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Scott J. Meiners, Steward T. A. Pickett and Mary L. Cadenasso
Excerpt
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1 Goals, concepts and definitions

> "Every one [sic] has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that ancient Indian ruins in the Southern United States, which must formerly have been cleared of trees, now display the same beautiful diversity and proportions of kinds as in the surrounding virgin forests. What a struggle must have gone on during the long centuries between the several kinds of trees, each annually scattering its seeds by the thousand; what war between insect and insect – between insects, snails and other animals with birds and beasts of prey – all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees."
>
> Charles Robert Darwin, *The Origin of Species by Means of Natural Selection* (1859)

As has often been noted, you can go back to the writings of Darwin and see most of modern biology contained within his keen observations. Succession is clearly no different. Within his text we see a pluralism of mechanisms; invoking the action of competition, consumers and seed dispersal. We also see an early example of one of the major conflicts in the development of succession – the idea that communities will repeat themselves in time, returning to some pre-disturbance state. Of course Darwin is not particularly well known for his work in succession, but rather his views on population ecology. If we look back over the history of succession, we can generate a "Who's Who" list of ecological thinkers from the last century – Braun, Connell, Cowles, Clements, Gleason, Grime, Keever, Odum, Oosting and Whittaker among many, many others who have all contributed to our understanding of succession.

Based on this long history of work, shouldn't we have a pretty good handle on everything by now? Perhaps we should, but in preparing this text we have learned that there is much still left to be done. Much of what is considered conventional wisdom regarding succession isn't as clear cut as we would like. Ecologists have been very good at examining community dynamics from a one-driver approach and have built a strong body of theory that supports the role of those drivers. Where we have failed is in embracing the multiplicity of simultaneous drivers and contingencies that constrain both community dynamics and the importance of individual drivers. Perhaps we have also been too quick to dismiss succession as an important phenomenon of study just because we have been working on it for well over a century. Researchers have been examining competition for nearly as long and certainly no one would regard that avenue as passé or having outlived its conceptual usefulness (Trinder *et al*., 2013). In fact, several authors have specifically touted the relevance of succession to modern ecology and to our contemporary environmental problems (Davis *et al*., 2005; Walker *et al*., 2007; Cramer *et al*., 2008; Prach and Walker, 2011). We certainly believe that succession has retained its importance in ecology, not just for the reasons cited in those critiques, but because it offers real insight into the dynamics and structure of all plant communities. You may not care specifically about successional communities, but the lessons learned from them may be applied to any ecological system. It is with this overarching vision that we have undertaken this book.

In this chapter, we will not only outline our motivations and define our terms; we will attempt to be very clear about what we are trying to do and what we are not trying to do. We will also build a context for succession and the data that we will be presenting. This is an important first step, because if there are any misunderstandings in how we are using terms or what our perspective is, our message may be lost. This is the "getting to know you" chapter of our book. As with any conversation, the first moments are not always the most exciting, but they lay the groundwork for all that follows.

The goals of this book

Our goal in writing this book is simple – to develop a greater understanding of plant community dynamics. We came at this challenge from having worked to further our conceptual understanding of community organization and from conducting empirical studies on community dynamics. The resulting book is part monograph and part conceptual treatise. This structure was not based on our inability to agree on how the book should be developed, but rather from a strong conviction that the two approaches are necessary to form a full understanding of plant communities. Empirical studies are wonderful in that they isolate drivers of community structure and dynamics, and lead to clear and compelling, publishable papers. However, at the end of the day/career, it can be difficult to see exactly how the individual pieces that result from this work all relate to each other. On the other hand, conceptual approaches to ecology can stimulate ideas that may generate new experimental studies or research linkages that were previously unexplored. The drawback to this approach is that the broader the framework, the less specific it necessarily becomes. At broad levels it can be difficult to see how a particular conceptual organization applies to an individual system and so we often default back to more specific theories. Our approach has been to develop both the conceptual and empirical aspects of succession simultaneously. We will present a conceptual framework that organizes our thoughts on community dynamics and place it into the historical context of other successional ideas. We will then use the conceptual framework to guide our analysis and discussion of a long-term study of successional dynamics. We do this to specifically test the utility of our conceptual approach and to ensure that the data that are presented (and there are a lot) build a broader, integrated understanding of the system and of community dynamics in general.

