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Tamm Review

An historical perspective on forest succession and its relevance to ecosystem restoration and conservation practice in North America

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ABSTRACT

Eugene Odum's 1969 paper, *The Strategy of Ecosystem Development*, marks a watershed moment in approaches to the study of succession, ecosystem change caused by discrete disturbances. He argued that succession is unique from other kinds of change with regard to mechanisms (modification of the physical environment by the community), trajectory (orderly, directional and predictable), and endpoint (a stable climax ecosystem in which "maximum biomass and symbiotic function between organisms are maintained per unit energy flow"). Odum also argued that understanding successional change was central to the management of a great variety of environmental challenges. Given the important role of disturbance in these ecosystems, this is particularly true for management aimed at restoration and conservation of forests. Although there was considerable debate among ecologists regarding successional mechanisms, trajectories and endpoints in the decades preceding his exegesis, the views outlined by Odum generally prevailed. These significantly influenced answers to three central restoration and conservation questions during that era. (1) What should we restore and conserve? Climax ecosystems. (2) How should boundaries be set for restoration and conservation areas? This was not an important matter. (3) How should restoration and conservation be accomplished? Because succession would inexorably lead to the ultimate climax goal, forest ecosystems should be protected from disturbance. Over the past five decades, virtually every aspect of succession theory as presented by Odum (1969) has come into question. We now understand that there is no single unique or unifying mechanism for successional change, that successional trajectories are highly varied and rarely deterministic, and that succession has no specific endpoint. Answers to the three restoration and conservation questions have changed accordingly. (1) Restoration and conservation goals should include the full range of variation in species diversity and composition associated with disturbance and the succession that proceeds from it. (2) Pattern, scale and context influence patterns of both disturbance and succession, and preserve design really does matter. (3) Restoration and conservation practice must be tailored to the unique mechanisms and post-disturbance ecological legacies that determine the trajectory and tempo of successional change in each particular ecosystem. The search for a grand unified theory of succession apart from other kinds of ecosystem change is futile. Nevertheless, the change caused by discrete disturbances remains an important matter for concern for restoration and conservation practitioners.

Contents

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1. Introduction

No single paper shaped the research agenda for my generation of ecologists interested in the dynamics of ecosystems more than Eugene Odum's *The Strategy of Ecosystem Development* (Odum, 1969). Since its publication, this paper has been cited over 8000 times, several hundred times in the past year alone. Its influence and durability are certainly due in part to its clear synthesis of the prevailing textbook wisdom on succession as it stood in 1969. Even more, by succinctly articulating his so-called "trends to be expected in ecosystem development" in a single table, Odum put up stationary targets that catalyzed hundreds of research projects on succession, just at a time when interest in this topic was ebbing. Odum defined succession simply as the change that occurred in ecosystems following a disturbance. Although he did not explicitly define disturbance, White and Pickett's (1985) definition, "a disturbance is any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment," is implicit throughout his paper. Odum argued that this process of ecosystem change is quite different from other temporal variations in ecosystem composition and structure, and it is uniquely defined by three features: its mechanisms, trajectory and endpoint. First, succession "results from modification of the physical environment by the community" or, as an earlier generation of ecologists would put it, by 'biotic reaction.' Second, succession is an "orderly process of community development that is reasonably directional and, therefore, predictable." Odum did note that the rate of change and the specific nature of its endpoint were often determined by characteristics of the physical environment. Third, he asserted that succession ultimately "culminates in a stabilized ecosystem in which maximum biomass and symbiotic function between organisms are maintained per unit of available energy flow."

With definite purpose, Odum described this process combining the then controversial language from the applications of game theory to evolution with that of the emerging field of ecosystem science[1]. The strategy of succession was the ever increasing "control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations." In short, succession is the directional process of change propelled by the actions of organisms on their environment leading to maximum homeostatic control (i.e., stability) within the constraints of the physical environment. For Odum, succession was a genuine process in its own right in the same sense as other biological processes such as the development of an organism or the evolution of species, and it could be studied as such.

It is important and often overlooked that Odum dedicated over half of his paper to the relevance of succession theory to the management of Earth's ecosystems. He was certainly correct in his view that what we believe about the mechanisms, trajectory and ultimate endpoint of succession is central to ecosystem management policies and practice. In that regard, I focus attention here on management aimed at the restoration and conservation of wildland forest ecosystems.

Successful restoration and conservation of ecosystems ultimately hinges on the answers to three questions. (1) What should we restore and conserve? By this, I refer to the specific categories of things, as well as the items within those categories, that we deem worthy of our attention. (2) How should we set the boundaries for restoration and conservation areas? Here, I refer to what has come to be known as preserve design—where, how much and in what context should restoration and conservation efforts be dedicated? (3) How, exactly, should restoration and conservation be accomplished? What actions do we need to take to ensure restoration and/or conservation success? Answers to these questions—as evidenced by management practice and policy—have undergone considerable evolution over the past century.

The vast majority of land designated for restoration and conservation management in North America was formally set aside in the century preceding Odum's exegesis. Over that time, policies and practices were pursued with doctrinaire confidence (some would say *hubris*) based on certainty about the answers to the questions above. In the decades since 1969, confidence in those answers has been significantly shaken in large part due to changing views about successional mechanisms, trajectories and endpoints.

In this paper I use a broad brush to paint a general history of ideas about the mechanisms, trajectory and endpoints of succession that preceded Odum's paper, and how those ideas influenced forest restoration and conservation practices. I then consider how our understanding of successional mechanisms, trajectories and endpoints has changed and the implications of those changes for current restoration and conservation practice. Odum's paper deals with successional changes in a variety of ecosystem properties and processes, including productivity and nutrient cycles. I shall focus here on changes in plant species composition and diversity. Odum may have imagined his strategy of ecosystem development as a grand unified theory for successional change following disturbance. With respect to mechanisms, trajectories and endpoints, I shall argue that there is nothing to distinguish succession as unique from other forms of ecosystem change that are typically not considered under the heading of succession (e.g., shifts in species composition due to climate change, invasion of nonnative species, or changes in landscape structure). Thus, there can be no grand theory of succession as such. Nevertheless, this term and its associated concepts remain valuable to restoration and conservation practitioners.

