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Succession

Scott J. Meiners

Eastern Illinois University, sjmeiners@eiu.edu

Steward Pickett

University of Illinois at Urbana-Champaign

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South Africa has made substantial contributions to the international scientific knowledge base on biological invasions in the past. The formation of the CIB provides a platform and critical mass for further research on key issues relating to the management of invasive species. In its first four years, the CIB produced 246 primary research publications in peer-reviewed journals, supported over 100 graduate students and post-doctoral associates, and provided high-level input to policy formulation.

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SPREAD, MODELS OF

SEE EPIDEMIOLOGY AND DISPERSAL

SUCCESSION

SCOTT J. MEINERS

Eastern Illinois University, Charleston

STEWART T.A. PICKETT

Cary Institute of Ecosystem Studies, Millbrook, New York

Succession in a strict sense refers to the recovery and revegetation of an area following a disturbance such as the cessation of agriculture, the retreat of a glacier, or an intense forest fire. Succession is a special case of vegetation dynamics, although many early ecologists referred to all vegetation change as succession. Succession includes a series of compositional and structural changes, often in a directional manner. The common occurrence of natural disturbances coupled with the extent of human activity on the planet makes succession one of the most ubiquitous ecological processes. Because invasion is a crucial feature of succession, understanding the nature and controls of community dynamics is important for the science and management of invasive species.

CONTEXT OF SUCCESSION

The study of succession began as ecologists first struggled with the idea that plant communities were not static over time but were dynamic over both long and short time scales. The long history of successional studies has generated both progress and controversy, even in the way that succession is defined. Early work described successional dynamics as both directional and with a clear endpoint. Neither of these ideas is currently accepted without caveats. In many, if not most, cases succession will generate a directional change in communities over time. For example, succession in many mesic temperate environments will generate the recovery of deciduous forests, with successional transitions



FIGURE 1 A successional sequence from the Piedmont region of New Jersey. (A) Newly abandoned agriculture land. (B) Herbaceous stage, five years after abandonment. (Photographs courtesy of Steward Pickett.) (C) Increasing dominance of trees 40 years after abandonment. (Photograph courtesy of Scott Meiners.) (D) Mature forest. (Photograph courtesy of Helen Buell.) Data from this system are used in all of the examples illustrated.

from herbaceous to shrubby to forested communities (Fig. 1). However, the ecological literature is filled with examples where successional dynamics stall at some intermediate stage or reverse direction following some change in the environment. For example, the introduction of drought and fire to mesic succession may generate savanna or grassland communities instead of a closed-canopy deciduous forest. Some systems exhibit essentially cyclical dynamics, where each successional stage is continually replaced by another, with no stage able to regenerate itself. Cyclical successions typically occur as a function of the internal patch dynamics of a community rather than in response to a disturbance. The coarse-scale community would be an aggregate of patches in all successional phases.

Opinions on the existence of a successional endpoint, or climax community, have also changed over time. While succession generally does result in a community which has the ability to regenerate itself, these communities are by no means stable. All communities are dynamic; they just exhibit turnover and compositional changes at different time scales. If conditions change, then the inherent

dynamics of the community may also change and generate a new community structure.

SUCCESSIONAL DYNAMICS

The structure of communities tends to change dramatically during succession. Often, the disturbance that initiated succession produces openings within the community that are available for colonization by plants. The amount of bare substrate may range from complete, as in succession following volcanic eruptions, to very little, as in succession following hay production or forest clearing. Over successional time, this colonizable space decreases. There is also an increase in the total biomass of the community, as spaces fill in and larger plants replace smaller, disturbance-adapted species. In successions that regenerate forests, the increase in biomass will largely be due to the accumulation of woody material. Within successions to perennial grasslands or other herbaceous communities, much of this biomass may be accumulated below ground in roots and storage structures. Associated with the increase in biomass is the ability of the community to accumulate and