The major sub-theme of this book is integration, the opposite of reductionism. Reductionism excels at finding *an* answer and forms the foundational basis for much of what is presented here. However, it can be difficult to gain a broader understanding of ecological phenomena if all empirical studies do not find the same pattern/effect. Integration, in contrast, embraces contingencies by building a larger context in which a study may be understood. The lack of a conceptual framework and an appreciation of contingencies may lead to arguments and the development of simplistic dichotomies in science. Examples of such dichotomies include: Is diversity related to ecosystem function?; Does disturbance lead to invasion by non-native species?; Are communities individualistic? (as an aside, if your research question can be answered with yes or no, then you are way down on the reductionist scale in ecology). All of these questions have led to arguments in the literature and can suffer from the lack of an appropriate context. By moving from simple yes/no questions to understanding when a particular pattern/effect can be expected, one moves into the ecological realm of integration and contingencies. The more complex the system, the greater the number of contingencies, the greater the need will be for a conceptual framework to organize all drivers into a logical structure.

One analogy that can help to illustrate the utility of a conceptual framework is that of a jigsaw puzzle. When working a complex puzzle, people generally begin by sorting the pieces using some sort of rubric. Often, edge pieces are a key first step in that they delimit the boundaries of the system (puzzle). Pieces may then be sorted based on color or distinctive aspects of the image. This will help the researcher (puzzle worker) to assemble the puzzle more efficiently. Of course, this all assumes that you looked at the box top and know what the resulting image should be. In ecology, we rarely, if ever, know how the system works, which is why we are studying it in the first place. If you did not know what the target image was, the sorting structure (conceptual framework) may become even more important to assembling the puzzle. The pieces of the puzzle represent individual reductionist aspects of the system – competition between species A and B, availability of resource X, herbivore damage by a generalist, etc. It is difficult to know which piece(s) will be critical in forming an understanding of the image. Likewise, it is difficult to know a priori which individual interaction or driver will be more important than others in forming that understanding. The framework provides a way to organize the pieces so that you know how they relate to each other. If you have a very simple puzzle, organizing the pieces may not be necessary, though the puzzle would not be very intellectually stimulating. If you are dealing with a complex system, the contingencies (linkages among pieces) that generate the final image are multiplicatively greater and organization becomes crucial. Of course, in ecology, we rarely have all, or perhaps most, of the puzzle pieces. Our view of the final image is constantly changing as we find new ecological pieces on the conceptual carpet.

As integration is our goal, we have tried to form a more complete view of our study system. We of course acknowledge that there are many other ways to explore our data. While we have tried to be exhaustive in our conceptual development, we have not tried to be exhaustive in our literature citations. Our goal for each topic has been to represent the general ideas and move on. The literature that we have selected to include is primarily from successional systems, especially when it concerns succession in abandoned agricultural land – our model system. Whenever possible, we have focused on studies based in the same site as the data presented here. Much of this work has been done by our colleagues and students over the years. The remaining papers cited represent classics, personal favorites and other selections that have caught our eye for various reasons. We apologize if we offend in any papers omitted.

Why is succession relevant today?

Succession as a concept is foundational to the development of ecology (McIntosh, 1985). To a certain extent, the history of succession *is* the history of ecology. Setting that aside, there are many reasons why succession as a concept and successional systems as models are still of importance. As the economics and logistics of agriculture have changed, the rate of land being retired from agriculture has increased (Foster, 1993; Foster *et al*., 2004; Flinn *et al*., 2005; Hatna and Bakker, 2011). Historically, this has meant the abandonment of less financially lucrative lands, but now even fertile lands may be retired from agriculture. Much of this has likely been driven by the transformation of agriculture from small, family farms to a larger industrial mode of agriculture. Lands too steep for row crops would have once supported a family's livestock; but as animal production has shifted to feedlots and crop production to larger equipment, these areas have been allowed to undergo succession. Similarly, societal constraints on logging have pushed wood production to private landholdings leading to extended periods of forest regeneration in some areas. In tropical areas, shifting agricultural practices and human populations may at least temporarily generate secondary forests (Lambin *et al*., 2003). These socioeconomic changes mean that there is, and will continue to be, much more land experiencing succession. Understanding successional processes means that we will understand the forces regulating a significant portion of our modern landscape. This also means that the opportunity to remediate and restore these communities through manipulating succession is great (Clements, 1935; Luken, 1990; Cramer and Hobbs, 2007; Walker *et al*., 2007; Prach and Walker, 2011).

