



Alternative states and positive feedbacks in restoration ecology

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There is increasing interest in developing better predictive tools and a broader conceptual framework to guide the restoration of degraded land. Traditionally, restoration efforts have focused on re-establishing historical disturbance regimes or abiotic conditions, relying on successional processes to guide the recovery of biotic communities. However, strong feedbacks between biotic factors and the physical environment can alter the efficacy of these successional-based management efforts. Recent experimental work indicates that some degraded systems are resilient to traditional restoration efforts owing to constraints such as changes in landscape connectivity and organization, loss of native species pools, shifts in species dominance, trophic interactions and/or invasion by exotics, and concomitant effects on biogeochemical processes. Models of alternative ecosystem states that incorporate system thresholds and feedbacks are now being applied to the dynamics of recovery in degraded systems and are suggesting ways in which restoration can identify, prioritize and address these constraints.

Conservation efforts over the past decade have been shifting from a focus on the preservation and protection of intact systems to the restoration of degraded systems [1,2]. One major challenge to these efforts is that degraded communities often do not respond predictably to management efforts, producing inconsistent and sometimes unexpected results [3–5]. Recent experimental work indicates that unexpected outcomes are often due to the focus on restoring the historic abiotic features of the system, whilst ignoring changes in biotic factors and the feedback between biotic and abiotic factors that have developed in the degraded state. These feedbacks can make a degraded system resilient to restorative change [5,6]. Increasingly, research is documenting that degraded systems are often in a persistent, resilient, ALTERNATIVE STATE (see Glossary), requiring a unique recovery pathway (Figure 1, [3,7]). Here, we review this important conceptual development and how it is being linked to theoretical models of alternative ecosystem states. We concentrate on the restoration of herbaceous plant communities because they are the focus of much recent experimental work, although we emphasize general mechanisms that are applicable to other systems and trophic levels (Box 1).

Successional models for restoration

Traditionally, restoration efforts have focused on ways to re-establish historical abiotic conditions (primarily disturbance regimes) to promote the natural return of the vegetation [1,8–10]. This successional-based approach assumes that, once the historical physical environment is re-established, natural successional processes will return the biotic system to its original condition. There are many degraded systems that can be restored along successional pathways. For example, degradation of prairie pothole communities is often related to changes in the natural flooding regime. If hydrology can be restored and the seed bank has persisted, the original plant assemblage can re-establish [11]. Such results support a traditional successional trajectory: re-introduction of the natural flooding regime or hydrology enhances vegetation recovery. Similarly, prescribed burning of degraded grasslands can promote restoration of native plant assemblages, particularly if the fire management regime is applied according to historical patterns [12,13].

In other cases, restoration relying on successional recovery has been unpredictable. For example, Anderson *et al.* [14] found that re-introduction of fire to prairie barrens in southern Illinois after a 25-year hiatus shifted community composition but did not return it to a barren community. This departure was attributed to an increase in tree cover (primarily prairie willow *Salix humilis*)

Glossary

Based on [36,38]

Alternative states:

alternative combinations of ecosystem states and environmental conditions that may persist at a particular spatial extent and temporal scale.

Ecological resilience: speed at which a system returns to its former state after it has been perturbed and displaced from that state. In the context of restoration, resilience can refer to both a system's return to a restorative "goal" state following a degradative perturbation and a system's return to a degraded state following a management perturbation.

Ecological resistance: amount of change or disruption (or management perturbation) that can be absorbed before processes change that control the structure and behavior of a system.

Environmental condition: resource conditions and disturbance characteristics that influence the interaction between the biological community and physical environment.

Perturbation: disturbance or disruption, including management actions, which can force a system into another state.

Stable equilibrium: a combination of an ecosystem state and environmental condition that persists and to which the system returns following perturbations. Also referred to as an attractor.

Threshold: point where even small changes in environmental conditions will lead to large changes in system state variables.

