Community Succession and Assembly

Comparing, Contrasting and Combining Paradigms in the Context of Ecological Restoration

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Three ecologists explore two ways of thinking about the development of ecological communities and the relationships of these approaches to each other and to restoration.

"When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional number and kinds to what we call chance. But how false a view this is! Every one has heard that when an American forest is cut down a very different vegetation springs up; but it has been observed that ancient Indian ruins in the Southern United States, which must formerly have been cleared of forests, now display the same beautiful diversity and proportion of kinds as in the surrounding forests."

—*Charles Darwin,*
1872 (1958, pg. 84)

Restoration ecology is rooted in community ecology (Palmer and others, 1997; Young, 2000). One cannot restore individual bits of biodiversity unless appropriate communities and soil exist. There are of course population-restoration projects, or reintroductions, some of which overlay functional ecosystems. Nonetheless, it is in the restoration of complex communities that restoration ecology finds its greatest challenges and opportunities, and also its fullest expression (Young, 2000).

Therefore restoration ecology, in its search for conceptual bases, looks to theories of community structure (Luken, 1990; Packard, 1994; Lockwood, 1997; Pritchett, 1997). In particular, two conceptual models in community ecology have relevance to ecological restoration: 1) community succession, which dates back more than a century (Cowles, 1899) and 2) the more recently developed ideas of community assembly and priority effects (Palmer and others, 1997; Lockwood, 1997). Briefly, succession refers to an orderly, more or less predictable turnover of species composition at a site that has been cleared of species or otherwise disturbed, often back toward a predisturbance state. Community assembly is similarly intended to explain how communities form after a site is cleared of species. In assembly, however, community development is determined by random variation in species' colonization rates and the subsequent likelihood of their establishment and persistence in the community. Although, as we will discuss, these views are not mutually exclusive, there are a number of underlying differences between succession and assembly as they have developed historically (Table 1).

Both succession and assembly have enjoyed considerable theoretical and empirical attention from community ecologists, and have obvious connections to each other. In addition, both of these conceptual frameworks can be useful in providing a scientific foundation for the emerging field of restoration ecology. However, despite the inherent similarity between community succession and assembly, there has been little cross-fertilization between these concepts (but see Lawton, 1987; Drake, 1990; Walker, 1997; McIntosh, 1999). In this paper we examine both models, comparing and

Table 1. A summary of differences between succession and assembly as conceptual models in community ecology.

Characteristic	Succession	Assembly
Communities studied	Natural, semi-natural	Artificial (controlled), virtual
Dominant taxa	Vascular plants	(Invertebrate) animals and protists
Ecosystems	Mainly terrestrial (mainland)	Mainly aquatic and island
Types of models	Conceptual (verbal)	Simulation (mathematical)
End point(s)	A single "climax," or a few alternative stable states	Theoretically many alternative stable states. In empirical experiments, only a few.
Reasons for alternative states	Arrested (truncated) succession, disclimax, cyclic succession, exogenous disturbance	Priority effects and niche preemption, sometimes with a cascading effect
Process vs. product	Primary interest in the mechanisms of change, only secondary interest in how this results in a "final" state.	Primary interest in explaining the final state(s), with the process seen mostly as a means to get to this state (but otherwise ignored).
Life history differences	Central (colonization/competition tradeoffs)	Invoked only after species arrival, and only in some models
Processes	More deterministic than random	More random than deterministic
Dispersal limitation	Sometimes considered, species-specific	Central, but stochastic
Establishment and growth	Individual phenomena	Population phenomena
Species' residence times	Not much more than individual life span, often barely exceeding age of first reproduction	Usually far longer than individual life spans
Nature of facilitation	Within trophic levels, causes temporal change	Across trophic levels, causes alternative states
Number of trophic levels	One (except as modifiers)	Up to several

contrasting them from the perspective of restoration. At the heart of this discussion is a question that is at the very root of restoration ecology (Palmer and others, 1997): Do altered communities have an inherent ability to repair themselves and return to a structure and composition similar to the original, or can historical events and contingencies allow for more than one, and perhaps an indefinite number of (stable) community outcomes?

But this review is not simply about single as opposed to multiple stable states in communities. Succession theory has been dealing with multiple stable states nearly since its inception (see below). Assembly theory represents a particular framework for multiple stable states, but does so from an ecological perspective that differs in many ways from most succession theory. It is these differences that we will explore.

