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Implications from the Buell-Small Succession Study for vegetation restoration

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Abstract. Succession is relevant to restoration because managers have to prevent, enhance or replace natural vegetation dynamics. Features of a permanent plot study of post-agricultural succession in central New Jersey, USA, illustrate important implications of vegetation dynamics for restoration. In the past, such implications had to be drawn from chronosequences and coarse resolution studies, neither of which exposes the local contingencies relevant to site specific restoration. However, the fine scale and continuous nature of the current study reveal that succession is highly contingent on historical and local spatial heterogeneity. For example, the absence of one generally expected dominant stage, the demise of shrubs without replacement by later successional tree species, and the long and multimodal persistence of individual species suggest that neither the relay floristic or initial floristic models of succession is adequate to guide restoration. At the local scale, volleys of species appear through the succession, and reflect spatial contingencies such as neighboring vegetation and edge relationships, and patchy behavior of different functional groups. The role of introduced species and of plant consumers are additional sources of local contingency. These local and time-specific behaviors in the vegetation are the patterns that restorationists must understand either to choose appropriate reference states, to prevent unexpected local dynamics, or to design interventions that are appropriate to the specific site of interests.

Keywords: Community dynamics; Contingency; Functional group; Heterogeneity; Hutcheson Memorial Forest; New Jersey; Long-term study; Old field; Permanent plot; Vegetation dynamics.

Nomenclature: Gleason & Cronquist (1991) for plant species, life forms, and geographic origins of species.

Abbreviation: BSS = Buell-Small Succession Study.

Introduction

Restoration establishes vegetation in denuded sites, or modifies existing vegetation in an already occupied site. Although restoration is not equivalent to succession, because vegetation is a dynamic phenomenon, restoration can be considered to initiate a desired succession, replace an existing succession, skip certain stages of succession, or prevent succession from proceeding. In essence, all forms of vegetation design and management must manipulate or take advantage of vegetation dyanamics (Luken 1990). Restorationists attempt to bypass the limitations of succession, or thwart the successional impulse at a given site.

Given the relationships of vegetation dynamics and restoration, the understanding of succession can contribute in two ways to the knowledge base for restoration. One way is to reveal patterns of spontaneous change in natural systems, and the second is to reveal mechanisms of change in those systems. Those who practice restoration can use such information to meet several fundamental needs. Restorationists seek (1) appropriate reference points from the natural world, (2) an understanding of the functions that communities of a given structure can provide, and (3) a tool kit of methods that yield predictable results (Jordan 1993). The link between the study of succession and the practice of restoration is knowledge about the feasible points of reference, the possible and sustainable functions of communities, and what processes underlie those reference points and functions. This paper will explore what the Buell-Small Succession Study (BSS) – a long-term, fine resolution study of the process of post-agricultural succession – can contribute to restoration. There are notable contrasts between the classical theory of succession which is sometimes used as the reference for restoration and the contemporary theory (Pickett & Parker 1994) which can be illustrated by the BSS.

Restoration consists primarily of either (1) modifying or constructing habitats, assuming ‘if you build it they will come’, or (2) assembling a desired suite of species by planting and removal (Lockwood 1997).

Both of these approaches parallel key aspects of succession. Succession, or vegetation dynamics, occurs as a result of an arena for community change becoming available, the differential availability of species in or arriving at that arena, and the differential performance of species (Pickett & Kolasa 1989). Conditions of site availability reflect the characteristics of the substrate and the nature of the disturbance that initiates the succession. Differential species availability reflects the stored seed and propagule pool, and the seed and propagule rain at the site. Finally, differential performance results from the innate architectural and physiological features of the species life history strategies, and the interactions of plants with competitors, mutualists, and consumers, including disease. Studies of succession can help evaluate and inform both of the approaches to restoration by evaluating the assumption that habitat modification is sufficient for restoration, as well as by showing how species assembly actually occurs through time.

The understanding of succession rests on three main approaches. One is chronosequences, in which a successional sequence is inferred from comparing sites of different ages (Pickett 1989). For this method to be valid, ecologists assume that the different sites have the same initial environmental conditions, that they reflect the same history, and that species are equally available to all sites. The condition at a given age is most often represented as an average of presumably replicate sites. The second approach is simulation modeling. This approach also characterizes sites as uniform replicates. The third approach is idealized theoretical models (Czárán 1998). These three approaches yield clear patterns that serve as mirrors for restoration. However, chronosequences, simulations, and existing theoretical models neglect the fine scale, spatio-temporal structure of successional communities and largely ignore site heterogeneity. In part, such neglect is due to the rarity of continuous, fine-scaled studies of succession to motivate the construction of models matching the characteristics of fine scale, spatially explicit processes of post agricultural succession. Using the BSS as an example of a continuous, fine scale data set, we can assess what sorts of insights might be missing from the usual sources of successional information available to restorationists.

The information from chronosequence studies has provided simple, clear trends. For example, in mesic forest environments with moderate levels of resources, disturbed ground is usually dominated in order by the different life form groups of forbs, grasses, shrubs, and trees. It was this sequence of life form dominance that motivated Clements' (1916) theory of succession. Chronosequences, such as that by Bard (1952) in the vicinity of the Hutcheson Memorial Forest where the BSS is located, often revealed similarly simple and apparently robust trends at the coarse scale. One notable failure to generate a single clear chronosequence among early studies was Oosting's (1942) description of bottomland successions in post-agricultural fields in North Carolina. More recently, for example, simulations based on the detailed resource relationships, site conditions, and mortality responses of forest trees have yielded good predictions of forest succession (Canham & Pacala 1995). An important question which will be evaluated here is to what extent chronosequences and theoretical studies serve as a sound template for restoration. Do the trends survive examination at fine temporal and spatial scales? Based on prior long-term studies (e.g. Collins & Adams 1983), we expect that the local trends will not mirror the regional ideal.

The emerging paradigm in ecology suggests that spatial contingencies, specific site histories, and episodic events are crucial to the structure and dynamics of ecological systems (Pickett et al. 1992; Wu & Loucks 1995). Contingency simply means that the state of a system depends on the interaction between its specific history and spatial context. If the order of events or the spatial context in which those events occur were different, so too would the successional trajectory differ. The concept also appears in evolutionary biology (Eldredge 1999) where it has very similar implications for the history of life. Contingencies are the natural spatial and temporal influences that generate structure in specific biotic assemblages. Far from being problems to overcome or mere statistical uncertainty, they are likely the source of much of the order and diversity in the natural world. We hope that illustrative aspects of the BSS can help expose some important contingencies that can appear in succession, and hence can influence restoration. With such a fine scale, continuous data sets are ideal for both the assessment of spatial-temporal structure, and for revealing relationships that can be exploited in restoration.

