Identifying Linkages among Conceptual Models of Ecosystem Degradation and Restoration: Towards an Integrative Framework

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Abstract
We present an ecological framework for considering ecosystem degradation and restoration, particularly in rangelands and arid environments. The framework is a synthesis of three conceptual models previously developed by several rangeland and restoration ecologists. We focus first on distinctions and connections between structural and functional components of rangeland ecosystems and then on distinctions and connections between biotic and abiotic components of the ecosystem. We next show that the structural/functional and biotic/abiotic distinctions can be integrated with a stepwise, positive feedback model of degradation to help explain degradation processes and restoration approaches. Finally, we relate those concepts to a threshold model of rangeland degradation. By establishing the conceptual links among these different models, this synthesis provides a broader, more integrated framework for thinking about the dynamics involved in rangeland degradation and restoration. We conclude by presenting some approaches to restoration that are motivated by the suite of concepts that are brought together in the framework.

Key words: degradation spiral, ecosystem function, rangelands, restoration thresholds.

Introduction
In this study, we discuss ecological principles relating to ecosystem degradation and restoration and how those principles can play an important role in the development and success of restoration activities. We focus on rangeland ecosystems, but the principles developed here may have broader applicability to many other types of ecosystems.

Historically, the development of rangeland restoration practices has been largely driven by information gleaned from context-specific, empirical attempts to restore degraded landscapes. Some strategies seem to work well, whereas others often fail, and some strategies work well in one situation but not in another. As a result, the information available for guiding the development of future restoration projects is often very anecdotal, which makes it hard for restoration practitioners to formulate sound strategies for novel situations or to learn from one another’s successes and failures (Hobbs & Norton 1996; Choi 2004).

There is, however, a great deal of ecological theory that relates to landscape and rangeland degradation, which has been well developed, debated, and tested (e.g., Connell & Slatyer 1977; Noy-Meir 1985; Laycock 1991; Hobbie 1992; Milton et al. 1994; Tongway & Ludwig 1994; Callaway 1995; Schlesinger et al. 1996; van de Koppel et al. 1997; Briske et al. 2003; Mayer & Rietkerk 2004; Cingolani et al. 2005; Ludwig et al. 2005). A salient endeavor of restoration ecology has been to emphasize and develop the relationships between such theoretical works and their application to restoration practices. To this end, several insightful conceptual models have been generated, which explain different components of degradation and focus on their relevance to restoration (Aronson et al. 1993; Milton et al. 1994; Aronson & Le Floch 1996; Ludwig et al. 1997; Whisenant 1999; Breshears et al. 2001; Perrow & Davy 2002a, b; Gomez-Aparicio et al. 2004; Mayer & Rietkerk 2004; Temperton et al. 2004). In many instances, the various conceptual models do not directly conflict with one another. Instead, they focus on different components of degradation or restoration or they address dynamics in different contexts. Even the debates between equilibrial, threshold, and nonequilibrial models of rangeland dynamics have been recently reviewed and to some extent reconciled as largely compatible and complementary perspectives within a broader contextual spectrum (Briske et al. 2003; Mayer & Rietkerk 2004; Vetter 2005).

The above recent reviews illustrate the importance of revisiting conceptual models to explore their links in order to integrate disparate components and build a more useful and complete understanding of ecosystem dynamics and restoration practices. Linking together disparate conceptual models to create a broader conceptual framework can prove useful in several ways to the development of practical restoration plans. Using a set of guiding principles that
are disjunct or context specific can lead to restoration plans that only deal with a portion of relevant dynamics or place improper emphasis on some dynamics, whereas others are neglected. When there are clear logical links between multiple components of an integrated framework, the suite of concepts becomes more intuitive and can be more effectively applied as a foundation for planning or evaluating restoration projects. Because they include multiple and complementary perspectives, integrated frameworks can also help both researchers and practitioners better evaluate why some strategies may succeed and others fail and judge the potential advantages and disadvantages to using a given strategy in a novel situation. An integrated conceptual framework can thus provide a powerful tool for making ecologically sound translations between broad generalizations and context-specific or ecological process-specific information.