Historical context
Community Succession

Interestingly, these two views of community dynamics recall a classic dichotomy established among early plant community ecologists. Darwin wrote about succes-

sional phenomena (see opening quote), and indeed, some of the first research in modern ecology was based on the idea of succession (Cowles, 1899). Henry Cowles's classic research on the dynamics of vegetation on dunes on the shores of Lake Michigan helped to establish the idea that the development of a plant community could best be described as a sequence—or succession—of species and associations of species replacing one another through time in a more or less orderly and predictable way. Building on these and other observations, Frederick Clements (for example, 1916, 1936) championed the view that communities represent an alliance of species that reaches maturity in a stable "climax" community. Although there were several underlying hypotheses in Clements's work, the predominant paradigm to emerge was that communities "succeed" along a fixed trajectory toward a single, more or less well-defined end state.

Two kinds of observations of disturbed plant communities have inspired much of the research on succession. The first is that they progress through a set of different community states, with certain common characteristics ("early and late successional") in

a wide variety of ecosystems. The second is that they tend to develop back to a state similar to the original one, even from very different starting points. Despite the current aversion to the classic notion of community "climax" (see below), the fact remains that many terrestrial communities do tend to return to predisturbance states in a more or less predictable way (for example, van Breeman, 1995; Sheil, 1999; Buddle and others, 2000; Leps and others, 2000). Conceptual models of succession date from the early days of plant ecology (Clements, 1916), and continue today (Pacala and Rees, 1998). These models focus on mechanisms of change within successional communities, and have been reviewed elsewhere (Pickett and others, 1987; Luken, 1990; Van Andel and others, 1993; McCook, 1994).

In the context of successional theory, ecological restoration can be seen to represent an attempt to accelerate or jumpstart the successional sequence, bypassing earlier successional stages (Palmer and others, 1997). Understanding the processes that drive succession, we can suggest practical ways to speed the rates at which the desired states are achieved (see below).

While Clements emphasized the coherence and unity of the community, his primary antagonist, Henry Gleason (for example, 1927), was impressed by the individuality of species within communities, and placed a greater emphasis on the role of species-specific processes and history in determining eventual community composition. Gleason was the first in a long line of ecologists to propose and document a more pluralistic view of plant succession. Interestingly, Gleason presented a surprisingly modern view of the role of community assembly history on the development of community composition in this passage describing how emergent wetland plants colonize and come to dominate small ponds in a region: "Only the chances of seed dispersal have determined the allocation of species to different pools, but in the course of three or four years, each pool has a different appearance, although the environment, aside from the reaction of the various species, is precisely the same for each." (Gleason, 1927). Tansley (1935) later coined the term "polyclimax" to describe such alternative stable states.

Community Assembly

The development of assembly theory did not occur until almost half a century later. It was based on Jared Diamond's (1975) studies of bird communities on Pacific islands and was developed by several zoologists, who did not recognize that Gleason, and later Frank Egler (1954), had anticipated many of the main points of the assembly model. This conceptual framework attempts to explain the existence in sites with similar environmental conditions of communities composed of different individual species (or relative abundances of those species), even though a much broader pool of species has access to the community. As we define it here, community assembly refers to the process by which species colonize, interact with other species, and establish a community in such a way that multiple stable community states may result. We are *not* referring here to the related theory of "assembly rules," which seeks to explain non-random similarities in guild structure across communities differing in their component species (Weiher and Keddy, 1999).

When assembly biologists use the term "multiple stable states" (Lewontin, 1969; May, 1977; Drake, 1991; Knowlton, 1992; Law and Morton, 1993; Drake and

Are aquatic ecosystems, such as this vernal pool, more likely to develop alternative stable states than are the more terrestrial systems in the surrounding uplands of Oregon's Agate Desert? Such differences between systems may account for different ideas of system dynamics ecologists have developed over the years.   *Photo by R.T Huddleston*

others, 1996; Samuels and Drake, 1997; Chase, 1998, 1999a) they restrict its meaning to a process in which the final outcome depends heavily on historical contingency—that is, all else being equal, more than one final (stable) composition can result, depending only on the details of the community's history.

In assembly theory, "multiple stable states" refers only to situations where all species have equal access to communities, and where differences in eventual community composition are due to variations in

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the *timing* of colonization. Thus, it is not correct to invoke assembly theory to say that a community with, for example, some large herbivore species exists in an "alternative stable state" to one that does not (Strohmayer and Warren, 1997; Rietkerk and van de Koppel, 1997; Kim, 1997). Rather, in assembly theory alternative ecological states driven by herbivores exist only when the herbivore has equal access to both communities, but plays a functionally different role depending on the timing of its arrival in the community, which is considered to be random (see for example, Dublin and others, 1990). Succession biol-

ogists recognize a wider range of causes for multiple stable states (see below).

In contrast to restoration efforts based on the assumption that degraded communities tend to proceed through succession back toward the predisturbance state, restoration based on the idea that a community that can exist in multiple stable states will be less straightforward, and can represent a severe limit to our ability to appropriately restore ecological communities. Nevertheless, if we can understand explicitly the nature and structure of these multiple stable states, restoration recommendations will be much better informed (see also "Implication for ecological restoration" below).

