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How to combine two methods to restore populations cost effectively

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Abstract. Ecosystems worldwide have become degraded due to global change, and therefore, restoration of these ecosystems is critical for the prolonged provision of ecosystem services. Specifically, major restoration efforts are directed toward the restoration of key species that provide important services and functions. There are often several alternative methods to restore a species population, such as the reintroduction of its individuals, improvement of its habitat quality, and removal of competing invasive species. However, these methods can be expensive, and hence, it is important to determine how to cost effectively combine them over time. In this paper, we use optimal control theory and we find a general rule of thumb for combining two restoration methods. The general rule, which applies to a wide variety of ecosystems, is that cost-effective restoration entails one of the following two strategies: (1) using a single method until the system approaches a "restoration threshold" or (2) combining both methods to approach an "investment benchmark," which is a certain configuration of the system that does not depend on the system's initial state. After either the restoration threshold or the investment benchmark has been approached, investment should stop and the system should be left to recover naturally. Therefore, finding the restoration threshold and the investment benchmark is key for guiding effective restoration, and we demonstrate a simple method for finding them.

Key words: bioeconomics; conservation; ecosystem services; optimal control; restoration; Stochastic Programming.

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Introduction

It is widely recognized that ecosystems provide important services with both economic and aesthetic values (Assessment 2005). Sustainable management, aimed at avoiding over-harvesting and maintaining ecosystem functions despite human activity, is a worldwide goal (Groom et al. 2006). Nevertheless, ecosystems are often becoming severely degraded and even collapsing, either because efforts to conserve the ecosystem have not been made in time or because some unexpected factors, such as invasive species or storms, have perturbed these systems significantly (Coomes et al. 2003, Hulme 2006, Day et al. 2007, Richardson et al. 2007, Bergstrom et al. 2009). Active restoration of these systems may yield significant economic benefits, and therefore, restoration has become an integral part of sustainable management (Dobson et al. 1997, McBride et al. 2010, Seddon et al. 2014). Specifically, many restoration efforts are directed toward the populations of species that (1) provide an important ecosystem service (Tri et al. 1998, Coen et al. 2007), (2) provide some important function and may promote the recovery of other populations (Byers et al. 2006, Mann and Powell 2007, Brumbaugh and Coen 2009, Chapman 2013, Breckheimer et al. 2014,

Seddon et al. 2014), or (3) are endangered (Lampert et al. 2014).

A variety of populations can be restored via several alternative methods, which can be used either separately or jointly (Fig. 1; Hobbs and Norton 1996, McBride et al. 2010, Seddon et al. 2014). Common methods include (1) the introduction of the target species (including reintroduction and reinforcement, Breckheimer et al. 2014, Seddon et al. 2014), (2) the eradication of invasive species that compete with the target species (Lampert et al. 2014), and (3) the restoration of the species' habitat (Chapman 2013; e.g., via the introduction of some plant species or abiotic manipulations of the environment). One aquatic ecosystems example is the restoration of oysters, which managers can achieve by introducing living oysters (stock enhancement) or by introducing dead oysters (substrate enhancement; Mann and Powell 2007, Brumbaugh and Coen 2009). Another example is management for reversing eutrophication, a ubiquitous harmful phenomenon in aquatic systems in which algae bloom and fish die (Carpenter et al. 1999, Kemp et al. 2005, Coen et al. 2007). Eutrophication often results from phosphorous pollution, thus reducing pollution levels is one method used for restoration. But this is sometimes insufficient, and managers need to remove algae directly.

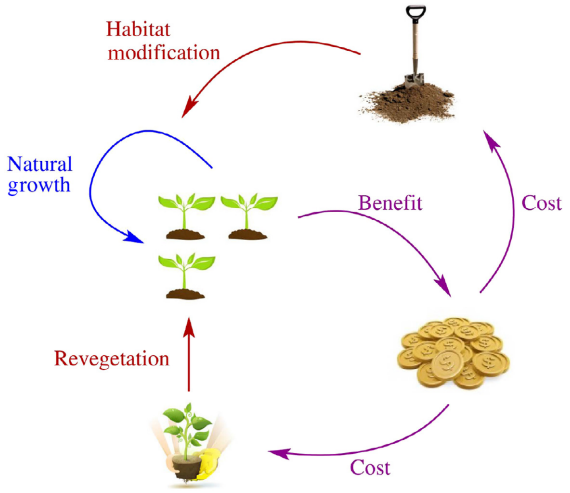

Fig. 1. Illustration of the model based on an example of a plant restoration. In this example, the manager can facilitate the growth of the target plant population using two methods: (1) planting individual plants of the target species and (2) modifying the habitat, which increases the growth rate of the target plant population. Both methods are costly, but a restored plant population yields some benefits.