The Buell-Small Succession Study

In 1958, Murray Buell, Helen Buell and John Small started a study of succession on land that had been farmed since 1701 by a colonial consortium and their decendents. Unlike much agricultural land in the Piedmont of the eastern United States, the Mettler's farm was regarded as well managed and reasonably productive. Agriculture ceased due to pressures for suburban development rather than soil exhaustion. However, the Penn series soils of the Triassic red shales in central New Jersey are droughty and not very fertile (Ugolini 1964). The founders began the study (1) to test whether the chronosequences previously studied in the region of the Hutcheson Memorial Forest (Bard 1952) gave a reliable overview of succession, and (2) whether Egler's (1954) initial floristic composition hypothesis was correct. The initial floristic composition hypothesis posits that woody species are present from the beginning of succession.

The data consist of visual estimates of cover in 1 m^2 permanently marked plots measuring 0.5 m × 2 m. There are 48 plots in each of 10 fields. Species are identified, and for canopy or subcanopy trees, the number of stems of seedlings, saplings and adults is recorded. If the cover of a tree species is contributed by individuals rooted outside the plot, the cover is coded to represent overhang. Further background on the Buell-Small Succession Study is found at http://www.ecostudies.org/bss

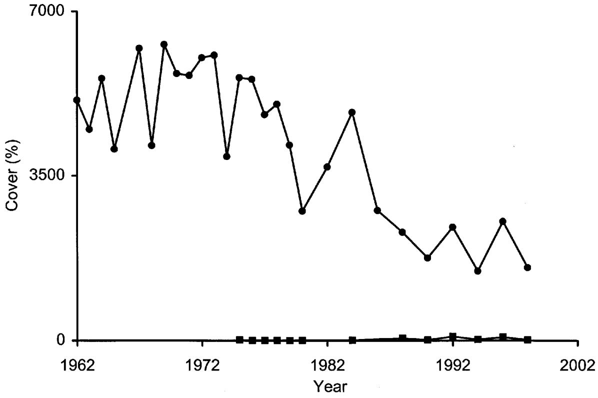

Fig. 1. Total cover of *Schizachyrium scoparium* (■) and all other herbaceous plants (●) including grasses in field E1. The percent cover is totaled over all 48 plots in the field. Plots can have greater than 100 % plant cover if multiple vegetation layers are present.

Contingency in succession

What succession has to contribute to the issues identified in restoration is related to the phenomenon of contingency. The issues for restoration are points of reference, the function of ecological systems, and reliable methods. These issues are all affected by contingency. The most fundamental classical assumption about succession is that it is deterministic. This classical assumption leaves little space for contingency. In fact, the deterministic drivers of succession were seen as arising from within the assemblage of plants itself. Therefore, ecologists often ignored historical events that reflected external conditions or processes that reflected the spatial context. The successional pathways often generalized in the eastern United States follow this assumption. How reliable are the simple patterns suggested by the classical theory of succession, such as the march of life forms from forbs to trees in the New Jersey Piedmont?

Dominant grass stage.

Chronosequences in the eastern US often identify *Schizachyrium scoparium* as the dominant short-lived perennial in early succession. Bard (1952) discovered that, among a collection of similar fields five to 40 years old, *Schizachyrium* was in fact a major dominant. However, in the fields of the BSS, *Schizachyrium* is only infrequently encountered and at low abundance (Fig. 1; Pickett 1983). The absence of this common old-field dominant is likely due to one or both of two factors. One contributing cause may be the relative isolation of the fields in the BSS from seed sources of *Schizachyrium*. The fields are bordered by the old growth forest on the south and west, by a hedgerow on the north, and by an abandoned pasture on the east. Beyond the hedgerow to the north are fields that remained in cultivation through the 1980s until converted to large suburban housing lots. Despite the fact that *Schizachyrium* is wind dispersed, dispersal is commonly limited to small radii around the seed parent (Pickett 1983). Thus, the BSS fields may be relatively inaccessible to *Schizachyrium*. This example suggests that the "if you build it, they will come" assumption sometimes made in restoration (Lockwood 1997) is weak, even for a common, wind dispersed species.

The second likely cause may be the absence of optimal resource conditions for *Schizachyrium*. *Schizachyrium* characteristically dominates communities on infertile or xeric sites. The BSS fields, farmed by the descendants of the original Dutch settlers for 254 yr until the fields were acquired by Rutgers University were perceived to be well manured and otherwise well cared for (H.F. Buell pers. comm.). Thus, in spite of a conspicuous loss of surface horizons compared to the old growth forest (Buell 1957), the field soils apparently maintained fertility. In such environments, broad leaved forbs tend to be the dominants. A combination of lack of seed source and suboptimal soil conditions may jointly limit the contribution of *Schizachyrium* to the succession in the BSS fields. Here contingency appears in the specific agricultural practices of the Mettler's compared to the general practice on other farms nearby.

Shrub demise. An additional example of contingency in the BSS is the pattern of demise of dominant shrub species through time. Important shrubs that appeared, as expected, in the BSS during its second decade included *Rhus glabra* and *Rosa multiflora*. Based on generalizations from chronosequences and general observation in the region, we expected these shrub species to give way to early successional trees or even forest trees. Both the widely spreading clonal *Rhus* and the dense arching *Rosa* showed sharp collapses in cover across an entire field