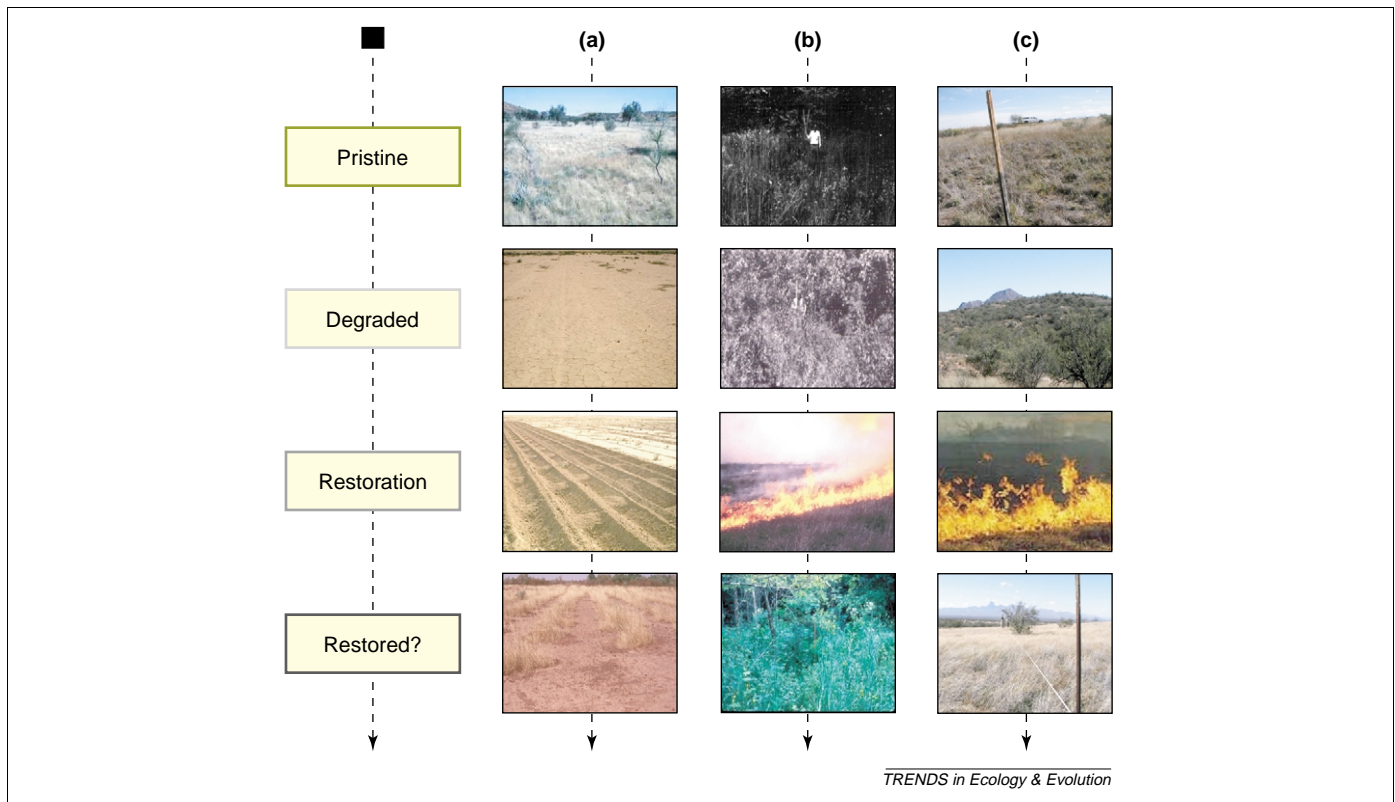


Figure 1. Examples of the complexity of outcomes in the restoration of degraded lands. (a) In Niger and the Chihuahuan Desert, abandoned agricultural fields have sealed surfaces and slow infiltration rates [7]. The little rainfall that occurs is lost to runoff, creating a positive feedback where drier conditions support less vegetation, and less vegetation holds less water. Without intervention, the system will not recover. Restoration treatments that roughen the soil surface can break this feedback. After the micro-catchments are dug and water is held, grasses regenerate spontaneously, creating a structure that catches more water, thereby reversing desertification. Photos courtesy of S.G. Whisenant. (b) In sand barren prairies (IL, USA), areas without frequent burning become dominated by woody vegetation [14]. Re-introduction of fire is not effective in reverting the system to prairie because the woody vegetation (primarily *Salix humilis*) influences the efficacy of the burning treatment. Photos courtesy of R. Anderson. (c) In semi-desert grasslands (AZ, USA), overgrazing can cause an increase in woody species, particularly mesquite *Prosopis velutina*. Burning can reduce mesquite cover, particularly at young size-classes, in wet years, and at high soil fertility. In addition, once propagules of non-native Lehmann lovegrass *Eragrostis Lehmanniana* have arrived at a site, fire can enhance the establishment of the problematic species at the expense of native species [64,65]. Photos courtesy of E. Geiger. The top picture in (c) and fire pictures in (b) and (c) are approximate for illustrative purposes.

