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A hierarchical consideration of causes and mechanisms of succession

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Abstract

Questions of successional pattern and causality have been central concerns in vegetation ecology. In this paper we address the limits of the overextended models of Connell and Slatyer by discussing problems encountered in field tests. To help prevent such problems, we define the essential concepts needed to understand succession: pathway, cause, mechanism, and model. We then suggest a more complete enumeration of successional causes, and place them in a three-level hierarchy. The highest level in the hierarchy defines the general and universal conditions under which succession occurs: (1) availability of open sites, (2) differential availability of species, and (3) differential performance of species at the site. To provide a more detailed understanding of succession, each of these causes is decomposed into ecological processes. A further decomposition results in the third level of the hierarchy, which is required to elucidate the mechanisms of succession at particular sites and to make detailed predictions. The hierarchy allows the appropriate causes to be chosen to answer questions about succession at the desired level of generality or level of organization. Recognizing the appropriate level(s) in the hierarchy is critical for the successful explanation of succession, design of experiments, statement of predictions, construction of models and development of general theory.

Introduction

Succession has commanded much of the attention of plant ecologists since the inception of the discipline. The majority of that effort has focused on determining the patterns of vegetation change through time. The study of mechanisms has been slower to develop due to the long time periods involved, but also due to the dominance of theories that gave preeminence to the climax, to stage-wise turnover, and to facilitative interactions (e.g. Clements, 1916). In addition, the causes of succession are complex, and this has hindered the development of a comprehensive body of theory.

Connell & Slatyer (1977) provided an antidote to several of the critical problems that had beset the study of successional causes. For example, they promoted an experimental approach to determining the mechanisms of succession and the view that succession can be the outcome of several mechanisms. However, application of the ideas of Connell & Slatyer (hereafter denoted C & S) has been problematical. Here we analyze these difficulties and clarify important concepts needed in the study of succession. (Occasional reexamination of the fundamental concepts in vegetation was long ago advised by Cooper, 1926). We then provide a causal hierarchy as a framework for the study of succession.

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Basic definitions

Four concepts are needed to describe, explain or predict aspects of succession.

(1) *Pathway*: The temporal pattern of vegetation change. A pathway may show changes in community types, system states, populations, or other parameters of vegetation. A variety of diagrammatic pathways presented by Horn (1981) and the analysis by Boerner (1985) exemplify the idea. A pathway for a particular succession appears in Fig. 1.

(2) *Cause*: An agent, circumstance or action responsible for successional patterns. Mechanisms, defined below, are one sort of cause. Complexity in successional causality will be illustrated and organized in the hierarchy introduced later.

(3) *Mechanism*: An interaction that contributes to successional change. A mechanism of succession, as an agent of change, is thus an efficient cause in the classical sense.

An important caveat in using the term 'mechanism' is that the specific interaction that is termed a mechanism depends on the level of organization a study addresses (Allen & Starr, 1982; Allen, 1987). At the community level, a mechanism may be a general ecological process or interaction, such as competition, establishment, or mutualism. Importantly, Connell & Slatyer's (1977) terms facilitation, tolerance and inhibition fit this description. But when considered at lower levels or organization, such as the population or individual levels, general processes must be decomposed into more detailed mechanisms. For example, 'competition' can be divided into mechanisms of differential resource uptake, stress effects on resource use, alterations in growth rates and allocation, and subsequent changes in resource availability. This example illustrates that what is called a mechanism on one level of organization can be considered an effect on another level. It is thus important to specify on what level of organization a mechanism is being sought. Such specification may avoid unproductive arguments, since ecological studies usually involve several levels of organization.

(4) *Model*: A conceptual construct to explain successional pathways or predict the course of particular successions by combining various mechanisms, specifying the relationship between the mechanisms and the pathway as well as one another. The general systems model of succession developed by MacMahon (1981), models for specific seres (Noble & Slatyer, 1980; Armesto & Pickett, 1985a), and simulation models (Shugart, 1986) all serve as examples (Fig. 1).Note that the phrase 'C & S model' refers specifically to the 'models of mechanisms' (their phrase).

Misapplication of Connell and Slatyer's models

Connell & Slatyer's (1977) paper (hereafter denoted C & S) has been the focus of some studies (e.g., Sousa, 1979; Hils & Vankat, 1982; Turner, 1983; Harris *et al.*, 1984), and has been a point of reference in many others (e.g. Keever, 1979).