A completely different value of successional communities comes from their importance to theoretical studies. Successional systems, particularly old fields, have become model systems for testing theories of biodiversity, competition, ecosystem regulation and many other contemporary ideas (Tilman, 1985; Carson and Pickett, 1990; Wedin and Tilman, 1993; Clay and Holah, 1999; Stevens and Carson, 1999; Symstad, 2000; Klironomos, 2002; Schmitz, 2010). Aside from the ubiquity and lack of conservation status of successional areas, these systems are particularly amenable to manipulation because they are dynamic over relatively short time scales. We may be more inherently interested in other ecosystems, but we can get results within a season or two in a successional system. The hope is that by understanding the dynamics and structuring forces of successional systems, we can apply these lessons to systems that are of much greater conservation concern and that experience dynamics over a much greater time scale. Finally, and we must be honest here, no one is concerned with protecting old fields. From an experimental view, this means that these systems can be manipulated in very severe ways with no societal consequences. Take, for example, the usage of old fields as model systems to understand how fragmentation alters the persistence and movement of small mammals (Robinson *et al*., 1992; Barrett *et al*., 1995). Doing similar things in forested landscapes, and with larger animals, would be much more difficult (e.g. Brookshire and Shifley, 1997; Laurance *et al*. 1998) and would require a massive, coordinated research effort, instead of a mower.

Interestingly, successional systems are somewhat of an oddity in nature. One can argue that logging mimics natural disturbance regimes, though the scale, periodicity and severity may be much different. Old fields, however, are very anomalous. What is the historical analog of abandoned agricultural land? Old fields on one hand could be envisioned as similar to very large forest gaps. A critical difference, however, is the long history of soil disturbances and the legacies that are generated by those disturbances which would be absent in gaps (Foster, 1993; Walker *et al*., 2010; Kuhman *et al*., 2011). If we look at the native species that dominate the herbaceous stages of succession, we find disturbance-adapted species that were once relegated to large forest gaps or persistent forest openings such as glades (Marks, 1983). As succession proceeds, herbaceous species are replaced by opportunistic woody species that would also likely colonize large gaps, persisting until canopy closure limited their recruitment. On top of this odd assemblage of native species is a large suite of non-native species that are typically dominant early in succession (Inouye *et al*., 1987; Bastl *et al*., 1997; Meiners *et al*., 2002a). These species were largely introduced intentionally and accidentally through agricultural practices, though some were introduced for ornamental purposes. What results is an odd assemblage of native and non-native species that have come together to form a community that covers a large portion of the planet's surface under relatively novel physical conditions.

Finally, we must address whether there is really anything new to learn in succession. After all, ecologists have been studying succession for over 100 years – have they been lazy? The answer is of course, yes there is more to learn and no, ecologists have not been lazy. The view of understanding succession as largely a completed task comes from confusing description with understanding. We have described successional dynamics from many, many areas and know many of the general transitions that occur over time. In addition to this work, decades of reductionist ecology have provided us with a long list of potential regulators of community dynamics that may or may not be important in any individual system. What we are still lacking is a full appreciation of the contingencies that constrain succession and the interactions that may lead to dramatic shifts in the trajectory of individual species or the entire community.

As an example of the importance of description vs. understanding, let us examine gene expression. Cell biologists know that there are regulators of gene expression that either encourage transcription or inhibit it (promoters, transcription factors, methylation etc.). These are the basic drivers of gene expression. Mechanistically, the basic drivers are known, and introductory textbooks can outline a simple process of control. However, there may be multiple genes that are involved (epigenetics) and so contingencies may occur based on the gene's context in a cell. The net effect of all controllers is an up- or down-regulation of a gene product. Of course reality is even more complicated in that another gene may be turned on that represents the same cellular function. The one-gene–one-product rule has, as well, been thrown out, as there can be manipulation after transcription. All this is to say that while we know the parts that may be involved, no one would (or should) walk up to a cell biologist and claim that we understand gene expression. There are quite simply too many contingencies at the cellular level to make broad sweeping statements. Similarly, we would argue that succession, or more broadly community dynamics, is still a fertile area for research.

Finally, successional biology contains many aspects of population and community ecology. For this reason it is a fabulous context to integrate often disparate fields of study. Succession touches on issues of allocation, tradeoffs and reproduction at the population scale; plant strategies, diversity and competition at the community scale; and nutrient cycling, productivity and consumer interactions at the ecosystem scale. One of us (STAP) has even announced at a symposium on ecological theory that "nothing in community ecology makes sense except in the light of succession" mirroring the famous comment by Dobzhansky on evolution. While this drew the hoped-for laugh from the audience, much can be made of the ability of succession to integrate ecology.