2. The paths to Odum: 1860–1969

In 1860, Henry David Thoreau read his paper to the Massachusetts Middlesex Agricultural Society entitled "The Succession of Forest Trees" in which he considered the consequences of cutting forests of different types—those dominated by pines compared to those dominated by hardwoods—on a New England landscape that was rapidly being reshaped by human activities (Thoreau, 1860). Besides being the first published use of the word "succession" in connection with ecological change, this paper is notable for two other reasons. First, Thoreau's reflections on the importance of species life histories, including seed dispersal and early seedling growth, and his recognition of the importance of landscape effects (i.e., spatial relationships) on forest succession clearly foreshadows key themes in successional research more than a century later. Second, he described succession as a *phenomenon* in which one forest type replaces another rather than an *integrated process*; that is, Thoreau used the word in much the same way one would describe any sequence of events without assigning a single mechanistic explanation or process to it.

The first systematic study of ecosystem change in this country was conducted in the late 19th century by Henry Chandler Cowles. In two monographic papers, Cowles described processes that had shaped changes in the geomorphology and vegetation of the landscape associated with the recession of Lake Michigan in what is today the Indiana Dunes National Seashore (Cowles, 1899, 1901). He called specific attention to the interactions between plant species and their environment as shaping the process of

[1] Although the word "ecosystem" had been coined by Sir Arthur Tansley (1935) over three decades before, ecosystem science was in 1969 still in its adolescence; the IBP (International Biome Project) was gearing up, and the National Science Foundation's Ecosystem Program would not be inaugurated for another decade (Golley, 1993).

succession—he did view it as a distinct process. At any particular place and time, the community of plant species at a place modifies their environment in ways that make it more hospitable for the plant species that succeed them than for themselves. But Cowles also noted that changes in the physical environment outside the control of the biological community such as sediment accretion around streams and lakes or land subsidence also played a role in succession.

Cowles insisted that succession was a complex process characterized by a variety of twists and turns. "Succession is not a straight-line process. Its stages may be slow or rapid, direct or tortuous and often they are retrogressive" (Cowles, 1901). We might identify a most complex and mature climax community in a particular region or situation, but the process of succession did not always lead to that climax. Indeed, it might retrogress or lead to less complex vegetation communities and landforms. Furthermore, the successional process is heavily influenced by changes in the environment within which it occurs. In a phrase that most certainly resonates among ecologists today, Cowles asserted that succession is "a variable approaching a variable rather than a constant" (Cowles, 1911).

Cowles' may have been one of the first systematic studies, but it is Frederic Clements who is credited with the first synthetic *theory* for successional change (Clements, 1916). Clements began his 1916 monograph with an assertion: the study of succession "necessarily rests upon the assumption that the – climax formation (i.e., ecosystem or community) is an organic entity. As an organism the formation arises, grows, matures, and dies." Succession can therefore be simply defined as "the universal process of formation development." Succession is a highly directional and deterministic process constituting, to use Clements' term (and he had an inordinate fondness for terminology), a sere from pioneer to climax communities. Seres, he argued are divisible into distinct seral stages, each recognizable by one or a few dominant plant species. The process might be initiated by a variety of different disturbance types (e.g., primary versus secondary succession) and under a variety of different conditions (e.g., hydrarch vs. xerarch seres), but seres invariably converged over time (perhaps long spans of time) to a single climax community or formation representing the most stable composition of species under the prevailing regional climate – the climatic climax (Clements, 1916, 1928, 1936). Importantly, Clements imagined that, in the absence of human influence, Earth's ecosystems were mostly of the climax type. This was most evident in his views regarding the role of fire in nature such as expressed in an influential paper entitled *Experimental Ecology in the Public Service* (Clements, 1935). "Under primitive conditions, the great climaxes of the globe must have remained essentially intact, since fires from natural causes must have been both relatively infrequent and localized."

Clements had no doubt that succession is a directional process, and almost by definition, dominant species play a central role in that process. Succession is initiated by a discrete disturbance or, in Clements' parlance, nudation which opens a site to immigration and establishment (ecesis) of new species. It is the biotic reactions of dominants – Clements' term for their influences on their environment – that determine the variety of associated species at any stage in the process. Competition among dominants and subdominant species sharpens the boundaries (ecotones) between seral stages, and results in the homogeneous characteristics of each individual stage. Dominance, biotic reaction and competition are the processes that organize communities and the process of change that produces them (these processes are reviewed in detail in Pickett et al., 2009).

Clements assigned great meaning to the origin of words. That "climate" and "climax" shared the same Greek root was for him strong evidence for the role of the former in determining the character of the latter (Clements, 1936). Similarly, the sequence or "succession" of distinct seral stages was a defining characteristic of the process of succession (cf. Thoreau, 1860). This point was important enough for Clements' contemporaries to dub situations where disturbances resulted in the direct replacement of dominant species by themselves as "autosuccessions" and the communities that produced them as "super climaxes" (e.g., Muller, 1940; Whittaker, 1953).

Clements' ideas were favorably received by many in the nascent discipline of ecology (e.g., Phillips, 1934, 1935; Nichols, 1935), but he also had vocal critics. Most notable among this latter group were William S. Cooper, Henry A. Gleason, and Arthur Tansley.

A student of Cowles, Cooper is best known for extensive studies of post-glacial succession at Glacier Bay, Alaska (Cooper, 1923a, 1923b and 1923c). He was most critical of Clements' views about the trajectory and endpoint of succession, particularly the notion of convergent change leading to a single climax community. He observed that succession in boreal forests is often retrogressive; changes in microclimate beneath the supposed climax white spruce forests often encourages their replacement by diminutive black spruce muskegs (Cooper, 1923c). For Cooper, succession is best understood in the analogy of a braided stream undergoing constant change. "Vegetation as we see it today is thus a mere cross section of this complex stream. The same is true of any point in past time. As to the future we may, from the study of present and past, prophesy a little distance onward with some degree of certainty, but more remote progress remains absolutely in the dark" (Cooper, 1926). Cooper defined succession simply as the process of vegetation change, therefore, "all vegetational change must of necessity be successional" and attributable to different mechanisms in different situations.

