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Using ecosystem engineers to restore ecological systems

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Ecosystem engineers affect other organisms by creating, modifying, maintaining or destroying habitats. Despite widespread recognition of these often important effects, the ecosystem engineering concept has yet to be widely used in ecological applications. Here, we present a conceptual framework that shows how consideration of ecosystem engineers can be used to assess the likelihood of restoration of a system to a desired state, the type of changes necessary for successful restoration and how restoration efforts can be most effectively partitioned between direct human intervention and natural ecosystem engineers.

Introduction

Restoration ecologists typically seek to re-establish native populations, communities and ecosystem processes following environmental degradation. However, restoration sometimes fails because ecological interactions are more complex or human intervention is more difficult than anticipated [1–4]. Sometimes, common restoration strategies of removing exotic species or preventing continued human impact, followed by reintroduction of desired (e.g. native) species are insufficient to overcome the inertia of an unsuitable abiotic environmental state [5–8] in which the desired species are unable to survive. Many restoration efforts therefore start by attempting to change the degraded abiotic state with the expectation that appropriate species and ecological processes will then recover [9]. However, even if the abiotic environment is changed enough to enable biota to re-establish, the changes might be insufficient to restore ecosystem functions that involve coupled biotic–abiotic processes (e.g. biogeochemistry). Thus, changing the interaction between abiotic and biotic states is often a necessary first step for successful system recovery [9–11].

Dam building by beaver, lowering of the water table by introduced *Tamarix* sp., or alteration of fire regimes by exotic cheat grass *Bromus tectorum* all substantially change abiotic environments. These are examples of ecosystem engineering, a ubiquitous process of abiotic environmental modification by species that often has consequences for populations, communities, ecosystem functioning and landscape structure [12–15]. Researchers studying restoration and biological invasions have long appreciated the large influences that some species can have on the abiotic environment (e.g. [16–18] and references therein), yet there was little theory addressing such influences before the introduction of the ecosystem engineering concept [12,13]. This concept provides a general framework for understanding interactions between species that are mediated through the effects of certain species on the abiotic environment. By reshaping the landscape, ecosystem engineers change the abiotic context upon which biotic interactions heavily depend. Consequently, we believe that a conservation framework that uses the ecosystem engineer concept can contribute to ecological applications such as ecosystem restoration and invasive species management. Here, we present a conceptual model that illustrates the influence of ecosystem engineers in moving an ecosystem between alternative states.

Ecosystem engineers as agents of system state change

Alternative system states are one explanation of why degraded systems are sometimes difficult to restore [10,19,20]. Didham *et al.* [11] suggest that the systems that are most resistant or resilient to restoration are those that are heavily abiotically controlled and also those that are most likely to exhibit alternate states (e.g. overgrazing of arid grasslands reduces vegetation, decreasing water filtration, further limiting plant growth and leading to persistent desertification). Given that we know that the abiotic environment can be greatly modified by some ecosystem engineers, it is likely that they are often the causative agents driving the transition between alternative system states [21], such as between a degraded condition and a restoration target.

Our conceptual framework illustrates how restoration efforts can be most effectively partitioned between the direct alteration of abiotic and biotic attributes by humans, and the modification of abiotic attributes and consequent response of biota instigated by ecosystem engineers. Explicitly incorporating ecosystem engineers into restoration frameworks could lead to increased

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restoration success while simultaneously reducing cost and effort. We illustrate the utility of the model by example and explore some of its general ramifications for restoration ecology, including how it could help guide practitioners' evaluation of intervention options.

A conceptual framework for restoration

Our model emphasizes the need to consider both abiotic and biotic conditions when attempting restoration, while illustrating the special role of ecosystem engineers. Unlike previous models of ecosystem engineers that focus on engineer dynamics [22–25], this general conceptual model focuses on environment states, with specific systems being viewed as special cases.