Evidence for Stability in Succession and Assembly

Both succession and assembly have received considerable theoretical attention from community ecologists in recent years. However, the current dearth of empirical, and particularly experimental, evidence that alternative stable community configurations are common makes it difficult to evaluate the relative utility of these two conceptual frameworks, particularly as a foundation for restoration ecology. Connell and Sousa (1983) pointed out a number of stringent requirements that are needed to show stability in a community, and especially to determine whether a community can exist in multiple stable states. They also suggested that, as of 1983, few experimental studies met those requirements. This is part of a broader debate in community ecology concerning the importance of inherent variability in community structure that dates back to Watt (1947).

In order to demonstrate the existence of the kinds of multiple stable states proposed by assembly theory, it is necessary to show that different communities can develop under conditions that are essentially identical except for variations in the timing of species arrival. Since such control is difficult to achieve in the field, the most successful early experimental studies exploring the existence of one or more stable states have involved microcosms (see for example Robinson and Dickerson,

1987; Robinson and Edgemon, 1988, 1989; Drake, 1991; Drake and others, 1993; Weatherby and others, 1998). Nevertheless, some experimental studies in natural communities have also provided evidence for multiple stable states (Sutherland, 1974; Paine and others, 1985; Bazely and Jefferies, 1986; Sutherland, 1990; Chase, 1998, 1999b and unpublished manuscript; Petraitis and Latham, 1999). Both of these kinds of studies (virtually all of which were carried out in aquatic systems) have demonstrated that differences in the relative arrival times of species can produce alternative communities that are relatively stable. In addition, a variety of models (both analytical and computer simulation) have been developed to simulate the assumptions and outcomes of assembly theory (Drake, 1990; Luh and Pimm, 1993; Law and Morton, 1993, 1996). It remains to be seen, however, how often and under what conditions communities converge toward a single stable state (whether or not we call this the climax), and when priority and historical legacy will lead to multiple stable states under identical environmental conditions (Ludwig and others, 1997).

Comparison and Contrast

One of the earliest successional models, the Initial Floristics Model of Frank Egler (1954), anticipated many of the basic concepts underlying assembly theory. Egler proposed a model in which variation in initial composition, unrelated to abiotic site differences, resulted in the establishment of different stable community types. Among late-successional species, those already present in the seed bank or arriving shortly after a disturbance event were able to establish in sufficient numbers that later arrivals were not able to change the course of community development (essentially a priority effect). Some of the earliest and best work on alternative ecological states within the successional context (see below) was done by Egler (1949, 1975) and his colleagues, most notably Bill Niering (Niering and Egler, 1955; Niering and Goodwin, 1974; Niering and others, 1986; Niering, 1987; Fike and Niering, 1999).

The paradigms of succession and assembly have much in common:

1. Both seek to explain community composition.
2. Both suggest that there is a historical explanation to this composition.
3. Both acknowledge that communities develop through time toward relatively stable states.
4. Both assume the importance of biotic interactions, especially competition.

Despite these similarities, these two approaches also differ in many ways. Table 1 summarizes some of the contrasting features of these two paradigms as they are conceived today. These are not intended as strict dichotomies, but rather as strong tendencies that may at least partly reflect the different characters of the ecological systems in which they are studied. It is striking that ecologists who work in terrestrial plant communities have generally thought in terms of succession, while most modern research on assembly theory has been carried out in aquatic (invertebrate) systems, and in virtual (computer) "communities." The reasons for this are not clear, although we suggest one possibility below (under "Mechanisms of establishment"). Ecological restoration has a primarily botanical orientation (Young, 2000), and so perhaps it is natural that succession theory has been a dominant paradigm in restoration (for example, see Packard, 1994; Anderson and others, 2000; Kettle and others, 2000).

Another key difference is that assembly theory is far more amenable to mathematical modeling than is succession. This apparent rigor makes assembly theory attractive to modern ecologists, but also depends on the simplicity of its underlying assumptions, such as the ecological niche equivalence of species and the absence of colonization-competition trade-offs. Indeed, if these computer models were to add the element that the better competitors in a community on average arrive later, the virtual communities these models produce might more closely resemble convergent successional communities.

Process versus Product

Theories of succession are designed to explain the changes in species composition that occur through time following a disturbance. They seek to explain the mechanisms that limit the establishment and persistence of species, and thus determine the relative timing of species' appearance in, and disappearance from, the community. They also seek to identify the traits of species that place them at different stages of a successional sequence, and the patterns or trends that characterize such a sequence. While it is true that succession theory often treats this as a process converging toward a predisturbance state, it does not usually attempt to explain this state except as the product of the sequence.

