
The Scale of Successional Models and Restoration Objectives

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Abstract

Successional models are used to predict how restoration projects will achieve their goals. These models have been developed on different spatial and temporal scales and consequently emphasize different types of dynamics. This paper focuses on the restoration goal of self-sustainability, but only in the context of a long-term goal. Because of the temporal scale of this goal, we must consider the impact of processes arising outside of the restoration site as of greater importance than restoration itself. Because ecological systems are open, restoration sites will be subjected to many external influential processes. Depending on the landscape context, the impact of these processes may not be noticeable, or, at the other extreme, they may prevent the achievement of restoration objectives. A second issue is to emphasize the nature of processes in the long term, that they are a complex of characteristics such as magnitude, frequency, and extent. Ecological systems are only adapted to a range of values in each of these characteristics. Restoration often combines goals that are of different scales. Models appropriate to these goals need consideration.

Introduction

The restoration and management of ecological systems has been conceptualized as intervention into the ongoing dynamics of a site, or "applied succession" (McIntosh 1980; Niering 1987; Luken 1990; Glenn-Lewin & van der Maarel 1992; Jordan 1993), even though a site may require considerable initial rehabilitation. Restoration ecology in this context requires specific objectives

(Cairns 1990), and in some cases these might be a particular composition, some functional process reestablished (like tidal flow in marshes), or comparison against a reference site. Intervention might require the reduction or removal of species or circumstances that might prevent site restoration, such as invasive species populations or toxic soil conditions. In other situations, the addition of specific species or the infrequent application of processes such as burning may be needed. The principal objective appears to be the creation of a species mix and environmental conditions that permit the site to become self-sustaining, if that is possible.

This model of restoration inherently implies a view of ecological systems as reflecting the dynamics of underlying processes. The pattern of the biological community and its composition and spatial distribution result from a history of processes at the site. Dispersal rate into the site is one of these processes, as are reproductive rates and interactions among the biological members of the site, changing edaphic conditions, climate, and other familiar abiotic impacts. Ecologists pair the terms "pattern" and "process" together as an indication of this perspective.

A number of implications for restoration arise from this perspective, such as how processes critical to maintaining a site may arise external to it or how a list of static characteristics used for assessing restoration success, like composition, diversity, or structure, may not adequately express the ongoing dynamics of the biological community as would terms expressing rates of change. If processes are dynamic in their spatial and temporal features, characteristics of a system to be considered need to be described from a dynamic perspective. Rather than composition, the rate of change in total composition or of a particular species set may be a more appropriate consideration, or the rate of cover or biomass change or other system attributes (Table 1). Characteristics can change in their rates at different seasonal or successional periods or climatic conditions. Such patterns of rate change are fundamental for understanding system operation and meeting restoration objectives.

Part of the problem of restoring sites using our current understanding of succession is that ecologists differ about what successional principles are established or accepted (McIntosh 1980, 1985, 1987; Shugart 1984; Pickett et al. 1987, 1992). Consequently, there can be dissension among scientists about the degree to which sites are self-regulating or about whether there are end points to succession (Pickett & Parker 1994; Aronson et al. 1995). These are important issues, but the problem is not really that in restoration, reference sites are overemphasized in some cases or that end points to succession are expected, or any of the other issues that ecologists question. At the center of these arguments is assessing and understanding the spatial and temporal scale at

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Table 1. Examples of characteristics of ecological systems from a static and a dynamic perspective.

<i>Static Characteristic</i>	<i>Dynamic Characteristic</i>
Species composition	Rate of change in composition
Diversity	Rate of change in diversity
Structure/spatial patterning	Patch dynamics
Mineral pools	Mineralization rates
Energy income	Food web development rate and dynamics or rate of change in productivity and biomass distribution

which mechanisms that drive and control succession are expected to operate (McIntosh 1980, 1985; Allen & Starr 1982; Shugart 1984; O'Neill et al. 1986; Carlile et al. 1989; Hoekstra et al. 1991; Brand & Parker 1995). This is the focus of this paper, and I approach it by considering only two issues. One of these is the degree to which restoration sites are impacted by influential processes originating from outside the site. Restoration sites occur in a variety of circumstances, and in each case, processes impacting the system may enhance, have no net impact on, or greatly constrain the success of the restoration effort.