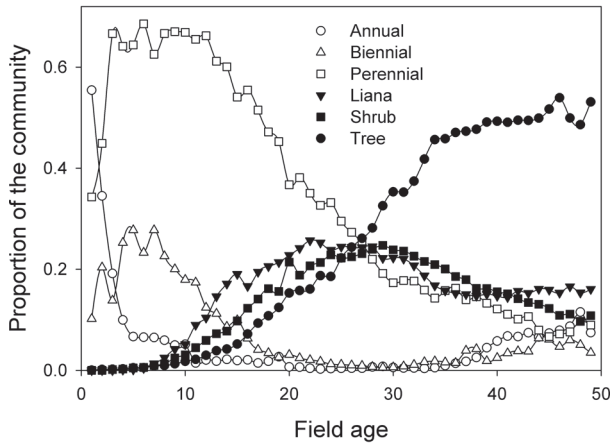


FIGURE 2 Successional transitions of life forms over time during succession from row crop agriculture to deciduous forest.

retain nutrients. While early successional communities often contain relatively low amounts of nutrients in the biomass and have little ability to retain these nutrients within the system, late successional communities tend to contain larger pools of nutrients in the biomass and have a greater capacity for retention.

The diversity of the plant community, and often the associated invertebrate, vertebrate, and microbial communities, changes during succession. In general, early successional communities are relatively low in diversity, being dominated by only those species that are able to either survive the initiating disturbance or quickly colonize following it. As succession proceeds, the community accumulates more species, many of which are not dependent on disturbance for their regeneration. This accumulation of species increases the diversity of mid-successional communities. However, as late successional species accumulate in the community, opportunities for the regeneration of early successional species decrease, eventually leading to their loss from the community. The greatest diversity in succession tends to be in mid-successional communities that contain a mixture of early and late species.

The simplest and clearest compositional transitions that occur during succession are changes in the life form of the dominant plant species (Fig. 2). As succession proceeds, the community shifts in dominance from short-lived herbaceous species to long-lived herbaceous species. In areas where the climate supports the growth of forests, these herbaceous species will be replaced by shrubs and lianas, and ultimately by trees. This does not mean that late successional communities lack other life forms. A late successional forest would also be expected to contain shade-tolerant herbaceous and woody species

in the understory, although canopy trees would clearly be the dominant life form. Succession on bare mineral substrates, which is limited by the availability of nutrients, may begin with extended periods that are dominated by cyanobacteria and mosses, which will precede dominance by herbaceous species.

Concurrent with the changes in life form would be other changes in the characteristics of the community (Fig. 3). In successions that produce forests, the community will become taller over time as short-statured herbaceous plants are overtopped and replaced by shrubs and then by canopy trees. The community will also shift over time from small-seeded species toward larger-seeded species that are more able to regenerate under the dense plant canopy. Related to this change in seed

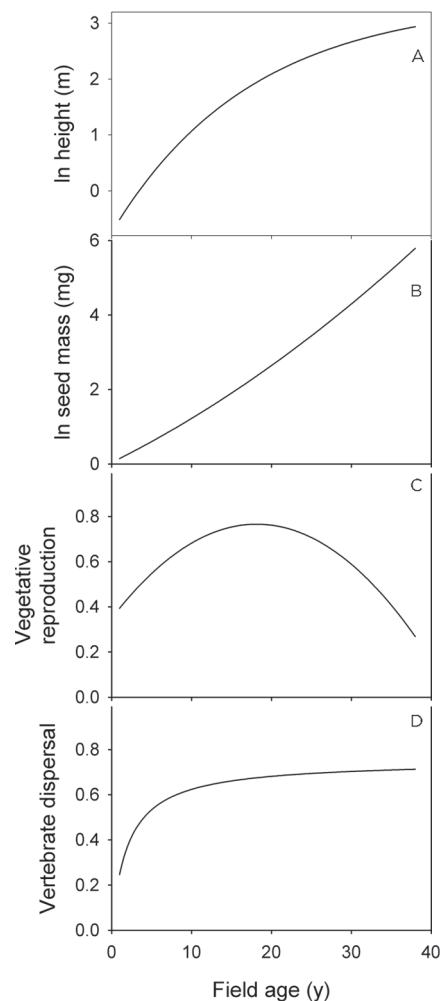


FIGURE 3 Functional changes during succession. (A) Plant height. (B) Seed mass. (C) Vegetative reproduction. (D) Vertebrate dispersal. Plant height and seed mass data are abundance-weighted means for the entire community, while vegetative reproduction and dispersal are the proportion of the community with each trait.

mass is an increased dependence on vertebrates, particularly mammals and birds, for seed dispersal. Smaller-seeded species tend to rely on abiotic mechanisms such as wind for seed dispersal. Vegetative reproduction often peaks in mid-successional communities and is strongly linked with the ability of species to take over and exploit patches of resources. Competitive ability and presumably vegetative reproduction are important in both succession and species invasion.