during the period of fire suppression that influenced the effects of burning when fire was re-introduced. Likewise, intense grazing often removes drought-tolerant grasses in semi-arid rangelands, which can facilitate the growth of woody species and soil degradation. Following these secondary changes, reduction of grazing intensity does not restore the grass dominance [15–17]. On coral reefs, human-induced disturbances can promote the establishment of fleshy algae that replace hard coral, and subsequent coral recovery is limited owing to the simultaneous loss of grazers from the system [18]. These and many other examples suggest that some degraded systems have shifted to a new state that cannot be restored to the previous conditions solely by re-establishing physical conditions or disturbance regimes. Successful restoration often requires bold and innovative management that

disrupts feedbacks and addresses constraints of degraded systems.

The degraded system as an alternative state

Models of alternative states incorporate positive feedbacks and alternative internally reinforced states. They are being increasingly used to predict when a system might suddenly collapse as a result of gradual changes in climatic factors, human exploitation of biotic resources, habitat loss and fragmentation (Box 2, [18–21]). These models also provide a constructive framework for developing management tools that can be used to restore systems that have already collapsed to a degraded state. The value of this approach is that it recognizes that the dynamics of the degraded state are very different from those in the pristine or target state and that the trajectory to recovery will probably be different from that of degradation. In these systems, restoration efforts might need to manipulate more than the single dimension (factor or process) that led to the original collapse (Figure 2) [5,21–23].

Increasing evidence of the ECOLOGICAL RESILIENCE of some degraded communities to restoration efforts supports the idea that these systems represent alternative states and that restoration efforts can sometimes send systems along unintended trajectories [4,20,24–26]. These ideas have been applied to management of arid

Box 1. The big picture

- Ecological dynamics in degraded systems can be very different from dynamics in less-impacted systems.
- For restoration, it is important to understand feedbacks and constraints in the degraded system.
- Alternative state models, which emphasize internally reinforced states and recovery thresholds, can help guide restoration efforts.

Box 2. Alternative state models and restoration ecology

A principal thesis of alternative state models is that the system can shift abruptly between two or more states (Figure 1a) [after 20–21,35,56]. SYSTEM STATE VARIABLES (see Box Glossary) refer to characteristics such as species diversity, abundance, composition or some desired ecosystem service. These state variables are determined by a combination of factors (e.g. grazing intensity, fire frequency, pollution or nutrient loading) that characterize the environmental condition. Critical thresholds of environmental conditions, E_1 and E_2 (Figure 1a, red dots), bound stable equilibrium (or attractors, Figure 1a, solid black lines) and UNSTABLE EQUILIBRIUM (or repellers, Figure 1a, dashed black line). S_1 and S_2 are alternative states (green and white) of the system.

These models have application to the degradation and restoration of systems, particularly in situations where the trajectories of collapse and recovery differ (Figure 1b). For example, at S_1 a shift in environmental conditions below E_2 will always result in the system returning to the 'green' ecosystem state S_1 . However if environmental conditions are shifted above E_2 , the system collapses to S_2 (the 'white' state). At environmental conditions between E_1 and E_2 , the system could return to either the green S_1 or the white S_2 state depending on the initial conditions (whether at S_1 or S_2 , for example). For instance, rangeland might persist in ecosystem state S_1 as grazing pressure increases from E_1 to E_2 (the green zone along the line in Figure 1a). However, if grazing pressure increased beyond E_2 the system would 'collapse' to a degraded system dominated by shrubs (S_2) because a threshold point has been exceeded. Once the system has collapsed to S_2 , it will not recover or return to the grassland state (S_1) unless grazing pressure (or some other factor) is reduced to E_1 . This recovery could be costly and slow compared with the collapse (Figure 1b), and depending on feedbacks, possibly could not occur at all. A perturbation (either natural or managed) could more directly influence the return trajectory. For instance, management efforts (e.g. shrub removal) that influence state variables (Figure 1b, the double-lined arrow) could return the system to S_1 without the accompanying need to reduce environmental conditions below E_1 .

