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Transition Dynamics in Succession: Implications for Rates, Trajectories and Restoration

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Succession provides a temporal framework in which to understand ecological processes. Studies of community assembly and changes in species diversity and nutrient cycling, for example, benefit greatly from the temporal perspective that succession offers. The temporal consequences of species interactions throughout the life history of each species are also well integrated into the conceptual framework of successional dynamics. With an emphasis on species effects on community dynamics, succession has been a nexus for physiological, population, ecosystem and landscape ecology as well as for biogeography, geology, soil science and other disciplines. With its temporal focus that demands recognition of the ubiquitous forces of change, succession thus provides insights into practical issues that involve restoration, land management and global climate change (del Moral and Walker 2007).

To evaluate how species replace each other over time and how trajectories of communities develop (the process of succession) requires grappling with concepts of stability and transition, equilibrium and non-equilibrium states. In the context of this paper, we define stability as persistence of a successional stage with or without the presence of a disturbance. The species composition of all communities is dynamic so even relatively stable communities can have substantial local species turnover (described by van der Maarel and Sykes [1993] as the "carousel model"). There can be a range of rates within a given sere (successional sequence). For example, on rocky lava, lichens and mosses may rapidly colonize but then not change for decades until vascular plants are able to colonize (del Moral 2000). Ultimately, successional communities can be characterized by a range of processes from quasi-equilibrium to non-equilibrium dynamics depending on the time scales involved (Briske et al. 2003).

Restoration research has benefited from (stable) state and transition models (Bestelmeyer et al. 2003, Grant 2006) because these models focus on mechanisms that cause transitions between successional stages and provide explicit goals for restoration. Transitions are integral to restoration as they are the process of community level change following a disturbance and may move the system either toward or away from the desired state. These transitions lead to sometimes predictable but often unpredictable or even novel patterns of community change. In the context of restoration, stability may be of less conceptual value than the idea of transitions because each organism is constantly responding to ever-present fluctuations in the environment. At the community level, relative stability can be achieved when the opposite forces of both abiotic and biotic disturbances and the biotic responses to the disturbances are in balance.

The ability to make accurate predictions of successional states remains elusive. However, accurate predictions are essential if succession is to be relevant to restoration (Hobbs et al. 2007b). While progress has been made in understanding immediate responses to forces of change, we still can predict only approximate patterns of longer-term community responses – despite 110 yr of observation of successional change and 40 yr of experimentation. Therefore, it may be more useful to model transition dynamics (and their antithesis – stable states) in order to develop insights for restoration of damaged lands. Such models can integrate across dynamics at scales of individual plants, stands, communities or landscapes.

In this chapter, we discuss how the study of succession offers insights into both transition and stability in terrestrial plant communities. To do this, we address how disturbance severity and species interactions influence whether a community is likely to be in transition or to be stable. We also explore the predictability of successional trajectories. Our perspective is that all communities are constantly in flux; however, at specified temporal scales, the rate of change may be reduced and a relatively stable state (prolonged or arrested successional stage) identified. Finally, we explore the beneficial and reciprocal interactions between mechanistic studies of succession and restoration activities.

Disturbance

Disturbance initiates succession by destroying biomass and disrupting how plants interact with other plants, soil and the atmosphere, thereby initiating new relationships (Johnson and Miyanishi 2007). Subsequent, less catastrophic disruptions may continue to alter trajectories of successional pathways. Allogenic disturbances are originally external to the ecosystem of concern and they can be abiotic (e.g., hurricane winds, flood waters) or biotic (e.g., invasive species, migrating herbivores). Autogenic disturbances arise from within the ecosystem and are either abiotic (e.g., local erosion, frost damage) or biotic (e.g., animal burrows, local herbivores). Disturbance therefore can also initiate transition in a successional system. Stability (no transition; fig. 1) can occur when disturbance is very infrequent (or mild), when disturbance is chronic or severe, or when disturbances counteract each other. Note that increases in frequency can be completely independent of (even inverse to) increases in severity, yet their impacts on successional stability are often similar. However, the stability and predictability of a successional stage can be low when infrequent, severe disturbances occur (e.g., a hurricane; Walker and del Moral 2003).

The near-absence of disturbance can lead to stable communities that are dominated by long-lived species (e.g., *Sequoia* trees; Stephenson and Demetry 1995), by species that are self-replacing following disturbance (e.g., *Pinus* forests [Buhk et al. 2006] or alpine meadows [Sarmiento et al. 2003]), or species that are both long-lived and self-replacing (direct succession; desert *Larrea* shrubs; McAuliffe 1988, Bolling and Walker 2000). Frequent disturbances can maintain a ruderal community that responds quickly but rarely changes in a successional sense (e.g., lawns; Austin 1980). Severe disturbances (that disrupt or remove most biomass) can promote stress-tolerant species where the species composition changes little over time (e.g., prairies; Knops 2006). An example of how disturbances interact is when floods, beaver, elk and river channelization all impact riparian shrub cover along a river floodplain in Colorado, USA (Peinetti et al. 2002). Total shrub cover was quite stable over a 60-year period. Shrubs benefited from meanders linked to beaver dams but declined where the river was more channelized and where elk-browsing pressure was high. This example can be viewed as many local cycles of disruption and succession producing a regional stability.