The restorations of terrestrial ecosystems can often be achieved by a single method of either introduction of some important species or removal of some harmful plant species such as a weed or an invasive, or by some combination of the two methods (Gómez-Aparicio 2009, Lampert et al. 2014). Gómez-Aparicio (2009) conducted a meta-analysis to investigate the interactions among plant species during the restoration process, focusing on how to combine the removal of competing vegetation with planting of plants that facilitate the target species (facilitation). She concluded that facilitation using planting of nurse shrubs and trees should be part of the restoration strategy, in addition to the more traditional removal of competing plants. Specific applications of this approach would depend on the choices of how much to spend on each of these two methods. Pueyo et al. (2009) compared the effects of direct abiotic amelioration and indirect amelioration through facilitation by planting *Suaeda vera* nurse shrubs on restoration of degraded semiarid grasslands. They concluded that a combination of both methods would be useful, with some direct amelioration required under the harshest conditions.

More broadly, there is an increasing number of studies that look at the introduction of ecosystem engineers as a method to restore ecosystems (Byers et al. 2006, Coen et al. 2007, Seddon et al. 2014). This method can complement other, more direct methods. Chapman (2013), for example, considered how burrows of the relic bilby (*Macrotis lagotis*) change rangeland habitat in ways that facilitate the establishment of other species. Thus, restoration can be achieved via increasing the population of bilbies and/or via increasing the population of plant species. This, in turn, leads to the question of how best to combine these two methods.

The examples above demonstrate that one of the greatest challenges in restoration is to determine how to cost effectively combine alternative methods over time, aiming at minimizing the costs due to both expenses of treatment and ecosystem damages until the restoration is complete. Most previous studies have focused on how to determine the target state, which specifies the desired species' abundance or its spatial structure

(Hyman and Leibowitz 2000, McAllister et al. 2000, Westphal et al. 2003, McBride et al. 2010). In this paper, we consider the target state as given, and we focus on the question of how to combine the alternative restoration methods to approach the target state in an optimal fashion, namely, how to minimize the net cost due to both treatment and damages over time. We use optimal control theory and Stochastic Programming to develop a novel and general method that enables to find a rule of thumb guiding how to use and combine the alternative methods. We demonstrate our method using models in which a population can be restored either via introduction of its individuals or via restoration of its habitat. Accordingly, the state of the system is characterized by two variables: population size and habitat quality. We find two general principles. First, investment in either method should stop when the system approaches either (1) the target or (2) a state that is sufficiently close to the target from which the population effectively recovers naturally. (This generalizes our previous result, Lampert and Hastings 2014 showing a similar rule for restoration using a single method.) Note that there are multiple such states at which the investment should stop (characterized by different combinations of population size and habitat quality), and we denote the set of all these states the "restoration threshold." The second principle is that, among the states comprising the restoration threshold, there may exist a particular state, an "investment benchmark," toward which managers should direct their actions. Specifically, managers should either (1) restore using a single method until the system approaches the restoration threshold or (2) combine both methods to approach an investment benchmark. In what follows, we develop and demonstrate a simple and general method for finding the restoration threshold and the investment benchmark without a need for finding the complete solution. We explain in the *Discussion* how our methods and results apply more broadly to other cases in which different restoration methods are used.

Model: Two Alternative Restoration Methods

We consider a species' population that can be restored via two methods (Fig. 1): (1) introduction of its individuals and (2) restoration of its habitat, where the habitat quality can be improved either via facilitation or via the removal of some harmful species or pollutants. We assume that a single variable, $n(t)$, characterizes the abundance of the target population at time t, between fully degraded ($n = 0$) and fully recovered ($n = 1$). Another variable, $\alpha(t)$, characterizes the quality of the species' habitat, where a higher α indicates a higher quality (e.g., better abiotic conditions or lower densities of harmful species). The dynamics of $n(t)$ and $\alpha(t)$ are given by

$$\begin{aligned} \frac{dn}{dt} &= f(n,\alpha) + R_n(t), \\ \frac{d\alpha}{dt} &= g(\alpha) + R_\alpha(t), \end{aligned} \tag{1}$$

where $f(n, \alpha)$ is the population's natural growth rate (increasing with α), $g(\alpha)$ is the natural rate of change in the habitat's quality, and R_n and R_α are the rates at which the restoration activities increase the population size and the habitat quality, respectively.