The state of any ecological system can be described by its abiotic (A) and biotic conditions (B) where A and B are usually multidimensional (i.e. many different variables contribute to composite metrics of the abiotic and biotic states). For example, the abiotic state of an estuary might include factors such as mean temperature, sediment redox potential, current water speed and salinity, whereas the biotic state might include attributes such as species composition, seasonal variation in biomass and the presence or absence of an endangered species. We assume multidimensional variables because we are presenting a model for ecosystem restoration, rather than for the restoration of just one system attribute, such as species richness. The selection of such composite variables is difficult; variables should best encompass the key differences between current and desired states and reflect a functioning system [19]. Because of the multidimensional nature of A and B, a large change in any single component variable might not necessarily correspond to a large change of the state of A or B. For example, a change in temperature might not significantly affect a forest that is also influenced by precipitation and hurricanes.

The need to restore a system implies that it has been perturbed from some former, desired state. Thus, in terms of both abiotic and biotic variables, there is a desired state that is the goal of restoration, D*, and the current state, S*. For example, a filled, weed-dominated lowland, S*, could be restored to a functioning wetland, D*. In real systems, there can be more than two possible attracting states. For the purposes of simplicity, we assume that there are only two stable states. Of course, the current and desired states might not be stable equilibrium points, but possibly something more complex, such as an oscillation or more complex dynamic. For example, D* might be