Disturbance frequency (return interval) and disturbance severity (damage caused) strongly modify transition dynamics. Frequency of a disturbance is relative to the life span of the species of interest. For example, a fire every 5 yr might not allow a slow-growing forest tree to reproduce and succession could be arrested at a shrub stage. If the fire is not severe, some trees might survive, but if it is so severe that even the shrubs die, a new trajectory might develop that is dominated by invasive grasses (Williamson et al. 2006). If the fire is so severe that all plant cover is lost, subsequent soil erosion may lead to a loss of site fertility and productivity in what is called retrogressive succession (Walker and Reddell 2007). Similar interactions occur with respect to grazing.

Humans have introduced many novel disturbances (e.g., urbanization, mine wastes, pavement) and exacerbated others (e.g., tsunami damage to coastlines; Dahdouh-Guebas and Koedam 2006, Stone 2006). When human disturbances have natural analogues (e.g., mine wastes resemble volcanic ash, pavement resembles lava), succession on these surfaces follows patterns broadly similar to those on natural disturbances (del Moral and Walker 2007). However, some disturbances (e.g., highly toxic wastes, extensive urbanization) may initiate unique retrogressive successional pathways that are not easily restored.

The relationship between disturbance, diversity and stability is complex, but higher diversity does not always correlate with increased stability (Walker and del Moral 2003). In fact, the opposite may be more common. Species diversity often peaks at intermediate disturbance frequency or severity (Connell 1978) while stability and predictability (Burrows 1990) tend to decline at intermediate disturbance (fig. 1).

Disturbances are rarely uniform in their effects across a landscape, so patches simultaneously support communities at different stages of succession. These patches may even diverge in their subsequent successional trajectories. Such spatial complexity with both fine scale transitions and larger scale trajectories argues for spatially explicit restoration goals (del Moral et al. 2007).

Multiple disturbances interact as a local disturbance regime and it is the net effect of these disturbances that determines overall successional trajectories (fig. 2). A more detailed examination of specific transition dynamics is needed to guide daily restoration decisions, but the overall successional context must ultimately be considered as well. Because disturbances are as variable as the community responses to them (at all temporal and spatial scales of interest), many successional trajectories are possible from an initial situation.

Succession

Successional studies emphasize overall patterns of community change. Despite numerous studies of mechanistic factors that drive change (e.g., dispersal, competitive inhibition, facilitation, soil nutrient availability), the focus of succession has been on the net result of multiple (and sometimes contradictory) interactions (Glenn-Lewin et al. 1992). However, the detailed dynamics of the process of change or transition to the next successional stage have been a productive line of research (Tilman 1988). Physiological thresholds and subsequent responses of plants to each other and to their abiotic and biotic environment, for example, provide the basis for many autogenic successional dynamics (Bazzaz 1996). The physiological responses of plants differ dramatically among the successive life history stages of each individual (dispersal, germination, establishment, reproduction, senescence). Successional dynamics are thereby profoundly influenced by the timing of forces of change relative to the life history stages of plants in the focal community (Noble and Gitay 1996). Additional autogenic drivers of succession include plant-soil organism feedbacks (Bever 2003) such as herbivores that retard early succession or accelerate later succession through their impacts on decomposers and nutrient supplies (Wardle and Peltzer 2007).

Studies of succession that examine the rate of change provide excellent insights into the stability of a given stage. Rates can be evaluated by direct measures of species abundance, species turnover or biomass accumulation in permanent plots, measures of similarity based on abundance or changes in positions in ordination space. Indirect measures include assumptions made from evaluating chronosequences. These approaches do not try to consider variation in rates as the trajectory unfolds. Rates may be slow, and then accelerate, only to be retarded as the system becomes dominated by longer-lived species. In such cases, it is usual to display the ordination position of the same plot in successive years or to plot abundance vs. time (del Moral 2007a). Alternatively, rates can be quantified by calculating changes between successive samples and analyzed by the degree of change over time. Useful comparative metrics include various similarity and ordination scores.

Succession rates are subject to the influence of any factor that affects recruitment and growth. They tend to be slower in unfavorable environments (dry, infertile, unstable, acidic, or remote) than favorable ones (Walker and del Moral 2003). Thus, restoration of at least structural complexity will benefit from site amelioration. However, amelioration will also alter the competitive balances and must be undertaken with caution and foresight. Succession rates are also determined by species characteristics (e.g., longevity, growth form, root exudates) and how these characteristics influence species interactions. Rates of succession vary during a trajectory, generally declining with time not only due to generally increasing life spans of the involved species but also because fewer species are added to older stages (Anderson 2007). Intriguingly, the overall rate of succession can be independent of the rate of transition from one stage to another (e.g., rapid threshold dynamics or more gradual transitions; see discussion of models below) because of the variable length of duration of each stage. Rates can vary for different ecosystem attributes. For example, species turnover may be quite slow while biomass accumulation is rapid.