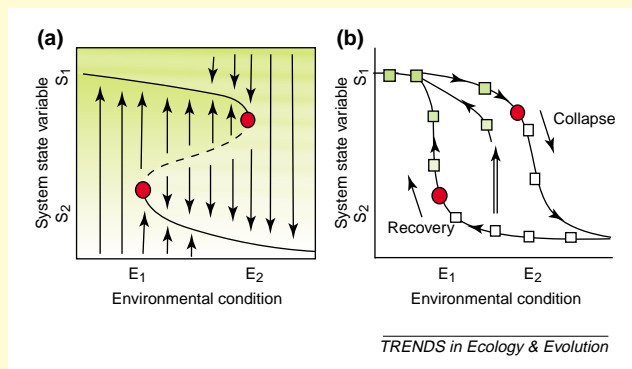


Figure 1.

Box Glossary

System state variables: features of the biological community (animals, plants, and microbes) and the physical environment that characterize the functions and processes of the system.

Unstable equilibrium: a combination of a system state and environmental condition that can only persist at the specified conditions; even minor perturbations will move the system away from these points. Also referred to as a repeller.

rangelands [14,15] and lake systems [27,28] for over a decade. Hobbs and Norton [29] argued for the use of alternative ecosystem state models as a conceptual basis for the general restoration of degraded systems. Although terminology differs (Table 1), this view is the basis of many

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recent efforts to develop a framework for the recovery of degraded systems.

Rigorous tests of whether a degraded system truly represents an alternative and STABLE EQUILIBRIUM [41,42] are beyond the scope of most restoration efforts. Although restoration management decisions for a particular remnant need to be decided relatively rapidly, it is difficult to detect internally maintained alternative states over small areas and short time periods, particularly in comparison to slow transient successional change [43]. Additionally, degraded systems probably will rarely meet the stability criterion that is central to this theory (Box 2) because most communities are continually subjected to new invasion and species turnover. However, experimentation and monitoring of the responses to management can provide evidence as to whether states are internally reinforced. Given the risk of inappropriate management sending the degraded system in an unintended direction, it might be more costly to assume that a single dimension controls system dynamics rather than that alternative states exist and are determined by interactions among many factors [44].

Feedbacks that increase resilience in degraded systems

Recent work indicates that biotic factors, such as the invasion of species that influence biogeochemical cycling, shifts in trophic interactions, loss of landscape connectivity and loss of native seed sources, are crucial elements that influence restoration. Feedbacks between these biotic factors and components of the physical environment constrain management efforts for restoration (Figure 2) [6,7,25,45]. These constraints can operate at multiple scales, and the dynamics at one scale can affect those at another [39,46]. In addition, the temporal sequence of changes can create priority effects [10] and shape landscape processes [47] that constrain other dimensions of recovery. Here, we examine four constraints that contribute to the ecological resilience (and/or ECOLOGICAL RESISTANCE in some cases) of degraded systems and, thus, the maintenance of alternative degraded states.

Species effects

Often a degraded system is characterized by species that respond differently (or not at all) to the historical disturbance regime that once maintained the structure and composition of the system in its former state. The new species (native or exotic) that comprise the degraded community often have distinctive traits that can change the ecosystem characteristics of the system, such as rates of resource turnover, nutrient distribution and disturbance regimes [48,49]. Once species have changed ecosystem processes, positive feedbacks can increase the resistance of the system in its degraded state and make it resilient to restoration efforts [3,20]. For example, introduced grasses in woodlands in Hawaii alter nitrogen cycling and promote fire, which further benefits introduced grasses at the expense of native shrub species, creating an internally re-enforced state that has proven very difficult to change [50,51].