Henry Gleason was critical of nearly every aspect of Clements' theory. He was among the first ecologists to advocate quantitative sampling (Gleason, 1920), and to recognize the importance of sample size and sampling technique on interpretations of vegetation distribution (Gleason, 1922, 1925). He was very aware of the limitations of inferring temporal change from chronsequences, samples of different localities at a particular point in time (Gleason, 1917, 1926).[2]

Gleason's definition of succession was considerably less inclusive than Coopers' and more similar to Clements'; "succession means the replacement of one association [assemblage of species] by another." However, Gleason and Cooper were in agreement regarding trajectories and mechanisms. "Different causes of succession may act simultaneously but at different rates or in different directions. The actual direction of succession may be likened to a resultant of forces" (Gleason, 1926). In other words, there is no fundamental reason to expect succession to move in any particular direction.

Gleason was especially skeptical of that most basic Clementsian tenet – ecological communities as organisms structured by the biotic reactions of dominant species. He proposed an *individualistic* concept of the plant community as an alternative to Clements' *organismic* theory (Gleason, 1917, 1926, 1939). His argument was simple – the environment (climate, soils, moisture, etc.) varies continuously in both time and space. The great variety of plant species vary in their abilities to grow and compete along such environmental gradients in a continuous fashion. The seeds of various plant species are widely distributed so that every species has some likelihood of arriving at a given place, and each place along the time–space continuum receives the seeds of many species. Thus, species

[2] Clements, too, recognized that studies of succession would ideally involve long-term studies at specific localities. In his 1916 monograph he noted that such studies require "concerted action such as is unknown at present, but there can be little question that continuous investigations of this nature will soon be organized by the great botanical institutions."

ought to be distributed along gradients of time or environment in an individualistic fashion. Clements' homogeneous seral stages are, an illusion caused in part by his focus on the most obvious (dominant) species and on sampling that purposefully avoided situations that did not meet the criterion of homogeneity—which Gleason argued constituted most of the world (Gleason, 1926, 1939). It may be valuable to classify vegetation into specific associations based on dominant species, but such classifications are necessarily arbitrary and utilitarian (i.e., not "natural"). Even when Odum published his 1969 paper, these contrasting world views continued to divide vegetation scientists (Whittaker, 1970).

Sir Arthur Tansley's 1935 paper, *The Use and Abuse of Vegetational Terms and Concepts* is a wonderful philippic, and few peers escaped his barbs. This paper is also famous for coining the word *ecosystem*. Much of the disagreement over the nature of succession hinged, he argued, on the disputants' affections for metaphors or analogies as if they were actually synonymies. "I think Cooper is somewhat obsessed by his image of universal vegetational change as a 'braided stream,' just as Clements and Phillips are obsessed by their 'complex organism'." On the basic question of whether succession constitutes a real process or simply a phenomenon, "I think the concept of succession involves not merely change, but the recognition of a sequence of phases (admittedly continuous from one phase to another) subject to ascertainable laws, otherwise why do we employ the term succession instead of change?" Ecologists had yet to ascertain those laws and to do so would require understanding communities of organisms and their environment as whole systems, "in the sense of physics," that is as *ecosystems.* "Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system." He went on to argue that ecosystems "develop gradually, steadily becoming more highly integrated and more delicately adjusted in equilibrium." "... normal autogenic succession is a progress towards greater integration and stability. The "climax" represents the highest stage of integration and the nearest approach to perfect dynamic equilibrium that can be attained in a system developed under the given conditions and with the available components." Explicit in Tansley's argument is the assumption of the "universal tendency to the evolution of dynamic equilibria." This sounds a great deal like Odum's strategy of ecosystem development.

Clements (1916, 1935) developed a complex classification system for successional trajectories and climaxes that deviated from his classical model, and most such deviations he attributed to human causes. At the most basic level, he differentiated between primary successions that "arise ... upon surfaces for the first time" and "secondary successions that arise on denuded soils." Because soil formation is generally slow, he argued that the rates of change are greatly accelerated in secondary compared to primary succession. Cowles (1911) argued that this distinction "seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and places together such unlike things as human agencies and the subsidence of land."

Cowles reservations notwithstanding, this basic distinction between successional types was and continues to be widely used by ecologists. Based on textbook case studies, Cowles dunes and Cooper's recently glaciated terrains have become the archetypes for primary succession in general. Virtually all textbook treatments of secondary succession showcase the revegetation of abandoned agricultural fields or, simply, old fields. It could be argued that this preoccupation with old fields is an accident of history. Cooper, who was then at University of Minnesota, trained several PhD students, notably Murray F. Buell and Henry J. Oosting, and Frank E. Egler[3], who took positions in ecology at prominent eastern Universities. Sharing the successional interests of their mentor, what these newly minted ecologists found in their new locations were landscapes devastated by nearly two centuries of land use and abuse – landscapes awash in abandoned fields, young stands of pine and beat up hardwoods. It was Oosting and his students who, in quantitative terms, not only fleshed out the details of this process, but elucidated the salient mechanisms underpinning that change. Over just a few years, old fields are dominated by a sequence of herb and grass species; these are eventually replaced by a thicket of pines. Pines subsequently develop in even-aged stands. Because they are unable to reproduce in their own shade, they are ultimately replaced by broad-leaved hardwood trees such as oaks and hickories (Billings, 1938; Oosting, 1942; Oosting and Kramer, 1946; Keever, 1950; Bormann, 1953). This work suggested that the processes driving successional change might be more complex than, as Egler (1954) called it, "relay floristics", that is, one species assemblage preparing the way for the next. Indeed, Keever's classic study of the early stages of this process demonstrated that much change was simply a consequence of differences in species life histories and which species arrived in what sequence (Keever, 1950).