Species interactions

Species interactions that drive successional change can be measured by species turnover, particularly when the role of abiotic disturbances declines. Members of a community form several categories: new arrivals (from seed bank, dispersal or vegetative spread); species that thrive (accrue resources and are competitively superior); species that survive but do not dominate (such as understory plants); or species that die (they are out-competed, succumb to disease, herbivory or abiotic disturbances or simply reach the end of their normal life span; fig. 3). With these four categories of species, one can address several types of vegetation change. These include colonization and sequential replacement in newly disturbed areas, direct replacement following disturbance of established vegetation, cyclic or fluctuating replacements, vegetation maintained by frequent disturbance, vegetation in equilibrium (no change for at least one generation of the dominant species), and millennial-scale changes (Burrows 1990). In most situations, succession is determined by changes in the status of the characteristic species. Change in dominance can result from either the success of new arrivals (“A” species) or the dominance of former, non-dominant survivors (“S” species), following loss of dominance of “T” species from disturbance, competition or senescence. Often, there is a hierarchy of relative dominance among a number of species. The rate of each transition is dependent on many internal and external variables.

Facilitative interactions between species promote change to the next successional stage most rapidly when the facilitator (often a “nurse plant”) is out-competed by the plant that it facilitates (contramensalism; Gaynor and Wallace 1998). This pattern of change fits the classic model (relay floristics) when the facilitative relationship is obligatory (species B does not establish without the presence of species A – as when shrubs like *Coriaria* with nitrogen-fixing symbionts are essential before later successional species such as *Griselinia* can colonize; Walker et al. 2003). There are other direct and indirect ways that facilitation alters succession (Table 1; Walker and del Moral 2003). Facilitation may promote stability at a landscape scale when cyclic succession occurs or when the positive relationship leads to coexistence of the two species rather than replacement (e.g., desert shrubs; Holzapfel and Mahall 1999). Facilitation also can affect several parts of the life cycle of a species (Table 2) and does not always involve a nurse plant (Callaway and Walker 1997). Facilitation is more likely in stressful than favorable environments (Kikvidze et al. 2001), although extreme environments may not favor either the nurse plant or facilitation (Brooker et al. in press). A nurse plant can affect different species with varying degrees of facilitation (depending on life stage or environmental severity), potentially leading to alternative successional trajectories. For example, *Lupinus lepidus* invaded small portions of pumice barrens soon after the 1980 volcanic eruption of Mount St. Helens (Washington, USA) to form dense colonies. After 23 years, it had facilitated succession compared to immediately adjacent areas (more species, higher diversity, much greater cover). Heterogeneity was greater and "lupine patches" formed communities distinct from adjacent sparse patches (del Moral and Rozzell 2005).

Competitive interactions between species can retard succession by impeding species turnover. Competitive effects either resist invasion (competitive inhibition) or out-compete existing species (competitive exclusion). When competition merely alters the relative dominance of the species involved it has no direct effect on succession. Competition thereby promotes stability of the existing community and arrests succession, as illustrated by species that form crusts, mats or thickets (Table 2; Walker 1994, Young et al. 1995). Arrested succession can occur at any time during succession (Walker and del Moral 2003). An alternative scenario that also arrests succession occurs when a species invades the community and resists its own replacement by competitive or by allelopathic means. Of course, if the initial invasion promotes species change, succession is temporarily accelerated. Arrested succession can be either beneficial or not for restoration, depending on whether the desired community has been achieved (Cortina et al. 2006).

Trajectories

Successional trajectories describe the changes in species composition but can also apply to changes in accompanying ecosystem function. For example, a progressive trajectory implies a sequential development of parameters such as biomass, structural complexity or productivity. A retrogressive trajectory implies sequential reduction of at least one critical parameter, often including fertility. Retrogression can occur at any time scale but is often noted only after many centuries without a catastrophic disturbance (fig. 4; Richardson et al. 2004, Walker and Reddell 2007). Disturbances can either trigger retrogression or reverse it. Retrogression has many interesting implications for transition dynamics but little has been examined about the rates of loss of ecosystem parameters or the duration of both stages and transitions. Both abrupt changes across thresholds and gradual, continuous transitions can characterize retrogression. Alternative retrogressive trajectories are certainly possible but poorly examined. Restoration efforts sometimes involve inducing retrogression in ecosystem properties such as soil fertility (e.g., by adding sawdust to immobilize soil nutrients and lower dominance by weeds; del Moral et al. 2007).

The mere act of identifying the type of trajectory does not explain the relative stability of each stage within it (see discussion of rates above). The direction of succession is driven by disturbance, propagule availability and both positive and negative species interactions, while the rate of succession is driven by both positive and negative species interactions. Hysteresis is one type of response by a community to a disturbance and conceptually integrates concepts of resilience, progressive and retrogressive succession, trajectories and restoration. When degradation drives ecological conditions below a threshold that precludes spontaneous recovery, subsequent progressive succession often takes an alternative trajectory, leading to an alternative stable state (see discussion of models below). It is when spontaneous recovery to a desirable state is arrested that restorative intervention is required. For example, if degradation has allowed the invasion of a noxious weed that precludes the return of native herbs or shrubs, competition from the weed must be alleviated and shrubs planted (Kulmatiski 2006). Subsequent restorative measures such as assisting recruitment where dispersal limitations are strong (Standish et al. 2007) or manipulating fertility to desired levels are likely to be required to guide the trajectory along a desirable path.