The use of C & S in the literature is often broader than intended (e.g. Harris *et al.*, 1984; Kruger, 1983; see Breitburg, 1985). Fig. 1 in C & S, entitled 'models of the mechanisms of succession' summarizes their focus on mechanisms of species turno-

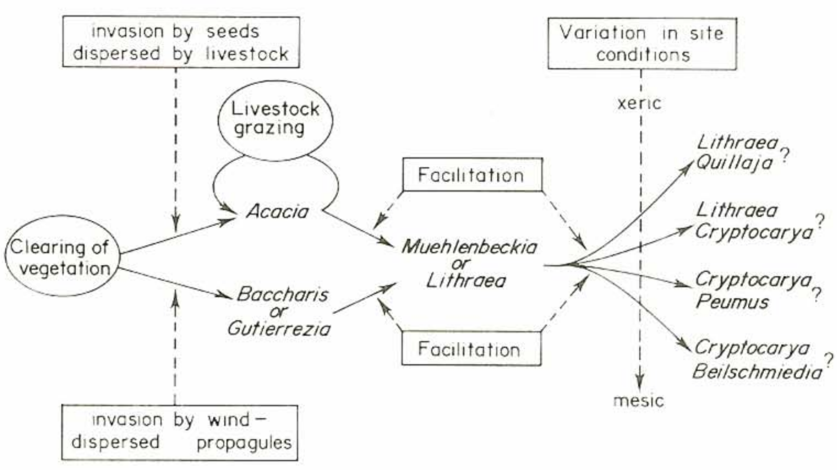

Fig. 1. A model of succession in Chilean matorral, composed of a pathway, indicated by solid arrows connecting stages labeled by their dominant genera. The mechanisms and causes of the succession are shown in boxes or circles, and their point of action in the pathway is shown by dashed arrows. (The difference between boxes and circles is unimportant for the current discussion). After Armesto & Pickett (1985a). Reproduced with permission of Revista Chilena de Historia Natural.

ver. The three models of C & S should be applied to specific plant-by-plant interactions (including the influence of mutualists and consumers) that result in successional turnover. They should not be applied to entire successions. Certainly, the C & S models are not alternative hypotheses about entire seres; attempting to 'test' them in that way is not likely to be productive (Quinn & Dunham, 1983). It is possible to analyze specific mechanisms of species replacement in succession within the broad categories of facilitation, tolerance and inhibition.

Another major limitation of the C & S models is the focus on species entry into the succession. Mechanisms by which species persist and mechanisms by which they yield space are not explicitly considered in the C & S models, although these events can be inferred from much of the rest of their discussion. The broad survey of successional causes by Clements (1916) provides the most inclusive framework for any discussion of successional mechanisms (Miles, 1979; MacMahon, 1981). Five non-teleological causes of succession appear in Clements' list: (1) Disturbance opening a site ('Nudation'), (2) Migration of propagules to the site, (3) Establishment of species at the site ('Ecesis'), (4) Interaction of organisms, (5) Alteration of the site by the organisms ('Reaction').

The nature of disturbance must be considered when succession is to be understood. C & S discuss disturbance in relation to community stability, but variations in features of disturbance do not discriminate among their three models of succession.

Migration is considered as a given or controlled factor by C & S, because they adopt an experimental approach. In field experiments the outcome of species removals or additions may depend in subtle ways on the presence or absence of species other than those being manipulated (Quinn & Dunham, 1983). In any event, understanding of the entire process of succession must include understanding the dynamics of invasion.

The C & S models are differentiable by the remaining three Clementsian causes. Establishment processes are key features of the three models. The obligate order of establishment is critical for separating the facilitation model from the other two. Finegan (1984) notes that facilitation may not require ordered establishment (i.e., relay floristics), but that refinement post dates the C & S models. Interaction among the species also differentiates the models. In the inhibition model, no invader can overcome the suppression of the initially established community, while in the tolerance and facilitation models, invasion is not depressed by the presence of the established plants. Finally, alteration of the environment by established plants has no impact in the tolerance model, although it does in the other two.

The examples to follow will consider both conceptual and practical problems in the application of the three mechanisms referred to in the C & S models. We will restrict our discussion to examples of inhibition. The complexity of all three mechanisms of species invasion are considered elsewhere (Finegan, 1984; Pickett *et al.*, in prep.).

