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Insights Gained from Succession for the Restoration of Landscape Structure and Function

Roger del Moral, Lawrence R. Walker, and Jan P. Bakker

Key Points

1. The study of succession provides valuable lessons for improving the quality of restoration programs.
2. These lessons suggest that restoration tactics should focus on site amelioration, improving establishment success, and protecting desirable species from herbivory and competition during their development.
3. Incorporation of physical heterogeneity in the early stages will foster mosaics of vegetation that better mimic natural landscapes.

2.1 Introduction

Restoration starts with the desire to improve degraded and destroyed landscapes or ecosystems. Land can be returned to utility through enhancing fertility, by reversing the long-term effects of agriculture, mining, or logging or by ameliorating toxicity. Plant communities also can be modified to resemble their former condition in an effort to provide conservation benefits (van Andel and Aronson 2006). In this chapter, we focus on insights from succession that enhance the rate and quality of restoration. Restoration outcomes are affected by aboveground and belowground processes, but are usually assessed as impacts on aboveground structure and function. We emphasize those processes that can be readily manipulated through a model that features “bottlenecks” to effective restoration. To establish a context for this model, we first discuss concepts central to restoration. Our approach highlights those crucial stages of succession where restoration efforts are most likely to be effective. Here, we highlight how understanding natural succession provides insight into creating effective restoration outcomes. We describe how both structure and function develop during natural succession in response to disturbances. Finally, we summarize the lessons learned from succession that are important in restoration.

2.1.1 Goals

The chances of success in restoration are enhanced if clear goals are established that describe measurable targets to be reached by a specific time. For example, a goal may be to achieve a complex of persistent, species-rich communities with wildlife habitats and opportunities for recreation. This goal could be evaluated by monitoring wildlife populations or plant species and by documenting human usage.

Several strategies might guide a project, but exact mimicry of natural successional trajectories should not be one of them. Because succession is affected by landscape factors and often proceeds slowly, careful intervention usually must occur and the early introduction of target species, those species planned to form the final community, should always be considered. For example, using legumes to enhance soil nitrogen and ameliorate site conditions can foster the development of complex structure decades faster than the direct and continued application of inorganic nitrogen. Restoration actions attempt to guide the trajectory toward desired targets more quickly than would occur spontaneously (cf. Díaz *et al*. 1999).

2.1.2 Ecosystem Parameters

Structure and function are crucial components of ecosystems. The structure of vegetation can be described by species composition (e.g., richness, abundance, dominance hierarchies), by growth form spectra, or by physiognomy. Ecosystem functions include productivity, nutrient cycling, and water use. Species may not contribute to ecosystem function in proportion to their abundance (Schwartz *et al*. 2000) and a few species can dominate functions. These dominant species may usurp resources (luxury consumption) and thereby lower productivity. However, the relationship between dominance and proportional contributions to functions remains debatable. Nearly complete functional restoration often occurs before structure is fully developed, but goals of restoration projects often emphasize structure over function (Lockwood and Pimm 1999). A system may be optimally productive, nutrient conservative, and structurally complex long before it hosts its full complement of species. While increased biodiversity can enhance productivity in grasslands of intermediate fertility, it remains unclear if this effect is proportional to biomass increases (Hector *et al*. 1999, Roscher *et al*. 2005). Plant species are also characterized by adaptive strategies (Grime 2001), in which growth rates and competitive abilities categorize species functions. The mix of strategies found in vegetation shifts during ecosystem development in response to fertility and competition and is therefore sensitive to modification, so trajectories can be under some degree of control. Biodiversity also changes with fertility because both hyper-fertile and infertile sites share low diversity, but have species of contrasting strategies (but see Chapter 6).

Díaz *et al*. (2004) showed that it is possible to predict ecosystem function using simple plant functional traits, so that selecting plants with particular traits can improve these functions. Traits such as leaf size, rooting depth, canopy architecture, seed size, and life span are correlated to productivity and to stress tolerance. By classifying species into functional groups, the task of monitoring ecosystem function is simplified. Even early in succession, these traits track vegetation dynamics. Often, a goal of restoration is to achieve substantial ecosystem structure quickly in order to optimize ecosystem function. Limits to productivity due to infertility and moisture (Baer *et al*. 2004) can retard succession (del Moral and Ellis 2004), so augmenting productivity is often central to restoration. Unfortunately, high productivity often only favors competitive species that produce dense vegetation and arrest structural development and limit biodiversity. Thus, restoration programs in relatively fertile sites, where the priority is to attain high biodiversity quickly, may fail unless fertility is limited and monitored.

2.1.3 Succession and Responses to Environmental Impacts

Succession is the process of species replacements accompanied by ecosystem development. Disturbances cause abrupt changes in or losses of biomass, usually associated with similar changes in ecosystem function. Succession occurs after disturbances that range from mild to severe. Mild disturbances, such as infrequent light ground fire regimes in fire-tolerant vegetation, do little damage. While relative proportions of species change following mild disturbances, species turnover is not directional. Nutrients may be lost and many individuals die, but most species survive. This process of recovery is sometimes called regeneration dynamics, not succession. It is uncommon that restoration will be required in such cases, unless diversity enhancement is required to overcome the consequences of overgrazing or intense fires.

Secondary succession occurs after more severe disturbances such as canopy fire (Beyers 2004) and flooding. Common anthropogenic examples include recovery when farming or grazing cease (Bakker and van Wieren 1998). A legacy of species may persist, but often it consists of undesirable nontarget species. Achieving structure and function comparable to developed vegetation may take decades if the only species that persist are those adapted to disturbances. In these cases, restoration can establish more complex, efficient ecosystems by early, targeted species introductions.

Primary succession occurs after severe disturbances that form new surfaces. Rarely is there a biological legacy, so regeneration is driven from outside the site. Familiar natural examples include lavas, surfaces revealed by retreating glaciers, landslides, and floods (Walker and del Moral 2003). The trajectory of development is unpredictable because the lack of survivors leaves a blank slate upon which many alternatives might be established.