Models of Transition Dynamics

In Chapter 1, Suding and Hobbs presented five models of transition dynamics. Here we discuss their links to succession. Note that these models are not mutually exclusive explanations of successional trajectories.

Threshold models invoke abrupt changes in state variables in response to small environmental changes. Successional transitions can occur in this way when a dominant species reaches its physiological tolerance to developing conditions, is removed by competitive interactions or is damaged by a sudden invasion (by a competitor, herbivore or disease; van der Wal 2006). Changes in nutrient availability can also trigger transitions. Threshold conditions do not necessarily result in changes to the next predicted stage; rather, successional trajectories can be deflected or be retrogressive (fig. 4).

Tipping points can occur when the critical mass of a key species is achieved, as in the transition from deciduous to coniferous vegetation under the influence of moose herbivory (Bardgett and Wardle 2003). Conifers were also involved in another tipping point on Mount St. Helens where a lahar is gradually developing vegetation following the eruption in 1980. Once the terrain was stable, it was colonized by low stature vegetation dominated by the nitrogen-fixing *Lupinus lepidus* and *Racomitrium* mosses. Where conifers became established in cracks, vegetative cover and species diversity were subsequently reduced. Many species were excluded by shade and dense leaf litter deposition from the conifers. However, other species were favored by higher surface fertility and reduced drought compared to vegetation in open sites. This conifer invasion altered vegetative structure, species composition and ecosystem properties (del Moral, unpubl.).

Herbivory can produce abrupt transitions between adjacent stable vegetation patches. Schmitz et al. (2006) removed insect herbivores from old fields in New England (USA). This sudden change in herbivore density resulted in a permanent shift from herbivore (top-down) control of community structure to plant (bottom-up) control. The experiment created patches that were similar to the existing vegetation mosaic in surrounding old fields, which suggested that it imitated natural fluctuations in herbivore density.

Alternative stable states (that we view as relatively long-lasting successional stages occupying similar habitats in the same area) arise in several ways and can occur in divergent, deflected, network or parallel trajectories or from a dynamic equilibrium between two stages within the same trajectory. Temporal and compositional stability are most likely at either low or high disturbance frequency or severity (fig. 1). Divergence can be caused by different initial physical or biotic conditions, variable recovery from a disturbance or random controls over dispersal and colonization (Wright and Chambers 2002, Schröder et al. 2005). Trajectory transitions may occur gradually or abruptly, from either allogenic or autogenic factors. Several kinds of natural disturbances (e.g., fire and insects) have produced two alternative stable states in northern Canadian spruce forests, whose understories are dominated either by mosses or by lichens (Jasinskim and Payette 2005). Different soil conditions induced by the vegetation can also produce alternative stable states, due to positive feedbacks caused by dominant species (Adema et al. 2002). Within a sere, largely allogenic forces that are both progressive and retrogressive can also result in alternative stable states (Sedia and Ehrenfeld 2003, Chambers et al. 2007, Schrautzer et al. 2007). Trajectories in the form of networks easily encompass this concept, especially when divergence is followed by subsequent convergence.

Slow-fast cycles introduce autogenic interactions with the environmental variables that control the characteristics *of* a particular sere. Such autogenic dynamics are more likely in secondary succession or later stages of primary succession where environmental controls are less consequential than in early primary succession. For example, late primary succession slack dune species in The Netherlands included pioneers that enhanced soil denitrification rates and arrested further development by competitive exclusion of plant species. A different, more productive community developed in adjacent areas under these same conditions when plant species established that did not lead to enhanced rates of denitrification (Adema et al. 2005).

Gradual continuous models are perhaps most applicable to later stages of both primary and secondary succession, where species replacement gradually occurs due to a combination of internal and *external* forces. An isolated sub-alpine ridge on Mount St. Helens demonstrated gradual transitions in species composition due to internal facilitative mechanisms (cf. del Moral 2007a). Between 1984 and 2006, species richness and percent cover increased, with the loss of only a few of the original colonists. Percent cover and growth of some species responded to pulses of *Lupinus* growth. Many examples of retrogressive succession also follow this gradual change as nutrients are depleted (often leached or transformed into unavailable forms as through soil acidification) and productivity declines (Wardle et al. 2004).

Stochastic dynamics dominate in early primary succession where forces that drive change are unpredictable and of widely varying nature and severity and links between vegetation and environment are tenuous (del Moral and Lacher 2005, Walker et al. 2006). Stochastic factors may produce priority effects and also may increase as either spatial or temporal scales decrease. Dispersal can be stochastic throughout succession but when strong biological legacies remain *following a disturbance (as in most secondary successions), successional trajectories are more* predictable (Turner et al. 1998). In primary succession, differences among plots are initially high due to stochastic invasions. Subsequently, some spatial pattern emerges and successional trends can be discerned (del Moral 2007b). Stochastic models appear to be less useful as the trajectory matures. However, predicting the overall trajectory does not necessarily lead to better predictions of transitions or duration and stability of each stage.