With two notable exceptions, virtually no one writing prior to 1970 was concerned about the possible influence of spatial scale or context – what we now call landscape issues—on the course of succession. The first exception was Thoreau (1860), who noted that the likelihood of a place on his New England landscape succeeding to either pine or hardwood was very much affected by the relative importance of these tree types in the vegetation surrounding that place. The other exception was Alex Watt's 1947 paper *Pattern and Process in the Plant Community*, truly one of the founding papers in the field of landscape ecology. Watt called particular attention to the spatially heterogeneous—"patchy"—nature of successional change in most areas. Patterns of succession he asserted are influenced by the size and arrangement of vegetation patches on the landscape. Most of the species that occur along an entire successional sere following a major disturbance, including pioneers, can also be found in smaller scale disturbances (In Watt's words, the "gap phase") within the climax community. In landscape jargon, Watt was arguing that successional processes are often self-similar over a wide range of spatial scales (Levin, 1992). In Watt's view, ecosystems are undergoing constant change driven by species' life histories and population dynamics. Furthermore, that change is often cyclic. The spatial scale and relative abundance of different patch types may be influenced by major disturbances, but he conjectured that they might come into some sort of equilibrium during the process of succession. It is in this sense that succession might be seen as directional.

3. Land restoration and conservation: 1860–1969

Coinciding with this period of scientific debate and synthesis on the role of disturbance and succession in ecosystems, the foundations of land restoration and conservation policy and practice were being laid and the majority of land in the US where we now apply those policies and practice was formally identified and dedicated. Five events were particularly important.

First, was the establishment of a system of National Parks beginning with Yellowstone in 1872.[4] Although 10 parks were added over the next four decades, the role of either restoration or conservation in that system was not clearly articulated. This changed

[3] Egler completed a masters degree with Cooper and did his doctoral work with Yale ecologist George Nichols. Nevertheless, Cooper's influence is evident in all of his work.

[4] It might be argued that Yosemite was actually the first such park. It was established in 1864, but its stewardship was turned over to the state of California. Unhappy with California's management, the federal government formally reclaimed management of Yosemite as a national park in 1890.

in 1916 (coincidentally the same year as the publication of Clements' monograph on succession) with the passage of the National Park Service Organic Act and the creation of the National Park Service. For the first time, conservation was front and center in the Park Service's mandate. The National Park Service "shall conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." The word "objects" in this mandate was especially important in subsequent conservation practice and policy in the parks (Sellars, 1997).

Second, was passage of the Weeks Act of 1911. The National Forest System and National Forest Service were created by organic acts passed in the previous decade, but their specific mission was the provision of wood and protection of water exclusively in western forests. Recognizing the extent of abused and degraded land, particularly in the East, this act authorized the acquisition of such land. Nearly all national forests east of the Rockies owe their existence to the Weeks Act. Importantly, the mission of the Forest Service was expanded to include both restoration and conservation on its lands. Passed in the year following massive wildfires in Montana and Idaho that claimed 82 lives, the Weeks Act also mandated federal and state cooperation to protect public and private lands from fire (Shands, 1992; Steen, 1976, 1992).

Third, policies to suppress all wildfires on public lands were codified in 1930 when the National Forest Service promulgated its so-called 10 AM rule for fire management – "the aim for any wildland fire shall be to obtain control by 10 AM on the day after it is first reported." This mandate was subsequently applied to all federal agencies involved in land management. Up to about 1940, the actual impact of the 10 AM policy on the majority of lands was probably minimal, except in areas that were reasonably accessible on foot or by vehicle. This changed around 1940 with the advent of smoke chasing and smoke jumping (Pyne, 1982; Christensen, 2009). The policy of complete fire suppression was emblematic of general beliefs about succession and the impacts of human management on successional change. Furthermore, much restoration management and policy is focused on changes in American forests caused or thought to be caused by this policy.

Fourth, was the establishment in 1951 of The Nature Conservancy dedicated to conservation of threatened species and ecosystems on lands, regardless of ownership (Birchard, 2005). Important in its own right, this event also catalyzed establishment numerous land conservancies dedicated to the acquisition, restoration and conservation of land across the country. Conservancy decisions regarding land acquisition as well as subsequent land management were and continue to be heavily influenced by prevailing wisdom regarding the role of disturbance and the nature of successional change.

Fifth, was the passage in 1964 of the Wilderness Act, arguably the first piece of legislation focused exclusively on the preservation of nature for its own sake. This legislation created the Wilderness Preservation System representing a new category of federal land, wilderness, in which "*the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain.*" Operationally, untrammeled meant no logging or mining, and only limited road construction. It is fair to say that most of us view "preservation of nature" as synonymous with this notion of wilderness. Lands in National Parks, National Forests, US Fish and Wildlife Refuges, and Bureau of Land Management Conservation Areas can receive formal wilderness designation by congressional action only. As of 2013, 109,512,000 acres, about 5% of US land area, are included in the US Wilderness Preservation System.

In 1969, there was general consensus with regards to my three general restoration/conservation questions, and that consensus was in many ways shaped by agreement about the mechanisms, trajectories and end points of successional change described in Odum's paper.

What should we restore and conserve? The clear answer for most lands was climax ecosystems. For the National Park Service, this was most obvious in its interpretation of the natural objects in its organic act mandate. In the words of the 1963 Advisory Board on Wildlife Management in the National Parks, the Parks should represent "vignettes of primitive America", interpreted to mean America absent of human influence (Leopold et al., 1963). This view is echoed in the 1964 Wilderness Act's definition of wilderness. For organizations such as The Nature Conservancy during this period, the emphasis on climax ecosystems was obvious in the definition of so-called "conservation elements" which boiled down to either rare species or iconic biological communities—"last great places". Conservation during this era was seen by nearly all to be equivalent to museum curation with a focus on the preservation of "objects" rather than the conservation of processes upon which those objects depend. The restoration goals for the Forest Service were most often focused on specific seral stages such as even-aged forests but still emphasized endpoints such as is captured in the goal to restore a "desired future state."