CAUSES OF SUCCESSION

Successional dynamics are the result of variation in three general classes of successional drivers—site availability, species availability, and species performance (Fig. 4). Much of the theoretical and experimental work on the mechanisms that generate succession focuses either on a specific mechanism within each of these general causes or on the importance of these general causes relative to each other. As specific mechanisms and their relative importance are likely to vary dramatically among locations, we will focus primarily on the general causes.

The conditions following disturbance are critical in determining the vegetation that will develop through succession. Disturbances of varying intensity or type will generate different successional trajectories. Even within the same region, disturbance from logging will generate a very different successional plant community than would be found on land retired from row crop agriculture or from grazing. Similarly, the spatial extent of the disturbance will influence the rate of succession; large disturbed areas will regenerate much more slowly and differently than smaller areas of disturbance. Of paramount importance is the condition of the soil following the disturbance. Agricultural practices often alter the fertility of soils, which may reduce the speed of recovery when fertility is low or may generate novel plant communities when fertilizer residues generate high fertility in normally poor soils. One of the major dichotomies in succession, that of primary and secondary succession, is largely based on the quality of soil available for regeneration. Primary succession typically occurs quite slowly as community dynamics are limited by fertility while the mineral soils accumulate

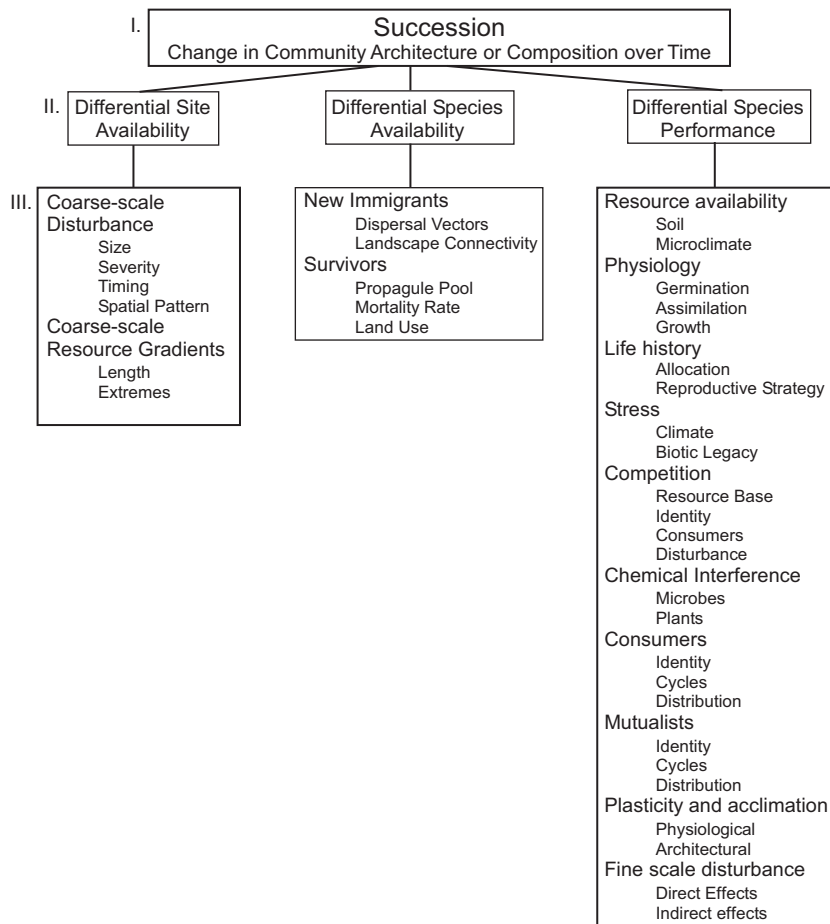


FIGURE 4 Hierarchy of successional drivers ranging from the broad classes of differential site availability, species availability, and species performance to the detailed mechanisms within each class. Successional dynamics within a site can result from one or many of these specific mechanisms within each broad class.

organic matter during succession. All of the site and disturbance variables function within the constraints of local climatic conditions. Succession in relatively moist areas tends to generate forests relatively quickly, while succession in dry habitats slowly produces more open communities composed of shrubs and grasses.

