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Introduction and background

Succession, ecosystem recovery, and global change

Forces of nature lead to innumerable local, regional, and sometimes global changes in plant community patterns. Even early humans undoubtedly observed vegetational change and may have used that change to their advantage. They saw the power of natural forces to change vegetation and used them, especially fire, to 'manage' ecosystems for their own needs. The exchange of materials between the atmosphere, the biosphere, and the ocean was largely controlled by natural events in the past but is currently being greatly modified through increased human activities (Fig. 1.1). Irrespective of the causes and the intensity of change, ecosystems are often naturally able to recover most of their attributes through natural succession. They can also be repaired through human intervention such as land reclamation. Because of the recent enormous rise in the human population and its per capita consumption of natural resources (Fig. 1.2), the earth is becoming increasingly occupied by successional ecosystems in various stages of recovery. With the recent heightened interest in the fate of the biosphere (e.g. Lubchenco *et al.* 1991, Woodwell and MacKenzie 1995), the emphasis on sustainable development worldwide and concern about the possible consequences of global climate change (Houghton *et al.* 1990, 1992, Vitousek 1994), the study of succession and ecosystem recovery takes on an added urgency. Successional theory will play a major role in ecosystem preservation, management, rehabilitation, and restoration.

Broadly viewed, succession is the recovery process of vegetation following any disturbance. Successional studies have focused on repeatedly observable transitions in community composition following either the exposure of new substratum (usually referred to as primary succession) or the disruption of existing communities by various agents of disturbance (secondary succession).

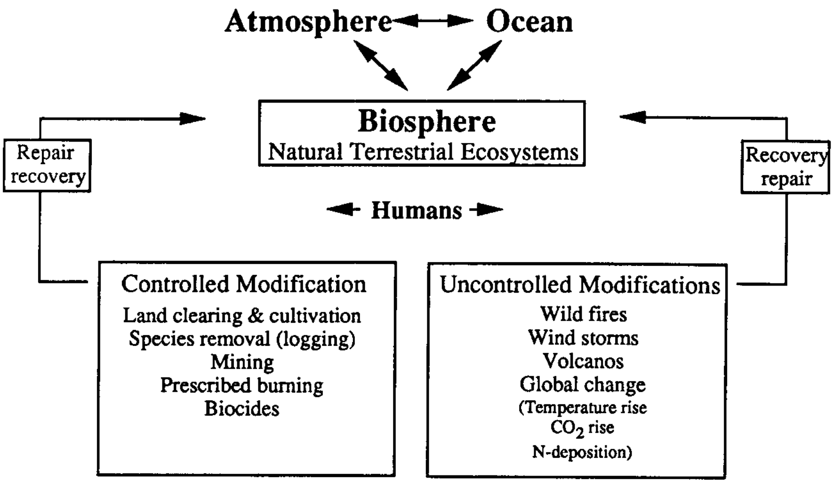

Fig. 1.1. The impacts of humans on atmosphere–biosphere–ocean interactions. Disturbance and recovery through succession.

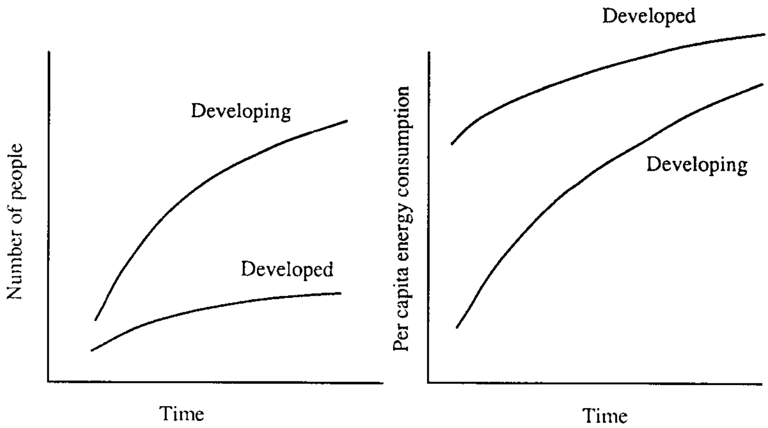

Fig. 1.2. Projected increase in human population and its impact on the environment through consumption of natural resources, in 'developed' and 'developing' countries.

Classically, succession was viewed as a subset of many different types of ecosystem recovery, from new colonizers filling in small vegetation gaps to regeneration during very large climatic changes such as deglaciation or global warming.