How should we set boundaries for restoration and conservation areas? Actions indicate that this was for the most part not an issue. Successional theory gave little or no consideration to possible role of spatial scale or context. Although Alex Watt's work suggested such a role, it also suggested that most of the biodiversity associated with successional change existed in relatively small patches within the climax community matrix. Thus, decisions regarding the size and boundaries of national parks, national forests and designated wilderness were taken as matters of economic and political expediency, with little or no concern about the implications for restoration and conservation.

How, exactly, should restoration and conservation be accomplished? Prevailing successional theory argued that, in the absence of disturbance, natural succession would inevitably lead to that ultimate climax goal. Thus, the best strategy for conservation was protection from disturbance. There was, however, debate among land managers on this issue perhaps best exemplified in the so-called "light-burning controversy". Aldo Leopold, then a Forest Service employee, cited evidence for the importance of frequent surface fires in arid forests of the Four Corners region in presettlement times and of the negative consequences of the loss of fire in these forests owing to cattle grazing and active fire suppression. With characteristic prescience, he argued that light burning was needed to restore healthy forest conditions (Leopold, 1924). Opposition to this position was emphatic and came from many quarters. For example, Leopold's boss, Forest Service Chief William B. Greeley, called the concept of light burning a fallacy and pejoratively dubbed it "Piute Forestry" (Greeley, 1920). Protection from burning prevailed.

4. The paths away from Odum: 1970 to the present

Perhaps the best measure of the general acceptance of Odum's classical successional model was the near absence of comment in the years immediately following its publication. Aside from a quibble over productivity differences during aquatic and terrestrial successions (McIntosh, 1969), there were no follow up papers or critical letters to the editor in the pages of *Science* magazine. It was not until the 1973 publication of a paper in the Journal of the Arnold Arboretum by William Drury and Ian Nisbett that serious questions regarding Odum's presentation were raised. They attacked Odum's 24 trends to be expected in a sequential and methodical fashion, and argued that data to support some of Odum's sweeping assertions were either tissue thin, contrary or nonexistent. In a postscript at the end of their paper they cite the hostile comments of many of the reviewers of their paper as evidence that these classical views of succession were still alive and well in the minds of many, if not most, ecologists. Surely Drury and Nisbett must have taken some comfort in the avalanche research and criticism of classical theory over the next several decades, much of it catalyzed by their paper.

Why was it that ecologists held so tightly to ideas supported at best by a thin tissue of evidence? And, why all of a sudden were these ideas challenged on so many fronts? There are probably several answers to the first question, but I think the most important is simply this: the Clements–Odum model portrayed natural change as most of us would prefer changes of all kinds to be—directional, with incremental improvement leading inexorably to that best (i.e., most stable) of all possible worlds. With regard to the second question, two things are perhaps most important. First, the field of ecology was evolving with an ever more critical eye on methodology and increased emphasis on quantitative sampling and concerns about sampling bias. The potential flaws in the chronosequence approach for understanding both the nature and mechanisms of the process were becoming particularly obvious (Drury and Nisbet, 1973; Christensen and Peet, 1981; Foster and Tilman, 2000; Walker et al., 2010). Second, ecological studies begun earlier in the 20th century now provided data sets that allowed ecologists of my generation to undertake longitudinal studies; that is, to actually examine successional changes at particular places over meaningful spans of time. Since Drury and Nisbett's paper, ecologists have challenged every one of Odum's assertions about the defining characteristics—mechanism, trajectory and endpoint—of succession. These challenges are summarized below.

Mechanism. *There is no unique or unifying mechanism for successional change*. Connell and Slatyer (1977) suggested that successional change could result from one or all of three alternative mechanisms. (1) Facilitation refers to situations in which a species or group of species modifies its environment so as to facilitate the invasion of other species. (2) Inhibition refers to situations in which early invading species usurp resources and prevent or limit the invasion of other species; succession proceeds only when populations of those early invaders decline. Tilman's (1988) suggestion that species replacement during succession results from competitive effects on the ratio of potentially limiting resources is a specific example of this mechanism. (3) Tolerance might be viewed as the null model in which succession proceeds largely as a consequence of the dispersal abilities, life histories and longevities of various species. In many ecosystems, all three of these mechanisms are important simultaneously. This is certainly the case with regard to old field succession (e.g., Keever 1950, 1983; Pickett et al., 1987; Walker and Chapin, 1987; Zanini et al., 2006; Peet et al., 2014). Furthermore, distinguishing among these mechanisms can be very complicated (Pickett et al., 1987). For example inhibition is generally assumed to result from competition by established species. But such competition also influences competition among potential invading species, facilitating the success of some species relative to others (Peet et al., 2014). By providing habitat and food for birds and mammals, early invading trees facilitate the dispersal and establishment of a variety of other tree species, while competitively limiting their growth (e.g., McDonnell and Stiles, 1983). None of these mechanisms is unique to succession (defined as change deriving from discrete disturbance events) as compared to other forms of ecosystem change.

The concept of ecological legacies represents another thread in the discussion of successional mechanisms. The historic distinction between primary and secondary succession was based on the presence or absence of soil following disturbance; rates of change were much faster on sites with soil. But, as Cowles (1911) argued, this binary distinction between primary and secondary succession is overly simplistic. Successional change is initiated along complex gradients of disturbance conditions—from scratch in the case of succession on newly exposed rock to old fields where succession begins on soil stripped of its seed bank and fertile horizons, to clear cuts and postfire situations where seed banks and soil horizons are left intact, to less severe disturbances of forest canopies in the case of plant disease or ice damage. Although farmland abandonment has declined considerably on the landscapes where old field succession was originally studied, it has accelerated exponentially worldwide (Cramer et al., 2008), and remains a something of a type specimen or model for successional change in general. Nevertheless, old fields usually retain few ecological legacies, such as seed banks and soil organic matter and nutrient capital, and they often represent an extreme situation compared to most other secondary disturbance types (e.g., change following fire or logging). We now understand that ecological legacies—such as soils nutrients, woody debris, seed banks and residual vegetative growth—play a critical role in the patterns and rates of change along gradients of disturbance intensity (Franklin et al., 2000; Foster et al., 2003; Cramer et al., 2008; Swanson et al., 2011).