Each of these models helps to clarify how transitions can occur between successional stages but they only indirectly illuminate what controls community composition or stability long enough for a recognizable stage to be formed. Further, the conditions of each stage (state variables) respond variously to thresholds, disturbances and transitions depending on such characteristics of species as life history stage, nutrient use efficiency, and competitive standing in the community. Further influences on transitions include the number, spatial distribution and influence of similar or dissimilar transitions and states occurring in that community. Understanding a transition under one set of conditions will not guarantee understanding it elsewhere. Any transition is a result of the unique combination of forces resisting and promoting a transition at a given site (Table 1). Using the community-level approach of succession can help in the search for generalizations about transition dynamics and the implications of such complex interactions for restoration must be evaluated.

Restoration

The goal of restoration is to establish persistent and diverse communities that are dynamically responsive to a variable environment. To facilitate this goal, one tactic is to incorporate physical heterogeneity that promotes patchiness in the vegetation. Other tactics focus on site amelioration, the initial establishment phase, and protection of desirable species from herbivory and competition (del Moral et al. 2007). Attempts to restore vegetation to static successional stages are unlikely to succeed without continual effort to preserve the desired condition. However, an understanding of the local successional dynamics can greatly improve chances for successful restoration outcomes.

Successful restoration relies on an understanding of disturbance, species life histories and how they interact as well as some awareness of likely successional trajectories. Unfortunately, such specific information is rarely available. Consequently, trial and error provides practical local lessons. The ability to extrapolate broadly applicable generalizations is hindered by the frequent lack of rigorous data collection and analysis (Hobbs et al. 2007b). Nonetheless, we offer some insights from successional studies that can help improve restoration success (Table 3).

It is essential for restorationists to recognize that disturbance is likely, either from within or from outside the ecosystem of concern (Hobbs et al. 2007a). When the likely timing, frequency and severity of allogenic disturbances are known (e.g., mean spring flood height along a floodplain), planning is possible. In cases of severe disturbance, this may mean no restoration actions are possible. When the disturbance is frequent or regular but not severe, care can be taken to use weedy species that rapidly establish between disturbances, perhaps moderating the severity of subsequent disturbances. However, the timing of most disturbances is difficult to predict, so redundancies in number and positioning of species can help. Autogenic disturbances are also a reality (e.g., local herbivory or erosion) but may also be hard to predict. Using species with a variety of growth rates, a spectrum of life forms and multiple reproductive strategies will ensure some natural sorting and some survivors of those disturbances.

Species interactions drive succession and occur from initial colonization through dominance to senescence and replacement (Table 3; fig. 3). Colonization can be aided in many ways (e.g., direct sowing of seeds, perch trees to attract dispersers, addition of surface structures to trap seeds) and is often essential to accelerate succession. The success of certain species can be promoted by manipulating soil fertility, but care should be taken not to overfertilize, which often promotes dense vegetation that can arrest succession (Walker and del Moral 2003). Facilitative interactions can greatly advance restoration goals when properly understood, but vary with fertility and disturbance as well (Callaway and Walker 1997).

Restoration to original, pre-disturbance conditions (*sensu stricto*) is unlikely, but often a mosaic of alternative states is suitable. Working from a prior understanding and overview of possible divergent successional trajectories and the forces that create transitions between stages is optimal but rarely achieved. Instead, most projects rely on broad criteria for success (restoration *sensu lato*). Sometimes alternative trajectories are accidentally or intentionally promoted and alternative stable states achieved. In most cases, progressive trajectories are desired, but sometimes it is desirable to reduce fertility, biomass or diversity, essentially driving succession back to a former state. Manipulation of such retrogressive processes is still poorly understood (Schrautzer et al. 2007, Walker and Reddell 2007).

Harnessing knowledge about how species interact during each phase of their life histories and coupling it with models of transition dynamics will provide a framework within which to address future restoration challenges. Where thresholds have been passed, restorationists must either exert extreme effort to overcome the threshold or abandon restoration efforts (Hobbs and Harris 2001). Alternative stable states reflect the prevalence of overlapping or network trajectories and allow restorationists welcome latitude in their goals. Abrupt transitions driven by autogenic factors can be hard to anticipate and manipulate, so modeling can help predict when they are likely to occur. In generally, unpredictable events are more likely than gradual, predictable change, so restoration goals need to stay general, focusing more on restoring some basic ecosystem functions than on particular species compositions.

We expect successional concepts will continue to have an important role in the development of future restoration frameworks. In turn, carefully recorded restoration experiments can elucidate poorly understood successional dynamics (Walker et al. 2007). For example, efforts to ameliorate abiotic constraints, consequences of various (sometimes novel) species combinations and persistence of given successional stages can all be obtained from restoration activities, whether they were "successful" or not.

Conclusions

We must understand how successional stages are maintained and how they undergo transitions in order to manipulate succession better. Disturbance dynamics initiate and control successional trajectories. Intermediate disturbance promotes transition among successional stages by thinning dominant species, while low and high disturbance frequency and severity usually promote stability of stages. Species responses to disturbance are controlled by their physiological traits at each successive life history stage. Rates of succession are controlled by both abiotic factors (slowest in unfavorable environments) and biotic factors (life spans, growth forms, species interactions). Despite over a century of study, predicting successional trajectories remains problematic. Various recent models help us examine the details of transition dynamics but models need to better address the mechanisms promoting stability of each stage between the transitions. There is little information on the life histories of key species in most restoration efforts, although some systems such as arid lands (e.g., Walker and Reddell 2007; Chamber and Miller 2004) and certain wetlands (Schrautzer et al. 2007; Zedler in press) are better understood than others. A successional perspective on community change is a useful and realistic framework to incorporate transition dynamics because it provides the necessary temporal perspective needed for successful, long-term restoration.

