

Changing Perspectives in Community Dynamics: A Theory of Successional Forces

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The classical concepts of succession and climax were burdened with intractable assumptions and were difficult to apply to the field. Conceptual refinements and more realistic assumptions have been proposed to identify the useful essence of the original ideas. The contemporary theory of community dynamics emphasizes process rather than end point, accommodates the richness of causes of succession, and motivates diverse research approaches.

There are many active, contemporary research topics in succession. These range from ecophysiology to plant-plant interactions based on competition and life history, and plant-animal interactions such as herbivory, predation and dispersal, to plant-environment interactions involving resource use and disturbance¹. Comparative, experimental and modelling approaches²⁻⁴ are employed to address questions concerning the process of succession, with a corresponding reduction in emphasis on the end point of the dynamics⁵. In addition, the modern focus is on plant-by-plant interactions^{6,7}, and collective properties of ecosystems, such as biomass and nutrient pools^{8,4}. There is also great interest in unification and generalization among different successions^{9,1,3}.

Although the classical theory of succession is of limited use for such contemporary interests, the ideas of succession and climax continue to be useful and powerful¹⁰. We wish to identify the useful kernels implicit in those concepts, and explicitly summarize the contemporary paradigm that motivates the diversity of process-oriented research questions. Such a paradigm can organize and relate the complex array of mechanisms recognized by contemporary community ecologists.

Classical ideas and assumptions

The idea of succession arose when the emphasis of research was on the description of static communities¹¹. In 1899, Cowles codified the revolutionary insight

that communities are dynamic¹². Recognizing the universal dynamism in communities was a major change in ecology. It added realism to the study of communities and included both compositional and structural changes.

Succession

Succession was assumed to be orderly, directional and predictable^{12,13,6}. Early research documented the directionality of patterns, but unfortunately paid less attention to process. Succession was further assumed to be autogenic, that is, governed by biotic interactions within the community. The overriding mechanism accepted by the classical theory was reaction¹³ or 'facilitation'¹⁴, whereby early communities alter the environment to their detriment and favor later-successional assemblages¹⁴. Finally, early concepts focused on the replacement of entire communities driven to an equilibrium by regional climate^{13,15}.

When the concepts of succession were applied to the field, especially using long-term studies, the assumptions were found wanting¹⁶. Trajectories were disorderly, precise predictions failed, and some successions cycled or 'reversed'^{17,5}. Allogenes, or the control of community dynamics by factors originating outside its boundaries, was common and often dominant¹⁸. Finally, inconsistent use of scale plagued the discipline. Although some workers focused on climatic and geomorphic regions, most focused on local stands, and contradictory patterns emerged.

Climax

Climax is the complementary concept to succession, and specifies the expected result. Although the composition and structure of successional communities were characteristic of a floristic region or resulted from a specific disturbance, all successions ended in a generalizable equilibrium state,

the climax. The concept is therefore an abstraction, allowing communication and application worldwide.

The climax is also an 'ideal', like the idealization of the frictionless pendulum. The idea of climax was defined so as to isolate it from influences other than regional climate. The idea served as an important tool for bounding the study of succession. Without it, the great variety of specific trajectories and states that communities could exhibit would have been difficult to order. Unfortunately, an implication of perfection and harmony was associated with the climax concept. Clements¹³ himself took the climax and its connotations to be concrete on the coarse scale.

The assumptions about climax were challenged soon after the concept appeared¹⁹⁻²¹. Other factors were found to override climate. Concrete climaxes were rarely found, and ecologists needed to abstract across many sites to document climaxes¹⁵. Finally, with the refinement of paleoecology, climate itself was seen to be unstable in the long term²².

In order to accommodate the variety of supposed climaxes found in the field, a complex vocabulary was developed, including such terms as 'disclimax', 'plagioclimax', 'subclimax', etc., reflecting control of the community by factors other than climate^{21,23}. In the classical system, the exceptional climaxes were still developmentally related to the climatic climax and were thought to be local or anthropogenic. Although other workers ignored¹⁰ or modified²¹ parts that did not fit their field experience, a complete, alternative framework was slow to emerge⁷.