Historical perspective

We do not know if scholars of older cultures in China, the Middle East, and the Americas formally considered community change, but we do know that Western philosophers and naturalists from Theoprastus to Thoreau thought and wrote about vegetational change. The study of plant community dynamics in Western science seems to have first appeared in the formal sense in the nineteenth century, in A. Kerner's description of the vegetation change in the Danube River Basin. In the United States, H. Cowles pioneered the study of 'primary succession' on newly exposed habitats with his classic work on zonation of vegetation of the sand dunes of Lake Michigan. However, F. E. Clements is better remembered as the father of successional theory. Clements derived much of his intellectual framework form German phytogeography, and his research experiences were restricted largely to the stable communities of the American midwest. His views were also influenced by the then predominant paradigm in geology: peneplaination, or the long term erosion of mountains to plains. As a result, he viewed plant communities as complex quasi-organisms and succession as the progressive development of the quasi-organism to a predetermined climax.

With only a few exceptions (e.g. H. A. Gleason), early ecologists considered succession a community-level phenomenon. They sought to identify the 'stages' of succession, the sequence of their appearance, the duration of their persistence, and their orderly progression to uniform and predictable endpoints or 'climaxes.' In contrast, more recent views of succession claim that succession is a multidirectional, probabilistic process which can have more than one endpoint (review in Pickett *et al.* 1987). Views about community organization, while not clearly allied with succession, are inextricably linked to successional theory. The apparent disjunction of community organization theory from successional theory stems from the fact that the former has been the domain of animal ecologists and the latter the domain of plant ecologists, and for a long time the two have been developing independently of each other. The debate over the Clementsian and Gleasonian views about the nature of the plant community is legendary (see McIntosh 1980) and it continues unabated today. There is probably no subject in plant ecology that has been so extensively treated. Unfortunately, many plant ecologists have spent much of their energy and time debating these views about communities, and have rarely paid the appropriate attention to the scale at which the issues are being considered (see Allen and Starr 1982, O'Neill *et al.* 1986).

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Scale

Appropriate consideration of scale clarifies much of the debate and resolves what may appear to be irreconcilable views. That there are physiognomically predictable communities on a regional scale cannot be denied. For example, coniferous forests dominate a huge area in the United States and Canada and stretch across Europe and much of Siberia, and temperate deciduous forest dominates most of the eastern United States. However, patchiness can be detected at several finer scales within these regions. Various combinations of species are present in each patch and different successional trajectories are possible. Moreover, individuals in a stand do not behave independently from their neighbors; they interact with each other through the shared or contested resources of the habitat. They are part of each other's environment. Although plant species have distinct genetic make-ups that influence their physiologies and distributions (Gleason 1926), individuals do interact with neighbors and can therefore modify each other's activities and distributions. Because of overlap in requirements for growth and reproduction, species can occur together in combinations as recognizable communities (Weaver and Clements 1938). Confusion between the 'stand' (which in plant ecology is a tangible unit of the landscape that can be measured and manipulated) and the 'community' (which is an abstraction obtained from observing and measuring several stands; Oosting 1956) has caused additional confusion in successional theory and plant community ecology. A critical appreciation of the importance of scale can clarify some fuzzy concepts in plant community ecology. This clarification can go a long way in successfully embedding successional studies into functional ecology, which could explain extant communities, their past, and their evolutionary pathways.

The consideration of successional processes at the ecosystem level, initially motivated by the writings of Ramon Margalef, began with the publication of E. P. Odum's paper, 'Strategy of Ecosystem Development' (1969). Based on studies of succession in oldfields in the southeastern United States, Odum proposed a list of attributes of successional populations and ecosystems. This seminal paper, more than any other, has stimulated and motivated much of the research in ecosystem dynamics. Disturbance ecology and the study of ecosystem recovery during succession have moved to positions of prominence, particularly with the publication of the work of F. H. Bormann, G. E. Likens and their associates on the Hubbard Brook watershed in the northeastern United States (see Bormann and Likens 1979). Controls on primary productivity, nutrient dynamics, and transport

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across system boundaries have become subjects of study in many systems worldwide. The former International Biological Program (IBP) and the more recent Long Term Ecological Research (LTER) network are integrated activities for, and large scale expressions of interest in, understanding ecosystem dynamics.