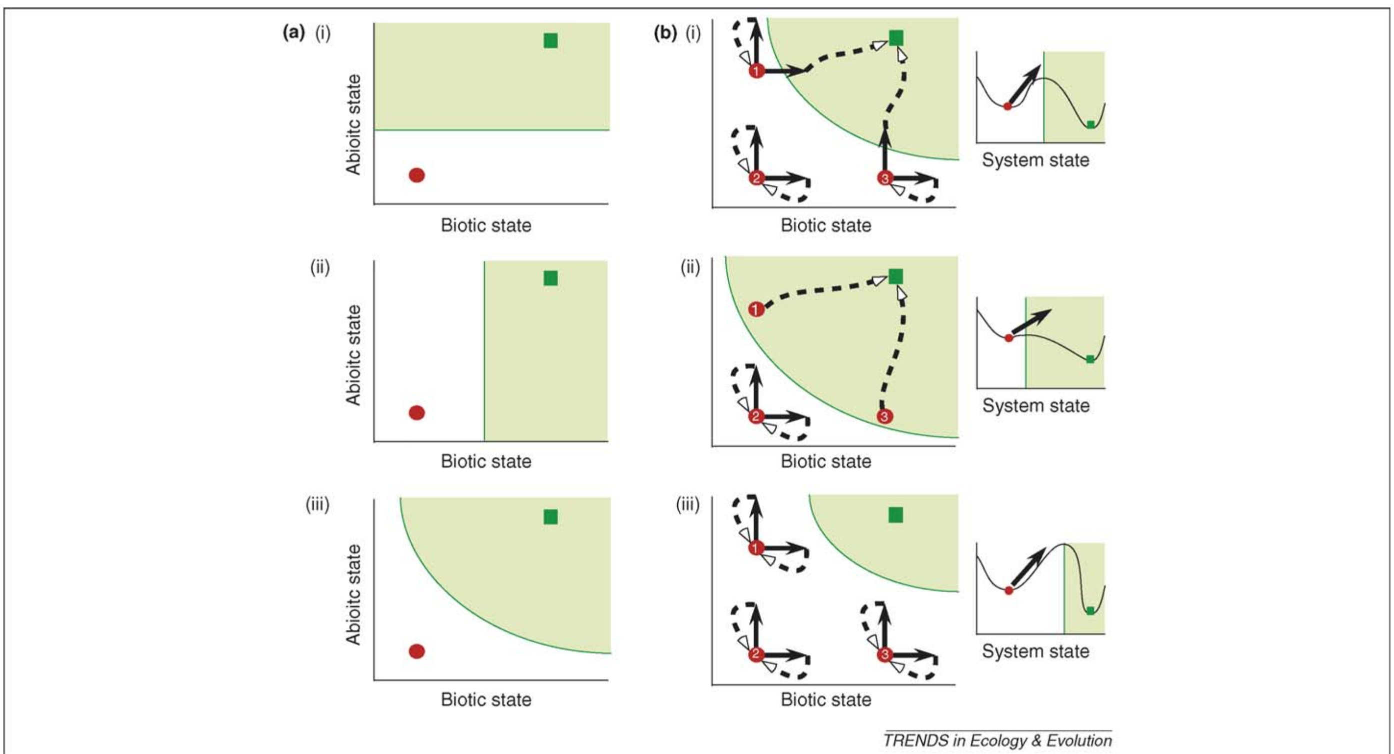

Figure 1. Models of alternate system states. Both the current state, S* (red circles), and the desired state, D* (green squares), are locally stable system states defined by a multidimensional expression of the abiotic and biotic states of the environment. The green-shaded area represents the set of conditions that leads to the restoration goal (i.e. the basin of attraction for the desired state, D*). **(a)** represents a system in which the basin of attraction for D*, and thus the switch between system states, is driven by changes to: (ai) abiotic conditions alone; (aii) biotic conditions alone; (aiii) both abiotic and biotic conditions. **(b)** illustrates the effects of restoration efforts and ecosystem engineers under alternate system states, where solid arrows represent human intervention on biotic and/or abiotic properties, and dashed arrows represent the post-intervention, natural readjustment of the system. Three potential current system states, S*, are shown as numbered circles to correspond to examples in the main text and Boxes 1–3. (bi) No ecosystem engineer added to the system; (bii) restoration-facilitating (i.e. desirable) ecosystem engineer added to the system; and (biii) restoration-inhibiting (i.e. undesirable) ecosystem engineer added to the system. Adding a single engineering species, although itself a small biotic change, instigates large changes in the abiotic state and in abiotic-dependent interactions that move the basin of attraction for D*. Small inset figures to the right of each of (bi–iii) represent a cross section of the topology between the current system state at point 2 (S*, red circle) and the desired system state (D*, green square). In this depiction, the restoration target is achieved with: (bi) considerable, appropriate intervention with no ecosystem engineer in the system; (bii) the least human effort with a desirable ecosystem engineer added to the system; and (biii) not achieved for the illustrated effort with an undesirable ecosystem engineer present.

the continued alternation between a high humidity, forested environment and a low-humidity, fire-recovery meadow. But for ease of exposition, we consider D* and S* to be locally stable equilibrium points.

At the extremes, one can think of the equilibrium states of natural systems as being determined completely by either abiotic or biotic factors. For example, a system can move from a forest to a tundra, mediated almost entirely by rainfall and temperature, in which case the switch between the current and the desired state is solely a function of abiotic conditions [i.e. $dA/dt = g(A)$; Figure 1ai]. Likewise, in some cases, biotic factors only might determine the locally stable system state. For example, the switch from kelp forest to denuded urchin barren owing to the loss of urchin predators is determined primarily by biotic, trophic interactions [i.e. $dB/dt = f(B)$; Figure 1aii]. In most systems, however, both abiotic and biotic factors determine dynamics; therefore, the boundary between the set of abiotic and biotic conditions that enable the system to move towards D* (i.e. the basin of attraction for D*) is determined by A and B [i.e. $dA/dt = g(A,B)$, $dB/dt = f(A,B)$; Figure 1aiii].