In fairness, our characterization of the climax as an abstraction and an idealization was arrived at in retrospect, and depended on the tests of its assumptions that have accumulated over time. Clements and his early disputants did not

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Box 1. Important characteristics of theory

Abstraction: The identification of certain features of a phenomenon as relevant to the study at hand, often involving generalization from among several instances.

Causal repertoire: The complete array of causes that can affect a phenomenon.

Causal spectrum: The identity and magnitude of the causes actually at work in a particular case.

Hierarchy: The nesting of entities or phenomena within other entities or phenomena. Applied here to the structure of theory, it indicates that general theories are constituted of more specific models, concepts and other components. The high-level aspects of a theory are most widely applicable while the lower-level aspects permit local and precise application.

Idealization: The focus on a phenomenon in isolation from certain factors that might appear in its environment.

Theory of forces: One dealing with a process and the suite of influences determining its dynamics. Force refers to any cause, mechanism or interaction determining system structure or dynamics.

Zero force law: A generalization, applicable within its specified universe, that states the balance of forces resulting in no net change in either the state or the trajectory of an entity or phenomenon.

New conceptual insights

There are two sources of new insights to apply to the concepts of succession and climax: philosophy of science and hierarchy theory (Box 1). Ideas from these areas help us to analyse the changing meaning of succession and climax. In addition, theories of forces, as in classical mechanics or population genetics²⁴, have a structure that is relevant to ecological theories²⁵. Theories of forces allow understanding of dynamic, multicausal processes, and have two relevant properties.

First, theories of forces provide 'causal repertoires', by compiling all possible forces or causes of the dynamics²⁶ (Fig. 1a). Specific studies can draw from the causal repertoires to determine which ones act or dominate in particular sites. For example, in an oldfield community, particular attention must be paid to interactions based on different life history characteristics⁷, dispersal interactions²⁷ and resource availability³. In contrast, recent experiments and surveys have shown that fine-scale disturbance is relatively unimportant in certain

oldfields²⁸. Comprehensive causal repertoires are needed to construct specific explanations in other systems, and to put theoretical models²⁹ into context.

Second, theories of forces explain dynamics by specifying 'zero force' laws, which indicate under what conditions the forces acting on the system produce no net change²⁴. 'No change' refers to either states or trajectories. For example, Newton's first law of motion is a zero force law that indicates under what balance of forces a body will either remain at rest or maintain a particular trajectory. Zero force laws operate only under certain ideal circumstances, and deviation suggests that other circumstances need to be specified to explain or predict the dynamics²⁴. For example, the Hardy-Weinberg principle is a zero force law that specifies the conditions under which gene frequencies will not change from generation to generation. Net genetic change alerts evolutionists to seek forces, such as mutation, drift, selection, etc. Climax supplies a zero force law for vegetation dynamics. It specifies the conditions under which an equilibrium state (climax) would occur.

Although zero force laws are central to theories, complete theories are conceptual systems having empirical content, hypothetical models, integrating frameworks and testable output²⁵. The theory of evolution is the richest and most widely applicable biological theory²⁴, and the law of natural selection is its most general component. To apply this higher-level law to particular cases, specific lower-level models of fitness must be used^{24,1}. The often repeated but powerful couplet in ecology, 'pattern and process', is hierarchical. Pattern exists on one hierarchical level, but the processes causing it reside at least one level lower³⁰.

Vegetation dynamics as a theory of forces

The concept of climax is clearly an ideal, equilibrium point of reference. However, contemporary usage (Box 2) explicitly incorporates non-climatic factors that might generate equilibrium structure and composition of communities^{21,9,31}. For example, soils, herbivores and disturbance regimes are among the

make explicit the role of abstraction and idealization in succession theory. We have also had the benefit of new conceptual insights to apply to the climax and succession concepts.