Assembly theory, in contrast, is primarily concerned with the explanation of stable community composition, and in particular, the similarities and differences among communities that explicitly are not due to transient dynamics. Simulation models do implicitly incorporate process (they "assemble" communities), but their explicit goal is to explain differences in eventual community composition. Certainly, priority effects are inherently temporal, but there is little else in assembly theory that explicitly addresses the process or mechanisms of community change or development through time.

Alternative Stable States or Convergence?

What a struggle must have gone on during the long centuries between the several kinds of trees each annually scattering its seeds by the thousand; what war between insect and insect—between insects, snails, and other animals with birds and beasts of prey—all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees!

—*Charles Darwin*,
1872 (1958, pg. 84)

The most fundamental difference between succession and assembly as conceptual bases for community and restoration ecology is how they treat alternative stable states. The stereotype of community succession theory is that it predicts a single stable state—the climax. The stereotype of assembly theory is the existence of many stable states. Superficially, these represent highly divergent views, with profoundly different implications for restoration. However, empirical evidence from actual studies of successional communities and assembly experiments suggest that this difference is less dramatic.

In reality, the difference is not, as some have suggested, that assembly theory recognizes or predicts many alternative stable states, while succession recognizes only one. Successional theory has long recognized alternative stable states, and assumes that communities not returning to the predisturbance state have failed to reach it for reasons that can be explained (for example, see Reynolds and Pacala, 1993; see also below). Assembly models may predict highly divergent community compositions, but both in the field and in experimental ecosystems the number of alternative states produced is usually very limited. In practice, both succession and assembly theories are associated with a small number (one to a few) of stable ecological states.

Succession theory arose in part to explain a perceived convergence of disturbed sites to a single community type. When ecologists began to recognize alternative "stable" states, they responded not by discarding the idea of succession, but by elaborating and refining it. Alternative states were considered merely variations on the theme of succession, not failures of succession theory. These states have been called arrested succession, truncated succession, polyclimax, and disclimax. Modern succession theory offers several classes of explanations for alternative stable states:

1. A disturbance generated by community traits keeps the community in an arrested successional state. This force could be fairly constant (herbivory) or sporadic, but predictable (fire).
2. An exogenous random disturbance (droughts, storms, wave action, landslides) can occur often enough that the communities of a natural landscape display a variety of successional states, but rarely reach local stability.

Planting needlegrass (*Nasella pulchra*) at a grassland restoration site near Davis, California. Does planting of particular species establish their competitive priority in ways that affect long-term community dynamics, thus running the risk of short-circuiting succession? *Photo by Truman Young*

3. Cyclic succession occurs when all successional states are intrinsically unstable, with each yielding to another within the cycle (Watt, 1947; Olff and others, 1999). Some examples involve single-aged stands of woody plants that are not self-replacing (Yeaton, 1978; Agnew, 1984; Young and Lindsay, 1988), but which can establish among other species in successional communities (Young and Peacock, 1992).

4. Succession theory recognizes that there are some early-successional (or exotic invasive) species that are highly suppressive of later-successional species, and that when these get established in sufficient densities early in succession, succession can be arrested for long periods of time, or even halted in an alternative state. Natural examples include shrublands, balds and fernlands in forests (Tappeiner and others, 1991;

Maxwell and others, 1993; Mallik, 1995; Young, 1996; Holl, 1999; Fike and Niering, 1999; Chapman and Chapman, 1999), fertility mosaics in grasslands and savannas (McNaughton, 1983; Belsky, 1986; Young and others, 1995), forest mosaics (Davis and others, 1998) and marine mussel and algal beds (Petraitis and Latham, 1999). Egler (1949, 1975) provided management examples in rights-of-way through forests.

5. Egler's Initial Floristics succession model explicitly considered the possibility that stochastic differences in the arrival and establishment of different late successional species could lead to alternative ecological states (see also Gleason, 1927; Tansley, 1935).

It is these last two processes that match most closely the multiple stable states of assembly theory, although with a

very limited number of alternative stable states. Modern succession theory is less fixated on the concept of a single "climax" but nonetheless still considers both progression and convergence to be common in regenerating communities in nature.

Assembly theory, on the other hand, arose out of a set of observations opposite to those that inspired succession theory. Here, it was the multiple stable states themselves that drove theory (Diamond, 1975). In the 1970s, plant ecologists were increasingly recognizing multiple stable states in some systems (suppressive shrubs in forests being a classic example) and were elaborating successional theory to account for them. At the same time animal ecologists, in their development of assembly theory, were paying little attention to succession theory in their attempts to account for variations in community dynamics. Assembly theory assumes that there is considerable niche

similarity among species, and that random differences in colonization and establishment at a given site can result in alternative mixes of species that are resistant to invasion by others.