For generality, we consider the boundary between the basins of attraction to be determined by an arbitrary, non-linear function. Thus, in the language of dynamical systems, the basin of attraction of S* does not include D*. If one can change the current state of the system so that the system enters the basin of attraction of D*, then the long-term dynamics of the system will tend towards D*. We do not pursue it here, but our model can be extended to

Box 1. Restoration of eutrophic lakes with phosphorous-rich sediment

Lakes that have become eutrophic as a result of phosphorous-rich sediment are systems where restoration is sensitive to biotic change, but resistant to abiotic change (point 1, Figure 1b, main text). High phosphorus concentrations in lakes cause algal blooms, resulting in sediment anoxia, reduced water quality and declines in aquatic species [32,33]. Even if phosphorus inputs are reduced, anoxic sediments release phosphorus into the water column, exacerbating eutrophication. An abiotic manipulation often used to address this problem is sediment aeration: in shallow, stratified lakes, aeration counteracts sediment anoxia, resulting in sediment phosphorus immobilization, particularly when iron is present [34–36]. However, even when effective, aeration requires costly, continuous human intervention (Figure Ia).

Biotic manipulations of the food-web structure that control algal abundance can shift lakes to the desired state, permanently reducing eutrophication in some circumstances [37–39] by moving the system state over the basin boundary (Figure Ia). Manipulations include removal of zooplanktivorous fish to increase zooplankton, addition of phytoplanktivorous fish, and removal or addition of fish at higher trophic levels to create an appropriate trophic cascade.

An example of co-opting desirable engineers is adding submerged aquatic macrophytes, which sometimes recruit naturally following food-web manipulations (Figure Ib) [40–44]. Although these plants take up phosphorus from the water column and inject oxygen into sediments around the roots, it is their engineering effects that are most important. Their roots stabilize sediments while submerged canopies attenuate turbulent mixing, with both actions reducing wind-driven sediment resuspension. In addition, canopies reduce the light available to algae, and the plant structure can provide refuges for juvenile fish that are part of the biotic food-web manipulation. The addition of the ecosystem engineer alters the system dynamics such that the basin of attraction of the desired state is now much larger (Figure Ib).

Problematic ecosystem engineers are benthic bioturbators such as carp (Figure Ic) [33,45]. By disturbing sediments through foraging, such species can increase phosphorus resuspension, exacerbating eutrophication and potentially offsetting positive influences of food-web manipulations. Carp can also uproot macrophytes, impeding restoration efforts based on desirable engineers. In this case, the boundary of the basin of attraction of the desired state moves further away from the current state (Figure Ic).