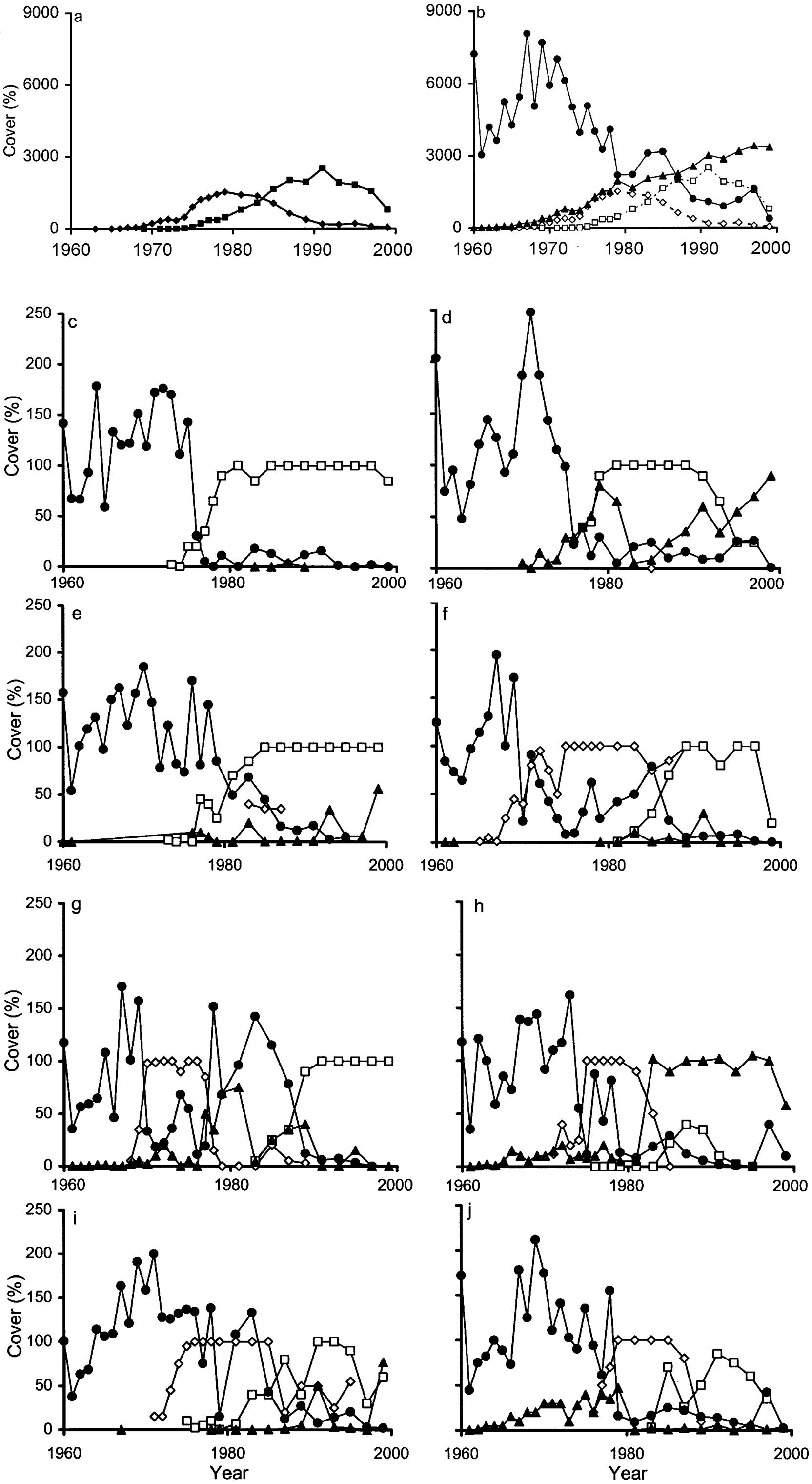

Fig. 2. Temporal patterns of ascendency and decline of two important mid-successional shrub species. **a.** Total percent cover over all 48 plots in field D3, abandoned as bare ground in 1960 from soybeans and sorghum for *Rhus glabra* (diamonds, closed or open) and *Rosa multiflora* (squares, closed or open). **b.** Total cover of the life form groups of herbs (●) and trees (▲), and of *Rhus glabra* and *Rosa multiflora*. **c-j.** Cover of the tree and herb life forms and of *Rhus glabra* and *Rosa multiflora* in all of the specific quadrats in field D3 where at least one of the shrub species reaches cover of 80 %.

(Fig. 2a). However, the patterns for the two species differ, and patterns of decline in individual plots suggest differing local mechanisms of decline. During the periods of collapse of these shrub species, trees did exhibit an apparently compensatory increase in cover over the entire field (Fig. 2b). In particular, the demise of *Rhus glabra* was associated either with an increase in *Rosa* (Fig. 2f, h-j), or with an increase in non-forest herbs

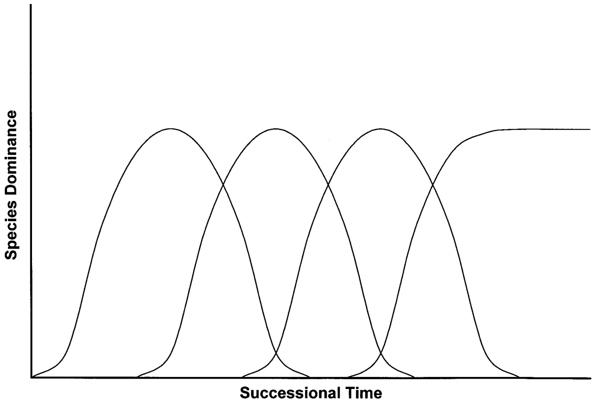

Fig. 3. Idealized sequence of species appearance, dominance and decline often depicted for successional sequences, where each curve represents a different species.

(Fig. 2g). In the remaining plots, there is not sufficient *Rhus* to suggest an association. *Rosa* is apparently replaced by trees in some individual plots (Fig. 2b, i). The sharp demise of *Rosa* often leaves the ground layer relatively devoid of plants. However, *Rosa* either does not decline (Fig. 2a, c, g), or has a relationship with trees that is still sorting out as of the most recent sampling dates (Fig. 2j). A particularly telling case is the plot in which dominance by trees precedes the rise of *Rosa*, and in which *Rosa* remains at low densities (Fig. 2h). In general, it is clear that those plots vacated by *Rhus* and *Rosa* have not become uniformly dominated by tree species in this field (Fig. 2b). The plot-specific patterns contrast with the common successional expectation. At present, the decline of *Rhus* may result from its limited life span as a fast growing successional dominant, or its replacement by the more dense-canopied *Rosa*. *Rosa* appears to yield to overtopping trees. The field-wide pattern of turnover must be understood as reflecting the contingent, actual invasion, persistence, and replacement dynamics of individual plots.

Individual species persistence.

Contingency also appears in the temporal patterns of invasion and persistence of individual species (Myster & Pickett 1988) and in the multiplicity of successional pathways (Myster & Pickett 1990). Ecologists have idealized dominance and demise of species populations in succession as unimodal and discrete curves (Fig. 3). However, initial analysis of a single field of the BSS through its first 20 years of succession falsified this idealization (Pickett 1982). For the majority of species in that analysis, the peaks of dominance were temporally narrow and species often had several peaks separated in time. In addition, the tails of the distributions either preceding or following the period of dominance were quite long. Examining the remaining nine fields and extending the analysis from 20 yr to the full time span available has confirmed that initial observation. For example, *Chrysanthemum leucanthemum* and *Acalypha rhomboidea*, two species representing the early herbaceous perennial community, show multiple peaks of abundance and long periods of presence in one field (Fig. 4).