The predictability of restoration can be improved by introducing species expected to form the fundamental structure of the desired system (Turner *et al*. 1998). Definitive model communities for restoration (“nature target types”) exist for The Netherlands (Bakker 2005), and could be developed for other regions from available descriptions of plant communities (Rodwell 1991–2000, Schaminée 1995–1999, Wolters *et al*. 2005). Choosing a model community, or suite of communities, depends on the historical context of the target. Restoring rural landscapes to include examples of meadows under moderate grazing, for example, requires data from 19th century descriptions (Bignal and McCracken 1996). However, we emphasize that restoration for biodiversity conservation should aim at multiple targets and a mosaic of habitats. In some cases, no target or model community is known in detail, so target communities must be improvised.

2.1.4 Structure and Function

If an ecosystem has suffered only minor disturbance, structure and function may develop together. Few of the missing elements require immediate replacement because survivors, being physiologically and morphologically plastic, can compensate until others return. Sites that impose physiological stress on plants, such as mine tailings, recover slowly, and have low biodiversity for decades, but functions such as production rates are maximized more quickly than are ecosystem characteristics, such as vertical complexity and biodiversity.

Complex structure can be inconsistent with achieving low erosion, high productivity, and tight nutrient cycles in a short time. For example, if most of the species are annuals, much of the surface will be barren during part of the year. High species diversity can be achieved by limiting fertility and competition, but this could reduce productivity and limit nutrient uptake. Much of the literature describing the effects of biodiversity on ecosystem structure concerns species loss, not species additions. Smith and Knapp (2003) showed that net production was scarcely affected by excluding rare species compared to a quantitatively similar reduction of the dominant. However, they suggested that the lack of uncommon species could reduce productivity, thus leading to less inefficient ecosystems. Rosenfeld (2002) suggested that function would be best maintained if the functional group diversity, not species diversity, were maximized. Several biodiversity–ecosystem function experiments in grasslands support this view because the number of functional groups was positively related to ecosystem processes (Hille Ris Lambers *et al*. 2004, Spehn *et al*. 2005).

If functions such as the rate of productivity and nutrient uptake increase more rapidly than does diversity, then restoration can concentrate on dominant species to provide a framework of structure with substantial functioning. This could provide an acceptably stable system with low diversity. Over longer periods, additional species and functional types (*sensu* Díaz *et al*. 1999) can be encouraged to assemble to provide greater long-term resilience.

2.2 Conceptual Scheme of Succession

Natural ecosystem recovery displays an inspiring diversity of responses to equally diverse disturbances. Sites made barren by human activities were once ignored while succession ran its fitful and inefficient course, leading to landscapes replete with exotic species and with limited productivity. The scarcity of productive land and effective biotic reserves now dictates that these sites be restored. Succession provides a framework, not a precise model to enhance restoration efficiency. Restoration often is driven by the real need to achieve effective vegetation cover in a short time. However, where conservation goals are paramount, early successional communities often form a significant component of the resulting landscape. One goal that would mimic nature would be a shifting mosaic of vegetation types that reflect, at any given time, an array of communities attuned to different combinations of fertility, disturbance, and competition, but dominated by native species.

Egler (1954) was among the first to emphasize the vagaries of succession. His initial floristic composition model stated that succession started with whatever propagules were available, even if the species were normally common in late successional stages. Many numerical models emphasize particular aspects of vegetation dynamics, but few usefully predict precise trajectories of all species over long periods (Walker and del Moral 2003). Our model (Fig. 2.1) is not

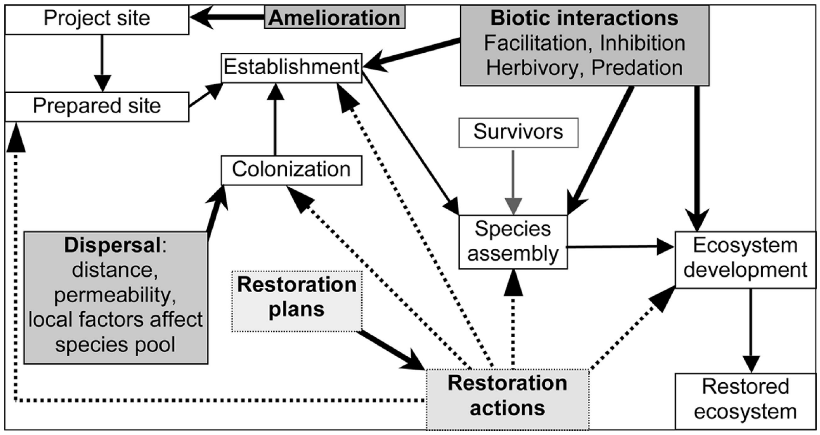

Figure 2.1 Simplified mechanisms of ecosystem change. Restoration plans drive the process and continue to be important throughout the project. The three dark boxes represent natural mechanisms that alter the success of organisms and are linked to processes by thick arrows. Restoration actions and five dotted lines emanating to process boxes indicate restoration actions that may act initially on the project site and subsequently on four phases of restoration. Thin, solid arrows indicate the course of succession. The restoration process starts with planning, in which critical stages are identified. It ends with the formation of the restored ecosystem. Further disturbances, not shown, can affect development at any stage.

comprehensive but does emphasize those constraints that limit and direct species assembly and ecosystem development that can be applied to restoration actions (see Chapter 1).

Three sets of mechanisms direct natural colonization and establishment (shaded boxes, Fig. 2.1): physical amelioration, dispersal, and biotic interactions. After establishment, species form distinct combinations with some becoming dominant as soils develop and biotic interactions intensify (Table 2.1). Restoration actions can alter colonization, establishment, and species accumulations and through these affect ecosystem development. Below we summarize five major phases of succession and suggest how restoration can use this model. At each phase, we first indicate how succession normally occurs and then the relevance for restoration.