Differential availability of species to a disturbed area can have large effects on the successional processes that occur. Plant species vary dramatically in their dispersal ability and in their ability to survive a given disturbance. Many species may be present immediately following a disturbance, persisting as vegetative fragments or as seeds dormant in the soil. These species often dominate the earliest successional communities. Other species must disperse into the disturbed area. Which species arrive, and their relative abundances, will be determined by the spatial location of reproductive individuals in the surrounding landscape, the efficiency and behavior of dispersal vectors, and the landscape connectivity of the disturbed habitat to source populations. As the seed production of some plant species is temporally sporadic, the composition of successional communities may vary stochastically based on which species reproduced when the site became available. The abundance of an invasive species in the surrounding landscape may determine the initial importance of the species in the successional community, but once the species becomes reproductive, it may spread throughout the community.

Finally, differential performance generates much of the ecological sorting of species seen during succession. Species performance is determined by a variety of characteristics of a species. Factors such as life form and longevity determine the physical constraints on a species and how long it may potentially occupy a particular spot within the community. Other factors include physiological characteristics such as growth rate, shade tolerance, response to herbivory, and competitive ability, to list a few. These characteristics will together determine the outcome of individual plant–plant interactions at local scales. At broader spatial scales, compositional changes within the community will be the sum of all of the individual interactions. Of course, all interactions occur within the constraints of the original site conditions and may vary dramatically from place to place. For example, annuals are typically rapidly displaced by longer-lived species. However, when soil fertility is maintained at artificially high levels with fertilizers, annuals may persist and even dominate the community for years.

While the individual successional drivers are discussed separately above, a plant species must integrate across all of these factors to be successful in a plant community. As

no species can be perfectly suited to all conditions and interactions, tradeoffs must exist that allow species to succeed within particular types of environments experienced during their evolutionary history. These tradeoffs generate the ecological strategies employed by the species, which in turn determine the ability of species to capitalize on a specific successional phase. From a plant strategy perspective, early successional communities will be dominated by short-lived species, which are able to either survive the disturbance or quickly disperse into the site. These species maximize their growth rates but are largely dependent on disturbances to maintain their populations. Early colonizers are replaced by mid-successional species, which employ a competitive strategy of rapidly expanding and capturing resources. Competitive species tend to disperse relatively well but are initially slower to grow and reproduce. Many mid-successional species expand vegetatively via stolons or rhizomes and generate large patches where they dominate local resources. Finally, late successional species expand most slowly of all but can regenerate under earlier successional species or replace them as they die. These species are the longest lived, but they often disperse poorly owing to their large seed mass. Of course, due to spatial heterogeneity within the habitat and stochastic effects on populations, natural communities contain species with strategies adapted for all positions along the successional gradient, not just the phases described here for convenience.

PLANT INVASIONS IN SUCCESSION

Early successional communities worldwide are typically heavily invaded by a diversity of nonnative species. The dominance of nonnative species, particularly in secondary succession, is probably driven by a combination of two factors. First, the disturbances that initiate succession also tend to generate conditions favorable for nonnative species. As disturbance is clearly linked with invasion, it is not surprising that disturbance-adapted nonnative species are also important components of successional systems. Second, the most abundant types of successional habitats are the result of agricultural activities. These activities, whether focused on grazing, row crops, or forestry practices, all support associated suites of weedy species, many of which are nonnative. Agricultural activities increase both the abundance of these species within the landscape and their contribution to the successional flora.