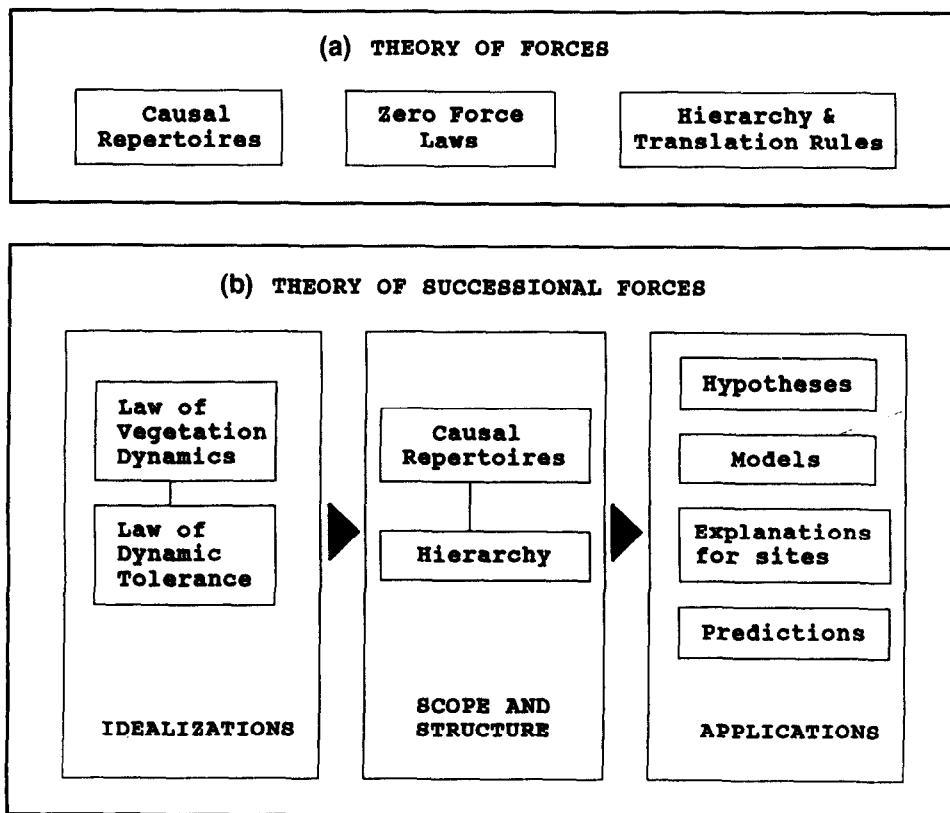


Fig. 1. Schematic representation of (a) some components of general theories of forces and (b) the relationship between idealizations, scope and structure, and applications of the theory of successional forces²⁵. Translation rules are important concepts or models permitting application of the abstractions of the theory to the field or in experiments¹.

factors that can be considered to determine community equilibrium on certain spatial and temporal scales³².

The refinements of the early ideas of succession, and the difficulty of translating the ideal climax to nature, have led to a shift in emphasis. Rather than emphasizing the end point, most contemporary work attempts to understand the patterns of the community dynamics and evaluate their causes^{33,34,2}. An idealized end point is not central to a process-oriented approach, but a scheme that identifies the major causes of vegetation dynamics is required (Box 3). Focusing on a particular site, we can state a 'law of vegetation dynamics' (Law 1, Box 3). (Because this generalization has broad applicability, and is in conditional form, it can be called a law.) This law suggests the scheme that organizes the contemporary, process-oriented approach to community dynamics. It identifies the site, organism availability and organism performance as the major concerns. Site availability, being partially dependent on disturbance and other factors external to the plant community, is not a zero force factor¹⁸, but rather embodies initial conditions. Likewise, the particulars of dispersal are far from ideal, and can be accounted for in stochastic or other models, but cannot serve as the generalizable core of vegetation dynamics theory²⁷. Therefore, differential species performance emerges as the core process, and the remaining two processes, the opening of sites by disturbance and species availability, define the initiation and boundaries in which differential performance can act.