We consider a manager whose objective is to minimize the net cost, taking into account the cost due to both treatment and damages over time (Born et al. 2005, Epanchin-Niell and Hastings 2010, Wilson et al. 2011). The manager determines how much to invest in each restoration method over time. Therefore, to assist the manager, we need to find $R_n(n, \alpha)$ and $R_\alpha(n, \alpha)$ that maximize the net present value (minimize the net present cost; Clark 2010), $\mathcal{V}$, given by

$$\begin{aligned} &\mathcal{V}(R_n, R_\alpha, n_0, \alpha_0) = \\ &\quad -\int_0^\infty [C_d(n) + c_n(n,\alpha)R_n + c_\alpha(n,\alpha)R_\alpha]e^{-\delta t}dt \end{aligned} \tag{2}$$

where $C_d(n)$ is the cost due to the degradation of the ecosystem (decreases with n), c_n and c_α are the per-unit costs of species introduction and habitat restoration, respectively, and δ is the discount rate that assigns lower values to future gains and losses. The initial conditions are given by $n(0) = n_0$ and $\alpha(0) = \alpha_0$.

In the following, we consider three special cases characterized by specific forms of the growth function $f(n, \alpha)$, while $g = 0$. In case I, we consider logistic growth, where the population

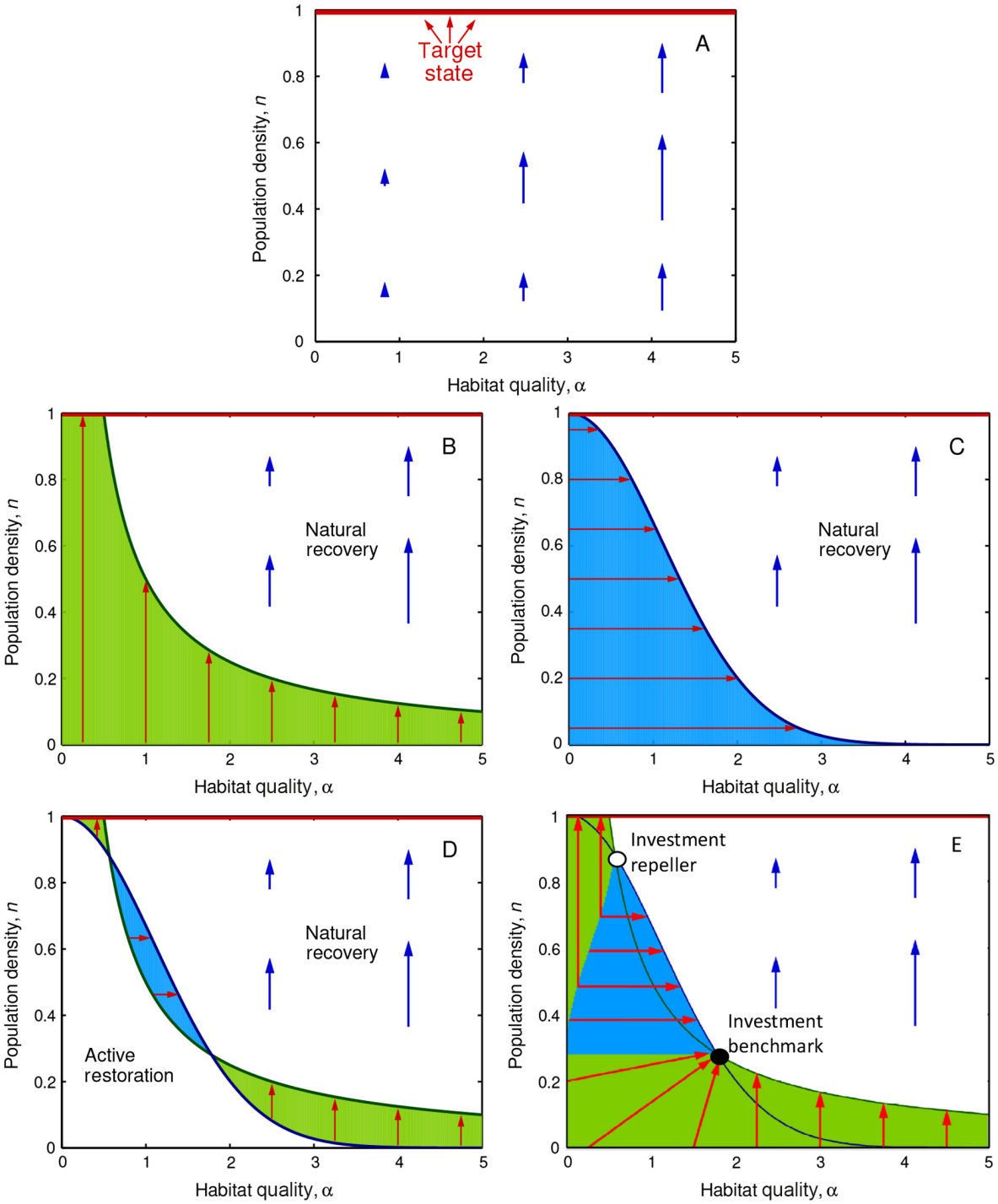

Fig. 2. Optimal restoration dictates either (1) using a single method until the system approaches the "restoration threshold" or (2) combining the two methods until the system approaches the "investment benchmark." (A) Demonstrated are the dynamics of the system given by Eq. (1) without restoration ($R_n = R_\alpha = 0$), where f is given by Eq. (3) and $g = 0$ (case I). These dynamics lead to recovery, but this recovery may be slow. (B) In some states of the system, restoration via introduction of the target population should be prioritized over natural recovery

(Fig. 2. *Continued*)
(green). (C) In some other states, modifying the habitat to enhance the recovery rates should be prioritized over natural recovery. (D) The two region boundaries demonstrated in panels B and C determine the optimal restoration strategies in all the states between these boundaries. The restoration threshold is given by the curve that is closer to the target state and separates the colored region and the white region. (E) The complete solution for the optimal restoration of the system includes an investment benchmark and an investment repeller that are located at the intersections of the two region boundaries. The red arrows show how to optimally restore the system from various initial states. Restoration should either focus on a single method, or combine the two methods toward the investment benchmark. Parameters: $C_d(n) = \max(1 - n, 0)$, $c_n = 20$, $c_\alpha = 20$, $\delta = 0$.

growth rate, when rare, is given by α. Specifically, we consider (Fig. 2A)

$$\text{case I}: f(n, \alpha) = \alpha n(1 - n) \tag{3}$$