Trajectory. *Successional trajectories are highly varied*. Indeed, Walker and del Moral (2003); (Walker et al., 2010) describe 9 "common" trajectories of successional development. As discussed earlier, ecologists have long suggested that succession is not always directional and or always deterministic in the sense of ever increasing stability (Cowles (1901, 1911) was emphatic about this). Cooper's braided stream metaphor might imply directionality of a sort, but hardly deterministic. Gleason explicitly rejected both directionality and determinism in his assertion that succession is the result of multiple forces. From his studies of heathlands and beech forests, Watt (1947) suggested that successional change following disturbance in many (if not all) ecosystems proceeds first through a regenerative phase characterized by rapid growth followed by a degenerative phase as individual plants senesce. Successional retrogression continues to be an important theme, particularly with regard to changes in nutrient cycles and the relative availability of nitrogen and phosphorus over very long spans of time (e.g., Vitousek, 2004; Wardle et al., 2004; Walker and Reddell, 2007; Peltzer et al., 2010).

Endpoint. *There is not one*. Nearly all considerations of trajectory are inevitably tied to discussion of exactly where (or not) succession is headed. Convergence, for example, has been a prominent theme in considerations of successional trajectory, but convergence on what? For Tansley and Odum, that *what* is stability. However, many studies suggest that, as succession proceeds, many ecosystems actually become less stable and more prone to disturbances such as fire, wind and ice, generating cycles of change. Such change cycles have since been documented in a wide variety of ecosystems visited by different types of disturbance. These include the pattern of "wave regeneration" in fir forests of the northeastern U.S. maintained by disturbance from wind and ice (Sprugel, 1976; Sprugel and Bormann, 1981), and the millennial thaw-lake cycle in the wet tundra of Alaska's North Slope (Billings and Peterson, 1980). Indeed, Odum was well aware of such cyclic patterns of change and dubbed them "pulse stable". Calling attention to the homeostatic relationship between ecosystem change and the disturbances that stabilized such cycles, he argued that cyclic succession was an exception that proved the rule. That is, as ecosystems develop following disturbance, they undergo change that makes them more prone to disturbance. In this view, disturbance cannot be seen as an externality occurring independent of the status of an ecosystem. To a greater or lesser extent it is an integral part of the process of succession.

This notion of cyclic change has been especially important with regard to the role of fire in a wide variety of ecosystems. By the 1950s and 1960s, the phrase "fire cycle" was in wide use in the forest and range management literature (e.g., Weaver, 1951; Biswell, 1961; Cooper, 1960; Hanes, 1971; Heinselman, 1973). Immediately following fire in southern California chaparral, for example, communities are very diverse and productive, but relatively nonflammable. As succession proceeds, diversity and productivity decline, and flammable live and dead fuels accumulate. This continuously increases the probability of the next fire which initiates the next cycle of change (Christensen and Muller, 1975). Ecologists (including myself) studying fire during this period were particularly taken with the notion of pulse stability and the fire cycle, focusing much of our attention on the estimation of fire return intervals and the historic range of variation in those intervals through time (Kilgore, 1973; Christensen, 1981). Mutch (1970) went so far as to suggest that natural selection had favored the evolution of flammability in species in fire-prone ecosystems to ensure maintenance of fire cycles upon which they depended for successful reproduction.

Although successional change is a driver for repeated episodes of disturbance in a great many ecosystems, lake sediment and tree ring data demonstrate that the historic range of variation in such episodes has been very large historically, and that few ecosystems or landscapes experience regular pulse stable cycles of change (e.g., Swetnam, 1993; Clark and Royall, 1996; Swetnam and Betancourt, 1998; Anderson et al., 2008; Jacobs and Whitlock, 2008; Whitlock et al., 2010). Indeed, Whitlock et al. (2010) suggest that the phrase "fire cycle" be abandoned altogether. Research in a variety of ecosystems suggests that variability in fire regimes is the norm and that it contributes significantly to the biological diversity of landscapes at a variety of spatial scales (e.g., Turner et al., 1993; Turner and Romme, 1994; Turner, 2005; Baker, 2009).

The notion of convergence is complicated even where succession is thought to be generally directional. For example, Christensen and Peet's (1981, 1984) study of old field succession in over 200 forest stands in the North Carolina Piedmont revealed that understory plant diversity and species composition in pine forests do not converge in a linear fashion with increasing stand age toward the putative hardwood climax. Instead, it is intermediate aged pine understories that most resemble their hardwood counterparts. They show that this more complicated trajectory is the result of demographic changes associated with the development of the even-aged pine stands and their eventual transition to uneven-aged forests in which gap-phase processes are important (Peet and Christensen, 1980; Christensen and Peet, 1984; Peet et al., 2014).

We live in a world of accelerating change, including changes in climate, landscape patterns and biogeographic distributions. Succession is occurring in the context of that change, a "variable approaching a variable," and discerning successional change proceeds from discrete disturbances such as a fire or an abandoned field from other sorts of change has been the focus of much recent work. For example, old-field succession is generally thought to account for the vast majority of variation in species composition and diversity in forests on the piedmont of the southeastern U.S., but much of the change in these forests over the past four decades is unrelated to such succession. Peet and Christensen's permanent plots were resampled 23 and 35 years after their establishment in 1977. There was considerable change in diversity and composition in all of these stands that was consistent across stand ages. Most important, this change did not correspond in any way to successional changes predicted based on the 1977 samples (Taverna et al., 2005; Schwartz, 2007; Israel, 2012; Peet et al., 2014). In other words, regardless of successional status, the majority of the change in species composition and diversity on this landscape over the past three decades relatively little to do with old-field succession! Rather, it appears to have been driven by a combination of factors, including invasion of non-native species, greatly increased deer browsing, historical exclusion of fire (e.g., mesophication, Nowacki and Abrams, 2008), recent hurricanes, and climate change (Peet et al., 2014).