State-transition Models

Faced with the realities of disclimax, arrested succession, and habitat degradation, some ecosystem managers responded with a new kind of community model—the state-transition model (Westoby and others, 1989; Lockwood and Lockwood, 1993; Allen-Diaz and Bartolome, 1998). State-transition models were initially developed by rangeland ecologists, and still are used mainly in that context. Like assembly models, they are based on the idea of alternative ecological states. However, these states are not merely the result of priority effects, but are often the result of different forcing factors in the environment: grazing, drought, fire, or soil modification, for example. It is the purpose of these state-transition models not only to identify the factors causing alternative states, but also to identify remedial actions to bring about transitions from less desirable states to more desirable states. Because of their emphasis on exogenous processes, state-transition models do not relate directly to our comparison of succession and assembly, but their emphasis on management alternatives does make them valuable models for restoration ecologists.

Priority Effects and Niche Similarity

Central to assembly theory is the idea of priority effects (Belyea and Lancaster 1999). Priority is established by the species that are the first to arrive and can therefore become dominant in the community. These species then inhibit invasion by other species, particularly those with similar niches. The strength of the priority depends on 1) arrival time, and 2) the attributes of species after arrival (for example, competitive ability, fecundity, or population growth rate). Temporal priority may confer a competitive advantage on a species that is normally an inferior com-

petitor (Hodge and others, 1996). Multiple stable states are possible because different species may by chance arrive earlier at different sites, establish themselves, and exclude later arrivals.

Because established plants tend to have local priority in any community, succession occurs when this priority (inhibition, or resistance to invasion) is over-

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come either by more competitive species, or by changes in the environment brought about by the plants themselves (facilitation). But succession theory has also incorporated the idea of priority effects more directly. Working in an eastern deciduous forest where he saw the effectiveness of clonal shrubs in suppressing forest succession, Egler (1954) was one of the first to suggest that the initial species composition on a site would determine the eventual outcome of community development (but see also Gleason, 1927). Two decades later, Connell and Slatyer (1977) elaborated this idea in their inhibition model, which presents priority as a mechanism driving successional processes. Initial floristic composition and inhibition by early-arriving species are important processes in succession, but these represent only a few of the many mechanisms that interact during succession. Competitive inhibition may delay succession and create temporary alternative states, but the general assumption is that given enough time, the community will progress toward the predisturbance state.

Both succession and assembly theories recognize that some species will always be better competitors regardless of the order in which they arrive, and others will always be poor competitors, even if they have had a long time to establish in a community. In assembly, priority effects can explain why in some areas species coexist and in others there is competitive exclusion. In areas where the poor competitors arrive first, become established and are subsequently invaded by a better competitor, their populations are significantly reduced, but the species is able to persist in the community. However, if the better competitor arrives first, the less competitive species are unable to invade the community and are therefore excluded (Drake, 1991).

Successional models generally explain the coexistence of early- and late-successional species at the landscape scale as a result of disturbance. Stochastic disturbance events in the community remove some of the more competitive species and allow the less competitive species to exist locally and temporarily. Disturbance may occur on a large scale, returning large areas to an earlier state of succession, or on a small scale, creating a mosaic of different successional stages within the larger community. In addition, successional models explicitly incorporate the idea of a colonization-competition trade-off. The species that are most likely to arrive early are also competitively subordinate, and eventually are replaced by late-arriving species that are competitively dominant. This colonization/competition trade-off is a central process in successional change. Although currently absent from assembly models, it could easily be incorporated, and would probably result in more robust models that more closely resemble succession.

Recruitment Limitation

Recruitment can be limited at either of two stages: dispersal or establishment. Recruitment limitation is central to restoration ecology (Bakker and others, 1996; Strykstra and others, 1998; Bakker and Berendse, 1999). In many communities, the availability of propagules is a limiting factor in successful restoration (Robinson and Handel 1993; Gorchov and others, 1993;

Guariguata and others, 1995; Keenan and others, 1997; Parrotta and others, 1997b; Lamb and others, 1997; Stampfli and Zeiter, 1999). One of the primary activities in ecological restoration is planting and assisting in the establishment of native species. This work is a specific attempt to overcome the factors that limit recruitment. Conversely, the control of invasive exotic species often occurs at the stages of dispersal and establishment. We will compare how succession and assembly theories treat both stages of recruitment limitation.

Dispersal Limitation

Dispersal limitation was recognized as central to community development in the early theories proposed to explain successional processes. Clements (1916) and Egler (1954) were among the first to recognize the influence of dispersal limitation on plant communities by suggesting that the failure of potentially dominant species to arrive at a given site could dramatically alter the trajectory of community development. Later models such as Connell and Slatyer's (1977) tolerance, inhibition and facilitation model make only passing references to dispersal limitation, and focus instead on the processes occurring after propagules arrive at a given site. Recently there has been a renewed interest in the role of dispersal limitation in community dynamics. The proximity of seed sources, differential timing of maturity and age of reproduction, annual seed production, and timing of disturbance have all been found to influence the spatial and temporal aspects of community development (Del Moral, 1998; Hughes and Fahey, 1988; Fastie, 1995; Holl, 1999).