In this case, restoration may not be necessary for recovery, but natural recovery may be slow, and therefore, it may be beneficial to invest in restoration to accelerate natural recovery. In case II, we consider a population that does not recover naturally if the population abundance and the habitat quality are below a certain threshold (hysteresis, Fig. 3A). For sufficiently small n and α, the natural dynamics (without restoration) lead to an undesirable stable state; only if either n or α is sufficiently large, the natural dynamics lead to the desirable (target) state. Specifically, we consider (Fig. 3A)

$$\text{case II}: f(n, \alpha) = \left(n(n-1) + a\alpha^b\right)(1 - n) \tag{4}$$

where a and b are parameters determining how the habitat quality affects the population growth. In this case, restoration is necessary for recovery if both n and α are below the threshold. But, as in case I, restoration may be beneficial even when n and α are above the threshold, because it accelerates natural recovery. We also consider case III, a stochastic version of case I, which we describe and analyze in Appendix S3.

In our numeric solution (Figs. 2, 3), we assume $g(\alpha) = 0$ (Eq. 1), but the method we develop applies more broadly. The complete solution can be found using Stochastic Programming (Clark 2010), as described in Appendix S2. Nevertheless, since computing the exact solution may be difficult, and since the exact solution may be sensitive to uncertainty in the parameters, our goal is to develop a general and robust method, which will allow finding the essential properties of a robust solution in a few steps.

Robust Method to Guide Restoration: Emergence of the Restoration Threshold and Benchmarks

Region boundaries

As a first step, we assume that the manager can only restore the population via the introduction of its individuals (increasing n, e.g., via reintroduction or rehabilitation). Note that restoration is beneficial if the per-unit cost of the introduction is lower than the cost of the damages avoided by a given unit of the species introduction (marginal benefit is greater than marginal cost; Appendix S1). Our results show that, if n is sufficiently low, then the introduction of individuals is beneficial, whereas if the population is already close to full recovery, it is optimal to let the system recover naturally (Figs. 2B, 3B; see also Lampert and Hastings 2014, Lampert et al. 2018). Moreover, if the habitat has a higher quality, the natural recovery is more effective, and therefore, the introduction of individuals should stop at lower population levels (Figs. 2B, 3B). More generally, two regions can be identified (Fig. 2B or 3B): one where n and α are sufficiently small and restoration via introduction of individuals is beneficial (green), and one where n and α are sufficiently large and it is not beneficial (white). The boundary that separates these two regions (hereafter, the first region boundary) defines, for each α, the critical value of n where it is no longer beneficial to introduce the species (Appendix S1).