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Table 1. Forces that resist and that promote the transition from successional stage A to B.

Resistant Forces	Promotional Forces
Disturbance	
That maintains A or resets succession	That damages A but favors B
Competition	
Inhibition (of dispersal, germination, growth) that slows establishment of B	Indirect facilitation if competitors of B inhibited, favoring B
Facilitation	
Indirect inhibition if competitors of B facilitated, so B not favored	Facilitation (of dispersal, germination, growth) with negative impact on A
Herbivory/Disease/Allelopathy	
If B damaged	If A damaged

Table 2. Facilitation and competition affect different life history stages of a plant (modified from Walker and del Moral 2003).

Life history stage	Mechanism of facilitation	Mechanism of competition
Dispersal	Bird perches	Dense canopy
	Seed entrapment by vegetation	
Germination	Scarification in animal guts	Leaf litter mats
	Site amelioration	Soil crusts
Establishment and growth	Site stabilization	Resource preemption
	Mycorrhizae	Thickets (less light, water; more herbivory, litter
	Less herbivory	
	Site amelioration	
Reproduction	Alternate food for pollinators	Frugivory, competition for pollinators
Survival	Less herbivory	More herbivory
	Less disturbance	More disturbance

Table 3. Succession-related topics, lessons from succession and applications to restoration. F = disturbance frequency; S = disturbance severity. Adapted from various sources including Walker and del Moral (2003), del Moral et al. (2007), Hobbs et al. (2007b).

Topic	Lessons from Succession	Applications to Restoration
Disturbance		
Allogenesis	Off-site factors can alter trajectories	Adjust goals to realities of disturbance regime
Autogenesis	Within-site factors drive small changes	Consider species interactions
Low F, Low S	Trajectory predictable	Minimal impact by disturbance. Address competition instead.
Low F, High S	Impact unpredictable	Difficult to plan for. Introduce stress-tolerators?
High F, Low S	Fast-growing pioneers dominate	Utilize or address problems of weedy species
High F, High S	Little biological legacy	Evaluate if restoration even possible.
Interactions	Complex impacts on trajectories	Aim for range of life spans and disturbance adaptations
Novel Types	There are often natural analogues	Experiment with species found in natural analogues
Diversity	High at intermediate disturbance	Promote or allow some disturbance
Patchiness	Supports multiple stages	Use spatially explicit methods. Overlapping stages okay.
Species Interactions		
Colonization	Survival low, dispersal stochastic	Add excess of desired species from multiple life forms
Replacement	Direct, sequential, cyclic, fluctuating	Apply methods best for dominant type of replacement
Dominance	Often but not always arrests change	Avoid unless dominant species belongs in desired community
Facilitation	Importance varies with fertility	Use selectively to promote change
Competition	Can increase diversity or arrest change	Avoid thicket-forming species
Trajectories		
Progressive	Most often desired	Promote short-lived stages
Retrogressive	Sometimes desired	Reduce fertility or diversity
Arrested	Relative to time scale; common	Promote only if matches goal
Hysteresis	No system lacks history	Actions impacted uniquely by each system
Models		
Thresholds	To overcome, extra input needed	Avoid tipping points; commit extra effort or abandon
Alternative Stable State	Arrested with positive feedbacks	Encourage network trajectories, diverse outcomes
Slow-fast Cycles	Different rates on adjacent plots	Manipulate autogenic factors
Gradual, Continuous	In late or retrogressive stages	Be patient! Change will be slow.
Stochastic	High in early and primary stages	Aim for restoring function, not composition

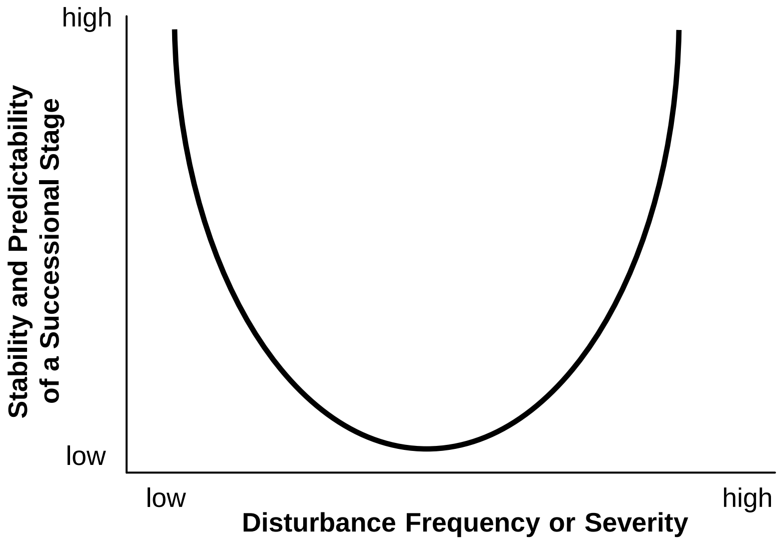

Figure 1. A proposed relationship between stability and predictability of successional stages and disturbance frequency or severity. Maximal stability and predictability are reached when disturbances are either minimally or maximally frequent and severe.