2.2.1 Amelioration

Infertility is the most common obstacle to effective restoration. Drought, lack of organic matter, surface instability, and toxicity are among many factors that can also be problematic. These adverse conditions can be created by natural phenomena (e.g., volcanic eruptions, floods) or by human activities (mining, logging). It is rare that destroyed sites will recover both complex structure and substantial function without some applied amelioration (Snyman 2003). During primary succession, natural processes normally improve growing conditions for plants. Winds deposit dust, pollen, seeds, and insects crucial to reducing infertility (Hodgkinson *et al.* 2002). Amelioration can include water erosion that removes overburden (del Moral 1983), frost–thaw cycles that fracture rocks, and wind erosion that creates microtopography to form safe-sites.

Table 2.1 Comparison of lessons from succession and applications to restoration. Topics refer to boxes in Fig. 2.1.

Topic	Lessons from succession	Application to restoration
Amelioration	Stress restricts establishment; safe-site creation important; low fertility may increase diversity	Create heterogeneity and reduce infertility and toxicity
Dispersal	Regional species pool limited; chance is important	Introduce poorly dispersed species in early stages
Colonization	Disharmony characterizes early vegetation; survival probabilities low and stochastic	Introduce array of life-forms; natural dispersal does not provide most colonists; plant more species than required
Establishment	Affected by local variations in stress; oases are of minor importance; safe-sites crucial	Create heterogeneity and safe-sites
Facilitation and inhibition	Nurse plants important; strong dominance reduces diversity; priority effects common	Ameliorate site factors and dominants in mosaic; plant "seral" species at the start to direct trajectory
Herbivory	Animals can eliminate potentially successful species	Project plantings from large grazers; protect seeds from small seed predators; intermix plantings
Species assembly	Affected by chance, biotic interactions; alternative trajectories are common, sometimes induced by differential herbivory	Accept that there are several viable structural and functional results
Development	Strongly affected by biotic interactions, later disturbances	Plan for more disturbance response; manage biotic effects

During restoration, amelioration is usually needed to alter fertility or reduce toxicity. Reid and Naeth (2005) bravely attempted to revegetate mine tailings under subarctic conditions. Kimberlite tailings lack surface stability, organic matter, and nutrients, but do have excessive magnesium from serpentine rocks. By amending soil with organic matter to improve structure and fertility, they established grass cover. However, excessive fertility can reduce biodiversity by promoting only a few competitive species. Biomass responses to fertility are a major control of diversity, at least in grasslands (Grime 2001). Moderate disturbances from mowing or grazing by vertebrates can enhance diversity in more fertile sites by reducing competitive dominance. In some systems, dense, low-diversity vegetation may be desirable to reduce invasion by weeds or to survive intensive use.

Less attention is paid to spatial heterogeneity in physical properties and to variations in fertility, yet these conditions potentially enhance survival of less competitive species and permit sites to develop at different rates. The resulting mosaic enhances overall biodiversity. Huttl and Weber (2001) showed that pine plantations were more successful on coal tailings where acidity varied naturally, providing roots and mycorrhizae opportunities lacking in homogenous acidic soils. Heterogeneity initially present often disappears due to erosion or plant development. Soil heterogeneity in restored prairies near Chicago (USA) declined as C-4 grasses achieved dominance (Lane and Bassiri Rad 2005). Monitoring soil parameters and spatial patterns of dominant species should be included in traditional monitoring, with contingencies to augment heterogeneity if the system becomes too homogeneous. One general method is to import soils with contrasting properties (e.g., acid soils in limestone regions). Alternatively, species that produce litter with qualities distinct from the common species could be introduced.

2.2.2 Dispersal

The ability of most species to disperse is more limited than generally realized, so dispersal can limit colonization (Fuller and del Moral 2003; see Chapter 6). Isolation favors colonization by species with small, buoyant seeds. If the seed rain is sparse, then chance plays a role in species assembly and alternative compositions in similar habitats can develop (McEuen and Curran 2004, Svenning and Wright 2005). Sites that have been severely damaged often have a depleted seed bank with little chance of replenishment (Bakker and Berendse 1999).

Landscape permeability, that feature which resists or promotes dispersal, varies greatly. Permeable landscapes may contain barriers, but also stepping-stones and corridors (Fig. 2.2). Some habitats are impermeable to some species, but not to others (Honnay *et al*. 2002). Barriers and inhospitable habitats reduce permeability and therefore can limit the diversity of functional types that reach a site unaided. Restoration activities can eliminate dispersal problems by planting most species expected in the community. This is rarely successful because residual species resist the newly planted species and swarms of invading alien species can overwhelm the site. Many species that could be effective in a particular project, even though they may not be present in local examples of the target vegetation, are valid candidates for planting. Martínez-Garza and Howe

Figure 2.2 Refugia with shallow pumice depths allowed some species to survive the 1980 eruption of Mount St. Helens (right side of picture). However, the surroundings were impermeable to colonization by the survivors because of deeper pumice deposits. These deposits were colonized by invading species such as *Chamerion angustifolium* shrubs shown in the center of the picture.

(2003) showed that dispersal of rain forest trees into abandoned pastures was severely limited and that planting trees shortened succession by at least three decades.

The restoration of diverse meadows from pastures is particularly difficult when the existing ruderals resist the establishment of meadow species. In such cases, dispersal can be promoted by the introduction of hay from a reference site (Hölzel and Otte 2003) and by adding top soil and litter with seeds of target species and appropriate soil organisms (van der Heijden *et al*. 1998, De Deyn *et al*. 2003).

2.2.3 Colonization

Isolated sites are unlikely to receive large-seeded species common in later succession, so early communities are a disharmonious selection of the local flora. Species that do arrive are usually small-seeded and without large energy reserves. While a few individuals may establish, early development is commonly limited to very favorable sites (see also Wagner 2004). Seedling failure rates are also high. When understory species were planted in *Fagus* forests in Belgium, survival was higher in cleared sites than in the controls (Verheyen and Hermy 2004). Colonization by *Pinus sylvestris* in Spanish old-fields was restricted both by competition from meadow vegetation and by seed predation (Castro *et al*. 2002). Such failures to establish slow the rate of ecosystem development.