In this study, we present a synthesis of three conceptual models relevant to rangeland degradation and restoration, showing how the different concepts relate to one another. The goal is to thereby generate a broader, more integrated ecological framework for thinking about ecosystem restoration and facilitating effective restoration practices. The first concept we explore focuses on distinctions and connections between structural and functional components of rangeland ecosystems and also on distinctions and connections between biotic and abiotic components of the ecosystem. Next, we show how those distinctions add to our appreciation of another conceptual model that depicts degradation as a stepwise positive feedback cycle. Finally, we relate both of those conceptual models to threshold models of rangeland degradation. We conclude by presenting some approaches to restoration that are directly motivated by the suite of components that are brought together in the framework.

Structural versus Functional Approaches

Structure versus function is a common and widely useful dichotomy in ecology. Extending that dichotomy to restoration, Whisenant (1999) made a distinction between structural versus functional approaches in restoration strategies (Fig. 1). When assessing degradation, the structural approach focuses upon static patterns, whereas the functional approach instead aims to assess the dynamic processes that contribute to those patterns. And in terms of restoration strategies, the structural approach tends to focus upon mechanical manipulations of components of ecosystem structure, whereas the functional approach instead attempts to manipulate the interactions and dynamics—the ecological processes—which have been degraded.

The difference in approaches has direct bearing on how the desired outcome of restoration is conceived and achieved. Under the structural approach, restoration is considered successful if the degraded patterns are altered to more closely resemble the predisturbance state. Such restoration tactics can rapidly transform the structural components of degraded system to more closely resemble a healthier ecosystem, providing a “quick fix”. However, because the dynamics and processes that generated the degraded patterns are not directly considered or manipulated, this approach offers little certainty that the restored patterns will persist over time. The functional approach, on the other hand, evaluates restoration success based on the recovery of ecological processes and dynamics. If the processes that sustain ecosystem recovery are reinstated, it follows that this approach will result in a higher certainty of long-term sustainability of the restoration effort. Reinstating an integrated set of ecological dynamics and feedback cycles is often a slower and more gradual process, so this approach may not generate the rapid structural repairs that mechanical manipulations can achieve (Whisenant et al. 1995; Tongway & Ludwig 1996; Whisenant 1999). The structural and functional approaches are not mutually exclusive, but the dichotomy illustrates the two extremes of a continuum of approaches.

Biotic and Abiotic Factors

In addition to distinguishing between structural and functional components of ecosystems, one can also make distinctions between abiotic and biotic components. We can now visualize a $2 \times 2$ matrix, with structure and function as two columns and abiotic and biotic as two rows (Fig. 2). Characterizing ecosystem attributes in this way draws attention to distinctions among different ways to assess rangeland degradation and among different approaches to improve the status of the assessed indicators. To help make these distinctions clearer, we consider a few examples. An example of an abiotic component of rangeland degradation is soil erosion. Structurally, erosion may be indicated by eroded landforms, with rills and gullies. A structural approach to restoration would be to fill in erosion gullies and create mechanical barriers, thereby manipulating the degraded structure. From a functional point of view, soil erosion indicates degraded soil-water dynamics, such as low water infiltration, high surface water flow, and soil loss during rain. When erosion is viewed from a functional perspective, the way to repair it is to modify the degraded processes, such as increasing water infiltration into the soil and improving soil structure (Tongway &
changes continue to feedback on one another to cause a spiraling decline in ecosystem structure and function. This model represents the basic ecological dynamics of degradation in rangelands, drawing together decades of empirical work and ecological theories of ecosystem dynamics. It provides an explicit framework of the links between different ecosystem components, with causal steps indicating that changes in one elicit changes in a subsequent component. But the model is not in itself a complete view of the process. By exploring its conceptual links to other models, complementary ideas may be identified that, when considered together, provide additional insight into degradation processes and restoration options.