Differential species performance has most often been discussed as differential tolerance to physical and biotic factors^{7,14,1,2}. At the most general level of application, it is a net effect of the different autecologies of species³⁵. It expresses the zero force dynamic of vegetation theory, which can be called the 'law of dynamic tolerance' (Law 2, Box 3). This zero force law is so fundamental that it has underlain, albeit tacitly, all the major work on succession in the last two decades, and has motivated the contemporary process-oriented approach. It was adumbrated by Gleason³⁶ in

1917. The concept of initial floristic composition also embodies sorting among a suite of species present at the start of succession, based on their differential tolerance³⁷. The empirical inputs, needed to predict whether the ideal dynamics based solely on tolerance will appear in a particular site, are the species autecologies, including ecophysiology, architecture, etc.¹ The order in which contrasting autecological types dominate a particular site will depend on whether resources increase or decrease in availability during a particular succession. The specific mechanism of tolerance will depend on the balance among limiting resources through time³.

Evolutionary basis of the zero force relationship

The zero force relationship in community dynamics has an evolutionary basis. Differential tolerance among species is explained by the principle of allocation, which states that an organism partitions its limited assimilated energy among competing functions^{38,39,3}. Although this profound principle has sometimes surfaced in problematic dichotomies such as *r*- versus *K*-selection, the difficulties of those applications do not discredit the basic idea. When patterns of allocation are genetically determined, they can be summarized as strategies. Strategic contrasts between early- and late-successional species appear in many processes, e.g. plasticity, photosynthesis and transpiration, canopy architecture, anti-herbivore defense, propagule banking and dispersal^{38,2,40}. The existence of mutually exclusive allocation strategies^{7,3} are expressed in community dynamics as species individuality.

Species individuality takes two forms: pattern individuality and process individuality⁴¹. Pattern individuality appears if species distributions are statistically independent on a gradient. Whether an individualistic *pattern* appears depends on the degree of discontinuity or steepness of the underlying gradient²¹. The degree of individuality in species pattern may also depend on the methods and parameters used to examine communities along gradients. Species presence/absence versus species cover data, and multivariate versus

Box 2. Important terms in community dynamics

Climax: Generally to be avoided, to prevent tacit acceptance of the incorrect assumptions of classical theory and their attendant connotations of perfection and permanence. Contemporary usage is merely convenient shorthand to recognize the tendency for vegetation to equilibrate with the prevailing environment and disturbance regime.

Sere: An entire successional trajectory.

Species individuality: Can refer either to statistical independence of species distributions along environmental gradients or, more fundamentally, to the fact that species distributions depend on individual ecophysiology, architecture and other life history characteristics, regardless of the pattern of distribution that results.

Succession: Contemporary usage is a near synonym of vegetation dynamics when focus is on the decadal scale. While some degree of directionality is implied, neither monotonic change, progress nor stable termination is necessary.

Vegetation dynamics: Any change in plant communities, including seasonal, successional or post-glacial. Emphasis is on the process rather than the end point.

univariate assessment of pattern, may yield different estimates of species individuality over the same gradient⁴².

Whether species distributions appear to be individualistic or not, the underlying processes generating distribution along environmental

Box 3. Components of a contemporary theory of community dynamics

Law 1: Law of vegetation dynamics: A universal generalization that is applicable to species and assemblages, and that specifies the three major categories of cause influencing vegetation dynamics: If a site becomes available, and if species are differentially available at that site, or if species perform differentially at that site, then vegetation structure or composition will change through time.

Law 2: Law of dynamic tolerance: A universal generalization specifying the cause of vegetation change in isolation from the influence of differential species availability and assuming availability of a suitable site: An assemblage of species having differing tolerance to the abiotic environment and differing capacities for interaction through resource use, will sort through time in order of their tolerance.