The life history traits of individual species can also play a central role in successional processes. Ridley (1930) suggested that dispersal strategy involves a compromise in energy expenditures between growth and reproduction. Species with short generation times, prolific reproduction and efficient dispersal mechanisms tend to be favored in open environments where they can grow and reproduce before slower-growing but more competitive species become dominant. Some species are adapted to shift resources

from reproduction into vegetative growth as resources became limiting (Houssard and Escarre, 1995). The consequence of such tradeoffs is increased variability in the seed rain and seed bank, which can

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Assembly theory emphasizes the random timing and order of arrival of species, like numbers coming up in a game of roulette. Succession, in contrast, may be likened to slowly developing a winning hand in gin rummy.

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ultimately influence successional dynamics (Clark and Yuan, 1995).

Assembly theory is typically based on the assumption that all species have an equal probability of colonization, and that the long-term absence of a species from a given site is not due to lack of access. These models typically ignore species-specific differences in colonization ability, as Gleason (1927) noted in an early discussion of how community composition can be determined by the stochastic processes of species colonization history, and as is implicit in some recent models of the assembly process (for example, see Drake, 1990; Law and Morton, 1993, 1996; Morton and others, 1996). The emphasis is on the random timing and order of arrival of species, like numbers coming up in a game of roulette. Succession, in contrast, may be likened to slowly developing a winning hand in gin rummy.

Ecologists have examined assembly theory using numerous models and experiments designed to reveal the effects of arrival order, invasion intensity (the

amount of time between successive invasion events) and species attributes (Drake, 1991; Lockwood and others, 1997; Weiher and others, 1998). However, to our knowledge the effects of species' dispersal abilities and/or colonization competition trade-offs have not been examined in the context of assembly theory. It is also interesting to note that one of the studies often cited in support of the multiple stable states predicted by assembly theory is a study by McCune and Allen (1985) of the development of different coniferous forest communities on similar sites in Montana. They cite several historical factors that may account for the different forest communities, including variation in seed production, timing of seed crops relative to disturbance, differential tolerances of the species to climate conditions, herbivory, and local availability of seed source. Given these variables it seems unlikely that all species had an equal opportunity to colonize all of the study sites.

We suggest that the assumption of equal probability of colonization is unrealistic in many natural situations, and that future models of community assembly should allow for the different dispersal abilities of species. In addition, if such models were also constructed to include species' life history attributes and differential colonization and competitive abilities, the differences between succession and assembly may not be as great as they now appear.

Mechanisms of Establishment

Just as they treat dispersal differently, theories of succession and assembly deal in very different ways with the process of establishment and growth following arrival. In assembly theory, growth and establishment are regarded as population-level phenomena. The basic model is one of rare propagules arriving, and either reproducing to establish a growing population or failing to do so. Differences in population growth rates are allowed, and priority effects are achieved when the differences in arrival times are sufficient to overcome differences in subsequent population growth.

In succession theory growth and establishment are usually treated as properties of individuals. Multiple propagules arrive, and

The persistence of shrub cover in this right-of-way suggests that restorationists may sometimes have opportunities to select from alternative stable states in defining management objectives. In the case of this site in western Kentucky, the herb and grass cover under the power lines may be as stable as the surrounding forest. *Photo by J.O. Luken*

either succeed in germinating and growing past vulnerable stages, or they do not. For most successional species, populations have already begun to decline or are at least stable before individuals reach reproductive maturity. One of the definitions of climax is that it is a community in which populations replace themselves locally. This is in contrast to early successional stages, which rarely last much longer than the generation times of their component species.

Variations in the post-dispersal growth rates of individual plants are correlated with both dispersability and life span along a gradient from early- to late-successional species. Temporary priority effects are achieved when the differences in arrival times are sufficient to overcome differences in the growth rates of competing individuals. Indeed, many alternative ecological states in terrestrial plant ecosystems are relatively stable because the individuals that make up the alternative community are themselves clonal and

long-lived—good examples would be ferns or clonal shrubs in forest ecosystems (Tappeiner and others, 1991; Maxwell and others, 1993; Mallik, 1995; Young, 1996; Holl, 1999; Fike and Niering, 1999; Chapman and Chapman, 1999).

This difference in mechanisms of establishment may be partly due to inherent differences between terrestrial plants (succession) and aquatic invertebrates, microbes, and algae (assembly). The latter are characterized by determinate growth, high intrinsic rates of increase, and generation times usually much less than the species' residence time in the community. In contrast, vascular plants in terrestrial succession have indeterminate growth, relatively low population growth rates, and species' residence times in the community that are often not much longer than individual life spans.