There is a temptation to depend on spontaneous recolonization because it is economical (see Chapter 6). Prach *et al*. (2001a) suggested that spontaneous succession (i.e., depending on volunteering colonists) might be useful, at least for reclamation, where any vegetation at all is beneficial. Ideally, spontaneous species will facilitate the establishment of woody species in forest environments, but this is uncertain. The nature of volunteer species is contingent on the landscape, and trajectories started by ruderal species often diverge in unexpected ways and lead to vegetation that provides few values (Prach *et al*. 2001b). Unless economic resources available for restoration are scarce, even a favorable seed rain of spontaneous species should not preclude the introduction of target species. Under vegetation conditions typical of restoration programs, where the surroundings are disturbed and mature vegetation is scarce, spontaneous vegetation often will be dominated by exotic species (Bakker and Wilson 2004) and active introduction of species will be required when biodiversity conservation is a goal. There are several ways to enhance the colonization of spontaneous species, though each has limitations. Installing perches creates centers of dispersal for species dispersed by birds (Toh *et al*. 1999), but better still is to use trees and shrubs that attract birds and that can protect seedlings (Slocum and Horvitz 2000). This nucleation process is a crucial form of colonization in many types of natural succession and can accelerate the establishment desirable species.

2.2.4 Establishment

The establishment phase is critical, and surfaces can be hostile. A seedling must grow rapidly to reach better conditions, a feat constrained by infertility, drought, excessive light, surface heat, and other unfavorable conditions. Establishment is promoted by mechanisms that trap seeds to increase the odds of germination, by stable surfaces, and by safe-sites appropriate to each species (Walker *et al*.

~~in press~~). Jones and del Moral (2005) noted that seedlings on a glacial foreland were normally found in microsites that offered substantial protection, while Tsuyuzaki *et al*. (1997) showed that even minimal surface instability restricted seedling establishment on loose volcanic substrates.

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Establishment success may be improved if several species in each of several functional groups (functional redundancy) are employed early in restoration. Even if some species fail, ecosystem functions are likely to develop more quickly than if too much reliance is placed on a few species. Using functional redundancy may prove beneficial in view of unpredictable global change.

2.2.4.1 Facilitation

Biological facilitation is the process by which established plants improve the performance of other plants. Facilitation has been the process emphasized during establishment, largely because of early studies of succession that were focused on this process (Walker and del Moral 2003). Facilitation is physical when established plants improve soil moisture availability, temperature, or light conditions or reduce wind. Rocks and small channels augmented seedling survival early in succession on Mount St. Helens (del Moral and Wood 1993; Fig. 2.3), but plants also provide physical amelioration (Barchuk *et al*. 2005). Established plants may be “nurse plants” and facilitate seedling establishment (Henríquez and Lusk 2005). Nurse plants may inhibit one species, thus releasing other species from competition. Legumes are particularly likely to have such complex interactions (del Moral and Rozzell 2005). Eventually, the fostered plant may eliminate the nurse plant (Temperton and Zirr 2004). Shrubs often

Figure 2.3 *Anaphalis margaritacea* is one of several species that were able to establish early in succession, following the 1980 eruption of Mount St. Helens, by lodging among rocks. Rocks, as well as other microsite features, enhance moisture and nutrients, while protecting seedlings from herbivory.

protect forbs from herbivory by physical (Garcia and Obeso 2003) or by chemical means (Jones *et al*. 2003), while late successional species such as *Quercus robur* can establish among spiny *Prunus spinosa* (Bakker *et al*. 2004). However, facilitation should be used carefully so that it does not become inhibition.

Physical amelioration tactics are well-known. In addition, site heterogeneity should be enhanced to improve the number and variety of safe-sites. Rocks, hummocks, and rills foster heterogeneity, provide refuges, and help to insure against unforeseen events. Even small variations on hostile surfaces can facilitate seedling establishment, so small restoration efforts create favorable microsites. Existing heterogeneity on relatively level terrain should be preserved and natural processes mimicked. Heterogeneity can be augmented by the introduction of rocks large enough to protect seedlings from drought or herbivory and by introducing inorganic mulch of variable depths. The creative use of low windbreaks can conserve moisture and reduce desiccation of seedlings. A mosaic imposed at the start of a project, for example by patches with different fertilization regimes, may reduce the need for intense long-term maintenance. Physical amelioration aimed at creating heterogeneous conditions can lead to the development of alternative, but stable and desirable communities.

2.2.4.2 Inhibition

The inhibitory potential of plants during succession is crucial but little appreciated. Such negative effects of one species on another can slow, arrest, or deflect succession. Competition for resources and allelopathy are the main types of inhibition. Although nitrogen-fixing plants may ultimately facilitate other species, their immediate effect can be inhibitory, particularly when a dense sward or thicket forms. The facilitative effect can be delayed until the nitrogen-fixer dies (Gosling 2005). Such an inhibitory effect of nitrogen fixing plants may be more common than generally realized (Walker 1993). Inhibition often causes problems during restoration. Aggressive invaders suppress plantings or nurse plants suppress desired target species. By planting saplings in scattered clusters to provide mutual support, followed by selective thinning, the growth of species expected to form the framework of mature vegetation can be accelerated. Selective thinning of nurse plants and competitors can also facilitate the development of target species (Sekura *et al*. 2005).

2.2.4.3 Herbivory

Seed predation and other forms of herbivory can reduce establishment (Ramsey and Wilson 1997). However, herbivory can also promote seed dispersal, add nutrients, and facilitate seedling recruitment (Bakker and Olff 2003). Such interactions have been observed to involve livestock, burrowing mammals, and ungulates such as the North American elk on Mount St. Helens. Herbivory during establishment is a major cause of restoration failure. In many cases, plantings must be protected from herbivores by fences or individual exclosures until they become established.