The second issue is that the systems we are attempting to restore are historically contingent, and this creates many of the problems of interpreting and applying influential processes on a system. What I mean by this is that communities result from numerous assemblies, disturbances, invasions, shifts in climate, and gradual changes in environmental conditions such as erosion or soil development. Some ecologists think of succession as an individual by individual replacement process (Horn 1975; Pickett 1976, 1980), as a struggle among species in which adaptations permit the success of some over earlier occupants. This provides the mechanistic process by which orderly progression or at least some prediction can be based. Even though we can develop "laws" of succession if we restrict the scale sufficiently (Pickett & McDonnell 1989), such a viewpoint constrains completely our expectations and can lead to unexpected failure (Brand & Parker 1995).

Expanding our scale temporally and spatially on succession also reveals the multidimensional nature of ecological processes. We can overcome the history of a site with respect to composition by introducing species into a site or removing others. However, to maintain their ongoing dynamics, restorationists must also introduce or restrict processes so that the influential set of processes at a site are reflective of the history of conditions supporting the patterns of biological organization and dynamics we are interested in establishing. While it is well accepted that disturbances such as fire or canopy gaps have several dimensions, for example, frequency, magni-

tude, area and season, which together are expressed as a "regime" (Pickett & White 1985), clearly all processes that influence dynamics, whether they are abiotic impacts such as windthrows or biotic interactions such as herbivory, have these dimensions, and that gives them a historical characteristic within any particular community. For restoration, re-creating these environmental regimes within their historical range is the principal objective (Cairns 1990; Pickett et al. 1992; Beechie et al. 1996).

What are restoration goals? Ecologists have interpreted dynamics of ecological systems from a number of temporal and spatial scales; all of these scales are valid, yet they demonstrate the differential importance of processes, depending on the scale considered. If we are rehabilitating sites and establishing any type of community, then short-term, small-scale approaches will be effective. However, often the goal is to develop communities that are self-sustaining, and this is a long-term issue. Much of the diversity of successional models and principles is the result of the scale at which they were developed. If we limit our goals to initiating a certain composition and leaving the system alone after that, then models that focus on biological interactions and organism adaptation to initial conditions are appropriate. If self-sustainability is also a goal, then larger spatial and temporal scale models are fundamental. This paper starts with the assumption that one of the goals is self-sustainability. Given that, then processes arising external to the site and the longer-term characteristics of processes are much more critical to understand and incorporate (Botkin 1992; Arseneault & Payette 1997; Caley & Schluter 1997).

Process Scales and Site Context

Processes that underlie observable patterns of a diversity of ecological communities arise from a range of spatial scales and temporal durations (Allen & Starr 1982; Allen & Hoekstra 1992; Dayton et al. 1992; O'Neill et al. 1986; Steele 1978, 1989; Weins 1986, 1989; Menge & Olson 1990; Brand & Parker 1995; Parker & Pickett 1998). Many familiar biological processes are those contained within the site, such as competition and symbiotic mutualisms between individuals, and abiotic processes, such as soil drying during droughts. On the other hand, processes arising external to the site can have considerable impact as well. Dispersal of individuals into a site can result from adjacent or distant locations (Carlquist 1981; Fowler et al. 1992). Metapopulation models are based on these probabilities (Hanski 1991; Hanski & Gilpin 1991). The impact from external processes can be gradual, such as the predicted global climate change, or be a single event, such as a rainstorm during the passing of the Chernobyl radioactive fallout cloud over California (DeSante & Geupel 1987). Simi-

larly, processes may impact only a portion of a site or selected organisms within a site, or the whole site being restored may be impacted (Figure 1). The range of temporal durations and spatial extents of processes suggests that we should think of sites as impacted by a continuum of process scales (Parker & Pickett 1997, 1998).

We can arbitrarily divide this continuum into several categories. One is those processes contained within restoration sites. These would include biological processes such as competition, parasitism, and mutualism, that is, most processes involved in interactions among individuals. Restoration sites are found within a spatial context of other ecological systems that may or may not contain a similar array of species. Within urban areas, for example, a major influence on the success of a site's restoration is the continuous propagule input of aggressive invasive species dispersed from adjacent habitats. Such dispersal represents an example of a process arising external to the site. Other processes originating externally may include runoff and erosion, mineral flow, pollen flow and pollinator activity, as well as other constraints or enhancements. Finally, we can also divide up processes into regional or global ones. Historically, these larger scales of processes changed at rates too slow for the time scale of restoration ecology objectives. Currently, however, regional influences can include new invasive species, general warming of an area, atmospheric pollution, impacts from agricultural practices, differential inputs of dust and minerals, and acidified rain, among others. Globally, these human influences are reflected in seemingly rapid changes in climatic variability and atmospheric composition.