A critical problem in interpreting information from field experiments designed to assess the three mechanisms arises because succession is fundamentally a plant-by-plant replacement process (Horn, 1976; Peet & Christensen, 1980) and interactions at the scale of neighborhoods are significant (Aarssen & Turkington, 1985a, b). Thus experiments focused on the entire assemblage of plants may fail to discriminate clearly among mechanisms (Breitburg, 1985). The clearest focus for discriminating among the mechanisms is at the level of individual replacement. Uncertainty resulting from confounding these scales appeared in the experiments of Hils & Vankat (1982) who were not able to confidently discriminate between the tolerance and inhibition mechanisms, although their results did contradict the predictions of the facilitation mechanism. Hils & Vankat (1982) suggested that different mechanisms may act simultaneously or consecutively. This is confirmed by Breitburg's (1985) analysis of marine cases and subsequent experiments on the fine scale (Armesto & Pickett, 1985b).

The role of species of *Rhus* in the invasion of trees into grasslands or oldfields (Petranka & McPherson, 1979; Werner & Harbeck, 1983), provides another example of difficulty in interpreting the inhibition mechanism. *Rhus typhina* increases the survivorship of trees invading a Michigan oldfield by thinning the dense herb cover that had formerly inhibited the trees (Werner & Harbeck, 1983). Thus, the interaction between *Rhus* and trees would be labeled facilitation. However, as Breitburg (1985) points out for marine cases, such interactions are asymmetrical. From the point of view of the grasses, the situation is inhibitory. Furthermore, if an experiment were done late in the interaction among the *Rhus*, grasses and trees, when the grasses had decreased substantially in cover, the trees would likely be released as a result of removing *Rhus*. The interaction would then be labelled inhibitory to the growth of tree seedlings. In order to fully understand the dynamics of tree invasion in an oldfield the mechanisms of invasion, persistence and mortality of the interacting species need to be known. Classifying the interaction as one of the three alternative types discerned by C & S may leave much unlearned about the interactions in a particular sere (Finegan, 1984).

Gap phase dynamics, common in mesic forests (Brokaw, 1985; Runkle, 1985) offer additional examples of the problems of interpretating the inhibition mechanism. Setting aside the problem of asymmetry in interactions, ascent of late successional trees into the canopy depends not only on disturbance removing the inhibitory canopy individuals, but also on the tolerance of the late successional seedlings or sapling trees (e.g. Canham & Marks, 1985). Consequently, part of the entire interaction involves more than one mechanism (see Finegan, 1984).

For some questions concerning successional mechanisms and causes, it will be necessary to go beyond the particular C & S models.

A causal hierarchy

We suggest that the causes of succession be arrayed in a hierarchy for several reasons. A hierarchical arrangement spans all levels of inquiry. At the most inclusive level, the hierarchy presents a general explanation of succession, while at the most specific level, it comprises specific predictive factors. The hierarchy also encompasses all causes that operate at all levels of ecological organization. The specific research questions and objectives will determine where in the hierarchy causes are examined. Presentation of the hierarchy is not an admonition to incorporate all possible mechanisms or causes of succession in any particular study. Rather, it allows studies of part of the range of causes to be put in context, and guides the choice of interactions and constraints that must be considered to answer a given question.

The hierarchy has three levels. The highest, most general level is composed of the answers to the question, What causes succession? The answers that generally apply to any situation are that: (1) open sites become available; (2) species are differentially available to an open site; and (3) species behave differentially at the site. In the next level of the hierarchy, the three general causes of succession are divided into ecological processes or relationships. The first general cause, site availability, is determined by disturbance. The second differential species availability, is a function of the processes of dispersal and the dynamics of the propagule pool. The third, differential species performance, can be broken down into relations of the following: (1) resource availability; (2) ecophysiology; (3) life history strategy; (4) stochastic environmental stress through the sere; (5) competition; (6) allelopathy; and (7) herbivory and predation.

Each one of the processes or phenomena at the intermediate level in the hierarchy can in turn be understood in greater detail by examining the factors that determine its outcome and impact in a particular succession. It is these specific factors of the lowest, most detailed level of the hierarchy, that must be assessed or modeled to make specific predictions about the course of succession at a particular site. Similarly, certain of these factors need to be known to explain fine scale variation in succession. See Table 1.