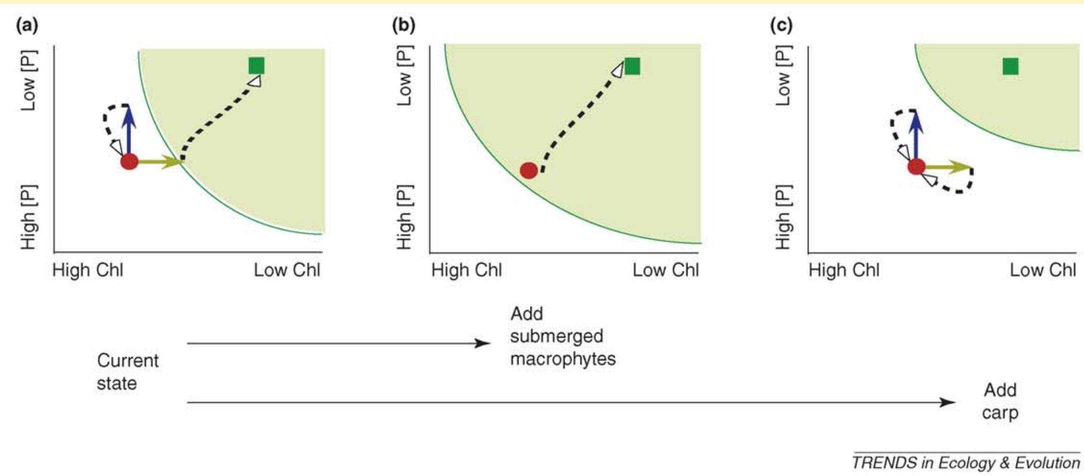

Figure I. Application of the ecosystem engineer model to restore a eutrophic shallow lake. Both the current state, S* (red circles), and the desired state, D* (green squares), are locally stable system states defined by a multidimensional expression of the abiotic and biotic states of the environment. The green-shaded area represents the basin of attraction for the desired state, D*. For illustrative purposes, composite variables on each axis have been simplified. The abiotic state variable is the phosphorous concentration in the water column that comes from its release from the sediment, representing eutrophication potential; the biotic state variable is the chlorophyll a (Chl) concentration, representing algal biomass and its relation to food-web structure. Solid-colored arrows represent human intervention on biotic and/or abiotic properties, and dashed arrows represent the natural post-intervention readjustment of the system. **(a)** The blue arrow represents human abiotic intervention (e.g. sediment aeration) that does not move the system to D*. The green arrow represents human intervention to alter the biotic state, (e.g. food-web manipulations to enhance phytoplanktivory) that moves the system to D*. **(b)** The addition of desirable ecosystem engineers (aquatic macrophytes) facilitates restoration. **(c)** Some ecosystem engineers (e.g. bioturbating carp) make the desired state harder to achieve.

include variability, where system behavior depends upon the initial conditions of the system.

The role of ecosystem engineers

Influential engineering species have such large magnitude effects on abiotic conditions that the introduction of even one such species, which in and of itself is a small biotic change, could drastically alter the abiotic system state, triggering a consequent response in the biotic state. For example, by changing terrestrial and riparian habitat into submerged aquatic habitat, beavers affect relationships between many species and the physical environment. The strong influence of the engineer occurs because the large and dynamic nature of the abiotic alteration and its biotic consequences, including feedback to the engineer species itself, inherently alters the system. The change in the basin boundary represents how ecosystem engineers change relationships between abiotic properties and organisms, influencing context-dependent outcomes of species interactions (Figure 1b).

The introduction of ecosystem engineers can thus fundamentally influence the basin of attraction, shifting the boundary either further from or closer to D*, and therefore requiring more or less effort to reach D*, respectively (Figure 1bii, iii). In effect, the ecosystem engineer (EE) is such an influential component of the system that the abiotic and biotic dynamics depend upon it [i.e. $dA/dt = g(A,B;EE)$, $dB/dt = f(A,B;EE)$].

Model application to restoration

How does this model framework relate to ongoing restoration efforts and the potential use of ecosystem engineers? This way of thinking about ecosystems guides the selection of restoration goals, provides insight into past problems with restoration efforts, and helps us to evaluate the particular efforts required to achieve restoration goals and how ecosystem engineers will influence these. Briefly, the framework explicitly states that both abiotic and biotic ecosystem characteristics must be considered to be able to restore a system to a desired state. In Boxes 1–3, we present restoration examples for three different systems to illustrate the utility of the model, while providing insights into real restoration issues and how this approach helps us to better understand the systems involved.

Setting restoration goals

The choice of the restoration goal (D*) is of paramount importance because it dictates how easily restoration will be achieved and whether the system will self-regulate at that point [10]. Some desired states might not be stable and are therefore attainable only with large and perpetual effort (e.g. a riparian forest below a dammed river where reduced flows are insufficient to support recruitment and germination of dominant tree species [26]). In such cases, restoration attempts might result in the system returning to S* in the absence of continuous human intervention. For D* to be self-maintaining, restoration efforts have to take

Box 2. Restoration of Australian salt pans

Salinized land is often resistant to abiotic and biotic restoration efforts (point 2, Figure 1b, main text). Winter wheat *Triticum* spp. has been grown in Australian drylands since the 1900s. Before land clearing for cultivation, native vegetation had a variety of rooting depths, transpiring water throughout the soil profile, preventing salt-layer formation and keeping groundwater at depth. By contrast, winter wheat has a shallow, uniform rooting depth and a water demand only in a short growing season. The reduced vegetation cover, high evaporation and low evapotranspiration results in salt accumulation in a layer below the soil surface and rising groundwater that carries salts to the surface [46]. Since the introduction of winter wheat, millions of hectares of land have become saline with substantial loss of production [47,48] (Figure I).