These results notwithstanding, natural and human-caused disturbances are ubiquitous, and they remain important agents of change on many landscapes. In fact, many impacts of changes in climate, immigration of non-native species and changes in landscape structure are likely to be most obvious in earliest stages of succession (dominated by early life history processes such as seed germination and seedling establishment as opposed to long-established herbs, shrubs and trees) following such disturbances. With respect to climate change, for example, the impacts of even significant increases in temperature or evapotranspiration on late successional or mature forests may be small and difficult to detect, but they are likely to be quite apparent in the patterns of change in early successional communities. For example, recent studies suggest that rates change in early stages of secondary succession in many temperate forest ecosystems are increasing as a consequence of changes in climate, landscape change and patterns of species invasion (Wright and Fridley, 2010; Fridley and Wright, 2012).

Recent work on multiple stable states, regime shifts and change thresholds focuses on post-disturbance change trajectories in shifting environmental contexts (e.g., Gunderson and Holling, 2002; Scheffer and Carpenter, 2003; Folke et al., 2004; Schröder et al., 2005; Brock and Carpenter, 2010). Ecosystems are often depicted as marbles rolling about on a complex terrain representing the wide range of different environmental conditions and ecosystem structures. Movement on this terrain represents change, some of which is related to succession following disturbance. Mountains and valleys represent unstable and stable configurations of environment and species composition. Non-successional changes in such factors as climate, the abundance of non-native species, or the connectivity of habitat patches constantly restructure this terrain, resulting in new regimes of stability and instability. The relationship between such regime changes to disturbance and succession is illustrated with regard to global changes of three quite different kinds. In the Great Basin the widespread invasion of non-native cheat grass (*Bromus tectorum*) has increased the amount of very flammable fuel in sagebrush ecosystems. As a result, intense and frequent fires have virtually eliminated sage brush in many locations; the now-abundant cheat grass ensures the continuation of this new disturbance regime (e.g., Billings, 1990; D'Antonio and Vitousek, 1992; Valiant et al., 2007). Sea level rise in eastern North Carolina threatens to shift coastal vegetation zones such as between coastal marsh and adjacent pine forest. High evapotranspiration rates in the forest stabilize this zonation until a disturbance such as logging or fire, after which forest is no longer able to establish (Poulter et al., 2008). Warming climate in the Arctic is creating conditions favorable to large fires in boreal forest and tundra. This combination of climate change and fire is not only setting in motion new patterns of successional change, it is increasing the net flux of greenhouse gases from these ecosystems and, thus increasing warming (Kasischke et al., 1995; Kasischke and Turetsky, 2006; Field et al., 2007; Mack et al., 2011).

Criticism of classical models of succession over the past several decades returned to Watt's (1947) assertions about the importance of spatial and contextual relationships in successional change. Levin and Paine's (1974) study of the dynamics of rocky intertidal communities catalyzed much of the work that followed. They showed that these dynamic landscapes are composed of a mosaic patches populated by unique communities of organisms and representing different histories of disturbance and trajectories of change. Over the entire landscape, the composition or proportion of different patch types may remain about the same, but individual patches are constantly changing. Furthermore, patch size and, especially, the identity of adjacent patches play a significant role in the dynamics of each individual patch. This patch mosaic model has been shown to be relevant for a great variety of terrestrial landscapes. Successional change within patches on such landscapes is neither linear nor perfectly cyclic; instead it is often characterized by multidirectional change with multiple, relatively stable community types. Studies on a variety of landscapes show that change is influenced by the nature of surrounding patches which not only affect the immigration of species, but also the spread of disturbances like fire or human land use from one patch to another (e.g., Urban et al., 1987; Turner, 1989, 2005; Turner et al., 1998).

Pickett and White, 1985 suggested a demography-based framework for disturbance and patch dynamics on landscapes. The course of change within any particular patch is influenced by within patch legacies and processes such as competition (e.g., Peet and Christensen, 1987), patch size (e.g., Phillips and Shure, 1990; Turner et al., 1997), the character of surrounding patches (e.g., Turner, 2005), changes in disturbance severity and patterns of spread (disturbance regimes, e.g., Gardner et al., 1992) and changes in the overall environmental context (Scheffer and Carpenter, 2003; Brock and Carpenter, 2010). The concept of minimum dynamic area–the minimum area of a landscape necessary to include not only all of the pieces of its mosaic, but also to stabilize its dynamics through time—has particular importance to the restoration and conservation of ecosystems in a world of change.

5. Restoration and conservation implications

The evolution in our understanding of the mechanisms, trajectories and endpoints of succession has had significant consequences for ecosystem restoration and conservation practice which are discussed here with respect to the three questions posed earlier.

What should we restore and conserve? *Restoration and conservation goals and strategies should include the full range of variation in species diversity and composition associated with disturbance and the succession that proceeds from it.* At scales from forest gaps to large landscape patches, much biodiversity is associated with disturbance and the succession that proceeds from it (e.g., Turner, 2005; Swanson et al., 2011). Ecosystem restoration and conservation cannot be viewed as the curation of "natural and historic objects" in some sort of "tree museum." Instead, we must define goals in terms of the dynamics of landscapes and the disturbances and the processes that produce those dynamics.

Restoration and conservation goals are often articulated in terms of "desired future condition" when they ought to be focused on "desired future change." Restoration "targets" should be viewed as moving targets. This fixation on condition rather than change was reflected in Forest Service Chief William B. Greeley's advocacy of the 10 AM rule to make U.S. forests "as fireproof as possible" (Greeley, 1920). He could not of course have understood that fire suppression would encourage change that would have quite the opposite effect in many western forests. But, the focus on future condition rather than change continues. Under the aegis of the 2003 Healthy Forest Restoration Act, federal land management agencies have undertaken ambitious thinning and fuel reduction programs to "return our forests and rangelands to a healthier [i.e., less fire prone] state." However, little attention is being paid to the inevitable change that such fuel treatments are now facilitating (Christensen, 2009).