Principle of allocation: The generalization that organisms have limited assimilated energy available and therefore that energy allocated to particular structures or functions is unavailable to others. This limit is expressed in the concept of strategy when genetic control exists.

Strategy: A genetically determined pattern of allocation of assimilated resources by an organism. May be considered to have architectural implications, and therefore to summarize the evolved basis of species autecology which is expressed in the law of dynamic tolerance.

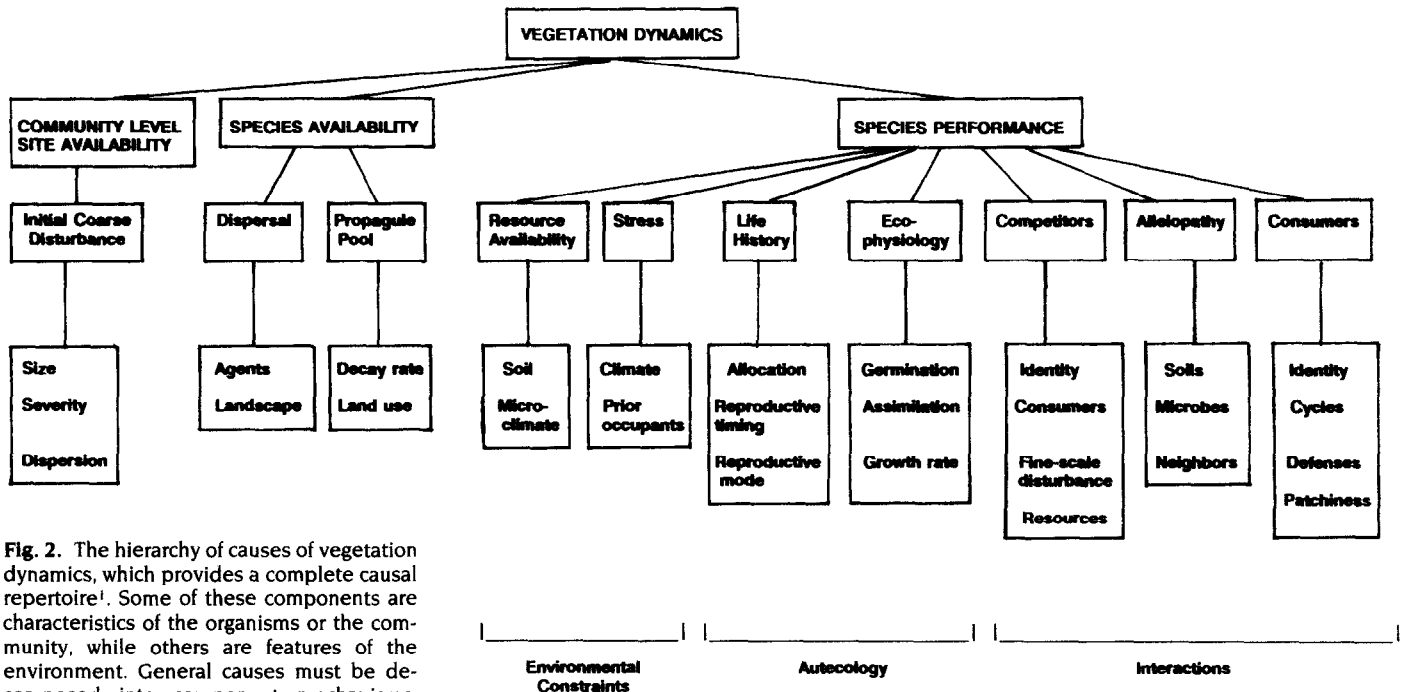


Fig. 2. The hierarchy of causes of vegetation dynamics, which provides a complete causal repertoire¹. Some of these components are characteristics of the organisms or the community, while others are features of the environment. General causes must be decomposed into component mechanisms, constraints or interactions to design experiments and construct models appropriate to specific sites. Site availability, differential species availability and differential species performance can be considered to act in sequence after a catastrophic disturbance, or to act in different patches in a mosaic landscape⁸. In a closed community undergoing gap phase dynamics, only fine-scale disturbance is likely to be relevant. Note that some general causes, such as initial coarse-scale disturbance, are decomposed into characteristics that correlate with environment, rather than into the detailed environmental factors themselves. See Ref. 1 for further details.