The desired management state is reduced soil salinity, restored agricultural productivity and remnant native plant conservation [49]. However, in hypersaline areas, restoration options are constrained by the severity of the abiotic changes [50]. Options for abiotic state modification by humans are limited to expensive, logistically complex removal of saline surface soils and groundwater. Human intervention to alter the biotic state is also limited because few plants can grow in hypersaline soils [50,51]. Neither a large abiotic nor biotic intervention can readily move the system across the basin boundary to the desired state (point 2, Figure 1bi, main text).

One solution involving ecosystem engineers is the establishment of salt-tolerant (halophyte) trees and shrubs (including non-natives) with a variety of rooting depths, promoting the downward movement and more even distribution of salts in the soil profile while lowering the water table [50,51] (Figure 1bii, main text). The initial establishment of these species is not easy and can require initial human modification of the abiotic environment [52]. Once a more-even distribution of salt has been achieved, salt-tolerant non-native species could be removed and replaced with native species that could re-establish under reduced soil salinity while maintaining the differential rooting depths and evapotranspiration rates necessary to prevent salt-pan accumulation and rising groundwater.

Halophytic engineers are necessary, but halophytes that are salt excluders (i.e. do not take up salts internally), are more desirable than salt excretors or accumulators. The latter types will continually bring salt back to the surface via excretion, litter and woody debris. If such species take up so much salt that there is no net downward salt movement, they would be undesirable engineers (i.e. Figure 1biii, main text), requiring further human intervention to remove excreted salts and salt-rich plant material continuously to achieve long-term salinity reductions.

Figure I. Hypersalinity in the Western Australian wheatbelt near Bruce Rock, Western Australia. Reproduced with permission from CSIRO, Australia. Copyright CSIRO Land and Water (http://www.clw.csiro.au). Photography by Willem van Aken.

Box 3. Enhanced productivity of the Negev Desert

Desert productivity is sensitive to abiotic change, but resistant to biotic change (point 3, Figure 1b, main text). The fundamental constraint on arid land plant productivity is the capacity to use limited precipitation before it evaporates. If water is redistributed, locally concentrated and stored, substantially greater productivity and diversity can be supported [53,54]. One option for the modification by humans of the abiotic environment is adding water via drip irrigation, although this requires continued maintenance and is impractical for large areas. Alternatively, humans can make sink or source structures. The creation of runoff sources (impervious sloped surfaces) and adjacent runoff sinks (permeable soils with high infiltration and storage capacity) is a basic approach to reversing desertification. Sink structures include soil pits and mounds (1–10 m^2), whereas source structures can be natural runoff sources such as rock, or can be made by compacting soil [55–58]. In the Negev Desert, Israel (Figure I), the use of sink–source relationships has substantially increased annual plant productivity and diversity and supports many native and domesticated grazers [55].

In contrast to these abiotic environmental modification options, humans have no viable options for directly changing the biotic state of deserts other than manipulating engineers. Seeding annual plants over large areas under such arid conditions has no effect unless accompanied by increased water [53] (i.e. point 3, Figure 1bi, main text). However, numerous ecosystem engineers in the Negev can be co-opted with limited human intervention. For example, microphytic crust communities (cyanobacteria, algae and fungi) form an impervious surface on the soil, generating runoff during rain [59,60]. Many engineering species of plants and animals create hydrological sinks. For instance, shrub canopies intercept windblown dust, slowly forming uncrusted soil mounds (c. 200 years) that function as hydrological sinks, creating small islands of fertility that are rich in annual plants [61]. Porcupines dig pits, ants make mounds and geophytes thrust up soil mounds, which all have sink functions [62]. The conservation, reintroduction or manipulation of these engineering species creates a large basin of attraction for the desired state (i.e. Figure 1bii, main text), preventing or reversing desertification.