Next, we perform a similar analysis for restoration via habitat quality improvement. We assume that the manager can restore only via habitat restoration (increasing α), and we find the states where the habitat restoration is beneficial (Figs. 2C, 3C). Our results show that, in both case I and case II, the manager should restore the habitat if n and α are sufficiently low (blue). If n and α are above a certain threshold, it is better to

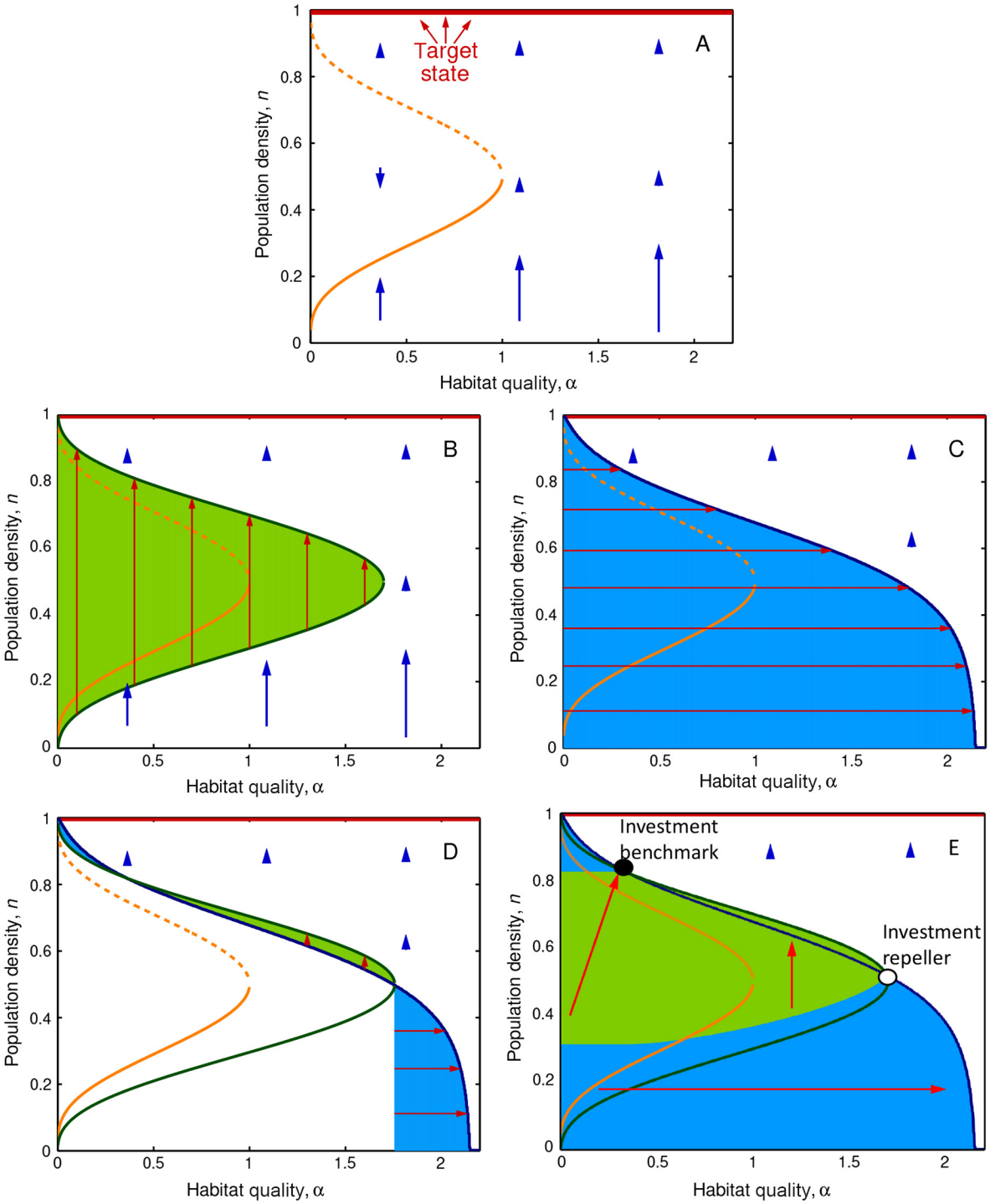

Fig. 3. When restoring the system from one stable steady state to another, more desirable steady state, the manager should either (1) focus on a single method or (2) combine the two methods toward an investment benchmark. (A) Demonstrated are the dynamics of the system given by Eq. (1) without restoration ($R_n = R_\alpha = 0$), where f is given by Eq. (4) and $g = 0$ (case II). These dynamics encompass two alternative stable steady states: a desirable one (solid red line on the top) and an undesirable one (solid, orange line). (B) Demonstrated in green is the region where