Because the plant's environment is ever-changing on a number of time scales, there is little in the ecology of plants that is unrelated to succession in the broad sense. Therefore, successional theory can form the basis for much of the life history evolution, population dynamics, competitive interactions, nutrient dynamics, and community organization of plants. Practical issues in ecology, such as restoration of damaged ecosystems and predicting consequences of global change, also draw heavily on theories of succession. With the now firm understanding that all communities are dynamic and patchy at several scales, there should be no distinction between plant community dynamics and successional studies. Ecosystem dynamics and successional change are best viewed as one and the same (Miles 1979). In fact, the distinction between community and ecosystem is itself misleading. 'A community does not become an ecosystem by adding the abiotic environment; it is an ecosystem because it is inseparable from the abiotic environment' (Bazzaz and Sipe 1987). While community ecology emphasizes the producers, no community exists in nature without the critical involvement of other trophic levels. It stands to reason, then, that whatever influences successional rates and trajectories also influences ecosystem structure and function. A mechanistic understanding of the fundamental and generalizable principles of succession, and their applications to global change questions, requires great depth and breadth in several areas of ecology. Knowledge of some aspects of molecular biology, plant physiology, population and community (ecosystems) ecology, and mathematical modeling is necessary to satisfactorily answer questions about succession and climate change. The ability to communicate in the language of the physical scientists is becoming more and more important for the profitable exchange with the physical scientists of information needed for assessment of the impact of global change.

A list of important works on succession can include hundreds of citations. Interest in succession has become even more prominent under the new heading 'disturbance' (reviews in White 1979, Mooney and Godron 1983, Pickett and White 1985). Extensive treatments of succession by Clements (1916), Loucks (1970), Drury and Nisbet (1973), Horn (1976), Pickett (1976), Connell and Slatyer (1977), Hayashi (1977), Gorham *et al.* (1979), Miles (1979), McIntosh (1980), Noble and Slatyer (1980), Peet and

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Christensen (1980), Van Hulst (1980), Bornkamm (1984), Finegan (1984), Shugart (1984), Huston and Smith (1987), Pickett *et al.* (1987), Numata (1990), and Osbornová *et al.* (1990) have been particularly illuminating. These reviews present extensive information on the history, philosophy, classification, causes, and mechanisms of succession. Amazingly, despite this great volume of work on the causes and mechanisms of succession, the phenomenon is still without a general theory (see Huston and Smith 1987, Huston 1994). The development of such a theory (assuming there can be one) will help to address some of the emerging and relevant issues of global change and their consequences for human welfare, sustainable development, and the preservation of biological diversity. The recent applications to this field of chaos theory, fractal geometry, vector calculus, and the strong emergence of the new science of complexity can profoundly impact such theories of succession. Needless to say, exciting and challenging times lie ahead for new generations of ecologists who will be armed with these new skills to solve fundamental questions in ecology.

The scope of this book

This book does not focus on the details of successional history and the progress toward the development of classical successional theory. These aspects have been thoroughly addressed before by several authors (see Pickett *et al.* 1987). Instead, this book considers the broader view of disturbance and recovery, from filling of small gaps to the revegetation after clearing of large areas for agriculture and forestry. The book integrates and synthesizes information on how disturbance changes the environment, how species function, coexist, and share or compete for resources in populations and communities, and how species replace each other over successional time. Furthermore, the book shows how we used a diverse array of plant species from different successional positions to examine fundamental questions in plant ecology by integrating physiological, population, and community processes. The basic philosophy of our work is that the physiological activities of individuals and the ecology of populations do not happen in a vacuum. Individuals in a population are embedded in a community matrix, and are influenced by the presence and activities of other individuals and populations of the same and of other trophic levels. Furthermore, there is a reciprocal effect, in that physiological and population processes strongly influence community composition and dynamics. This complexity makes the study of ecosystem recovery at once difficult, challenging, and exciting. It also dictates simultaneous work in micro-

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environmental measurements, physiological responses to these changes, feedback loops, and population and community ecology.

This book draws heavily on work carried out by me and my associates first at Illinois and later at Harvard in oldfields, temperate forests, and tropical rainforests. But it is not only a monograph; this work is integrated with the relevant literature, although it is not intended to be a comprehensive review of the literature. The book does not present a 'special case,' but uses our findings from these diverse ecosystems to develop a broad understanding of species' responses to rapidly changing environments, especially during vegetation recovery after disturbance. In our studies and throughout the book, we emphasize that even small disturbance events that initiate succession can modify the levels of resource availability in a profound way and can greatly influence many interconnected responses of plants to these changes, including negative and positive feedbacks at the individual, population and community level (Fig. 1.3).