However, livestock at high densities are undesirable engineers because their hooves break the microphytic crust. At low densities, hoof prints create small hydrological sinks [63], but at high densities the crust is destroyed over large areas, resulting in the loss of its crucial water-concentrating hydrological source function and in increased desertification (Figure 1biii, main text) [64,65] (Figure I).

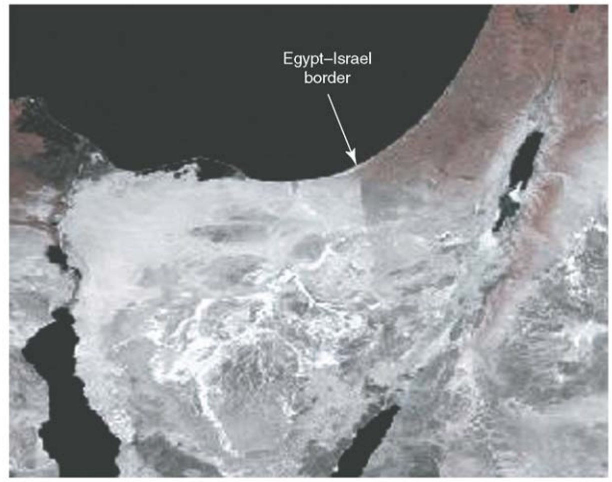

Figure I. The Negev desert at the Egypt–Israel border on the Sinai Peninsula. High densities of free-ranging livestock in Egypt have resulted in widespread desertification owing to excessive trampling-induced destruction of the microphytic crust and overgrazing of shrubs, both of which normally function as ecosystem engineers that generate and collect runoff, respectively, thus concentrating sparse rainfall. Densities of livestock are lower in Israel, and there are large areas of intact crust and shrubs and, thus, a more productive desert. The image shows the decrease in the infrared signal in Egypt that is exclusively due to the loss of the soil crust. NOAA-AVHRR image, January 1998; color composite: RGB = 2,2,1; 1-km resolution. Photo reproduced with permission from Arnon Karnieli at The Remote Sensing Laboratory, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Israel (http://bidr.bgu.ac.il/bidr/).

the system across the boundary that divides the basin of attraction for S* from D*.

The model guides consideration of the important biotic and abiotic variables in the system (i.e. Figure 1b model axes; Box 1 Figure I), including quantifying the differences between S* and D*, and establishing the amount of change needed to reach the latter [19]. Even a rough construction of the boundary (Figure 1b) of the model requires a great deal of knowledge and intuition about a system, specifically the identification of the important processes and interactions among variables, and what actions might enhance or hinder them (Figures 1bii,iii). Once the important elements and interactions within the system are identified, one can focus on how to execute these changes (i.e. Figure 1b model arrows) by determining what action should be taken and whether humans, an ecosystem engineer, or a combination of both would be most likely to effect change toward D* (Boxes 1–3).

Restoration problems

Not all restoration efforts are successful; sometimes even large efforts will not move a system to D*. Our model can explain why some restoration efforts are not attaining locally stable states and will therefore require continual maintenance. For example, an area cleared of exotic weeds might return to its invaded state and require continual weeding if there is no attempt to otherwise change the abiotic environment so that it is no longer suitable for weeds. In some cases, even large changes to abiotic conditions achieved by human intervention will not result in the basin boundary being crossed and, upon termination of this intervention, the system will return to S* (point 1, Figure 1bi). In other cases, large changes to biotic conditions alone might fail to restore the system (point 3, Figure 1bi). In yet other cases, simultaneous changes to both the abiotic and biotic variables are needed to restore a system, because changes to either alone would leave the system outside the basin of attraction of D* (point 2, Figure 1bi).

Suggestions for restoration: the role of ecosystem engineers

The particular suggestions for restoration efforts, as well as the consequences of these actions, will depend on the specific shape of the boundary between the basins of attraction for S* and D*, and the relative positions of these states. The shape of this boundary is determined by the specific underlying relationships among the factors that make up the composite abiotic and biotic variables. The influence of an ecosystem engineer on abiotic and biotic variables can thus be either a restoration benefit or a disaster.