(Fig. 3. *Continued*)
introduction of the target population should be prioritized over natural recovery. (C) Demonstrated in blue is the region where habitat restoration should be prioritized over natural recovery. (D) The two region boundaries demonstrated in panels B and C determine the optimal restoration strategies in all the states between these boundaries. (E) As in Fig. 2, the full solution shows that restoration should either focus on a single method or it should be directed toward the investment benchmark. Parameters: $a = 0.25$, $b = 0.28$, $C_d(n) = \max(1 - n, 0)$, $c_n = 25$, $c_\alpha = 0.917$, $\delta = 0$.

let the system recover naturally (white). The second region boundary is given by the line that separates the blue and the white regions. Specifically, the second region boundary defines, for each n, the critical value of α where it is no longer beneficial to improve the habitat quality. Mathematically, the region boundaries are the curves given by

$$\frac{\partial \mathcal{V}(R_n = 0, R_\alpha = 0, n, \alpha)}{\partial n} = c_n \tag{5a}$$

$$\frac{\partial \mathcal{V}(R_n = 0, R_\alpha = 0, n, \alpha)}{\partial \alpha} = c_\alpha. \tag{5b}$$

We find closed-form solutions for the region boundaries for cases I and II in Appendix S1.

Restoration threshold

As the next step in our method, we consider again the original model in which both restoration methods are possible. We then ask what we can learn from the two region boundaries. We have seen that, in both case I and case II, if the system has crossed a region boundary, the manager should no longer use the corresponding method (Figs. 2B, C, 3B, C). This implies that, if the system has crossed both region boundaries, the manager should not use any of the two methods thereafter, and should let the system recover naturally (Figs. 2D, E, 3D, E). In particular, we call the "restoration threshold" to the boundary that separates the region where the manager should use any of the two methods to restore the population from the region where they should leave the population to recover naturally. (The restoration threshold is the line separating the colored region from the white region shown in Figs. 2D, 3D and Figs. 2E, 3E.) Therefore, one general rule is that the manager should use some method, or methods, when the restoration endeavor begins, but should stop when the system approaches the restoration threshold (see also Lampert and Hastings 2014).

Investment benchmark

The next question we attempt to answer is, which method, or methods, the manager should use until the system approaches the restoration threshold. In our model, there are no diminishing returns on restoration efforts (the cost of the methods is linear in R_n and R_α, Eq. 2). Therefore, it follows from the Pontryagin's maximum principle that the optimal action at any given state of the system, (n_0, α_0), is one of the following: (1) invest in increasing n from n_0 to $n_0 + \Delta$ as fast as possible; (2) invest in increasing α to move from α_0 to $\alpha_0 + \Delta$ as fast as possible; or (3) do not do anything (Appendix S2). In other words, the optimal strategy would be to restore at once whenever the restoration is profitable (bang-bang strategy, Clark 2010, Lampert and Hastings 2014). Therefore, we should ask, which state, among all states on the restoration threshold, the manager should aim toward. To answer this question, we should look at the optimal restoration method when the system is sufficiently close to the restoration threshold. Specifically, note that if the system has crossed only one region boundary, then the manager should use the action that corresponds to the other region boundary, until the system approaches the other region boundary (Figs. 2D, 3D). In this way, the region boundaries incorporate the complete solution dictating what to do once at least one of the region boundaries has been crossed. Furthermore, note that a state of the system where the two region boundaries intersect determines which methods should be used to approach the restoration threshold when the system is sufficiently close to that state (Figs. 2D, E, 3D, E). Specifically, depending on the direction in which the two region boundaries intersect, a given intersection defines either: (1) an "investment benchmark," toward which it is optimal to direct the restoration efforts, or (2) an "investment repeller," which should be avoided by using alternative restoration methods (Figs. 2E, 3E).

The manager should aim to approach the investment benchmark if the initial values of both n and α are lower than their values at the benchmark, whereas if the initial value of either n or α is larger, then the manager should restore using a single method (Fig. 4). We use Stochastic Programming to verify the results and to calculate the optimal solution for all the states of the system, including the more degraded states that are far from the region boundaries (Appendix S2; Figs. 2E, 3E).