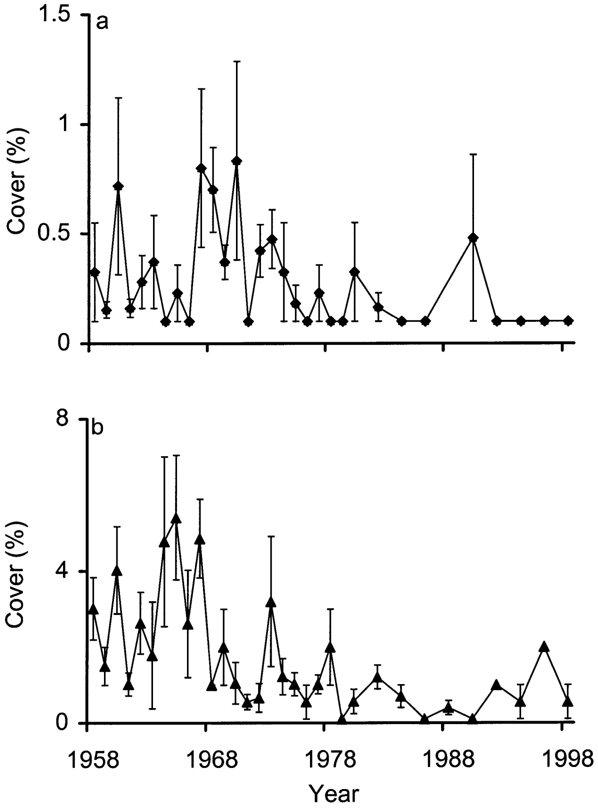

Fig. 4. Mean percent cover (± SE) of two early successional, short-lived perennials in field C3. The field was abandoned in 1958 after harvest of a crop of soybean (*Glycine max*) and sorghum (*Sorghum vulgare*). **a.** *Acalypha rhomboidea* and **b.** *Chrysanthemum leucanthemum*.

For woody species capable of being forest dominants in the region, the data set has quasi-demographic utility. Because individual stems are not marked in the BSS, true demographic analysis is not possible. However, the fact that in the early years of the succession, tree stems appear and disappear repeatedly in some individual plots (Fig. 5) suggests that (1) woody species are capable of invading very early in the succession, (2) repeated invasions are often required for successful colonization, and (3) some plots invaded by trees relatively early maintain a tree component continuously thereafter. Therefore, a modified form of the pattern predicted by initial floristic composition (Egler 1954) is

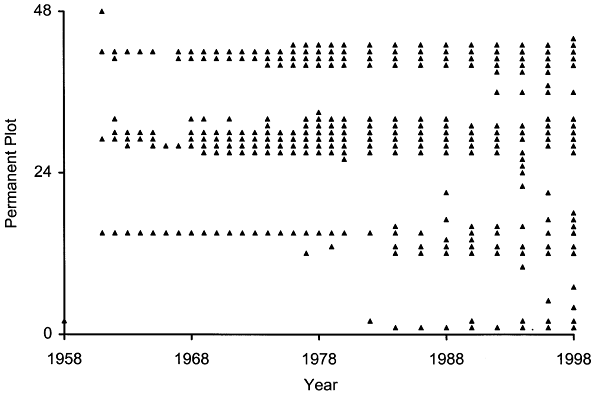

Fig. 5. Pattern of invasion and extirpation of *Acer rubrum* in each of the 48 permanent plots of field C3, abandoned in 1958. A triangle represents the presence of one or more stems of *A rubrum*. The field was sampled each year until 1980, and every other year thereafter. Hence, the standard for extirpation between 1958 and 1980 is a 1-yr gap, while from 1980 the standard is a 4-yr gap.

appropriate to describe this succession. Forest species do not necessarily have to wait until late in the succession to invade (cf. Rankin & Pickett 1989). Rather, they may probe the environment repeatedly before becoming established. In restoration, manipulations may profitably follow this strategy. Indeed, the common practice of seeding or planting late successional species is the practical parallel to this natural pattern.

The patterns of dominance, invasion and persistence, and repeated establishment of species suggest a more complex reality than the idealized hypotheses often used to characterize succession. There are two contrasting hypotheses concerning invasion. The relay floristic hypothesis is related to the classical theory of succession. The classical theory implies unimodal curves and discrete periods of persistence in succession (Fig. 3) and facilitation of later dominants by early species (Connell & Slatyer 1977). Clearly the patterns of relay floristics are inadequate to explain the BSS. Although there is a general temporal separation of dominance, the examples of multiple peaks for single species denies strict relay floristics. But if the pattern of relay floristics gives an incomplete picture, so too does the hypothesis of initial floristic composition. Elements of patterns suggested by both of the extreme hypotheses appear in the BSS. The initial floristic composition hypothesis posits that later successional species, particularly woody species, are present from the start of the succession. In support of the initial floristic composition hypothesis, it is true that some species, including later successional woody dominants, appear quite early in succession. In contrast, it is true that many of them exhibit repeated periods of arrival and demise, and that frequently the earliest invasions of later successional species fail (Buell et al. 1971; Rankin & Pickett 1989). Such patterns of early arrival and long periods of low abundance once species have established, suggest some inhibition of later species by early invaders. In support of the relay floristics model, it is also clear that some later successional species do not succeed in the absence of an established community or the presence of a specific life form. Mechanisms of such facilitation include frost heaving, which can be responsible for the failure of many tree seedlings in the first or second year of succession before an insulating litter layer builds up (Buell et al. 1971). Facilitation may be shown by woody vines, which do not begin to attain dominance before shrubs are present.

Taken together, the complex patterns of invasion, persistence, and demise in the BSS suggest that the metaphor of ‘volleys’ may be more appropriate than either strict relays or initial floristics. There is some validity to components of each of the simpler metaphors that can be captured in the combined metaphor of volleys of species in succession.

Persistent stages.

It is too early to evaluate the notion of stable end points using the BSS. However, some insights into persistence of assemblages through the early periods of succession can be offered. First, the succession has been relatively rapid in some fields adjacent to the old growth forest (Myster & Pickett 1994). In five of the eight fields adjacent to the forest, a canopy of *Acer rubrum* and various species of *Quercus* extends well into the fields (Fig. 6). In the remaining fields, trees of various species are well established at the forest edges of the fields, but shrub zones at forest-field edges are important components of some of the plots (Fig. 7). These shrub borders are notable because they are composed of thorn-bearing plants and they appear to be associated with lower cover and number of trees. In general, the fields in the BSS are proceeding rapidly through succession. As a result, the stationary stages are relatively short, and can be described by dominance of different life forms rather than by dominance of specific species. Future analyses will address this phenomenon in fine spatial and temporal detail. However, it appears in post-agricultural fields that have not been highly degraded, that relatively stationary periods are not prominent. This does not deny that selective or targeted management might not maintain fields in desired states for long periods (Niering 1987).