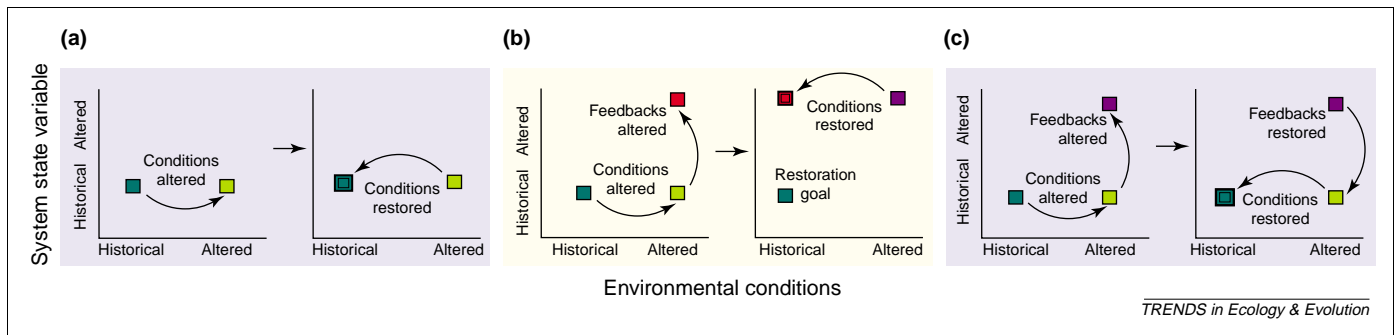


Figure 2. Three alternative restoration scenarios: two that meet their restoration goals (in blue) and one that does not (in yellow). In case 1 (a), changes in the system result primarily from alterations of historic environment (e.g. the disturbance regime or abiotic conditions), and re-establishment of historic environmental conditions returns the system along a successional trajectory (from the light-green to the dark-green square). In case 2 (b), changes in the historic environment are accompanied by changes biotic processes that shift the internal dynamics of the system (e.g. shifts in plant–soil feedbacks or limitation of propagules). The re-establishment of the historical environmental conditions can have unintended (or no) effects on the system state and can shift the system along another trajectory (to the red square). The restoration goal is not met. In case 3 (c), biotic constraints are addressed, shifting the internal feedbacks in the system (from the purple to light-green square). Then, disturbance/abiotic re-establishment might be sufficient to return the system to historical conditions. The major difference among these cases is the presence (and strength) of internal controls within the degraded system. Recent work suggests that system thresholds and feedbacks are common in degraded systems and restoration that takes these controls into account (i.e. case 3) is often very effective. Although these scenarios assume that the goal of the restoration is to a state approximating pre-degradation conditions, these scenarios also apply to other goals (i.e. designed ecosystems).

Trophic interactions

Patterns of herbivory and other trophic interactions are often altered in degraded systems in ways that increase the resilience to restorative efforts. For instance, herbivory by deer slows the recovery of woody species in riparian systems because they selectively feed on regenerating saplings [52]. In rangelands, redistribution of herbivores causes positive feedback between reduced herbaceous plant cover and increased losses owing to grazing, contributing to the further collapse of the system [16,17].

Landscape connectivity and seed source

The lack of landscape connectivity and sufficient local seed sources can also severely limit the regeneration of native species in degraded communities [6]. Declines of source populations of native species as a consequence of habitat destruction and fragmentation limit the effectiveness of regional pools as a source of propagules for recolonization. This, combined with the absence of native species in the degraded site and the loss of a native seedbank, limit the regenerative ability of many native species in restoration

Table 1. Concepts of restoration concordant with alternative ecosystem state ideas

Term	Description	Other related ideas	Refs
State-and-transition	Typically applied to the management of semi-arid rangeland systems, where vegetation exists in multiple states (e.g. grassland, shrubland, or desert) and changes in management or environmental factors (e.g. change in grazing pressure or fire regime) drive the transition from one state to another	Non-equilibrium persistent model of vegetation dynamics	[14,30–31]
Alternative equilibrium	The shift in lakes from a clearwater, macrophyte-dominated to a turbid, algal-dominated state has long been described as a shift between alternative states	Phase shifts	[18,27–28]
Directed succession	Alternative successional trajectories are possible in a system. Restoration can influence which trajectory of change occurs in the transition from degraded to desired state; e.g. applying topsoils to mined areas can ensure recovery to a particular community type by supplying propagules and soil resources	Active restoration; assisted revegetation	[26,32–34]
Catastrophic vegetation shifts	A relatively rapid collapse in ecosystem state to a degraded state that can be irreversible occurs as a result of a small change in the environment; e.g. a small increase in grazing pressure reduces vegetation cover below some threshold that results in increase erosion, diminished plant growth and increased grazing pressure, leading to desertification	Ecosystem surprises, unexpected vegetation developments	[4,16,20,35–36]
Restoration thresholds	Barriers to restoring degraded systems that result from feedbacks between the degraded state and internal or external factors; e.g. recruitment limitation of propagules of native vegetation in highly invaded systems and the fragmentation (or absence) of source pools in the surrounding landscapes	Resilience to management; synergisms among degradative factors	[3,6,37–39]
Non-equilibrium dynamics	Many authors refer to alternative states as reflecting (or resulting from) nonequilibrium dynamics in a system. The theory of alternative states assumes equilibrium dynamics, although it is unclear the degree to which the application to management depends on this distinction		[31,40]