Plant defense against herbivory, such as wood, terpenes, and tannins, generally increases during succession as a function of changing species composition and maturation of individuals. In secondary succession, N-based secondary compounds may defend forbs so herbivory is concentrated on grasses, deciduous shrubs, and trees (Davidson 1993). Because palatable plants often dominate intermediate successional stages, herbivory can retard or expedite succession. Each situation requires analysis to determine whether herbivores should be excluded, at least during crucial phases of the project. Excluding herbivores from parts of a project, but not others, could facilitate a desirable vegetation mosaic.

Herbivores can disrupt dominance and thus permit establishment of new species (Bach 2001). Bishop *et al*. (2005) demonstrated that various herbivores could reduce the rate of succession by slowing the rate of *Lupinus lepidus* expansion. However, herbivory also reduces competition by *Lupinus* and hastens the development of sites in which it had dominated. Herbivory may accelerate succession because some plant species may exhibit compensatory growth in the face of herbivory (Vail 1992, Hawkes and Sullivan 2001). While herbivory is more likely to spawn negative effects (e.g., promoting weed invasion or accelerating erosion), the possibility that it may be positive should be considered for each study (Belsky 1992). Established communities may be changed in unpredictable ways because the conditions of the restoration site may not have a comparable natural model. Howe and Lane (2004) established wetland prairies, and then exposed them to herbivory by voles. Voles caused dramatically divergent trajectories after four years, fostering a mosaic. Ants can hoard certain species to enhance the vegetation mosaic (Gorb *et al*. 2000, Dostal 2005).

2.2.5 Assembly and Ecosystem Development

Species can accumulate over decades, even while successive waves of pioneers fail. Populations expand and fill available space, thus increasing the use of resources. During this time, the character of the community emerges. Planned actions or responses to unexpected contingencies can lead to results that are more desirable, yet little attention has been paid to modifications during species assembly. It is during this period that adequate results can be sharply improved.

2.2.5.1 Biotic Effects

The composition of a developing community can be affected by the arrival of additional species, and, as is the case with establishment, by facilitation, inhibition, and herbivory. Facilitation and inhibition continue to have multiple effects (Fig. 2.4). For example, N-fixing taxa improve soil fertility, but they have complex interactions with other plants and with suites of herbivores as well (Bishop 2002, Clarkson *et al*. 2002). The competitive effects of these species often filter the species that could benefit from improved soil fertility. *L. lepidus* initially formed sporadic dense colonies on Mount St. Helens. Because this species is short lived and susceptible to multiple attacks from herbivores, the colonies expanded slowly, and their abundance cycled greatly. After several cycles, species able to establish during "crash" years have become abundant, but mosses make it difficult for other species to establish (del Moral and Rozzell 2005). The totality of how a species affects others, not just its net effect on the community, is crucial to understanding probable trajectories.

As species assemble, competitive hierarchies form and structure develops, but the overall net effects of competition and facilitation are difficult to predict. Hence, the trajectory of the community is also hard to predict. Species composition will adjust over time and usually lead to a functionally integrated

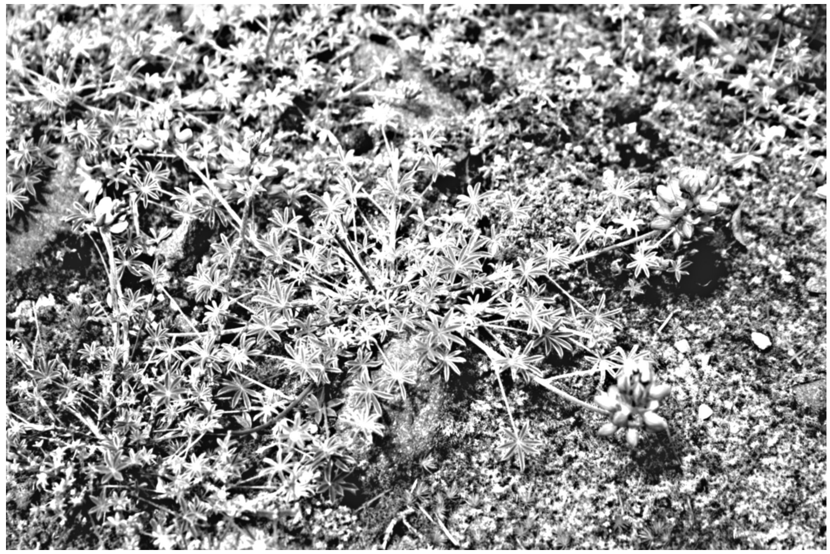

Figure 2.4 *Lupinus lepidus* and mosses interact to form a dense carpet on lahars at Mount St. Helens. Their net effects on other species are complex. While lupines enhanced nitrogen levels, the primary beneficiaries were mosses. Mosses inhibit the establishment of seed plants, while lupines competed with germinating seedlings.

ecosystem with substantial complexity and spatial variation. However, we note exceptions. If dense vegetation becomes established, subsequent development may be arrested. Dense growths of grasses, vines, ferns, bamboo, and shrubs can form thickets that defy change (Walker and del Moral 2003, Temperton and Zirr 2004). Thickets may be useful to restoration if they curtail erosion, reduce herbivory, or improve fertility and if the thicket eventually senesces. Artificial thickets can be created using dead branches to protect young plants. Planting late successional species in dense arrays can enhance their survival, promote heterogeneity, and limit weeds. If the goal is to produce low-maintenance vegetation dominated by shrubs, then shrub thickets can arrest succession (Niering and Egler 1955, Fike and Niering 1999). A mixture of species is usually superior to one because several species complement one another and provide more resources for wildlife (De Blois *et al*. 2004).

Nontarget species can be resisted by proper maintenance of existing target species. Using unpalatable species as “nurse plants” should be considered where herbivory is likely to reduce recruitment or harm young planted species. Callaway *et al*. (2005) described how unpalatable species produced indirect facilitation effects on palatable grassland species in the Caucasus (Russia). The benefits of using indirect facilitation include greater biological and functional diversity, though care must be exercised that the facilitators do not become dominant.