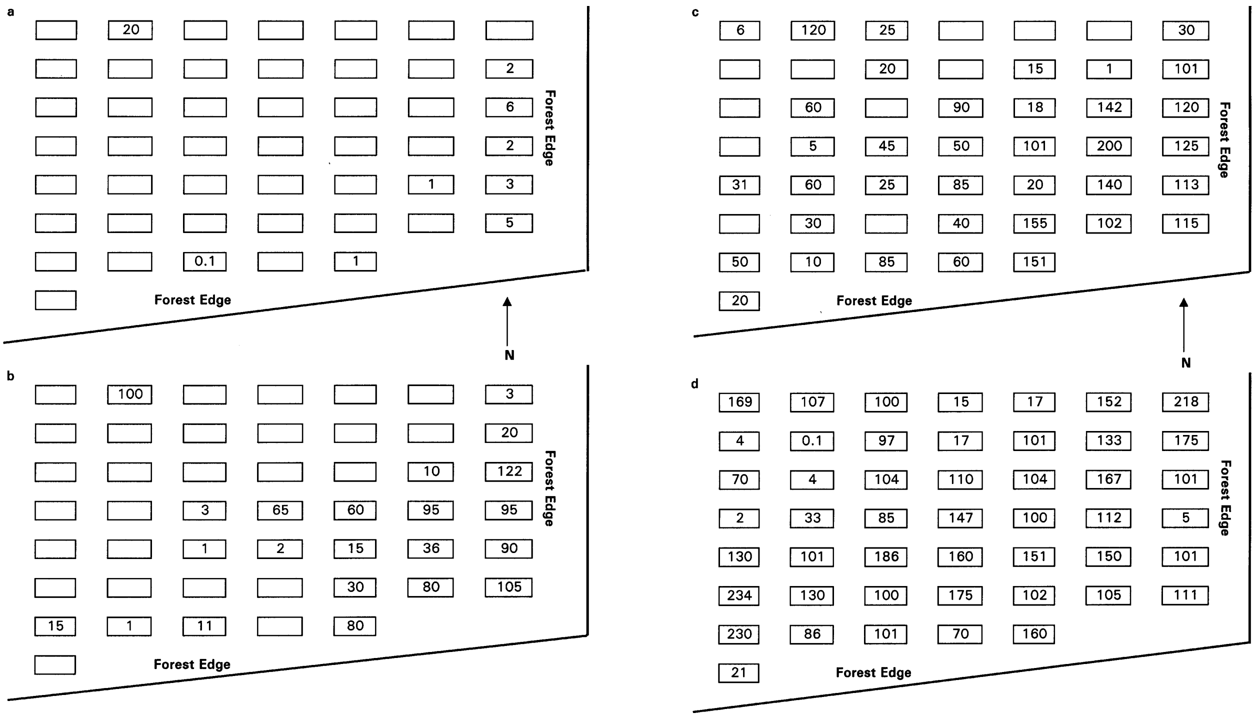

Fig. 6. Schematic map of the array of plots in field C3 and the percent cover of all tree species in each plot in **a.** 1965, **b.** 1975, **c.** 1984, and **d.** 1994. The solid lines represent the border between the field and the old growth forest. To the north is a field abandoned in 1960, and to the west is a field abandoned in 1966.

Sources of contingency and constraint

The three principal sources of community assembly in successional systems are (1) the spatial context, (2) local constraints, and (3) interactions within the assemblage. These have been captured in the hierarchical framework for successional processes that groups all specific interactions and constraints on succession as factors that affect either site availability, differential species availability, and differential species performance (Pickett et al. 1989). The assembly of communities through specific successions is affected by historical contingency of the factors acting at a specific site (Parker & Pickett 1998). The interaction between the evolutionary strategies, architectures, and allocation patterns of species have clear consequences for community assembly (Oborny & Bartha 1995).

The three sources of community assembly are each affected by contingency. Spatial context has been poorly documented in most successional studies. Indeed, few studies even state what the neighboring vegetation is. Therefore, most successional studies remain silent on the role of spatial context as a source of constraint and contingency. However, such features as the sizes of abandoned fields and the nature of communities that border them have been recognized as important constraints in some studies (e.g., Golley 1960). In the BSS, the successions in the eight fields abutting the old growth forest generally are more advanced toward broad-leaved canopies than the two fields that abut a roadside hedgerow of horticultural plane trees (*Platanus* × *hybrida).*

In particular, the successional trajectories and rates in plots within individual fields depend to some extent on the distance of the plot from the old forest edge (Myster & Pickett 1992). Woody species show relationships with the distance to edge (Fig. 6). In addition to the original forest edge, a structural boundary has developed around some fields on the edge between them and the system of access trails (Fig. 7). For bird dispersed species which are facilitated by the presence of perches (McDonnell & Stiles 1983), this may be due to birds landing at the edges of the successional fields after traversing the long distances across younger fields beyond the permanent study fields. For wind dispersed species, changes in turbulence at the boundary between the BSS and the shorter statured adjacent fields may be a contributing cause.

An additional source of spatial variation across individual fields is the differential and relatively localized behavior of different functional groups. We have defined functional groups (Fig. 8) on the basis of such features as clonal growth, above ground architecture, life cycle length, growth form, resource demand when

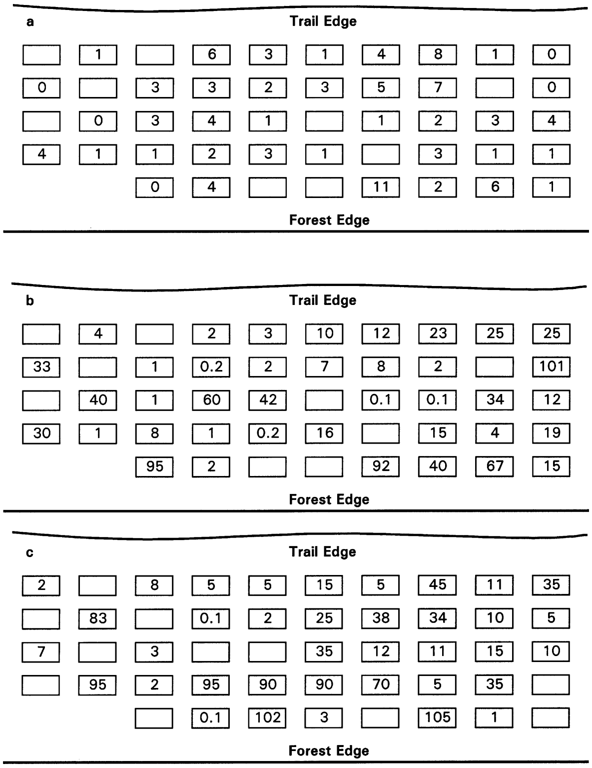

Fig. 7. Distribution of **a.** total tree stems, **b.** total percent tree cover, and **c.** total percent shrub cover in individual quadrats of field C4 in yr 19. The bottom of the figure represents the forest edge, while the upper edge abuts an access trail and a lower-statured field not part of the BSS. Field C4 was abandoned with plowing after a crop of soybeans in 1966. An 'O' in the plot indicates tree cover results from overhang. Light shading indicates tree density between 1-5 stems, while dense shading indicates densities of 6 or greater.

known, and modes of interaction. These features are among the important mechanisms by which species, species groups, and hence the entire community, reacts to historical contingency (Oborny & Bartha 1995). Different functional groups show contrasting spatial-temporal patterns of distribution (Fig. 8). These initial patterns suggest that the increased study of species functional attributes in the context of succession will be worthwhile. However, there are few studies of successional dominants that examine their functional similarities and behavior. In addition, although the within-field patch dynamics of functional groups may be related in some way to the larger landscape context, we have not yet investigated such relationships. The potential for interaction of the clear within-field heterogeneities of functional groups with the larger context is a major source of contingency (Bartha et al. 1995).

