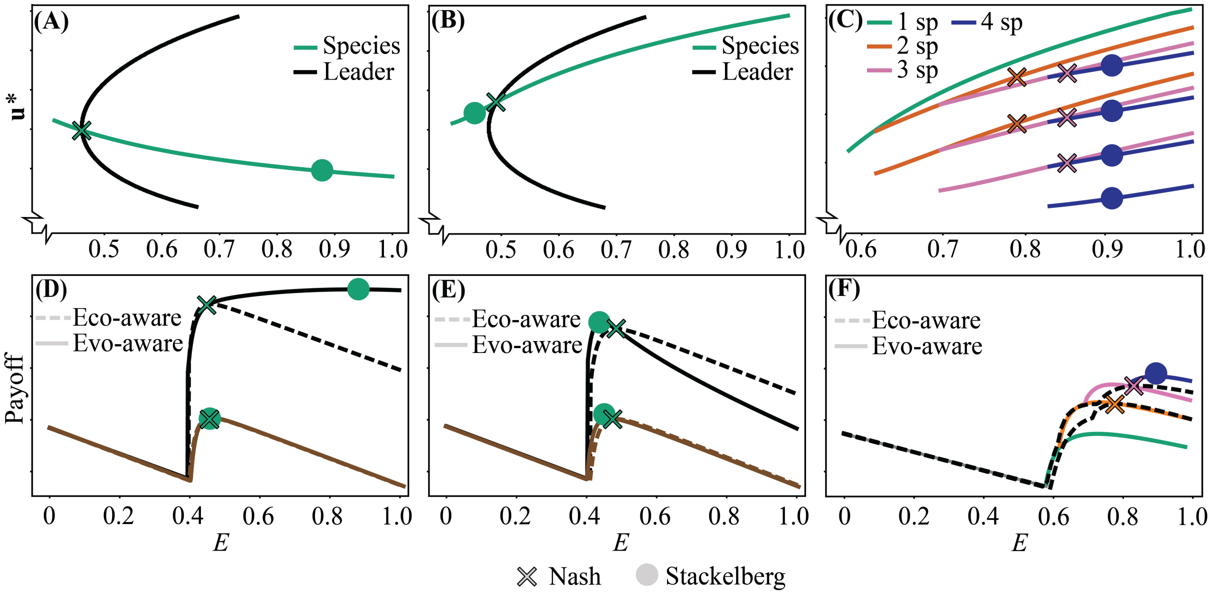

Figure 4: Best responses and manager's payoffs. Management outcomes under different density- and frequency-dependent assumptions and objective functions. Top row: species' best responses (trait values $\mathbf{u}^*$ at eco-evolutionary equilibrium as a function of E; colored lines) and the manager's best response (value of E that maximizes their objective; black line). Colors represent the number of coexisting species at equilibrium (one - green, two - orange, three - pink, and four - blue). In (C), each set of colored lines represent a distinct bifurcation branch in Figure 3 (A). The color of the solid circles (Stackelberg) and crosses (Nash) indicate the branches on which the Stackelberg and Nash equilibria lie respectively. Bottom row: Leader's payoff as a function of E under evolutionarily-aware (evo-aware, solid lines) and ecologically-aware (eco-aware, dashed lines) strategies. Note that the evo-aware payoff curve intersects the eco-aware payoff curve exactly at the Nash equilibria. (A,D) Density-dependent selection, single species. The Stackelberg equilibrium occurs at a higher E than the Nash demonstrating the manager's ability to steer the system to a more favorable outcome. The evo-aware manager's payoff (solid line in D) exceeds the eco-aware manager's payoff (dashed line). However, when the objective function does not explicitly include the trait (brown lines), the Nash and Stackelberg coincide. (B,E) Density- and frequency-dependent selection, single species. The Stackelberg equilibrium now occurs at a lower E than Nash. Yet the evo-aware manager's payoff exceeds the eco-aware payoff. When the trait is not included in the leader's objective (brown), the evo-aware manager's payoff is marginally higher. (C, F) Multi-species setting with density- and frequency-dependent selection. (C) shows the equilibrium trait values of one- (green), two- (orange), three- (pink), and four-species (blue) coexistence branches as a function of E. The Stackelberg equilibrium occurs at a higher E than both Nash equilibria. (F) shows the evo-aware payoff (solid colored lines, colors represent payoffs corresponding to the respective branches in (C) and Figure 3 (A)) and the eco-aware payoffs (dashed lines) corresponding to the two Nash equilibria in (C). In this multi-species setting, we only consider the case where the leader's objective explicitly includes the trait. The Stackelberg E occurs higher than both Nash E values, and with a higher payoff.