Alternative states and positive feedbacks in restoration ecology

Katharine N. Suding\textsuperscript{1,2}, Katherine L. Gross\textsuperscript{2} and Gregory R. Houseman\textsuperscript{2}

\textsuperscript{1}Department of Ecology and Evolutionary Biology, University of California at Irvine, Irvine, CA 92697, USA
\textsuperscript{2}W.K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, MI 49060, USA

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 \cite{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 \cite{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 \cite{5,6}. Increasingly, research is documenting that degraded systems are often in a persistent, resilient, \textit{ALTERNATIVE STATE} (see \textit{Glossary}), requiring a unique recovery pathway (Figure 1, \cite{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 \cite{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 \cite{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 \cite{12,13}.

In other cases, restoration relying on successional recovery has been unpredictable. For example, Anderson \textit{et al.} \cite{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 \textit{Salix humilis})

\textbf{Glossary}

Based on \cite{36,38}

\textbf{Alternative states:} alternative combinations of ecosystem states and environmental conditions that may persist at a particular spatial extent and temporal scale.

\textbf{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.

\textbf{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.

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

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

\textbf{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.

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

Corresponding author: Katharine N. Suding (ksuding@uci.edu).

http://tree.trends.com 0169-5347/$ - see front matter © 2003 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2003.10.005
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 Ia) [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, E1 and E2 (Figure Ia, red dots), bound stable equilibrium (or attractors, Figure Ia, solid black lines) and unstable equilibrium (or repellors, Figure Ia, dashed black line). S1 and S2 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 Ib). For example, at S1 a shift in environmental conditions below E2 will always result in the system returning to the ‘green’ ecosystem state S1. However if environmental conditions are shifted above E2, the system collapses to S2 (the ‘white’ state). At environmental conditions between E1 and E2, the system could return to either the green S1 or the white S2 state depending on the initial conditions (whether at S1 or S2, for example). For instance, rangeland might persist in ecosystem state S1 as grazing pressure increases from E1 to E2 (the green zone along the line in Figure Ia). However, if grazing pressure increased beyond E2 the system would ‘collapse’ to a degraded system dominated by shrubs (S2) because a threshold point has been exceeded. Once the system has collapsed to S2, it will not recover or return to the grassland state (S1) unless grazing pressure (or some other factor) is reduced to E1. This recovery could be costly and slow compared with the collapse (Figure Ib), 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 Ib, the double-lined arrow) could return the system to S1, without the accompanying need to reduce environmental conditions below E1.

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].

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 repellor.

Figure I.

(a) E1 E2
System state variable: S1
Environmental condition
(b) E1 E2
System state variable: S2
Environmental condition

http://tree.trends.com
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.

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 return a system to a particular community type, they also apply to other goals (i.e. designed ecosystems).

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

<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
<th>Other related ideas</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>State-and-transition</td>
<td>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</td>
<td>Non-equilibrium persistent model of vegetation dynamics</td>
<td>[14,30–31]</td>
</tr>
<tr>
<td>Alternative equilibrium</td>
<td>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</td>
<td>Phase shifts</td>
<td>[18,27–28]</td>
</tr>
<tr>
<td>Directed succession</td>
<td>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</td>
<td>Active restoration; assisted revegetation</td>
<td>[26,32–34]</td>
</tr>
<tr>
<td>Catastrophic vegetation shifts</td>
<td>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 increased erosion, diminished plant growth and increased grazing pressure, leading to desertification</td>
<td>Ecosystem surprises, unexpected vegetation developments</td>
<td>[4,16,20,35–36]</td>
</tr>
<tr>
<td>Restoration thresholds</td>
<td>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</td>
<td>Resilience to management; synergisms among degradative factors</td>
<td>[3,6,37–39]</td>
</tr>
<tr>
<td>Non-equilibrium dynamics</td>
<td>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</td>
<td></td>
<td>[31,40]</td>
</tr>
</tbody>
</table>
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
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].

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...
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.

Acknowledgements
This work developed from a prairie–savanna restoration project funded by the Michigan Department of Military and Veterans Affairs, with support from NSF-LTER Program (Kellogg Biological Station). Final synthesis and writing was conducted at National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0072909) and the University of California, whilst K.L.G. was a sabbatical fellow there. Discussions with P. Buston, P. Lundberg, E. Seabloom, T. Seastedt and the University of California, whilst K.L.G. was a sabbatical fellow there. Discussions with P. Buston, P. Lundberg, E. Seabloom, T. Seastedt and comments from S. Emery, F. Gerhardt, M. Smith, R. Smith and J. Zedler helped clarify the ideas presented here. This contribution #1005 of the Kellogg Biological Station. J. Zedler helped clarify the ideas presented here. This is contribution #1005 of the Kellogg Biological Station.

References


---

**Endeavour**

the quarterly magazine for the history and philosophy of science

You can access *Endeavour* online either through your *BioMedNet Reviews* subscription or via *ScienceDirect*, where you’ll find a collection of beautifully illustrated articles on the history of science, book reviews and editorial comment.

featuring

‘Dr. Steinaeh coming to make old young!’: sex glands, vasectomy and the quest for rejuvenation in the roaring twenties by C. Sengoopta

Cheese mites and other delicacies: the introduction of test objects into microscopy by J. Schickore

An herbal El Dorado: the quest for botanical wealth in the Spanish Empire by P. De Vos

Zones of inhibition: interactions between art and science by K. Davies

Global science: the eruption of Krakatau by M. Dörrries

Two pills, two paths: a tale of gender bias by M. Potts

Joseph Banks: Pacific pictures by P. Fara

and coming soon

Mr Blandowski misses out: discovery and loss of fish species in 19th century Australia by P. Humphries

The traffic and display of body parts in the early 19th century by S. Alberti and S. Chaplin

Exhibiting monstrosity: Chang and Eng, the ‘original’ Siamese twins by S. Mitchell

The ancient mariner and the transit of Venus at Hudson Bay by R. Griffin-Short

‘I got rhythm’: Gershwin and birth control in the 1930s by P. Viterbo

The market for Julia Pastrana by J. Browne and S. Messenger

Race mixing and science in the United States by P. Farber

Continental drift under the Third Reich by E. Buffetaut

The first president of the Royal Society by P. Fara

and much, much more . . .

Locate *Endeavour* in the *BioMedNet Reviews* collection (http://reviews.bmn.com) or on *ScienceDirect* (http://www.sciencedirect.com)