However, when dispersal is more limiting and dispersal events much rarer, species establishment may be driven by

local population growth through reproduction of earlier colonists, in a mode more like that assumed in assembly models. This can occur in primary succession (Fastie, 1995; Del Morel, 1998), understory herbs (Matlack, 1994), and perhaps some suppressive shrubs (Tappeiner and others, 1991; Maxwell and others, 1993).

Invasive Exotics

(All species) are not as perfect as they might have been in relation to their conditions; and this is shown to be the case by so many native forms in many quarters of the world having yielded their places to intruding foreigners.

—*Charles Darwin*, 1872 (1958, pg. 196)

The success of invasive exotic species is fundamentally a result of a breakdown in geographical isolation—the (usually

human-caused) elimination of geographic limitations to dispersal. In addition, disturbances of the native community, such as those caused by fire, cultivation, or grazing, can provide more opportunities for invaders to take advantage of the removal or breakdown of barriers to dispersal.

Assembly theory suggests that priority effects have a strong influence on the success of late arrivals and on eventual community composition. From this perspective, invasive exotics are an exception—species that aggressively displace species that established earlier. This looks more like succession than assembly and, in fact, there is a growing consensus that the relative success of invading exotic species depends more on their life history traits and edaphic limits than on the niche saturation of the invaded site (Rejmanek, 1996; Rejmanek and Richardson, 1996; Moyle and Light, 1997).

Nonetheless, disturbed systems are more susceptible than undisturbed ones to invasion by exotics (Groves and Burdon, 1986; McIntyre and Lavorel, 1994; Pyle, 1995; Kotanen, 1997), and invasion success seems to be negatively related to artificial variation (Tilman 1997, Symstad 2000), but not to natural variation (Stohlgren and others, 1999) in the species diversity of a community. These results are consistent with assembly theory. The newly invaded community is often relatively stable, but this is an alternative stable state only in a trivial sense.

In summary, succession and assembly offer only limited insight into the problem of invasive exotics that is of so much concern to restorationists. To quote James Drake and his colleagues (1996, pg. 673): "Non-native species are typically not bound by the rules of assembly that operate in the system they invade."

Facilitation

Some successional models explicitly describe facilitative relationships between plant species (Connell and Slatyer, 1977). Positive interactions between plants are usually mediated by the edaphic environment (Bertness and Callaway, 1994; Callaway and Walker, 1997). In succes-

sional models, early-successional plants may modify the microclimate or soil in a way that allows later successional plants to enter the community. Assembly models usually allow only for negative interactions within guilds or trophic levels, and so do not incorporate facilitation in the successional sense. Assembly models do sometimes include positive trophic interactions, both direct (plants provide food for herbivores) and indirect (predators allow certain prey species to co-exist by suppressing competitive dominants). Both of these mechanisms have long been a part of community ecology theory.

Interspecific facilitation can be an important force in ecological restoration, as when one suite of plants, including exotic species, is used to facilitate the regeneration of natural forest in both tropical (Geldenhuys, 1997; Oberhauser, 1997; see reviews in Lamb, 1998 and Parrotta and others, 1997a) and temperate forests (Choi and others,

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Both succession and assembly theories have developed with little cross-fertilization. We suggest that the time is ripe for a synthesis.

1988; see also Rousset and Lepart, 1999; Fike and Niering, 1999). These facilitations can be in the form of ameliorated microclimate (Scowcroft and Jeffrey, 1999), soil changes (Whisenant and others, 1995; Choi and others, 1998; Rhoades and others, 1998), or assisted seed dispersal (Robinson and Handel, 1993; da Silva and others, 1996; Parrotta and others, 1997a).

Prospects for a Synthesis

Both succession and assembly theories provide conceptual frameworks for understanding and studying how communities

are put together. Furthermore, these frameworks are useful to those involved in the restoration and management of ecological communities. However, these two theories have developed with little cross-fertilization. We suggest that the time is ripe for a synthesis, which we briefly outline here.

Succession and assembly theories share many underlying patterns and putative mechanisms. Indeed, the basic assumptions and conclusions of assembly theory were anticipated by plant ecologists, such as Gleason, Tansley and Egler, who were interested in modifying the successional paradigm. In recent years, however, succession ecologists have tended to explain multiple stable states by mechanisms that only occasionally refer these early explorations of random colonization and priority effects.

Succession theory focuses on the processes leading back toward a predisturbance community composition, and may assume a trajectory that will go towards that state, or examine reasons why the trajectory does not (resulting in multiple stable states). Assembly theory, on the other hand, not only explicitly allows for the possibility that multiple stable states can exist but typically downplays the role of transitional processes. Sometimes communities proceed toward a predisturbance state regardless of historical conditions (that is, community convergence), whereas at other times historical legacy and priority effects occur (i.e., community divergence) such that the eventual community configuration results from a complex combination of the species' biology and historical contingency (Belyea and Lancaster, 1999).