Along with viewing the size or duration of processes along a continuum is the observation that processes, regardless of size or duration, may impact only a portion of the site. Trails or roads facilitate processes like this, providing routes for movement of deer, other large animals or invasive species, and in the case of roads, differential pollution. Topographic variation, such as north-facing versus south-facing slopes, modifies frequencies and du-

ration of droughts or temperature extremes. Directional processes such as salt spray off of oceans or atmospheric pollution from point sources may differentially impact windward-exposed portions of restoration sites.

The extent of the impact of flows along boundaries, and into sites, strongly depends on the size and shape of the site, the types and conditions of surrounding habitat, and the overall landscape mosaic (Wiens 1992; Forman & Moore 1992; Forman 1995; With & Crist 1995). In some cases, processes impacting a site may differentially affect species, with only a portion of the community showing strong responses, as in situations in which physiological tolerances are reached, such as droughts or air pollution (Reich & Amundson 1985; DeSante & Geupel 1987). The overall context of a site, consequently, is a critical consideration, and two different restoration sites may completely differ in their post-treatment results because of differences in adjacent habitats that generate different types, frequencies, or magnitudes of processes.

Processes of External Origin and Site Dynamics

Planning for restoration, especially in terrestrial systems, often focuses on the problems and circumstances of the site itself. What species need to be introduced? What conditions need changing? However, dynamics of sites also depend upon processes arising outside of their boundaries. Sites containing communities isolated from other similar communities in the region often display different compositional or structural patterns than they would in a context of similar communities (Gaston & Lawton 1990). A number of species in a community may require spatially infrequent events for reproduction or high rates of immigration to maintain populations (Pickett & Thompson 1978). Each situation requires a careful consideration of what community can be maintained, what processes must be re-added, such as infrequent disturbances, and what new processes cannot be modified but must be accounted for.

Sites in which human impacts are significant, such as urban or agricultural areas, may be controlled by invasive species. Whereas studies on invasive species have been summarized recently (Drake et al. 1989; Simberloff 1996), the impacts of individual cases can be impressive. In Hawaii, *Myrica fava* (firetree) has modified mineral nutrient pools and shifted the system fertility to a range that has changed the succession dynamics of the forests and altered dominance patterns (Vitousek & Walker 1989). Sometimes the continuous introduction of invasive species over a long time period results in total changes in the system, such as the 95% dominance of San Francisco Bay by introduced aquatic organisms (Cohen & Carlton 1995) or the loss of native diversity in freshwater aquatic systems (Moyle & Leidy 1992; Moyle &

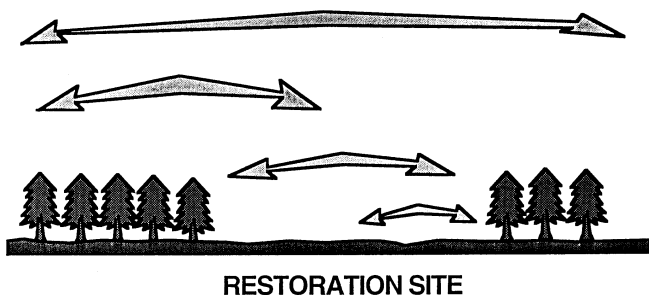


Figure 1. Illustration that processes impacting a restoration site can be of different spatial extents and can arise offsite yet be influential onsite.

Light 1996). In some cases, a single introduction, as in the case of a pathogen (e.g., Dutch elm disease), can change patterns of dominance throughout the range of the species infected.