Discussion

In this paper, we demonstrated two general principles that characterize the optimal combination of the two restoration methods. The first principle is that managers should invest in one or both methods only until the system approaches a state at which the natural recovery is sufficiently effective. Thereafter, the managers should leave the system to recover naturally (Figs. 2–4). (The natural recovery stage, in practice, may still entail some actions, such as monitoring and local interventions, but will generally cost less per-annum, Lampert and Hastings 2014, Lampert et al. 2014.) This implies that managers should not only decide what would be the ultimate goal for the restoration, but they should also determine the state of the system in which they should stop restoring actively and allow natural recovery. The second principle is that, if managers use both restoration methods, then they should combine them such that the system approaches a particular state that we denoted as the investment benchmark (Figs. 2E, 3E, 4). In turn, we constructed and demonstrated a general and robust method to determine the investment benchmark. Particularly, one needs to determine, for one restoration method at a time and assuming that this was the only possible method, at what states the investment should stop (region boundaries). Then, the restoration threshold and the investment benchmark can be determined using the same steps that we demonstrated here, where the investment benchmark appears at the intersection of the region boundaries and is a state in which both methods simultaneously become non-profitable (Figs. 2D, E, 3D, E).

In turn, to apply our method to a particular ecosystem, an estimate of the economic costs and

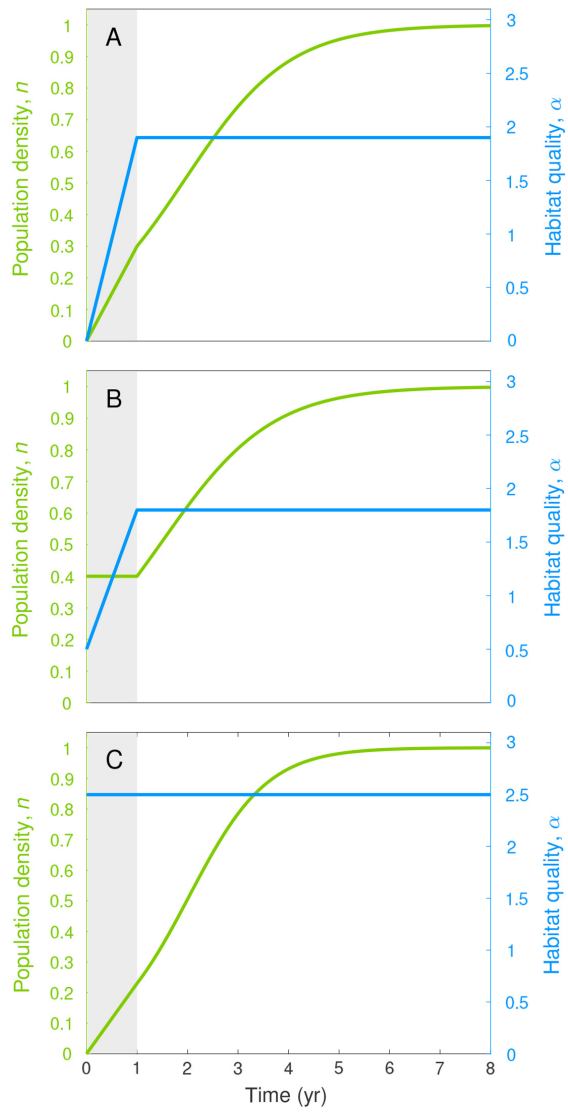

Fig. 4. Time evolution of the population density and the habitat quality following three different initial conditions. In the first stage (gray area), the manager uses the optimal strategy to restore the ecosystem described in case I (Fig. 2). (We consider a maximal investment rate such that the treatment takes one year.) Thereafter, the system is left to recover naturally (white area). (A) The initial conditions are $n(0) = 0$ and $\alpha(0) = 0$ and the manager restore until the system approaches the investment benchmark (Fig. 2E). (B) The initial population density is above its level at the investment benchmark and the manager restores only the habitat, until the system approaches the restoration threshold. (C) The initial habitat quality is above its level at the investment benchmark and the manager restores using species introduction.

the biological growth functions is needed. This includes the cost of each of the two methods, c_n and c_α, as well as the cost due to damages, C_d. In turn, the growth functions, f and g, depend on the ecosystem at hand. For example, when modeling the reversal of eutrophication (Carpenter et al. 1999, Kemp et al. 2005, Coen et al. 2007), n may be considered the "clearness" of the water, namely, $n = m_{max} - m$, where m is the density of algae and m_{max} is its maximal density. Then, $f(n, \alpha)$ would be minus the growth rate of algae, which depends on the habitat quality, α. In turn, the habitat quality increases with the efforts to prevent phosphorous pollution. For another example, when modeling vegetation via restoration of the target species vs. eradication of a competitor invasive species (Gómez-Aparicio 2009, Lampert et al. 2014), n would characterize the native species population density, while α would characterize the invasive species population density. Accordingly, $f(n, \alpha)$ would characterize the growth rate of the native species that decreases with α, while $g(\alpha)$ would characterize the growth rate of the invasive species. If the invasive species is subject to an Allee effect, our method may reveal how much below the Allee threshold one should bring the invasive population, as well as to what density one should bring the native population. Finally, for modeling restoration via ecosystem engineers (Byers et al. 2006, Coen et al. 2007, Pueyo et al. 2009, Seddon et al. 2014), f would characterize the rate of improvement of the environmental state, n, in response to the engineer population, α, while g would characterize the natural growth rate of the engineer.