This stepwise degradation model can be considered in terms of the above framework of structure versus function and abiotic versus biotic components. To draw linkages between the two models, each of the steps in Whisenant’s stepwise degradation model can be classified as structural or functional and biotic or abiotic (Fig. 3b). When this is done, it becomes evident that changes in structures affect function and vice versa. Also, changes in abiotic components affect biotic components and vice versa. When the distinctions between the structure/function/biotic/abiotic components of an ecosystem are overlaid onto the stepwise degradation diagram, the dynamic interconnectedness among the components becomes clearer (Fig. 4a). As an ecosystem is degraded, there are negative changes in all these components, and they feed back onto one another. Figure 4 is not necessarily meant to imply a consistent direction of feedback amongst the quadrants. Rather, the downward spiral is meant to generally illustrate that degradation involves feedback via interconnectedness among all the abiotic, biotic, structural, and functional components. If stresses continue to contribute to the degradation, whether they are biotic or abiotic, they can send the ecosystem spiraling towards worse and worse loss of structure and function (Fig. 4b). This feedback cycle, involving interplay between the structure and the function of biotic and abiotic components, reflects the conceptual links between the dichotomous models and the stepwise feedback model. Next, we will consider its bearing on restoration practices.

A conceptual framework that specifies categories for ecosystem processes and shows how those processes are dynamically linked can serve as a kind of map for restorationists to visualize the context of degradation. In terms of the framework, restoration ecologists and ecosystem managers seek to reverse the downward feedback spiral toward degradation. They want to restore functions and improve structures, for example, to improve water infiltration (abiotic function) and increase vegetation (biotic structure). The goal is to generate feedback loops that will initiate and promote the continued improvement of ecosystem components, thereby reversing the direction of the arrow of degradation (Fig. 4c). This is what is meant by the term autogenic recovery: self-sustaining feedback loops that lead to continued improvements in ecosystem attributes (Whisenant et al. 1995; Whisenant 1999). The

Ludwig 1996; Breshears et al. 2001). An example of a biotic component of rangeland degradation is weed encroachment. Structurally, this is assessed in terms of an undesirable pattern of species composition of the vegetation, which could be rectified by removing undesirable species and planting desirable ones. From a functional point of view, the degradation could be viewed in terms of competitive dynamics, wherein weedy species outcompete desirable species. Restoration would attempt to manipulate the competitive dynamics by, for example, altering the disturbance regime to favor desirable species establishment and persistence (Berger 1993; Eliason & Allen 1997; Sheley & Krueger-Mangold 2003).

The distinctions between structure and function, and abiotic and biotic ecosystem attributes, help the restorationist classify different possible approaches to restoration and see how those approaches are related to different restoration outcomes. However, the model does not elaborate on the relationships between structure and function nor the interactions among ecosystem components that occur during degradation or restoration. Designing restoration strategies to optimize short- and long-term restoration outcomes will require not only an understanding of the abiotic/biotic and structure/function distinctions but also an understanding of the interactions among them.

**Stepwise Degradation Cycle**

Whisenant (1999, 2002) proposed a separate conceptual model that does describe the interactive dynamics involved in degradation, characterizing them as a stepwise process with feedback (Fig. 3a). The model shows a sequence of changes in ecosystem components. These changes continue to feedback on one another to cause
framework illustrates that these components are all linked. But where does the practitioner intercede and target manipulations to start pushing the cycles back toward improvement? With which ecosystem components is it best to begin? With function? With structure? Abiotic? Biotic? Are there circumstances under which abiotic manipulations are more important than biotic ones? Although the model thus far is helpful for understanding the components, dynamics, and the nature of feedback among them, it still does provide much guidance as to where interventions should be targeted and under what circumstances. Linking the current framework with yet another conceptual model can bring us closer to answering those questions.

**Thresholds**

Figure 5 shows the concept of abiotic and biotic thresholds, following conceptual models initially put forward by Milton et al. (1994) and later developed by Whisenant (1999, 2002) and Hobbs and Harris (2001). There are three main stages of degradation, with thresholds between them that represent barriers to the potential ecosystem recovery. Starting at the left of the diagram, in the first stage, biotic function is degraded, but the system still has the capacity for autogenic recovery if the cause of degradation is removed. If degradation continues, the first threshold of recovery potential is crossed. The first threshold represents heavy damage to biotic function. If an ecosystem has crossed over this threshold and is in the second...
stage of the diagram, some manipulation of biotic components, beyond removal of disturbance, will be required for autogenic recovery to take place. Although abiotic functions may have been degraded in the second stage, they still maintain some resilience in terms of their capacity to recover without direct manipulation. Beyond the second threshold, in the third stage of the diagram, biotic processes are severely dysfunctional and abiotic function has been degraded beyond its resilience. In this final stage of degradation, abiotic components require manipulation in order to make autogenic recovery possible.