Within-field constraints can also operate as successional contingencies. Such constraints may operate on the scales of 1 through tens of meters. These constraints include the resource base, species pool, multi-trophic level interaction, and clonal architecture. The resource base is an important differentiating factor in succession. Low initial resources often characterize primary successions on new or reworked substrates. Relatively low resource rates may also characterize successions begun on degraded agricultural lands, while high resource rates likely characterize successions on such sites as fertile fields, hay fields and tree-fall gaps in forests. In the BSS, soil conditions do not differ quantitatively at coarse scales across the fields (Robertson 1982). However, fine scale variation expressed as locally eroded patches or those high on the gradual elevation contours, tend to support more species typical of low nutrient and low soil moisture conditions.

The species pool is a major local constraint in succession. One major source of contrast in seed pools is their content of exotic versus native species. The only significant difference in contribution of exotic and native species to the pool of available immigrants in the BSS is between fields abandoned after row crops versus those abandoned as meadows (Meiners et al. unpubl.). The two kinds of fields demonstrate very different starting species pools (in keeping with aspects of the initial floristic composition hypothesis). It takes 10 yr for invading species to overcome the dominance of the meadow grasses compared to the rapid turnover in fields abandoned after row crops (Myster & Pickett 1994). Qualitatively, additional differences appear in the species complement among some fields abandoned in different ways. For instance, two different early successional, wind-dispersed species dominate the first tree canopy in two contrasting fields abandoned in the same year. *Ailanthus altissima* trees dominated first in the field left unplowed at abandonment, while *Acer rubrum* dominated first in the plowed field (Fig. 8). Both species are present in all sorts of fields, yet their prominence is contingent upon the initial conditions, and may act as a cascading influence on differences in the different successions.

Interaction between plants and consumers is an important source of local constraint. These interactions have been exposed in fields that are similar to and near those in the BSS (Myster & McCarthy 1989; Cadenasso et al. subm.). Contingencies are especially likely in such interactions because of the cyclic or fluctuating nature of some mammal populations, and because of their dependence on large areas encompassing many successional habitats. The impact of mammal populations is exhibited by the observation that a mean of 48.5 % of tree seedlings planted outside of four replicate mammal exclosures in a first year field were killed by consumers while none were killed in the exclosures. Those differences were significant, and were associated with un-

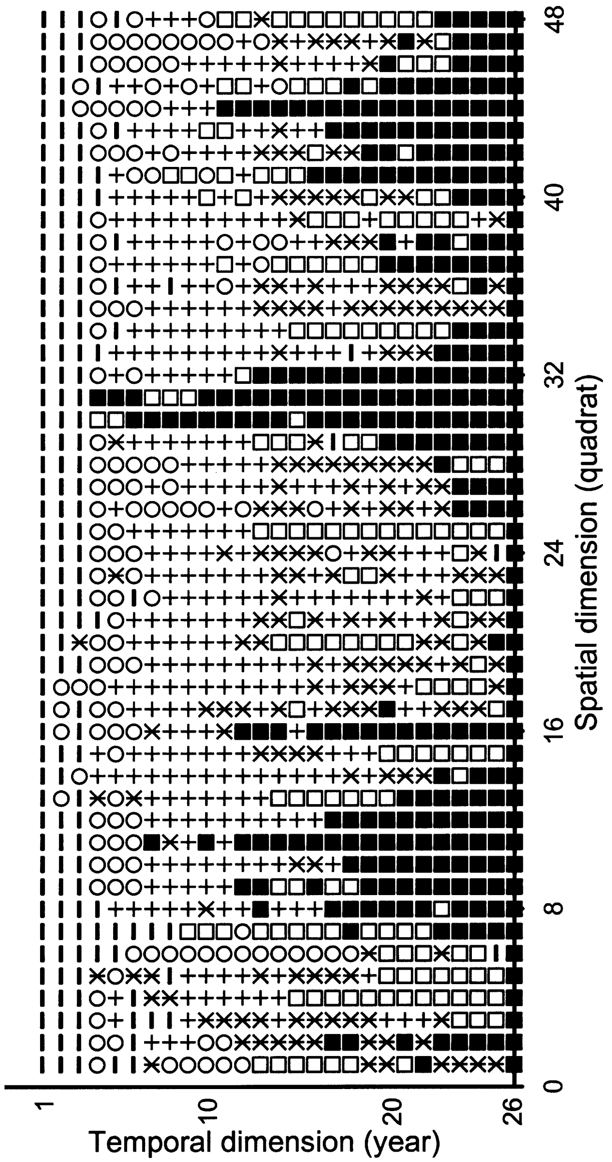

Fig. 8. Distribution of functional groups in space and time in field C3. Functional groups are short-lived species (|), erect herbs (✳), decumbent and guerilla grasses (○), phalanx grasses (+), shrubs and woody vines (□) and trees (■).

equivocal signs of damage by mammals. Furthermore, the order of dominance of trees in the succession – *Juniperus virginiana* and *Acer rubrum* early and *Cornus florida* and *Quercus rubra* late – is the same as their order of sensitivity to mammalian browsers (Cadenasso et al. subm.). In addition, those seedlings that appear in 20 cm diameter openings in the herbaceous canopy are significantly more likely to be damaged in older fields (45.7%) by browsers such as deer (*Odocoileus virginianus*) and rabbits (*Sylvilagus floridanus*) than seedlings surrounded by intact herbaceous vegetation (33.83%; M.A. Meadows unpubl.). Thus, contingency appears in trophic interactions based on the presence of herbivores and on their micro-scale access to seedlings.

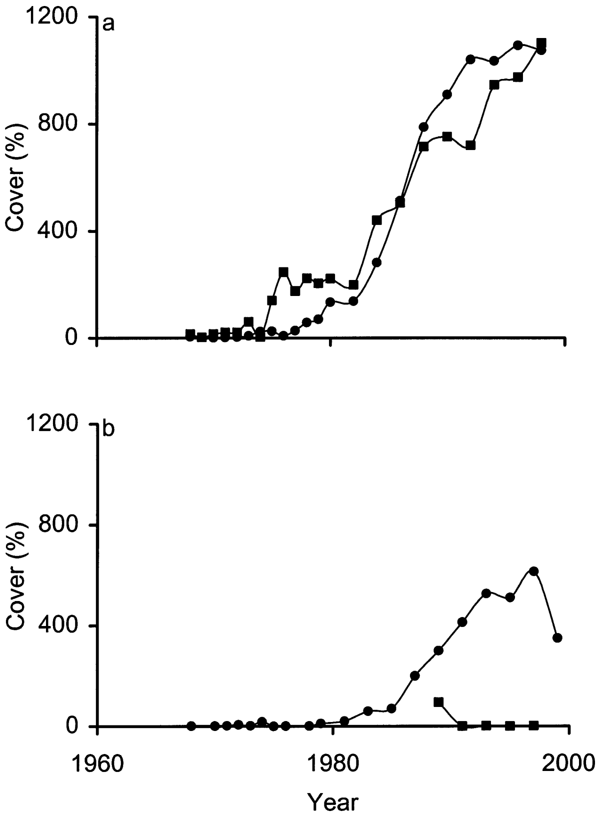

Fig. 9. Total cover of *Acer rubrum* (●) and *Ailanthus altissima* (■) in fields C6 (**a.**) and C7 (**b.**) of the Buell-Small Succession Study. Both fields supported orchard grass prior to release and were first sampled in 1964. The crop of orchard grass on C6 was harvested for hay in 1963, while C7 was plowed and disked in the spring of 1964.