projects [53,54]. Unfortunately, although native species often become demographically vulnerable as a result of habitat fragmentation, invasive or otherwise undesirable species are often well established in degraded lands. These problematic species can dominate the seedbank and seed rain of a degraded system and, thus, management efforts can have the unintended effect of facilitating the spread of these species. For example, in reviewing the effects of controlled burns, D'Antonio [55] found that fire more often facilitated rather than controlled exotic species.

Long-term change

Long-term changes in the mean or variability of climatic factors can also influence system dynamics. For instance, changes in the frequency of wet/dry years or severe droughts influence the effect of natural disturbance regimes and drive compositional changes that can impede or facilitate restoration [56]. Climatic warming might be a chronic contributing factor to degradation of a system that is accelerated by other human activities [17]. Similarly, chronic addition of atmospherically deposited nitrogen can change the effectiveness of natural disturbances and facilitate the invasion of species [57,58]. Degradation that is due to changes in global or large-scale regional factors, such as climate change, will be more difficult, and perhaps impossible, to reverse through local management efforts.

Putting the new perspective into practice

Management tools

The development of a new framework on which to base management decisions is accompanying the recognition that some degraded systems represent a resilient alternative state (Figure 3). Given the appropriate goals for a given restoration [59], more attention is being paid, both experimentally and observationally, to identifying the ecological constraints that create internal feedbacks. Both multiple and single factor constraints can make a system resilient to management, but, if there are multiple constraints, it is crucial to prioritize these and to determine whether they should be addressed singly or in tandem to reassemble the community [10]. It is becoming clear that most constraints will only be identified through experimentation and comparative synthetic analyses; site-specific trial and error approaches should be avoided [3,5]. Methods to predict the strength of constraints before actual restoration action deserve further attention and development.

If only a single constraint exists, decisions regarding restorative measures can be relatively straightforward. Such is the case for systems that can recover according to a successional model: often re-establishing the historical disturbance regime and/or physical process will enable the rest of the system to self-organize and assemble with little or no further management intervention [9,11].

However, if multiple constraints exist, prioritizing these constraints might be crucial. Research indicates that management actions that address multiple constraints simultaneously (e.g. burning and adding native seeds) often prove more successful than would either approach alone [5,24,60]. Although comparisons among different sequences of restoration has been limited [10],

actions to address constraints that produce strong feedbacks (e.g. removing species with strong biogeochemical effects) might need to be implemented before other tools will be effective. Ultimately, the allocation of resources (time and money) will also need to be considered in determining the order and extent of actions. If a strong constraint can be identified, but it is unclear what action would shift the system across a recovery THRESHOLD or if that action is cost prohibitive, then it might be necessary to either modify the restoration goal or allocate resources elsewhere.

Once constraints have been prioritized, the internal feedbacks that constrain restoration of the degraded state should be disrupted and the system perturbed in ways that will facilitate the transition to the desired state [7,29]. The choice of management action is dependent on which constraints are prioritized (Figure 3). In many systems, restoration requires a PERTURBATION that mitigates the biogeochemical and physical effects caused by a problematic species before the system can respond to any other management. For instance, topsoil removal, the mowing and removal of biomass, and/or carbon addition have been successfully used in systems in which enhanced fertility levels are a proximate cause of the degradation [24,53]. Repeated mowing and hay removal in chalk grasslands reduced the dominance of Tor grass *Brachypodium pinnatum*, a species that aggressively invades following agricultural abandonment, from 90% to <40% in seven years, and increased species richness by 90% [24]. Reducing nitrogen levels in tallgrass prairie plantings by adding carbon reduced weed biomass by 50% and increased the abundance of desirable prairie plants sevenfold [61]. Other systems require the enhancement of fertility, addition of specific nutrients and establishment of symbiotic relationships for successful restoration. Adding 10 cm of topsoil to a heavily invaded mine site increased species richness by 250% [60]. Selective removals of problematic species that have strong biogeochemical feedbacks have also been used with success in several systems [37,48]. Altering regional and local seed pools, both by managing surrounding areas and by translocating plants or adding seeds, facilitates the re-establishment of desired species [6,22,34,60]. For example, goose herbivory converts salt marsh swards to hypersaline mudflats off Hudson Bay. Although the reduction of herbivory does not facilitate recovery, salt marshes can be restored when plugs of *Puccinellia phryganodes*, a former dominant species, are transplanted into the mudflats [34]. Finally, although global climate change might be a contributing factor to the degradation, managers might be able to plan actions in conjunction with predictable variations in climate, such as El Niño events [56].