Our first model’s distinction between biotic and abiotic functions is particularly relevant in the threshold model, when viewed from the perspective of resource regulation and retention. Two significant generalizations arise. First, healthier and higher resource rangelands tend to be regulated more by biotic interactions, whereas in low-resource rangelands, resource loss is more abiotically mediated (Tongway & Ludwig 1996; Whisenant 1999). As a consequence, any given rangeland’s starting point on the x-axis in the threshold model depends on the inherent resource levels in the ecosystem. Arid rangelands “start” closer to degradation thresholds than wetter prairies. Second, degradation tends to shift resource regulation from biotic to abiotic processes. This shift from biotic to abiotic control usually leads to accelerated resource loss. The most severe degradation occurs when both biotic and abiotic functions are damaged, and there is nothing left to control resource loss (Schlesinger et al. 1990; Kassas 1995; Le Houerou 1996).

Another important aspect of this model is that it describes changes in function, not structure. This has important bearing on restoration goals and outcomes, as discussed earlier (see Structural versus Functional Approaches). When one manipulates the system to cross back over a degradation threshold, this model refers to the restoration of function. But there is no guarantee that the original structural components will or even can be restored. This is one way to define restoration versus rehabilitation. Restoration is usually an effort to restore original function and structure. Rehabilitation, on the other hand, is the effort to restore function, usually in heavily degraded systems that have crossed a threshold, with the realization or acceptance that the original structure may not be possible to attain. So by considering the threshold model in light of the structural/functional dichotomy, we find that the threshold model is more germane when the goal is restoring ecosystem function rather than recreating a historical landscape.
If we revisit the earlier questions regarding appropriate targets for restoration interventions, the threshold model indicates that, even though abiotic and biotic processes are linked through feedback loops, there is some basic level of abiotic structure and function that is necessary before biotic components can be established and functional. This is the reason why abiotic processes are often termed “primary” in threshold models (Whisenant 1999). Thus, to initiate autogenic recovery in severely degraded systems, restoring abiotic functions is a priority. However, if degradation is moderate, biotic manipulations should be adequate to initiate autogenic recovery. This provides a greater ability to prioritize restoration tactics, but it raises another critical practical question: is there any way to know if a given rangeland has crossed one of the degradation thresholds?

Researchers have developed a range of monitoring methodologies that evaluate ecosystem function by measuring various environmental indicators (e.g., Landscape Function Analysis [Tongway & Hindley 2004a], Rangeland Health Indicators [Pyke et al. 2002], and Vital Landscape Attributes [Aronson & Le Floch 1996]). In relation to Figure 5, evaluating ecosystem function can determine a system’s location on the y-axis. The next step is to interpret this level of ecosystem function in the context of the trajectory of degradation and thresholds along the x-axis. In order to determine where a given ecosystem lies on the trajectory of degradation, one needs to know more about the shape of the function describing how ecosystem function varies with stress or time. Measuring changes in ecosystem function over time or over a range of sites that have experienced different levels of disturbance, allows the construction of such a function and identification of regions of rapid change that represent thresholds. Landscape Function Analysis combines a protocol for measuring indices ecosystem functioning with an interpretive framework and has been successfully applied to several different ecosystems around the world, for which data were collected at multiple sites or multiple sampling times. The resulting trajectories of ecosystem functional change were typically sigmoidal, with an identifiable interval of rapid change that represents a threshold (Tongway & Hindley 2004b).

Ecosystem function assessments across a broad spectrum of degradation levels provide a powerful way for determining a site’s status along a degradation trajectory, but, in practice, such full information is rarely acquired or may not even possible to obtain. If ecosystem indicators are measured at one or just a few sites, or measured at a single point in time or over a short period of time, it can be very difficult to estimate the trajectory or to judge whether a particular site is near a threshold or has crossed one. In such cases, does the synthesis of concepts presented herein offer any potential solutions?