The difficult balance among biotic effects is illustrated by attempts to enhance the biodiversity of abandoned grasslands. Grazing and biomass removal is often insufficient to reduce fertility, a prerequisite to promoting higher diversity of target species. Topsoil removal (see Chapter 6) is a viable tactic, but nontarget species often invade and dominate the disturbed conditions. Sowing pasture grasses in an effort to smother nontarget species often creates a dense turf that inhibits target species (Bakker 2005).

2.2.5.2 Further Disturbances

Restoration projects are not immune from further disturbances due to grazing, fire, wind, or disease. Most disturbances are ephemeral, but some, such as herbivory, can destroy a project. Therefore, even after establishment, young plants often require protection, and exclosures against large animals are frequently needed (Koch *et al*. 2004).

Fire can destroy a restoration project, but often it merely serves to rejuvenate the vegetation and to promote the growth of target species. Frequent fires usually create herbaceous vegetation dominated by short-lived species, while less frequent fires can promote fire resistant trees (Hooper *et al*. 2004). Using fire to introduce or maintain heterogeneity can promote diversity at the scale of the project.

Atmospheric nitrogen deposits are a major disturbance that affects the structure and function of all ecosystems. Greater fertility lowers diversity by favoring only a few competitive species (Zavaleta *et al*. 2003, Suding *et al*. 2005). This effect is widespread, affecting not only industrialized regions, but also such isolated areas as the Mojave Desert, California, where atmospheric nitrogen deposits promoted alien plants and inhibited native species (Brooks 2003). Nitrogen deposition can also facilitate shifts in vegetation types (Kochy and Wilson 2005).

One approach to reduce excess fertility is to remove biomass. After long-term haymaking without fertilization, the output through hay was higher than the input from atmospheric nitrogen deposition. The critical input to maintain nutrient poor meadow communities in northern Europe is less than atmospheric deposition, suggesting that no fertilization is needed in these habitats (Bobbink *et al*. 1998).

2.2.5.3 Restoration Disturbances

Restoration is a unique form of disturbance, applied over time in a nuanced way. Adding fertility in a mosaic, for example, is a disturbance because it alters the existing regime in ways designed to alter species composition. The desired result is a vegetation mosaic with horizontal and vertical heterogeneity, even in grasslands and subalpine vegetation. Restoration tactics may deflect the trajectory of an assembling community in several ways. Species exerting strong dominance may be thinned. Fires or secondary disturbances may be introduced and, at some stage, it may be imperative to introduce mycorrhizae to foster more complete ecosystem function (Allen *et al*. 2005). There are many opportunities to introduce integral species incapable of independent establishment. Zanini and Ganade (2005) showed that perches that attracted birds to abandoned Brazilian subtropical pastures enhanced diversity of woody species. More seedlings were introduced where residual vegetation occurred, suggesting that a facilitative effect was also present. White *et al*. (2004) confirmed that spontaneous establishment is unreliable. In North Queensland forests, dispersal into isolated revegetated forest remnants was inundated by exotic species. Humans must intervene to introduce species into isolated recovering sites (Holl *et al*. 2000). Where restoration efforts occur on small sites, attracting bird dispersers may have little effect because the seed rain is dominated by wind-dispersed species that inhibit the few woody seedlings (Shiels and Walker 2003).

Relict and rapidly establishing vegetation present major challenges to restoration. Management is needed to overcome the inertia of survivors and exotic invaders. Hooper *et al*. (2005) demonstrated many barriers to regeneration of tropical forests on abandoned pastures in Panama. Competition from grasses, limited seed dispersal, and fire all restricted potential colonists. By planting native species in clusters, providing firebreaks and abstaining from fertilization, recovery was promoted.

2.2.5.4 Community Effects

Successful restoration requires an understanding of individual species, but relatively early in the process the focus must shift to community effects. Communities form as species proportions shift through competition and facilitation, colonization by species, and differential herbivore and disease pressures. Competition and facilitation vary in space and time, depending on the density of the participant species. While a canopy species can provide understory heterogeneity, biodiversity often declines (Morgantini and Kansas 2003). The results of the complex biotic interactions include divergent trajectories to both undesirable states that need to be redirected and to acceptable communities. The rates by which species facilitate or inhibit others differ with environmental stress, so succession rates will differ locally to create biologically heterogeneous conditions. By altering stress levels, desirable heterogeneity in a restoration project can be promoted. This heterogeneity can provide shifting spatial conditions so that no species achieves strong dominance during assembly. Once initiated, heterogeneity persists and provides greater structural complexity.

Restoration projects that are impacted by severe disturbances may not be able to recover the spectrum of species types found in mature, intact vegetation (Dana *et al*. 2002), or even recover their pre-disturbance functions. Dispersal limitations and local depletion of biodiversity can preclude many species from colonizing (Pyšek *et al*. 2005), so ongoing management could promote species with limited dispersal or reestablishment difficulties. If a project develops only from common species, structure will suffer and functions may be suppressed. Where the landscape matrix is agricultural, the promotion of species complexity may be more important as one way to provide habitats for species that can limit agricultural pests.

Under many conditions, restoration will be successful if there is complex growth-form structure with desired target species, even if biodiversity remains low. Over time, greater biotic complexity may accumulate, but it is likely that it will be much less than natural vegetation (Rayfield *et al*. 2005). During development, monitoring should continue to determine if interventions are needed. It is rare that they are not. Dominance by a few thriving species or to invasion of nontarget species requires attention. Disturbances from grazing, fire, pathogens, or wind all may require attention. Monitoring is also required to note the need to intervene to nudge the system along more desirable trajectories (de Souza and Batista 2004). In some cases, low biodiversity is acceptable because it reflects the natural situation (e.g., a salt marsh or a fen) and is the desired target. In other cases, limited biodiversity is an adequate result if community processes are adequate and the goal is to alleviate erosion or provide amenities.