Unfortunately, this reorientation complicates rather than simplifies our decisions about appropriate restoration and conservation goals. In a more deterministic world and with more confidence about our understanding of the interactions between successional change and other change agents, we could perhaps rely on current and historical patterns to frame such goals. In such a world we could set goals in terms of historic disturbance regimes or historic ranges of variation in such regimes and rely on succession to produce appropriate outcomes. Although improved knowledge of the historic range of variation in disturbance and succession should inform our conservation goals, we cannot assume that restoring past processes will result in restoration or conservation success (Parsons et al., 1999). Managers now acknowledge the existence and importance of change thresholds, but they have few tools to quantitatively define such thresholds (Yung et al., 2010).

In any case, goals cannot be stated exclusively in terms of the restoration and conservation practices we employ. Our interest should not be in restoring or preserving fire or other disturbances per se; rather we should focus on the biodiversity and key ecosystem processes that depend on these disturbances. Successful management depends on clear articulation of specific goals for biodiversity and ecosystem processes.

How should we set the boundaries for restoration and conservation areas? *Pattern, scale and context influence both disturbance and succession, and preserve design really does matter.* In this regard, managers should worry as much about the territories they do not restore or conserve as they do about the territory explicitly targeted for such management. In an ideal world, our attention would be drawn to defining minimum dynamic areas (MDA, Pickett and White, 1985) that would capture and stabilize all of the dynamics we wished to restore or conserve. We have repeatedly learned over the past several decades that most of the landscapes that we have set aside for restoration and conservation are far smaller than their MDAs, even under presettlement disturbance regimes. The frequency and size of many disturbances, including fire and hurricanes, appear to be increasing in association with other human-caused change, and this is increasing MDAs in many places. Successful restoration and conservation strategies must be developed with the explicit understanding that managed territories are almost always smaller than the MDA.

How, exactly, should restoration and conservation be accomplished? *Restoration and conservation policy and practice must be tailored to unique mechanisms and post-disturbance ecological legacies that determine the trajectory and tempo of successional change in each particular ecosystem.* A half century ago, restoration and conservation management in national parks, national forests and Nature Conservancy preserves was object-oriented, and centered on protection from disturbance; restoring and maintaining natural disturbance regimes and key ecosystem processes are now the highest priorities (e.g., Birchard, 2005; Christensen, 2005, 2009; Keeley et al., 2009; Aplet and Cole, 2010). Whether disturbances are in some sense natural (such as with fire) or human caused (such as with logging), managers now pay as much attention to what is left behind—ecological legacies—as they do to what the disturbance removes (e.g., Foster et al., 2003; Swanson et al., 2011). Understanding the potential role of competition from early invading species (i.e., inhibition), managers can intervene to accelerate successional change to restore ecosystems (e.g., Cramer et al., 2008). Recognizing that successional change is more stochastic than deterministic, and that it is occurring against a welter of global changes in climate, landscape structure and species biogeography, managers must acknowledge that policies and practices intended to simulate natural disturbance regimes or encourage "natural" processes of successional change can have undesirable consequences such as the loss of biodiversity or the invasion of non-native species (Chapin et al., 2010; Yung et al., 2010). More than ever, restoration and conservation management requires humility, rather than hubris. The complexity of ecosystem change, uncertainty about the future and our limited understanding of all of the consequences of our actions demand that management be adaptive.

6. Succession is dead: long live succession!

Is succession worthy of special designation apart from change in general? Pickett et al. (2009), for example, consider succession to be synonymous with "change in either species composition or the three dimensional structure of a plant community or both." Because of the history of more restrictive definitions, they suggest that the phrase "vegetation dynamics" be used in place of succession. However, given the widely recognized importance of discrete natural and human-caused disturbances in virtually all of Earth's ecosystems, the process of change that derives from them needs to be understood and, yes, specifically named. That name is *succession.* This is especially important in the realms of forest restoration and conservation. Intentionally and unintentionally, restoration and conservation management has historically influenced the nature, timing and severity of such disturbances. For decades, strategies were employed to protect forests from disturbance that, in the end, increased the likelihood and severity of those disturbances in some places and diminished them in others. Today, in the name of restoration and conservation, we strive to reintroduce and/or maintain those disturbances or their surrogates such as logging or thinning. In order to understand and evaluate the efficacy of these strategies relative to management goals, it has been and continues to be important to be able to measure the change—succession—they cause relative to changes caused by other agents.

I and other ecologists of my generation began our careers with the certainty of simple models of succession that validated strongly held beliefs about the way the world ought to be. To paraphrase Mark Twain, often, it is not what we do not know that gets us into trouble, it is what we know for sure that just ain't so. As we have learned more about succession in different places, initiated by different disturbances, and occurring in the context of other kinds of change, simple, deterministic, directional and widely applicable models of succession have been replaced by much more complex, stochastic, and situation-specific constructs. The mechanisms of succession following disturbance vary widely, but there is general agreement that they do not differ from mechanisms of change brought about by other agents such as shifts in climate, invasive species and landscape fragmentation. Furthermore, discrete disturbances can produce myriad change trajectories that defy such simple classifications as directional or cyclic. Although it may happen in some situations, there is certainly no evidence that post-disturbance succession invariably progresses towards "greater integration and stability" (Tansley, 1935) or "ever increasing control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations." Absent of unique processes or sets of processes, searching for a grand unified theory or strategy of succession such as proposed by Clements and Odum is futile. These are also important lessons for those concerned with the restoration and conservation of forests. Succession does not invariably trend toward increasing stability—often the opposite is true. Successful management requires recognition of the complexity and unique character of succession in each ecosystem.

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