Predictability in succession

Successional patterns.

Temporal aggregation or spatially coarse scale abstraction has exposed relatively predictable trends in succession. Field-wide trajectories, especially when averaged across the whole suite of fields sharing a major abandonment treatment, are quite striking (e.g. Fig. 2). In particular, the trajectories of life forms are relatively sound. A literal succession of dominance by herbs, shrubs, and trees occurs in the first 40 yr of succession in BSS. It was this sort of predictability, not necessarily the specifics of species composition, that Clements (1916) took as the core of his succession theory. Notably, in a post-agricultural succession in Kansas, the succession does not include the expected order of life forms derived from a regional survey (Collins & Adams 1983). While statistical averaging used to abstract the regional trends should not necessarily be expected to expose the same trends observed in one specific site, the contingencies that appear in the 10 fields of the BSS result from local, biologically comprehensible particulars. Explicable local uniqueness rather than random variation is the main point of difference between the patterns in the BSS and the chronosequence chosen by Bard (1952).

During this early successional period both at the Hutcheson Memorial Forest Center where the BSS is located (Meiners et al. 2000), and in the New Jersey Piedmont in general (Bard 1952), the dominance shifts from exotic species to natives. This trend may not continue into the future as new, forest-dwelling exotics such as *Alliaria petiolata* and *Acer pseudoplatanus* become more important in the region. The coarse scale trajectories are the result of the local contingencies and fine scale interactions exemplified earlier in this paper. Hence the mechanisms of the coarse scale trends are contingent and context specific. Restoration can seek to construct specific states from among those found at the fine scale in any successional stage. It can also discern methods by which desired states can be constructed or maintained by examining the contingent or local mechanisms that have yielded specific successional assemblages.

A second structural trend that characterizes the succession as a whole is the increase of spatial complexity through time. Detailed fluctuations within the general trajectory may have ecological significance. For example, periods during which dominance shifts from one major life form group to another may be periods of increased spatial heterogeneity, while those periods over which dominance by a life form is consolidated may be periods of lower heterogeneity. In addition, as dominance shifts to plants with larger body size, and hence different scale relationships compared to early herbaceous dominants, the scale of patchiness undoubtedly changes. Restoration may create heterogeneities of appropriate scales to generate desired compositions or community architectures. In addition, heterogeneity *per se* may sometimes be the desired goal of a restoration. Restorationists may manipulate heterogeneity itself, or the site conditions and characteristics of species combinations that may influence vegetation heterogeneity.

Successional processes.

Most of the large processes that drive succession have been identified for a long time (Miles 1979). Important expansions of the basic roster have occurred with the recognition of the role of animals, and of fine scale heterogeneity, for example (MacMahon 1981). The roster of processes can be related to one another in different ways, depending on the theoretical assumptions about the degree of determinism and closed nature of succession (Pickett et al. 1987). The state of the art is to recognize successional processes as relating to (1) the nature of the site at which succession occurs, including how and to what degree an existing community and soil is disrupted at the start of the succession, (2) the differential availability of propagules, whether from seeds or vegetative parts, and whether stored or migrating into the site; and (3) the differential performance of the species determined by their own autecological characteristics and their interactions with other plants, microbes, and animal dispersers and consumers. It is just these processes that must be manipulated to achieve restoration. This consistency of process is one of the generalizations from studies of succession that apply to planning and maintaining restoration projects. Yet how to apply the specific kinds of mechanism that each of the three processes includes is one of the key tools for restoration that emerges from understanding the fine spatial and temporal structure of succession (Luken 1990).

Discussion

The BSS, a fine-scale, temporally continuous study on succession in permanent plots, has yielded insights that can be applied to restoration. Spontaneous succession can expose key features of the points of reference restorationists can choose, the functions of ecological assemblages, and tools for restoring systems. Rather than rely on assumptions of environmental uniformity and deterministic interactions, the BSS points out mechanistic contingencies and constraints that can be used or managed in restoration. Similarly, the BSS reinforces conclusions from the literature that regional generalizations of successional trajectories do not necessarily inform local vegetation dyanamics, due to site specific contingencies.

The absence of one of the most widespread successional dominants of the eastern United States, *Schizachryrium scoparium* has pointed out the need to understand key mechanisms in succession, including dispersal and resource availability. The general description of a site as post-agricultural secondary succession leaves much contingency unexamined.

The demise of a dominant mid-successional shrub such as *Rhus glabra* without being replaced in all cases by later successional plants indicates an as yet unknown constraint on successional turnover. In some plots, *Rhus* is succeeded by trees. However, in other plots, it is replaced in dominance by *Rosa multiflora* or by a mixture of herbs that had been dominant earlier in the succession. Such patterns suggest that fine scale manipulation of invasion sites may be a more successful restoration strategy than assuming a deterministic replacement by trees in all cases. Such results suggest it is important to identify successional turnovers that may be susceptible to unpredictable switches at local sites. These turnovers may be especially crucial times for restoration or management intervention.

The multimodal form of dominance and persistence exhibited by species in the BSS suggests that they are often available to respond to changing conditions throughout the succession. It also means that species are likely responding to shifting weather conditions as well as to fine scale disturbances and the activities of animals and other plants. A parallel finding is the spatio-temporal patch dynamics exhibited by different functional groups. It appears that such groups are exploring different parts of the time-space matrix presented through succession. Whether there is practical value in constructing restorations to mimic such behavior is currently unknown. However, research is needed to determine the role of such shifting and multimodal patterns in succession and their relevance to restoration.

Patterns of invasion and persistence, especially those seen in tree species, indicate that species often probe and fail in specific plots, while they succeed in others. Whether there are fine-scale predictors of the success of trees needs to be investigated. However, at the least, the pattern shows the inadequacy of two major hypotheses about successional mechanism – the relay floristics hypothesis and the initial floristic composition hypothesis – for informing restoration. The reality is much more akin to volleys of invasion and persistence. The mechanisms of this more complex pattern may be important to restoration planning. In any event, the complex patterns discovered in this continuous, fine scaled succession study question the reliance on the “if you build it they will come” assumption as a foundation for restoration (Heimans 1954).