A more realistic view integrates revised versions of both the succession and assembly processes to allow for the possibility of multiple stable states along a trajectory of community change. This view also allows for the possibility that one stable state may be "stronger" or more resistant to perturbation than the others, rather like the climax of early succession theory. However, along the successional trajectory, as a result of historical contingency, several other states can be achieved and can remain stable indefinitely, or until

some large perturbation allows continuation along the successional trajectory.

Implications for Restoration

Restoration attempts based only on the simplistic versions of ecological succession may fail or be less likely to succeed, if, in fact, multiple stable states occur in some systems, regardless of whether we think of these multiple states in the context of succession or assembly. When alternative states are rare, as they are in many terrestrial plant communities, then restoration may appropriately be viewed as the task of simply assisting succession. On the other hand, in systems for which multiple ecological states are more likely, our search to determine the "reference" state to which to restore a community may be a difficult exercise involving several choices (Luh and Pimm, 1993). In addition, if multiple stable states exist as troughs along a successional trajectory toward the desired community composition, we cannot simply plant an assortment of species thought to be appropriate at a site and trust the process of succession to push the community toward a pre-disturbance composition (Holl, 1999). The desired state may be only one of many possible outcomes, and we must more fully understand the role of both assembly and succession if we are to devise successful restoration strategies. The existence of multiple stable states and priority effects should not be viewed as a barrier to restoration, but they do call for understanding of a more complex set of phenomena than is traditionally associated with simplistic (and outdated) forms of succession theory.

Once understood, the existence of alternative ecological states can even suggest management alternatives. Where ecological restoration must be sensitive to particular land uses, the practitioner may be able to choose the most appropriate from among several alternative stable communities, all of which may be considered ecologically and historically appropriate. For example, either shrub- or grass-dominated communities may appropriate in forested ecosystems where there is a need for visibility along transportation rights of way, such as or for fire control and access along power line corridors (Niering and Goodwin, 1974; Egler, 1975; Luken, 1990; Brown, 1995; Young and Chan, 1998).

Restoration: Experimental Tool for Ecology

Ecological restoration projects are an experimental ecologist's dream. They provide opportunities for large-scale manipulation of the very characteristics that we are beginning to suspect are fundamental to the ecology of populations, communities and ecosystems (Jordan and others, 1987), including those addressed in this review. For each of the following research questions, restoration projects offer ideal contexts for rigorous experimental tests, and the chance to integrate assembly and succession theory into an integrated concept of community structure and development. In addition, the concepts and theories involved are central to the development of restoration as an effective conservation and management tool.

1. How important are priority effects in different systems, and are there predictable patterns in the role they play in determining community structure? Most experimental research on this question has been carried out in microcosms and mesocosms (Weatherby and others, 1998), and most field work has been done in aquatic systems (Sutherland, 1974, 1990; Paine and others, 1985; Bazely and Jefferies, 1986; Petraitis and Latham, 1999; Chase, 1998 and unpublished manuscript). The latter represents a rare attempt to answer this important ecological problem in a rigorous way. Unfortunately for ecological restoration, none of these experiments has been done on terrestrial plant communities.

2. How important are the relative effects of individual growth and population growth in determining the species composition of regenerating communities?

3. How great do differences in arrival times and establishment rates need to be to overcome differences in competitive ability and establish priority effects?

4. Does the incorporation of competition-colonization trade-offs into assembly models produce transient dynamics more similar to those described by succession models?

5. How important is facilitation in the development of community structure and the maintenance of biodiversity?

6. How important is dispersal limitation in determining the rate and trajectory of community development? This long neglected determinant of community structure is currently being rediscovered, often in the context of restoration research (Robinson and Handel, 1993; Gorchov and others, 1993; Guariguata and others, 1995; Bakker and others, 1996; Keenan and others, 1997; Parrotta and others, 1997; Clark and others, 1998; Stampfli and Zeiter 1999).

Conclusion

Although theories of community succession and assembly may at first seem to make fundamentally different predictions with profound implications for ecological restoration, we propose that their real-world differences are not so large. It might even be argued that some lines of succession theory not only anticipate assembly theory, but fully incorporate it. We certainly believe that differences in the historical development of these two approaches, and in the taxa and ecosystems in which they have been studied, have tended to obscure the similarities between them, but have also allowed each to develop its own set of hypotheses. For each approach, comparison with the other often results in enlightening insights into particular restored communities and ecological communities in general. These insights provide a road map for future studies of community ecology, especially as they relate to restoration. Conversely, restoration provides uniquely powerful opportunities for experimental approaches to these same questions.

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