In cases I and II, we considered deterministic dynamics, whereas real restoration projects are subject to noise and uncertainty concerning the costs, growth rates, and the actual outcome of the methods (Beechie et al. 2008). In Appendix S3, we present a stochastic model (Appendix S3: Eq. S31) and examine how the region boundaries are affected. The results show that, the stronger the noise, the more it affects the region boundaries (Fig. 5; see also Lampert and Hastings 2014). Nevertheless, the general method that we described remains valid, namely, managers should determine the region boundaries with the stochasticity, and the intersections or the two region boundaries define, as in the deterministic cases, the investment benchmark.

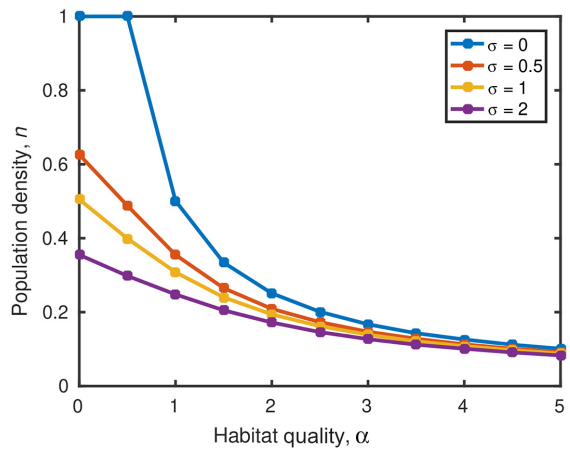

Fig. 5. Stochasticity alters the region boundary. Demonstrated is the region boundary that dictates where managers should switch from introduction of individuals to natural recovery. We consider case III, in which the dynamics are given by Eq. (1), where $g = 0$ and f is given in Appendix S3: Eq. S31. Each line demonstrates the region boundary for a different level of noise, characterized by the coefficient of the noise amplitude, σ. Without noise ($\sigma = 0$), Eq. S31 becomes identical to Eq. (3) and the region boundary is identical to that in case I (Fig. 2B). However, as the noise increases (σ increases), the region boundary shifts toward lower values of n.

Furthermore, note that stochasticity may cause the system to switch back from a state where natural recovery is recommended to a state where active restoration is recommended, and therefore, strong stochasticity may necessitate expenditures that are more flexible and variable over time (Lampert and Hastings 2014).

Our results provide a rule of thumb that rely on several simplifying assumptions. First, we assumed that there are no diminishing returns on the investment (linear cost functions, Eq. 2). The consequence is that managers should restore as fast as possible, and the net cost does not depend on the order at which the distinct restoration methods are being used. In turn, note that diminishing returns do not affect the restoration threshold (Figs. 2A–D and 3A–D remain unchanged if diminishing returns are considered). However, with diminishing returns, the order and the speed at which the restoration methods are being used may affect the treatment efficiency, and moreover, the system may end up at a state on the

restoration threshold that differs from the investment benchmark. Second, we assumed that the target state is given and that it would be cost-effective to restore the system. In general, however, the optimal treatment of some systems might be to abandon the restoration. For example, some invasive species inflict low damages and are costly to eradicate, and consequently, the optimal strategy is to leave them untreated (Clark 2010). Third, we considered cases in which a given method, once stopped, should not be resumed again when the state of the system becomes closer to the target. In case I, for example, this occurred naturally as we considered a concave per-capita growth rate function (f/n). In general, however, it may occur that restoration should be resumed at a later stages of the recovery process (Lampert and Hastings 2014), in which case, our method can only be used as an approximation.

The method that we demonstrated is simplified and robust in terms of planning. The investment benchmark is a more degraded form of the ecosystem than the target state, and therefore, finding a way to restore the ecosystem to the investment benchmark may be simpler. Furthermore, we showed that finding the investment benchmark does not require finding the complete solution, but rather, it is sufficient to find where to stop the restoration given one method at a time, while ignoring the diminishing returns on restoration efforts. Therefore, investment benchmarks are broadly applicable as a key for guiding restoration projects.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2552/full