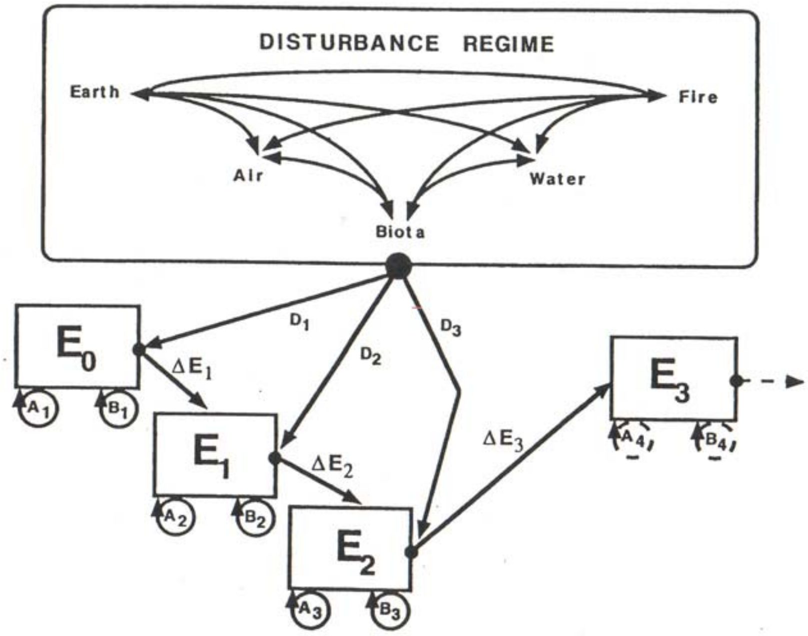

Figure 2. Ecological succession results from changes (ΔE_i) induced by the cumulative impact of a disturbance regime. A and B are abiotic and biotic feedbacks from the environment, D = disturbance, E = geographically explicit portion of the landscape occupied by an ecosystem. From Willig and Walker (1999) with permission.

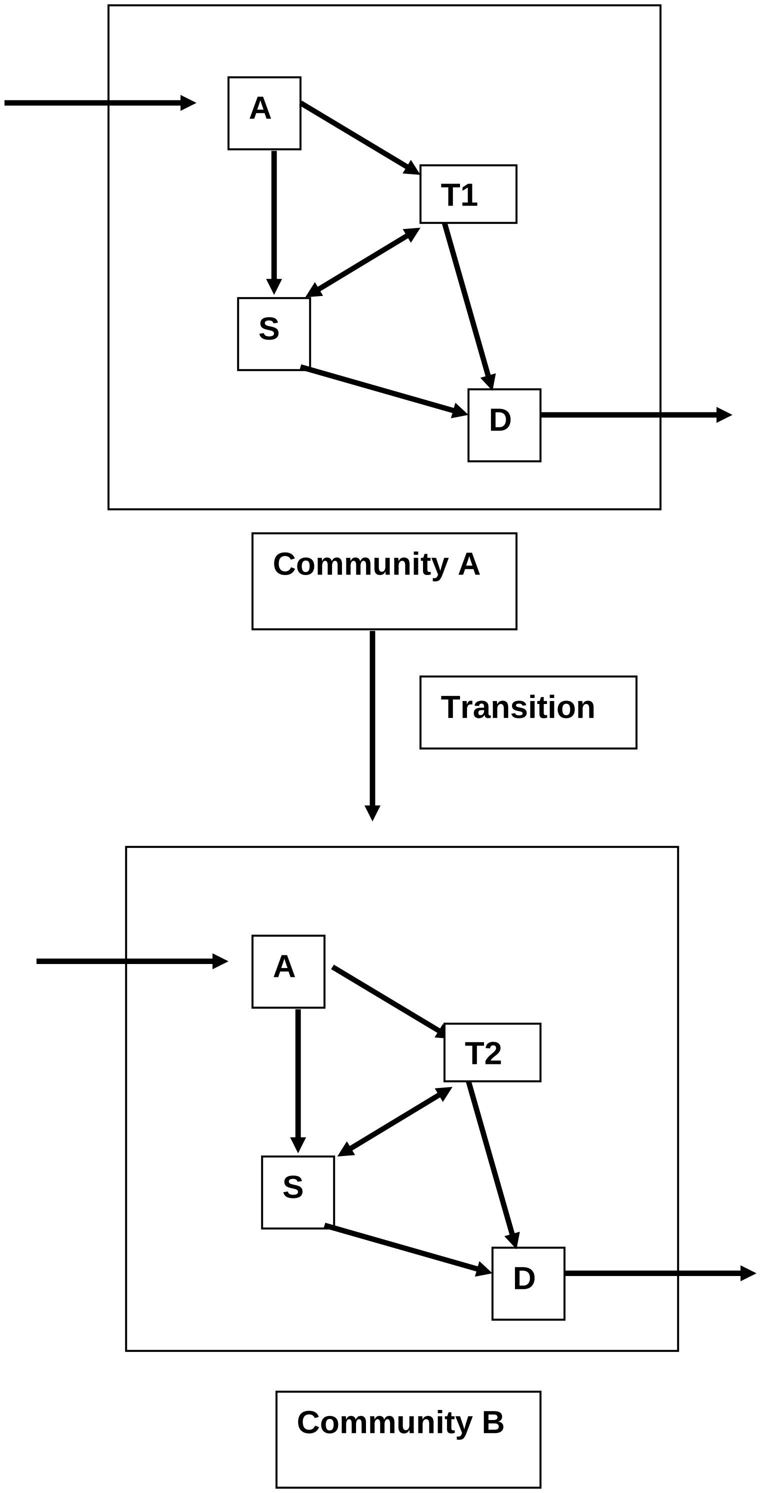
A
T1
S
D
Community A
Transition
A
T2
S
D
Community B