The introduction of a desirable ecosystem engineer will yield much abiotic change that can facilitate restoration of the biotic community by shifting the boundary to encompass S* within the basin of D* (points 1, 3, Figure 1bii). In this case, much of the work required to change the abiotic and biotic state of the system occurs automatically as a natural consequence of the presence of the engineer. Moreover, the human effort required to introduce the engineer might be small compared with the magnitude of change required to shift the system in its absence (Figure 1bi) because the engineer catalyzes movement from S* to D* (Figure 1bii). By contrast, the accidental introduction of an undesirable engineering species might hinder restoration. For example, introduction of *Spartina alterniflora* into the mudflats of Washington has dramatically altered that coastal system. *Spartina* impedes current flow, increasing sedimentation rates and elevating the tidal plain, conditions that are no longer optimum for many native species, but are favorable for many non-natives. Thus, *Spartina* has shifted the basin boundary away from S*, drastically increasing the effort required to cross into the domain of D* (Figure 1biii; Box 1, Figure Ic).

Ecosystem engineers can reduce the threshold of human effort needed to exact desired state changes (e.g. Boxes 1,3). Furthermore, provided that the essential resources required by the ecosystem engineer are present in the system, the solution is intrinsically self-sustaining. Ecosystem engineers might therefore be a cheaper, easier, faster, more sustainable and, in some cases, the only feasible solution to restoration problems (e.g. point 2, Figure 1b). Conversely, restoration that involves removal of an undesirable (e.g. non-native) engineer (Figure 1biii) might also be important. However, because engineers can produce structures or abiotic effects that persist long after their removal (e.g. beaver dams, soil salinity or the dead root masses of *Spartina alterniflora*), we must also be prepared to deal with their abiotic legacies [27].

A comment on trophic interactions

Although we have emphasized non-trophic engineering effects, we do not wish to minimize the important and often interacting role of trophic and other biological interactions (e.g. pollination or biocontrol) in restoration. It is interesting, however, that the trophic cascades that develop when manipulating food webs can culminate in important engineering effects because engineers themselves invariably belong to food webs [13]. For example, on the Channel Islands, California, failure to consider engineering aspects inhibited restoration objectives to remove invasive grazers and restore native vegetation. Exotic cattle and sheep were removed; however, managers were inadvertently removing important engineering species whose grazing had been controlling the physical structure of the environment. Their removal was followed by a rapid increase in the biomass and height of exotic vegetation, such as fennel *Foeniculum vulgare* [28,29]. Ironically, the increased vegetative cover then made it almost impossible for marksmen to see and shoot feral pigs, another targeted exotic animal that is a far more ecologically destructive engineering species ([30,31], R. Klinger pers. commun.). The ecosystem engineering dimensions of the problem suggest that pig removal should have preceded sheep removal, an option that resource managers considered but were unable to pursue for legal reasons.

Conclusions

The importance and influence of some engineering species has been previously noted, but the ecosystem engineer concept has yet to be formally and explicitly applied to restoration ecology. Our conceptual model provides a unifying framework for restoration and invasive species management by shaping the questions that researchers should ask. As illustrated in Box 1, the model forces explicit definition of the abiotic and biotic components of the desired system state, or restoration goal.

Identifying and managing probable engineering species and responsive ecosystems should be a key priority for conservation and this will necessitate a shift to a process-based understanding of the functioning of whole systems, a large and important step toward ecosystem-based management. The approach that we develop here provides an organized way to do this by guiding consideration of the entire ecosystem during restoration and enabling one to erect plausible restoration alternatives and consider their trajectories. As well as more efficient planning, this process also facilitates potential comparisons of the time and cost of different restoration approaches. Our model and its application to restoration, as illustrated by our examples (Boxes 1–3), suggest that explicit consideration of ecosystem engineers can usefully guide the restoration of ecological systems by sharpening our understanding of how to intervene most effectively.

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