Work in the Illinois fields

I started my work on plants of successional habitats with the aim of finding out as precisely as I could why certain species replaced each other, above and beyond what Clements and others already knew: that replacement had something to do with availability of propagules, differences in life cycles, competitive superiority, and site modification. I studied secondary successional stands in the hills of southern Illinois, where many fields had been abandoned because of poor productivity. The fields are located on thin, highly eroded, acidic soils and are thus deficient in nutrients. H. A. Gleason had done his Master's thesis work in the same area decades before me. At that time, the prevailing model for studying vegetation recovery was oldfield succession after forest clearing, agricultural use and subsequent abandonment. Research on oldfield succession was energized through the pioneering work of H. J. Oosting and his students, in fields of North Carolina and elsewhere that were abandoned during the Depression. Like several authors before me (e.g. Drew 1942, Oosting 1942, Bard 1952, Quarterman 1957), I wanted first to establish the patterns of change over time by sampling the vegetation of several fields known to differ in the approximate length of time since last cultivation. In so doing, I was substituting space for time. Having been educated under the influence of Clementsian thinking, I was hoping to find a uniform domination in each age group of fields by a few species, which could then be ranked by some measure of their

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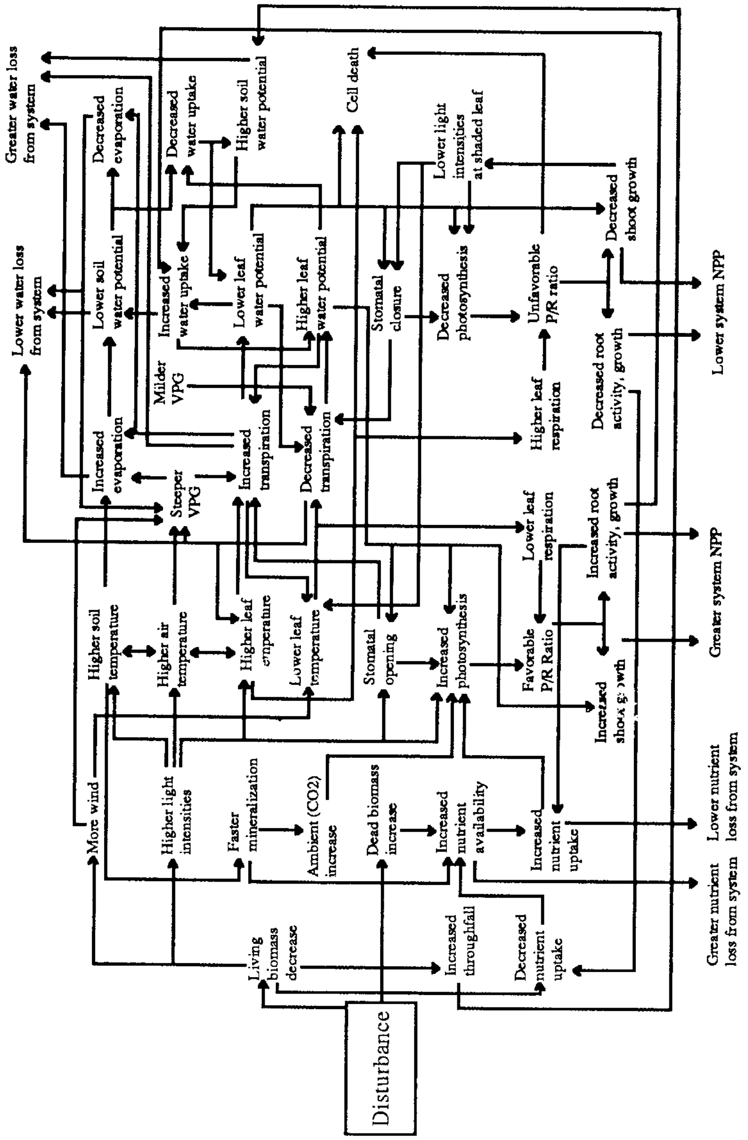

Fig. 1.3. The great complexity of physiological responses and their many feedbacks caused by a single disturbance event (modified from Bazzaz and Sipe 1987).

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relative importance, and from which a generalized community pattern of succession would emerge.