Commonly, the intermixing of natural habitats and human modified landscapes results in the addition of disturbances or abiotic influences or the suppression of processes critical to maintaining the diversity and structure of natural communities. Five decades of ozone pollution in the mountain ranges within 300 km of Los Angeles show shifts in the dominance of the forests from *Pinus ponderosa* (ponderosa pine) and *P. jeffreyi* (Jeffrey pine) to more ozone-tolerant species such as *Calocedrus decurrens* (incense cedar) and *Abies concolor* (white fir) (Miller et al. 1963; Miller 1992). Species with greater sensitivity, such as the lichen communities, have been eliminated from these systems altogether. The loss of diversity and function of the lichen component of these systems can have an impact on mineral cycling and food webs and further reduce diversity or modify biological structure (Sigal & Nash 1983). Human fragmentation of habitats also can constrain other processes such as migration or prevent the movement of fire across the landscape. The suppression of fire in particular can shift system dynamics into other successional trajectories or may yield a limited, more extreme range of fire intensities (Minnich 1989); in both cases, loss of biodiversity or a shift to a new community type results (Zedler et al. 1983; Christensen et al. 1989; Parker 1993). Fire is a good example of an often rare event that nonetheless is critical to the maintenance of site biodiversity, function, and dynamics on long-term scales. Other events can be just as critical for biodiversity and system function, and species that may not seem important within a system may dominate after such events (Tilman 1996). Species are adapted to the temporal patterns of these types of processes and can be profoundly impacted if the historical range of frequencies is exceeded. This is recognized in systems as different from each other as fire in chaparral (Zedler et al. 1983; Parker 1993) and watershed stream flows in salmon restoration (Beechie et al. 1996).

These examples suggest a number of circumstances that must be considered for restoration: What are the historical patterns of environmental regimes for the proposed community? Which are critical to the long-term dynamics or biodiversity of the proposed community? What are the constraints of the landscape context? What external processes can be managed and which cannot? How does this modify restoration objectives?

Scale and Interpretation of Successional Changes

Ecological systems are heterogeneous in time as well as in space; this temporal pattern requires a dynamic view of systems and of the characteristics we should measure

to determine restoration success. Many systems cannot be quickly returned to a relatively mature state, or in some cases, it may not be practical to return systems to a relatively mature state in which mineral cycles, patch dynamics, or other critical attributes are fully operative. System recovery may result from simply initiating the process of vegetation dynamics or succession. Because ecological systems are open, and because strongly influential processes are of a variety of spatial extents and temporal dimensions, successional trajectories can be readily modified by a number of processes (Pickett et al. 1987). The landscape context of a site is as important to understand and take into consideration as are characteristics of the site to be restored. Restoration may be an ongoing management process, and that blends into long-term vegetation management (Pickett & Parker 1994; Parker & Pickett 1997).

Finally, processes themselves are heterogeneous and are characterized by dimensions of magnitude, duration, frequency, extent, and other features. Processes of low frequency and limited duration, especially disturbances, may be critical to long-term dynamics of a site, but not at all necessary for short-term dynamics. Critical to restoration success is understanding this multidimensionality of processes, because we use processes to manipulate sites and direct succession or local dynamics. Unfortunately, all process dimensions have historical ranges to which dynamics will respond and maintain the system. Otherwise, site composition will reassemble into a new and perhaps unintended community. Remembering that systems may have multiple steady states while focusing on restoring natural historical ranges of processes is critical and leads to meeting restoration objectives.

Because the systems we wish to restore have historical dimensions, we must remember that we can only overcome certain of these aspects. We can achieve the desired composition in the short term by introduction of the appropriate species, but in the long term we have to ensure that a range of environmental processes is operative. Historically, ecologists have focused on how systems change during succession and how species are replaced. The principles developed from these studies are tested and often effective in restoration projects. It must be remembered, however, that these principles are scale-limited and work only in the context of changes after a disturbance (Brand & Parker 1995). These principles are spatially limited to the extent of the disturbance and temporally limited to the span of effects of the single initiating event. Long-term restoration goals, such as self-sustainability of a restoration, require a broader perspective. Habitat variation is no longer a set of initial characteristics that must be mitigated or considered; instead, the influence of the external processes and the long-term requirements for multiple disturbances or

other rare processes that maintain the diversity and function of the system (Brand & Parker 1995). The importance of considering the larger spatial and temporal scales will depend on the landscape mosaic of the restoration site. In the context of other natural systems with operative processes, focusing on initiating succession may be sufficient to meet restoration goals. However, in the context of disturbed or modified habitats, the longer-term issues become the dominating ones. Dynamics occur at a number of scales within natural systems; models developed at different scales are all valid but limited. Longer-term success of restoration depends on understanding longer-term dynamics and the governing processes.

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