gradients are necessarily individualistic⁷. Species must respond to the physical and biotic environments based on their strategies of growth, resource partitioning, architecture, and capacity for phenotypic plasticity. Soil resources and light are common currencies in the sorting out of species along environmental gradients in time and space, and they have been accommodated in many models of vegetation dynamics^{3,4}. Confounding pattern and process individuality may have contributed to the continuing debate about the individualistic nature of the community.

Application of the theory of forces to successions

The central law in vegetation dynamics (Law 1, Box 3) must be complemented by other factors⁴³ to apply it to the field or in specific models (Fig. 1b). Additional layers of mechanistic complexity are required (Fig. 2). A hierarchy of successional causes¹ provides a causal repertoire, and indicates factors that may override or modify differential species tolerance in community dynamics. The law of vegetation dynamics indicates the three realms of processes: site availability, differential species availability, and differential species performance¹. All three processes

must be decomposed into more specific causes⁴³, which include boundary and initial conditions (Fig. 2).

Status of community dynamics research

The law of dynamic tolerance predicts that the patterns of species turnover and dominance in succession should reflect species autecology. There are several striking cases of congruence between community pattern and species performance that have been discovered in the attempt to test this prediction^{2,3,6-8}. However, to extend such tests to other systems, and throughout successional time, contemporary research addresses several problems. First, long-term, quantitative studies of community composition and structure through time are remarkably rare. Indeed, there are very few successions in which resources and other environmental factors have been measured along with population turnover. Combined study of the demographic mechanism and assessment of its environmental basis is a major goal of contemporary succession research. Much more research is needed into the autecologies of mid- and late-successional species.

In cases where species autecologies do not match the community trends, studies are required to de-

termine the factors other than environmental tolerance that control succession. Experimental tests of the relationships of species to resources in the field, and of the potential role of intervention by factors other than resources, are the next logical steps¹ (Fig. 2). Several promising areas include the role of herbivores⁴⁰, the quantitative impact of different modes of dispersal and landscape configurations²⁷, and the significance of fine-scale disturbances and biotically generated debris and litter in community turnover^{7,44}.

Other areas of concern are the determination of ecosystem parameters that are not simply summations of individual metabolism and interactions, and the linkage of aquatic and terrestrial systems through succession⁸. Most contemporary research on succession has focused on the population and community levels, leaving the explicit relationship between population performance and ecosystem function poorly known. Although the works of earlier generations of students of succession are replete with insights and profound qualitative observations, much remains to be quantified and addressed with long-term studies.

Comparative studies are one of the most promising of the tools available to contemporary re-

searchers. Many of the generalizations about succession derive from a very small number of cases, and forest and herbaceous community dynamics are poorly linked. Not only does the empirical basis of these generalizations need to be strengthened, as noted above, but their applicability across systems must be tested. A taxonomy of cases, based on the resource level of the site, disturbance regimes, species longevity, or other major controlling factors², needs to be erected to ensure that generalizations are properly framed. The fundamental role of resources as they relate to the law of dynamic tolerance requires comparative and experimental test.

The contemporary modelling efforts must be expanded. Resource-based models of biomass allocation and trends are indeed growing to include factors such as disturbance³. And the demographic models, so successful in simulating forest succession^{4,29}, need to be expanded to the entire range of secondary successions and to incorporate realistic dispersal and recruitment parameters. We hope, too, that the broad framework reviewed here, centered on differential species performance but showing the place and role of other factors, can be used to help unify the diverse and growing body of information on one of the universal phenomena of the natural world.

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