2.3 Restoration Planning

Planning to facilitate the recovery of a landscape from anthropogenic impacts requires knowledge of the site, of potential ecosystems that can be achieved, and of the bottlenecks to development (Temperton *et al*. 2004, van Andel and Aronson 2006). A clear idea of the nature of the site when active maintenance ceases should be part of any plan. Planning not only prescribes the procedures and protocols, but also provides for maintenance and management to reach specific goals. It specifies the criteria by which a project is evaluated. Effective planning includes proper monitoring that will be communicated in the open literature. In this way, effective methods will be disseminated and mistakes can be avoided. Restoration should focus on five stages (Fig. 2.1), though for practical reasons, most effort will be put on amelioration of the environment and establishment. Colonization occurs *de facto* when species are selected, but many programs ignore species assembly and ecosystem development.

Planning starts with goals. Because late successional vegetation under similar environments can be variable (McCune and Allen 1985) and because trajectories are unlikely to converge to predictable endpoints (Taverna *et al*. 2005), goals should be specified in functional terms after considering the landscape and its biota (Khater *et al*. 2003). Functional goals can reside within goals expressed as structural classes such as short swards or tall forb communities and their spatial arrangement (Bakker 1998). Biodiversity goals derived from community descriptions are available in many countries (e.g., Anderson 2005). The selected species should be capable of forming a functional community, and their life-history characteristics can be incorporated into planning (Knevel *et al*. 2003).

Before the start of major projects, existing soil conditions (e.g., fertility, moisture, microsites), surviving species (if any), and local topography must be determined. These parameters will help limit the range of feasible "targets." During planning, pilot studies with bioassay species (e.g., fast growing grasses) can help determine needs for site amelioration. In extreme cases, bioremediation may be required to reduce toxicity. At the same time, the ability of dominant species to establish under planned amelioration tactics should be determined in field trials (Palmer and Chadwick 1985). Pilot studies and field trials will provide a substantial return on their investment and significantly increase the probability of success.

Contingency planning requires a pessimistic view and a willingness to consider rescue programs. Potential problems are associated with competition, infertility, and herbivory. The competitive environment must be assessed. Plans to remove exotic and nontarget species and to thin target species should be in place, with specific triggers in the maintenance plans (Ogden and Rejmanek 2005). Fertility often limits development when initial stores of nutrients become sequestered in the standing vegetation (Feldpausch *et al*. 2004), so nutrient stress should be monitored. Other common problems, such as episodic herbivore damage, catastrophic weather events, and unforeseen changes in the local environment all need to be addressed.

2.4 Lessons from Succession

Effective ecological restoration of barren, derelict, and degraded landscapes requires attention to the messages produced by natural recovery of ecosystems. Restoration often involves sites without vegetation or those dominated by non-target species that are isolated from pools of natural colonists. Here, restoration starts with alteration of abiotic conditions. Other sites, however, require enhancements of their properties. Heterogeneity may be reintroduced, erosion and sedimentation controlled, and competition limited by grazing, mowing, or topsoil or sod removal. Succession is not the predictable process it was once believed to be. It requires dynamic management at each stage because of this unpredictability and multiple outcomes should be accepted, if not always entirely welcomed.

2.4.1 Restoration Phases

There are three major phases in the redevelopment of a community (Table 2.2). A major goal is to enhance the structure and function of the site to improve ecosystem health (Cramer and Hobbs 2002). Healthy systems are resistant to further impacts, experience only limited fluctuations in population numbers, and are productive. The type of enhancement is determined in part by local circumstances (Bakker and Londo 1998). For example, the desired level of biodiversity may be lower in an industrial park compared to a rural area. However, the tactics differ in each of the stages. Environmental restoration is sometimes appropriate in the aftermath of major natural disturbances (e.g., lahars) that create new surfaces, but it is more common in intensively affected cultural landscapes (e.g., mine wastes). Physical amelioration, such as erosion control, and species introductions dominate this phase of restoration as the community is directed toward defined targets. In degraded cultural landscapes, vegetation is dominated by ruderal species and turnover is rapid. These ruderal species have little conservation interest and little direct economic value, so they should be controlled.

Table 2.2 Characteristics of managed landscapes during community development [modified from Bakker and Londo (1998)]

Characteristics	Early stages	Developing stages	Late stages
Dominating processes	Environmental restoration	Biotic restoration	Maintenance
Biotic function	Low	Moderate, directed	High, maintained; heterogeneous
Biotic structure	Variable, not desired	Increasing, directed	High, heterogeneous
Strategies	Physical amelioration; species introductions	Manage biotic environment	Limited management of populations, environment
Examples	Restore topographic heterogeneity; amend fertility; introduce targets	Selective thinning; grazing regime fits target; limit competition	Replace failed target species; suppress nontarget species
Species characteristics	Ruderal	Competitive, mixture of subordinate species	Competitive, with stress-tolerant species; mixture of subordinate species
Community turnover	High; directed toward multiple targets	Declines as targets are approached	Low, with minor, turnover

During the second phase of recovery, vegetation is often actively managed to improve its conservation value. Additional target species may be introduced, though many can survive early introductions. Many species are competitive, so thinning or mowing may be needed to enhance biodiversity (Bakker *et al*. 2002). Nontarget species should be controlled so that trajectories are directed toward stated targets. Species turnover declines as the vegetation attains maturity. Finally, as the conservation interest of the vegetation is maximized, management becomes focused on maintenance. Monitoring directs management to maintain biodiversity through tactics such as thinning the canopy; reintroducing species that may have died out and litter removal, leading to a vegetation mosaic. The final community may change cyclically both in space and time and species populations will fluctuate, but turnover is low.

2.4.2 Heterogeneity

Even barren sites may have some desirable heterogeneity. Surviving physical heterogeneity should be preserved and incorporated into plans instead of being graded to uniformity. This may preserve safe-sites, foster biodiversity, and facilitate development of the ecosystem. Variation can be a hedge against the unexpected and can offer a refuge during times of extreme climate. Using several growth forms helps to ensure that extreme events will not destroy all species. Structural variation provides resilience by permitting cores of survivors even if catastrophes occur.