We choose disturbance because for the purpose of illustration its importance in determining the course of succession has often been neglected (Vogl, 1980; Vitousek & White, 1981). The characteristics of disturbance requiring attention in understanding the course of successions include these (Sousa, 1984; White & Pickett, 1985): (1) severity; (2) size and shape; (3) timing relative to season, succession and past disturbance; and (4) spatial distribution of disturbed patches. The severity of disturbance is a measure of its impact on the vegetation (White & Pickett, 1985). To what extent the existing community is opened by disturbance determines for which potential colonists the new environment is suitable. It also determines whether vegetative or sexual propagules survive the disturbance and can contribute to the successional community (Noble & Slatyer, 1980). In some systems, e.g. mediterranean-type vegetation, the dynamics may be completely dependent on the predominant mode and impact of disturbance (e.g. fire in matorral, Armesto & Pickett, 1985a). Size of the area opened by disturbance will affect the environment of the site (Runkle, 1985; Denslow, 1980). Shape will additionally affect the physical environment, but will also influence the pattern of invasion of the site.

In addition to the simple physical characteristics of individual disturbances, the relationship of modes of disturbance to one another (e.g., Collins & Barber, 1986) and to other environmental and organism characteristics is important. The timing of the disturbance relative to season may influence its impact on the structure of the vegetation, the resources that are made available, the species that are particularly susceptible to its impact, and the suite of species that are potential immediate colonists (Keever, 1979). The timing of the disturbance relative to the successional status of the com-

Table 1. A hierarchy of successional causes. The highest level of the hierarchy represents the broadest, minimal defining phenomena. The intermediate level contains the mechanisms of change or causation of the highest level. The lowest level consists of the particular factors that determine the outcome of the intermediate-level processes, and are discernible or quantifiable at specific sites. Whether a particular process or factor advances or slows succession must be determined experimentally in specific instances or by generalization among comparable cases. Other processes or factors may be recognized in specific situations. For simplicity, interactions among factors at each level are not shown.

General causes of succession	Contributing processes or conditions	Defining factors
Site availability	Coarse-scale disturbance	Size, Severity, Time, Dispersion
Differential species availability	Dispersal	Landscape configuration
	Propagule pool	Dispersal agents, Time since disturbance, Land use
Differential species performance	Resource availability	Soil conditions, Topography, Microclimate, Site history
	Ecophysiology	Germination requirements, Assimilation rates, Growth rates, Population differentiation
	Life history strategy	Allocation pattern, Reproductive timing, Reproductive mode,
	Stochastic environmental stress	Climate cycles, Site history, Prior occupants
	Competition	Presence of competitors Identity of competitors Within-community disturbance Predators and herbivores Resource base
	Allelopathy	Soil characteristics, Microbes, Neighboring plants,
	Herbivory, disease and predation	Climate cycles, Consumer cycles, Plant vigor, Plant defense, Community composition, Patchiness

munity will also have important implications for subsequent succession. Timing of disturbance must also be considered in relation to the life histories of species in the community (Armesto & Pickett, 1985b). Disturbance may have different effects based on senescence, reproductive or architectural status of species in the community.

The frequency of disturbance in a landscape will likely influence the rate and course of succession through influences on the species pool, dispersal of species through the landscape, and configuration of patches of various successional ages (Pickett & Thompson, 1978; Forman & Godron, 1981). This aspect of the analysis of disturbance as a driving process of succession points out an important characteristic of disturbance that is helpful in application of the idea in general. It may apply to other components of the detailed level of the causal hierarchy as well. Each defining factor can be applied at a variety of spatial scales. For example, disturbance can be considered as a discrete event. In that case, a particular community is affected at a specific time. However, individual disturbances are a part of a disturbance regime that is discernible at coarser spatial and temporal scales (Levin & Paine, 1974). At the scale of entire landscapes, changing the disturbance regime may alter the dynamics of the successions that occur there. It is important to keep the distinction between disturbance regime and individual disturbances in mind to avoid confusion. Altering the magnitude of individual disturbances may have different effects on communities than altering the frequency and clumping of disturbances of various types and magnitudes in a landscape. In the first case, a disturbance is altered, and the response of one to several individuals is affected, whereas in the second case, the entire disturbance regime is altered and assemblages or landscapes may be affected.

Using the hierarchical array of successional causes proposed here, and recognizing the impact of scale on individual components of the hierarchy should enhance insight into the relationship of different causes to one another and lead to increased precision making predictions to be tested experimentally.

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