**Implications for Restoration Practice**

The conceptual framework provides a suite of concepts to help understand the components and processes in rangeland degradation and restoration. From this broad conceptual map, we can distill a few key ideas, which taken together, can help in devising effective restoration strategies under a broad range of degradation levels, even if one cannot assess whether thresholds have been crossed. First, the framework indicates that the abiotic processes are primary to ecosystem function, but second, it also stresses that regulation of resources by biotic processes is more effective and is thus an important objective in rehabilitating a degraded rangeland. Third, degradation and initiation of autogenic recovery are both driven by the interconnections and feedback between abiotic and biotic processes.

Based on these ideas, a good general strategy under any circumstance would be to focus on manipulations that will positively affect both abiotic and biotic functions. This does not necessarily entail more effort. Instead, it requires careful and thoughtful selection of a restoration tactic, focusing on how different ecosystem processes will be affected. A restoration strategy should aim to create as much synergy between abiotic and biotic processes as possible and thereby enhance the potential of initiating autogenic and more complete recovery.

Now, we may consider topics relevant to maximizing abiotic and biotic function by strengthening the synergies between them. There is a wealth of information and excellent research on specific abiotic and biotic processes relevant to restoration (Perrow & Davy 2002a, b). In brief, the three main categories of abiotic processes are soil stability, hydrology, and nutrient dynamics. Biotic processes include the dynamics of plant resource availability, plant–plant interactions, soil microorganisms, terrestrial invertebrates, herbivory and other trophic interactions, pollination, and spatially oriented dynamics such as dispersal and effects of habitat fragmentation. Because of the linkages, restoration tactics can be derived that “push” on multiple abiotic and biotic components at the same time and enhance synergistic effects. One possible way to do this is by using biotic components to regain abiotic processes. This addresses the primary importance of reinstating abiotic function if the abiotic threshold has been crossed and also will help regain biotic control of resource dynamics as quickly as possible (Whisenant et al. 1995; Ludwig & Tongway 1996; Whisenant 1999). Facilitation and nurse-plant phenomena offer an excellent tool for this. Facilitator and nurse-plants are so called because they enhance the success of other plants around them, either through biotic interactions or through a variety of stabilizing effects on the abiotic sphere (Callaway 1995). For instance, they can improve soil structure, increase water infiltration, enhance soil retention and prevent erosion, contribute nutrients, and exert control over nutrient cycling (Franco & Nobel 1989; Garner & Steinberger 1989; Bertness & Callaway 1994; Milton & Dean 1995; Pugnaire et al. 1996; Schlesinger et al. 1996; De Soysa et al. 1997; Breshears et al. 1998; Carrillo-Garcia et al. 2000; Walker et al. 2001).
To illustrate the value of using biotic components to drive ecosystem recovery, let us consider a choice of soil surface treatments to reduce erosion and moisture loss from a degraded soil surface. The basic goal is to improve abiotic processes, but the overall impact on autogenic recovery will be greater if biotic processes are simultaneously improved as well. A strictly abiotic approach, such as gravel mulch, would indeed be effective in controlling soil and moisture loss, but a biotic mulch can potentially do much more (Ludwig & Tongway 1996; Slingerland & Masdewel 1996). If dead plant material is used, for instance, cut annual grass as mulch, this also provides the benefits of a pulse of nutrients and perhaps an increase in soil organic matter as the grass decayed. Better yet, if a woody perennial plant is cut and used as mulch, this strategy would additionally enhance soil microbe and invertebrate activity (to break down woody material) and promote tighter control of nutrient cycling because slower decaying perennials in general release their nutrients more slowly (Hobbie 1992; Connin et al. 1997). In terms of autogenic recovery, with the focus on process instead of pattern alone, resource regulation and retention in the system is more important than net amounts of resources, so perennial mulches may be more effective in promoting autogenic recovery, particularly in nutrient-poor systems where rapid nutrient cycling can favor invasive weeds (Carpenter et al. 1990). The most effective strategy of all, however, would be to use living plants as facilitators. They can act as ground cover to prevent erosion and evaporation but can also help reestablish all the links among the other biotic elements, such as mycorrhizal activity, sustained nutrient regulation through cycles of plant uptake and decomposition, litter, and seed trapping, etc. (Vetaas 1992; Ludwig & Tongway 1996).