To determine whether actions have forced a shift in system state, the system should be repeatedly characterized after the constraints have been addressed. It will become increasingly important to develop coordinated data collection and reporting systems to disseminate information concerning how systems respond to management in relation to their system state and changed ENVIRONMENTAL CONDITIONS. Synthesized quantitative

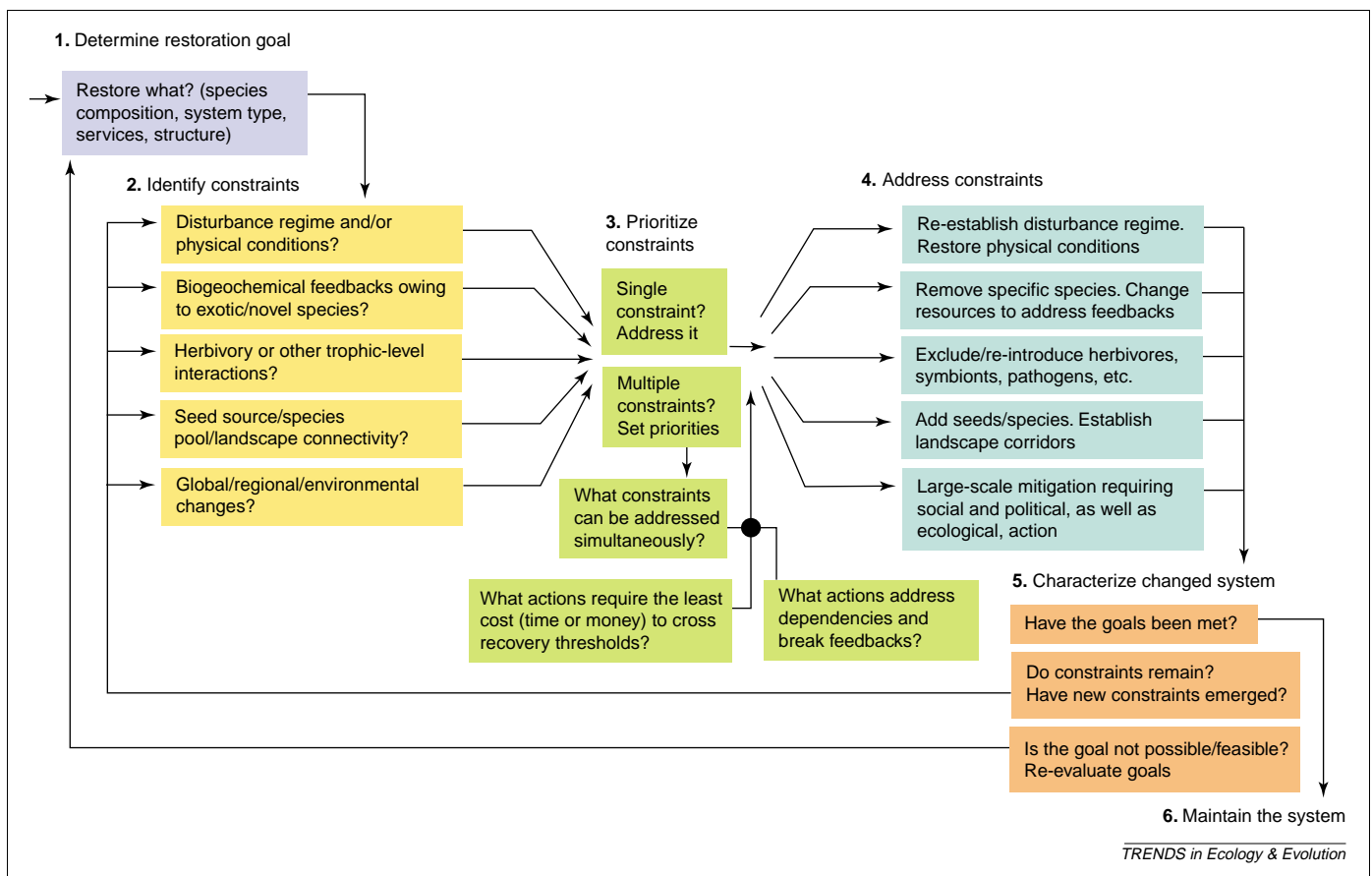


Figure 3. Incorporating alternative state ideas into restoration practice. First, the specific restoration goal should be determined. Usually, goals pertain to particular species composition, system structure or function. Although restoration goals generally concern the return of a system to a state approximating conditions before degradation, goals pertaining to the restoration and/or creation of particular services or functions might be more feasible in some cases. Second, constraints should be identified in the degraded system. In addition to disturbance and physical constraints, we describe four types of biotic constraints that are barriers to restoration: biogeochemical feedbacks, trophic-level interactions, propagule limitation, and regional environmental change. In most cases, experimentation is the best way to identify the constraints that exist in a given system. Third, these constraints must be prioritized, particularly in the all too frequent case when multiple constraints exist. High priority should be given to constraints that can be addressed simultaneously, require the least cost to cross recovery thresholds, and those that have strong dependencies or feedbacks to the rest of the system. Fourth, the prioritized constraints should be addressed. Actions depend on the specific constraints and, if possible, their efficacy should be tested before implementation. The fifth step would be to characterize the changed system. The monitoring program should determine whether the goals are being met and which constraints remain. Goals might have to be re-evaluated at this step and the process should be re-initiated at step one. If goals have been met, emphasis can shift from restoration to the final step, maintenance of the system, which could involve very different actions than those required to shift states.

information from these efforts would substantially enhance the predictive capacity regarding future restoration efforts.

Future questions and next steps