Spatial context is crucial in the successional patterns at the fine scale. Not only does the forest edge appear as a hot spot of succession, but so does the edge that many BSS fields share with adjacent, younger fields. The behavioral responses of birds and of wind turbulence to both edge types may cause the patterns. Restorationists already exploit perches as attractors for bird dispersal. Other fine scale structures may be worth investigating.

The interaction of the structure and composition of the plant community with browsers and their impact on tree invasion is a relatively new area of successional knowledge. New data suggest that the impacts of browsers may be manipulated either directly, through altering the structure of the plant community, or through manipulation of the invading woody individuals. Because browsers are themselves subject to the effects of landscape pattern, climatic fluctuation, and their own internal population dynamics, they may be a key lever for restoration.

The consistency of successional patterns across fields and large areas is an aggregate property. The local differences from these generalized patterns make a *laissez faire* approach to restoration risky. The variations in the coarse scale and long-term successional patterns are composed of the fine scale contingencies and spatial effects across many spatial scales in fields. Understanding how these contingent interactions and spatial constraints at different scales structure the plant community can generate knowledge that can be used in restorations. In essence, all restoration, because it relies on assemblages of interacting and flexible organisms, is an exercise in manipulating succession in local sites. Whether a restorationist wishes to slow or advance succession to attain some desired species composition or ecosystem architecture, the contingent, spatially explicit, and context-dependent processes of succession are relevant.

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References

Bard, G.E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecol. Monogr.* 22: 195-215.

Bartha, S., Czárán, T. & Oborny, B. 1995. Spatial constraints masking community assembly rules: a simulation study. *Fol. Geobot. Phytotax.* 30: 471-482.

Buell, M.F. 1957. The mature oak forest of Mettler’s woods. *William L. Hutcheson Mem. For. Bull.* 1: 16-19.

Buell, M.F., Buell, H.F., Small, J.A. & Siccama, T.G. 1971. Invasion of trees in secondary succession on the New Jersey Piedmont. *Bull. Torr. Bot. Club.* 98: 67-74.

Canham, C.D. & Pacala, S. 1995. Linking tree population dynamics and forest ecosystem processes. In: Jones, C.G. & Lawton, J.H. (eds.) *Linking species and ecosystems*, pp. 141-158. Chapman & Hall, New York, NY.

Clements, F.E. 1916. *Plant succession: an analysis of the development of vegetation.* Carnegie Institution, Washington, DC.

Collins, S.L. & Adams, D.E. 1983. Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass Prairie. *Vegetatio* 51: 181-190.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.

Czárán, T. 1998. *Spatiotemporal models of population and community dynamics*. Chapman and Hall, New York, NY.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412-417.

Eldredge, N. 1999. *The pattern of evolution*. Freeman, New York.

Gleason, H.A. & Cronquist, A. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*, 2nd. ed. The New York Botanical Garden, Bronx, NY.

Golley, F.B. 1960. Energy dynamics of an old-field community. *Ecol. Monogr.* 30: 187-206.

Heimans, J. 1954. L'accessibilité, terme nouveau en phytogeographie. (Accessibility: a new term in plant ecology). *Vegetatio* 5: 142-146.

Jordan, III, W.R. 1993. Restoration as a technique for identifying and characterizing human influences on ecosystems. In: McDonnell, M.J. & Pickett, S.T.A. (eds.) *Humans as components of ecosystems: the ecology of subtle human effects and populated areas,* pp. 271-279. Springer-Verlag, New York, NY.

Lockwood, J.L. 1997. An alternative to succession: assembly rules offer guide to restoration efforts. *Restor. Manage. Notes* 15: 45-50.

Luken, J.O. 1990. *Directing ecological succession*. Chapman and Hall, New York, NY.

MacMahon, J.A. 1981. Successional processes: comparisons among biomes with special reference to probable role of and influences on animals. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.) *Forest succession: concepts and applications*, pp. 277-304. Springer-Verlag, New York, NY.

McDonnell, M.J. & Stiles, E.W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* (*Berl.*) 56: 109-116.

Miles, J. 1979. *Vegetation dynamics*. Wiley & Sons, New York, NY.

Myster, R.W. & McCarthy, B.C. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56: 145-148.

Myster, R.W. & Pickett, S.T.A. 1988. Individualistic patterns of annuals and biennials in early successional oldfields. *Vegetatio* 78: 53-60.

Myster, R.W. & Pickett, S.T.A. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. *Am. Mid. Nat.* 124: 231-238.

Myster, R.W. & Pickett, S.T.A. 1992. Effects of palatability and dispersal mode on spatial patterns of trees in oldfields. *Bull. Torrey Bot. Club.* 119: 145-151.

Myster, R.W. & Pickett, S.T.A. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology* 75: 387-392.

Niering, W.A. 1987. Vegetation dynamics (succession and climax) in relation to plant community management. *Conserv. Biol.* 1: 287-295.

Oborny, B. & Bartha, S. 1995. Clonality in plant community – an overview. *Abstr. Bot.* 19: 115-127.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Mid. Nat.* 28: 1-126.

Parker, V.T. & Pickett, S.T.A. 1998. Historical contingency and multiple scales of dynamics within plant communities. In: Peterson, D.L. & Parker, V.T. (eds.) *Ecological scale: theory and application*, pp. 171-191. Columbia University Press, New York, NY.

Pickett, S.T.A. 1982. Population patterns through twenty years of oldfield succession. *Vegetatio* 49: 45-59.

Pickett, S.T.A. 1983. The absence of an *Andropogon* stage in old-field succession at the Hutcheson Memorial Forest. *Bull. Torrey Bot. Club* 110: 533-535.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-term studies in ecology: approaches and alternatives.* pp. 110-135. Springer-Verlag, New York, NY.

Pickett, S.T.A. & Kolasa, J. 1989. Structure of theory in vegetation science. *Vegetatio* 83: 7-15.

Pickett, S.T.A. & Parker, V.T. 1994. Avoiding the old pitfalls: opportunities in a new discipline. *Restor. Ecol.* 2: 75-79.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. 1987. Models, mechanisms and pathways of succession. *Bot. Rev.* 53: 335-371.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54: 129-136.

Pickett, S.T.A., Parker, V.T. & Fiedler, P.L. 1992. The new paradigm in ecology: implications for conservation biology above the species level. In: Fiedler, P.L. & Jain, S.K. (eds.) *Conservation biology: the theory and practice of nature conservation, preservation, and management*, pp. 65-88. Chapman & Hall, New York, NY.

Rankin, W.T. & Pickett, S.T.A. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. *Bull. Torrey Bot. Club.* 116: 182-186.

Robertson, G.P. 1982. Factors regulating nitrification potentials in primary and secondary succession. *Ecology* 63: 1561-1573.

Ugolini, F.C. 1964. Soil development on the red beds of New Jersey. *Bull. Hutcheson Mem. For.* 2: 1-34.

Wu, J. & Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* 70: 439-466.

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