Another strategy for building upon abiotic-biotic synergies to enhance restoration success is manipulations that reduce the spatial scale of interactions. Like the use of facilitators, this strategy also employs the use of biotic processes to control and restore abiotic ecosystem function. Landscapes that are in good condition generally possess biotic and abiotic components that control the flows of water and material across the landscape by providing barriers, which interrupt these flows at very local levels (Tongway & Ludwig 1994; Wu et al. 2000; Hobbs & Cramer 2003; Ludwig et al. 2005). Often degraded landscapes suffer from loss of abiotic resources, through erosion, decreased water infiltration, and loss of soil nutrients and organic matter (Fig. 6a). These are transported from the site of degradation to another site (Ludwig et al. 2000). These processes often have threshold velocities or rates. For instance, water has to be moving at a certain speed to begin removing soil particles, and these speeds are achieved over long interrupted distances (Tongway & Ludwig 1994). Reinstating biotic elements in such a system will be difficult due to the likelihood that overland flows will displace the biotic material. Reinstating biotic elements in the resource accumulation area of the system may be possible (Fig. 6b) but will not lead to overall improvement in system functioning. If, however, one can reduce the distances over which resources move uninterrupted, the resource loss can be reduced. As the resource movement distances are decreased, the transport all takes place within the site, rather than from the site to another area. Localizing resource movement can thus decrease net resource loss from a site (Fig. 6c). This can be achieved with microcatchments, but it can be even more beneficial to ecosystem recovery if it is combined with a biotic manipulation, such as establishing plants in microcatchments (Fig. 6d) (Tenbergen et al. 1995; Hysell & Grier 1996; Whisenant 2002). If transport distances are reduced to the spatial scale of individual plants, plants can then exert control over abiotic resource flows, beyond what manipulations of topography alone would achieve. Such a strategy not only deals with abiotic resource recapture but also reinstates biotic regulation over resource dynamics, which will help drive the system toward autogenic recovery.

Conclusion

The development of restoration ecology as a science depends on the continued development and refinement of the conceptual basis on which practice rests, which will allow the improved transfer of insights and knowledge from one system to another. In this study, we have aimed to continue the development of an integrated conceptual framework for understanding rangeland degradation and restoration, which identifies the distinctions between structure and function, stresses the feedback between abiotic and biotic processes, and recognizes the importance of degradation thresholds. From the framework, we have derived two strategies that maximize the recovery of both abiotic and biotic processes to enhance a degraded system’s capacity for autogenic recovery. Both of these strategies—using biotic tools for abiotic function repair and reducing resource movement to the biotic spatial scale—are already well known and often utilized in restoration ecology (Whisenant et al. 1995; Ludwig & Tongway 1996; Carrillo-Garcia et al. 1999; Maestre et al. 2001; Aronson et al. 2002; Castro et al. 2002; Gomez-Aparicio et al. 2004). The utility of the conceptual framework is that it aids in understanding why these strategies are effective. It also emphasizes the utility of strategies that target synergies between abiotic and biotic processes and their potential effectiveness under varying degrees of degradation. Thus, by revisiting established models and exploring the linkages among them, we can generate more complete, integrated conceptual frameworks that allow the development, implementation, and transfer of restoration solutions not apparent when models are considered individually. Such conceptual frameworks offer a common, process-oriented perspective for researchers and restoration practitioners in different systems, through which anecdotal experiences can be better understood and ecologically sound restoration strategies can be developed. We seek feedback from researchers and
practitioners as to whether this is the case and whether the framework can be further refined and developed.

**Implications for Practice**

- In this study, we attempt to draw together different strands of conceptual thinking in relation to ecosystem degradation and restoration, with a view to developing an integrated approach that may lead to better understanding of why particular restoration measures work in some cases but not in others and to more transferability of results from one case to another.
- Strong feedbacks exist between the living and the nonliving components of ecosystems. Degraded rangeland systems often have lost plant cover and degradation of the soil ensues.
- Restoration of degraded systems requires identification of where damage has resulted in loss of local control of water and nutrient flows, leading to a degradation “spiral.”
- Modification of soil surface or small-scale topography (such as by constructing “microcatchments”), together with the establishment of plants in these areas, is an effective way to restore local ecosystem processes.
- An understanding of the underlying processes allows methods used successfully in one ecosystem to be transferred effectively to other systems.

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