2.4.3 Landscape Effects

The surroundings are nearly as important as the characteristics of the site. They contribute propagules that could augment or inhibit restoration, so their net effects must be considered. Dispersal is inherently subject to chance, so the pool of potential colonists in fragmented landscapes may be drastically different from that of intact landscapes. Target species may be missing or isolated and their low probability of colonization can produce unpredictable results. Restoration must introduce target species at the correct time.

Complex vegetation requires a certain minimum area, and small sites are influenced by the invasion of dispersible species. The effects of the species-area curve have been documented for urban fragments (Murakami *et al*. 2005) and forests (Ross *et al*. 2002). Small sites lose species rapidly and never accumulate a full complement of species (Bastin and Thomas 1999). This suggests that planners should have expectations for complexity based on the size of a restoration project and its surroundings (Margules and Pressey 2000) not on large natural reference areas.

Which species reaches a site is one of the least predictable events. These pioneers can dictate subsequent development by altering soils, and possibly deflecting trajectories (Temperton and Zirr 2004). It is common for different trajectories to develop on the same site due to priority effects, that is, the impact of the first wave of colonists on later arrivals. Because colonization is episodic, initial natural succession is highly variable. Both spatial and temporal variation may be desirable for the development of the ecosystem, so planning should provide for such individualistic results and vegetation mosaics.

One consequence of priority effects and habitat heterogeneity is the development of a mosaic of alternative states, stable yet distinct vegetation types growing together under similar environments. Stochastic processes, differential rates of development, a shifting balance between facilitation and inhibition and secondary disturbances all foster mosaics. Examples are common in riparian vegetation (Baker and Walford 1995) where mature vegetation often exhibits contrasting composition (Honnay *et al*. 2001) and on broad plains recently freed from flooding (del Moral and Lacher 2005). Mosaics augment biodiversity and promote wildlife. A mosaic of types has several virtues, so a variety of targets is often warranted. Biodiversity is enhanced locally through the rescue effect (Gotelli 1991, Piessens *et al*. 2004) where colonists from other patches save target populations from going extinct and on a larger scale by differences among the mosaic elements. Multiple simultaneous trajectories are one way to insure against unforeseen consequences.

2.5 Conclusions

Fully applying the lessons of succession will improve the efficiency and quality of restoration programs by assuring that both structure and function develop well. It is difficult to predict restoration trajectories *a priori* by reference to "assembly rules" derived from species characteristics or studies under different conditions because young plants, planted sparsely, often lack a competitive environment. Studies that do demonstrate assembly rules typically are in competitive environments (Weiher and Keddy 1995, Bell 2005, Fukami *et al*. 2005). Rules can work at the level of functional traits and dispersal types, but are confounded by chance, competition from nontarget species and stressful conditions (Walker *et al*. ~~in press~~). Facilitation and inhibition by the same species is complex and dynamic, so that predicting patterns may require detailed knowledge of local conditions. Natural vegetation is the result of many contingent and stochastic factors so that existing mature vegetation is either only one of several viable alternatives or it is a mosaic. Thus, local mature vegetation may be a guide for planning, but not a detailed model. This is pragmatic because it permits several acceptable species compositions. The benefits of a community with several growth forms (or functional types) with multiple representatives of each may include greater productivity (Hille Ris Lambers *et al*. 2004), resistance to invasion (Symstad and Tilman 2001, Fargione and Tilman 2005), and enhanced ecosystem functions (Symstad *et al*. 2003) compared to a homogeneous site.

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The lessons of natural succession provide guidelines even if rules are contingent. Fragmentation, barriers, differential permeability, and isolation filter potential colonists, so that spontaneous recruitment rarely leads to an ecosystem with optimal structure and function. Further, the suite of first colonists will not represent the total pool. Even when economic constraints require dependence on spontaneous recruitment, amelioration helps to select for more desirable species~~,~~ and improve both the diversity and the density of colonists. Amelioration actions should produce variable substrates that will allow complex vegetation. Mosaics of communities usually characterize early succession. Homogeneous vegetation that results from application of similar procedures and vegetation throughout the project is better replaced by more nuanced actions designed to foster vegetation mosaics.

During the assembly of vegetation, conditions that filter immigrants change, leading to a different set of new colonists. At the least, moisture, nutrients, light, and biotic pressures change, altering the success of existing and immigrant species (Fattorini and Halle 2004). Diversity can be enhanced by the reduction of competition (Polley *et al*. 2005). One way to limit competitive dominance is to plant the less competitive species before putative dominants and to increase the number of species and functional groups early in the restoration process. Though it is appealing to mimic natural succession, planting sequences do not have to follow natural sequences. In nature, many species do not establish early in a trajectory either because they fail to arrive, or having reached the site, cannot establish. During restoration, species can be introduced early in the sequence if the conditions can be manipulated to help them establish. Slower growing species common in stable vegetation can be planted early in the process, in masses, to prevent them from being smothered by other species. This has the added benefit of enhancing the mosaic. Other treatments, including thinning and selective disturbances, may be feasible.

The use of herbivores to facilitate succession is poorly studied, though we know that moderate grazing can sometimes promote diversity. More often, restoration projects must be protected from vertebrates, and sometimes from invertebrates. Intermixing species can slow selective grazers and diverse plantings have other virtues.

Because the species composition of restoration projects can develop in unpredictable ways, composition alone is not the best measure of success. Rather, performance standards might be measured in terms of spatial mosaics, vertical complexity, overall diversity, and reproductive success among the shorter-lived species. Ideally, functions such as biomass accumulation rates~~,~~ and biofiltration efficiency can be used to measure performance.

There is much to be learned from succession. Restoration can help to improve the understanding of succession by monitoring and reporting the results of the application of succession theory (Young *et al*. 2005, see Chapter 1). At the same time, attention to the lessons learned from studies of succession will improve the quality, efficiency, and success of restoration.

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