While early successional habitats are often heavily invaded, the relative abundance of nonnative species typically decreases during succession (Fig. 5). While early

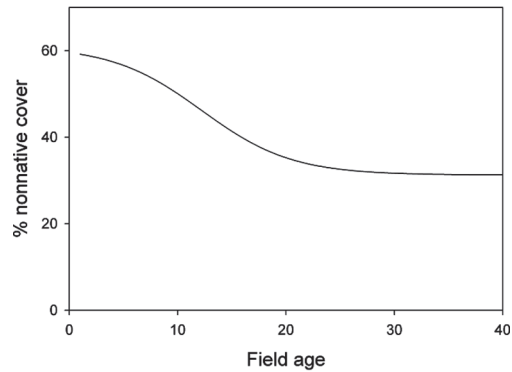


FIGURE 5 Change in relative cover of nonnative species during succession. While the relative abundance decreases sharply early in succession, nonnative species persist in later successional communities.

successional environments are dominated by disturbance-adapted species associated with agricultural practices, these species tend not to regenerate as the influences of agriculture decrease after abandonment. However, the successional replacement of nonnative species is expected only when the pool of nonnative species is dominated by early successional species. In contrast to agriculture, horticultural introductions may spread species from a variety of successional stages throughout the landscape. In communities where sufficient late successional species have also been introduced, the dominance of nonnative species may persist through succession.

Besides being important components of successional systems, invasive nonnative species may have direct impacts on successional processes. As many invaders are aggressive colonizers of disturbed areas, they may alter the direction of successional trajectories or reduce the rate of succession. This is particularly true if the invasive species is capable of regenerating in late successional communities or represents a life form new to the community. For example, woody invasive species in coastal areas may generate a persistent forested community in an area previously dominated by graminoids. Species-rich shrubby communities in South Africa (fynbos) are often replaced by near monocultures of nonnative acacias or pines. Similarly, the introduction of shade-tolerant shrubs into disturbed forests may generate much denser shrub layers that inhibit tree regeneration and the herbaceous layer. Most invasive species that are abundant in early successional communities will probably not become problematic, as they will be replaced by later successional species. However, any species that inhibits a successional transition may delay or even stall succession. In mesic environments that allow succession to forest, tree establishment is a key successional transition. If competition

with invasive species reduces or prevents the growth of trees, then a new, potentially persistent community may develop.

As successional areas often border areas targeted for conservation, they may also represent important propagule sources of invasive species. Invasive species may become abundant in the disturbed habitat and then disperse to the edges of the conservation area or colonize gaps within the community. The presence of successional communities may effectively increase the propagule pressure on the conservation area and increase local rates of invasion.

MANAGEMENT OF SUCCESSION

Much of ecological restoration involves the manipulation of ecological succession to achieve management goals. Typically, management involves increasing the rate of succession to achieve late successional communities more quickly, but this is not always the case. It may be necessary to retard succession in an earlier phase if an herbaceous species or its pollinator, or a grassland bird species, is the management target. Similarly, herbaceous communities in many climates are replaced by woody species during normal successional processes. If a meadow or other herbaceous community is the desired target, then either fire or mowing must be employed to inhibit the establishment of woody species. When management goals require the establishment of late successional communities or species, the successional drivers suggest several potential interventions. As late successional species are typically poor dispersers, seeds or seedlings may be installed to alleviate dispersal limitation. A complementary approach is to assess the factors limiting the growth of the species of interest. Competition and herbivory are two common processes that limit tree regeneration. Mechanical or chemical removal of competing vegetation and protection from herbivores may increase the growth rate of trees and hasten the transition from herbaceous to forested community.

Management of invasive species comes into play in two main ways. If the invasive species within a region are primarily early successional species, then succession, and management practices that increase its rate, will be sufficient to reduce the abundance of the invasive species. In contrast, if an invasive species inhibits successional transitions, then management intervention may be necessary to allow succession to proceed. For invasions involving species capable of regenerating within late successional communities, management of successional processes will have little influence. In these cases,

management of the invasion must focus directly on the removal of the species itself. However, following removal of the invader, it may be necessary to further restore the community to install species that may prevent recolonization of the site. For example, in forests with invasive shrub understories, invasive species should be replaced with suitable native shrubs that may compete with the invader. These management goals and activities are examples of the importance of understanding the processes of succession and the successional conditions that can affect invasive species.

SEE ALSO THE FOLLOWING ARTICLES

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