Figure 3. Classification of the status of species within a successional community (box). Successional transitions involve a change in the thriving (dominant) species but not necessarily in other types of species. A: a new arrival (from seed bank, dispersal or vegetative spreading; T: a species that thrives due to competitive dominance; S: a species present but merely surviving due to competitive inferiority; D: a species disappearing due to competition, damaged from disease, herbivory, abiotic disturbance, or senescence. Arrows denote species arriving or leaving the community or possible changes of status among species types within a community.

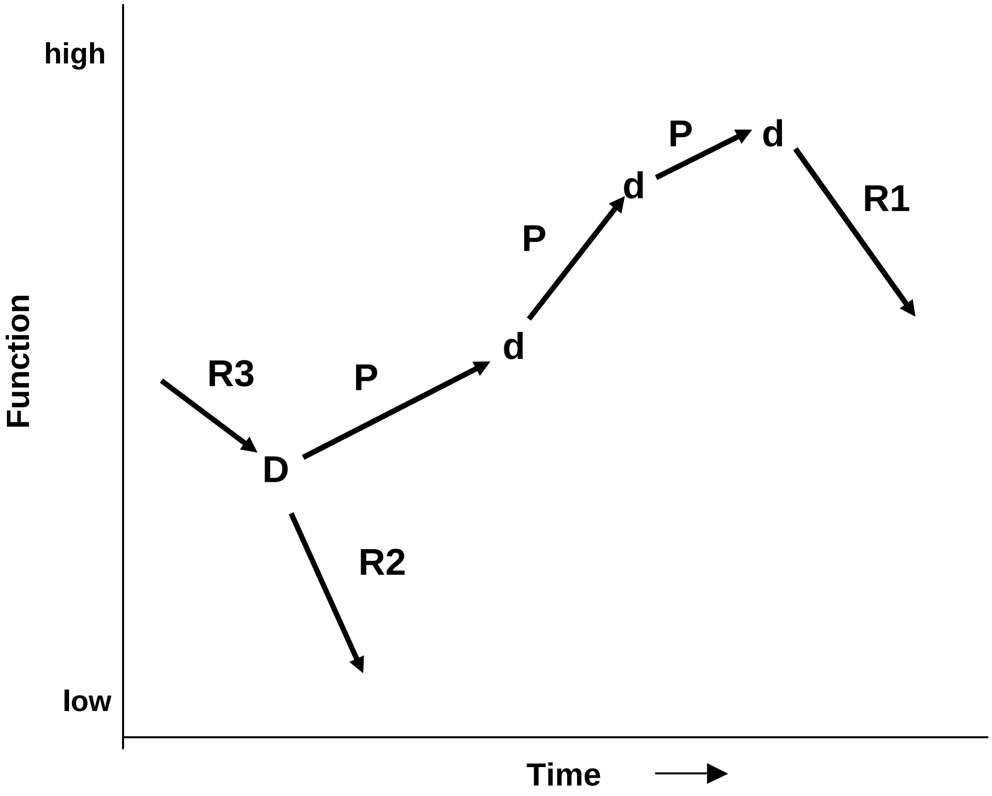

Figure 4. Possible inhibitory impacts on the trajectory of succession. a: Non-vascular plants; A1 and A2: concurrent colonists; I1 and I2: introduced native species; B, C and D: subsequent colonizers; J: aggressive alien invader. Competitive inhibition can occur early in succession (e.g., by non-vascular plants inhibiting colonization of vascular plants or an invader inhibiting succession of native species) or later in succession (e.g., by mid-successional species or invaders inhibiting later successional species). From Walker and del Moral (2003) with permission.

Figure 5. Disturbance triggers for progressive and retrogressive succession. Progressive succession (P) is typically initiated by a major disturbance (D) but the trajectory of increasing ecosystem function is altered by minor disturbances (d). Retrogressive succession (R) is usually initiated by a minor disturbance during a progressive succession (R_1) and is characterized by a loss of some ecosystem function (threshold or gradual continuous models; see text). However, retrogressive succession can be caused by (R_2) or diverted to progressive succession (R_3) by a major disturbance. R_2 and R_3 types of retrogression can be best described by alternative stable states, slow-fast cycles or stochastic models (see text). (this figure is missing)