My first surprise and a cause of some frustration and despair was that even in small fields of a few hectares that had been abandoned only recently, and which were apparently treated fairly uniformly prior to abandonment, there was much variation in vegetation. Adjacent patches with different dominants were quite common. Patches in older fields appeared to have vegetation typical of younger fields. Invasion of late-successional trees such as *Quercus* occurred only in middle-aged, clonally-spreading, patchily distributed thickets of *Sassafras* and *Diospyros* (Bazzaz 1968). In many fields, erosion created a soil-depth gradient on which different species occurred in different locations and with different breadths of occupation, some narrow and others quite broad (Fig. 1.4) (Bazzaz 1969). It became clear that certain of these species were good indicators of specific habitat factors throughout a large geographic region. The emerging notion of species diversity, a simple yet powerful central construct in community ecology, became rather complicated. Instead of the expected monotonic increase in species diversity over time, patterns were complex and difficult to scale in these patchy fields (Bazzaz 1975). With time and more experience, I realized that the Clementsian notions of uniformity, directionality, reproducibility, and the idea that succession results in uniform regional climaxes are uncommon and have only limited explanatory power in explaining vegetational change. That convinced me to go beyond description and to ask questions about where, when, and why species appear in succession. How are these patches created? What is their environment? What are their fates? Why and how are patches replaced by others? The scale at which field observations should be made and attributes expressed became major puzzles for me.

Beyond the Clementsian generalizations about causes of succession – 'denudation,' 'dispersal,' 'establishment and reproduction,' and 'site preparation' by one group of species for the next group to invade – there was limited information about the actual mechanisms of succession. The works of Catherine Keever (1950) on early stages and of F. Herbert Bormann (1953) on middle stages of temperate forest succession stood out as exceptions. Working from this foundation, I asked how different physiological characteristics and life history features of the species involved influence successional replacement. I only scratched the surface of this vast question in my Ph.D. dissertation, but I continued to explore it for several years afterward. My initial emphasis was on the controls of

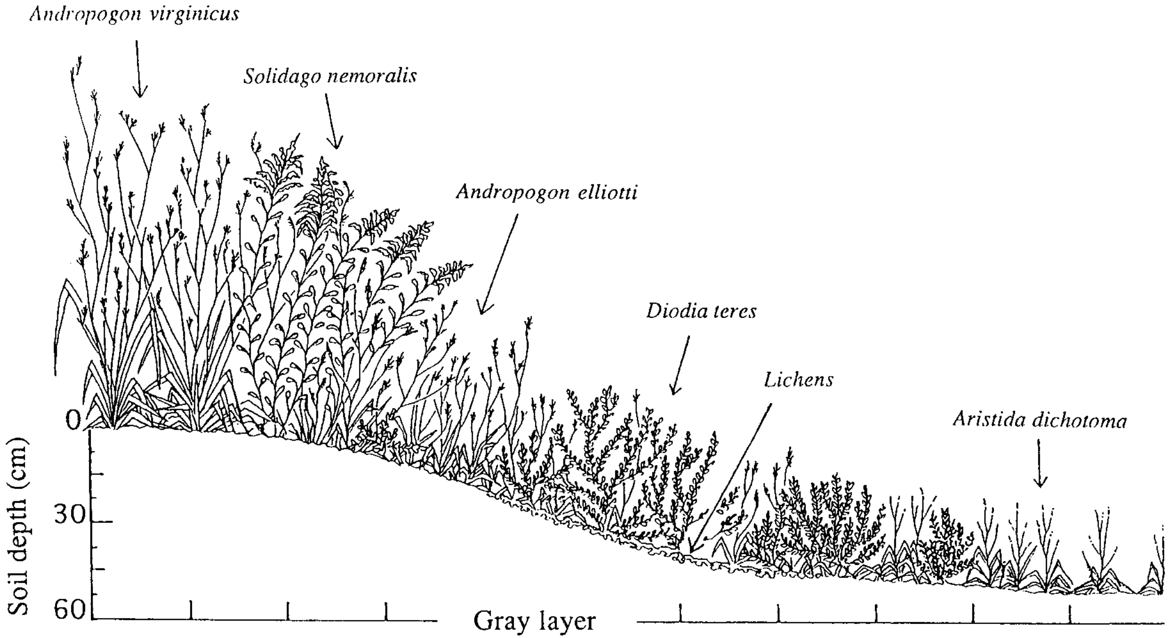

Fig. 1.4. The distribution of species along a soil depth gradient created by different degrees of erosion in a mid-successional field.