The emerging link between theoretical models of alternative ecosystem states and restoration ecology is an exciting development. It has the potential to advance both the practice of restoration and our understanding of the dynamics of degraded systems (Box 3). More small-scale mechanistic studies and large-scale landscape manipulations are needed to test which aspects of the theory are important, what system characteristics indicate the presence or absence of alternative ecosystem states, how to determine whether thresholds exist, and the relative strengths of different factors affecting resilience in degraded systems. Addressing these questions involves characterizing internal feedbacks that enforce the resilience of degraded systems [38], testing the relative effectiveness of different restoration tools across environmental gradients [53] and quantitatively synthesizing results from a range of projects to determine environmental contingencies [48,62–63].

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Conclusions

The challenge to develop effective tools to restore degraded lands will become increasingly important over the next few decades. Most restoration efforts have focused on

Box 3. Outstanding questions

- What are appropriate system-specific predictors of recovery thresholds? How can managers determine whether thresholds exist?
- Under what conditions are the assumptions of stability and equilibrium dynamics important in the application of alternative state models to degraded systems?
- Are there predictable characteristics that indicate when a system will follow a successional pathway and/or that indicate the presence or absence of alternative ecosystem states?
- What constraints are most likely to be irreversible? What are the relative strengths of different constraints and feedbacks in degraded systems?
- How does temporal and spatial variation influence restoration constraints? Do environments or systems predictably vary in the strength of particular constraints and/or in the efficacy of breaking those constraints?
- Is resilience to the restoration of cross-scale processes stronger than the resilience of local-scale processes?

identifying important elements that maintain community structure in pristine systems and on re-establishing these elements. However, recent work suggests that characterizing alternative controls of community structure and ecosystem function in the degraded state is essential for predicting how some degraded systems will respond to restorative measures. Models of alternative ecosystem states incorporate system thresholds and feedbacks that might explain why the degraded system is resilient to restoration. These models emphasize the need to identify how biotic and abiotic factors have been modified as a consequence of degradation. They suggest that carefully selected perturbations can release degraded systems from strong internal feedbacks and landscape controls. As a result, the linkage between alternative state theory and restoration ecology is advancing both the practice of restoration and our understanding of the dynamics of degraded systems.

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