Definitions and controversies

For such a foundational concept of ecology, succession has more than its share of controversies. To avoid these, we need to define our terms and place them into an appropriate historical context. This would seem a simple task, but as you will see, it can be tricky.

General ecology texts often contain simple definitions such as succession is the directional and predictable change in species composition in response to disturbance. This definition is perhaps suitable for the pre-med student who will never think too deeply on the subject, but it rapidly fails for those who pursue the ecological sciences. This is where the issues begin. We could add "more or less" and "often" in a few places, but that really just muddies the definitional waters. Interestingly, the restrictive conceptualization of succession in textbooks is a modern construct. Many early ecologists treated all vegetation change as succession (e.g. Warming, Watt etc.). This definition would certainly simplify things conceptually, but would be unsatisfactory for a great many people who view succession as a sort of special case. As a compromise, we pose that succession is a special type of vegetation change, bounded by certain constraints. We will define these constraints shortly, but it is important to realize that the general mechanisms and processes involved in successional and non-successional vegetation changes are the same. It is in this vein that succession can be used as a unifying concept in ecology (Davis *et al*., 2005).

Succession and disturbance are often conceptually linked, so we will start with defining these terms:

Succession – The temporal change in species composition or three-dimensional structure of plant cover in an area (Pickett and Cadenasso, 2005). This definition does not imply directionality, predictability or an endpoint, nor is it restrictive to only following a disturbance. Successional systems can be divided into primary and secondary, based on the lack or presence of established soil. Though the underlying processes should be the same in primary and secondary succession, relative importance of individual drivers will likely be quite different.

Disturbance – An event that alters the structure of vegetation or the substrate the vegetation is growing on, often resulting in a change in resource availability (Pickett and White, 1985; White and Jentsch, 2001). Missing from this definition is any mention of the time scale of a disturbance, though it does suggest a potential mode of effect via alteration of resources. This definition differs from that of Grime (2001) who defined disturbance solely as the destruction or removal of biomass.

These definitions seek to avoid the challenges posed by other conceptualizations of succession, largely espoused in the views of Clements (1916) as they advocated a clear starting point, directionality, predictable trajectories analogous to the development of an organism and, finally, a clear and stable endpoint (Pickett and Cadenasso, 2005; Pickett *et al*., 2009). Our definitions are broad enough to encompass the range of vegetation changes traditionally incorporated under the successional umbrella – cyclical community dynamics, progressive and retrogressive change, autogenic and allogenic drivers, the filling in of depressional wetlands, retreating glaciers and volcanic activity. They also allow for the contingencies and variability in dynamics that have come to characterize succession. If a more restrictive definition of succession that includes some form of directionality and a discrete disturbance is preferred, that will limit succession to exclude cyclical community dynamics, retrogressive changes and hydroseres. Though this is not our approach, this definition can work well and simply shifts more of the range of potential successional dynamics to the more inclusive vegetation dynamics (Figure 1.1). However, the delimitation between succession in a strict sense and vegetation dynamics in the broader is purely artificial. As the system that forms the foundation of this book represents succession on abandoned agricultural land, it luckily fits even the most restrictive definitions of succession.

If, as most contemporary ecologists, we reject the idea of a climax community as it is too entrenched with the idea of stability, how do we describe the end of succession? One candidate would appear to be the concept of dynamic equilibrium. In this concept, composition and structure at a landscape scale are maintained, despite constant turnover and compositional changes occurring within individual patches. While this addresses the idea that systems are constantly changing, the notion of stability at broader geographic scales seems unlikely in an age of global climate change, nutrient deposition, biological invasion and habitat fragmentation. Also, it does little to inform what is going on within an individual successional site. We might alternatively describe the end of succession as the point at which the dynamics of the site are no longer being driven by the event that initiated the succession. For hydric successions, this would be when soil development and the drying of the site no longer influence the composition of the site. Similarly, for old field succession, this would be when vegetation dynamics shift from being driven by the disturbance of the plow to being driven by other processes. In many instances this will also represent a shift to internal processes such as gap formation and regeneration. Of course this endpoint is difficult in application as land clearing often generates even-aged stands that more or less reach maturity and senescence at the same time, leading to

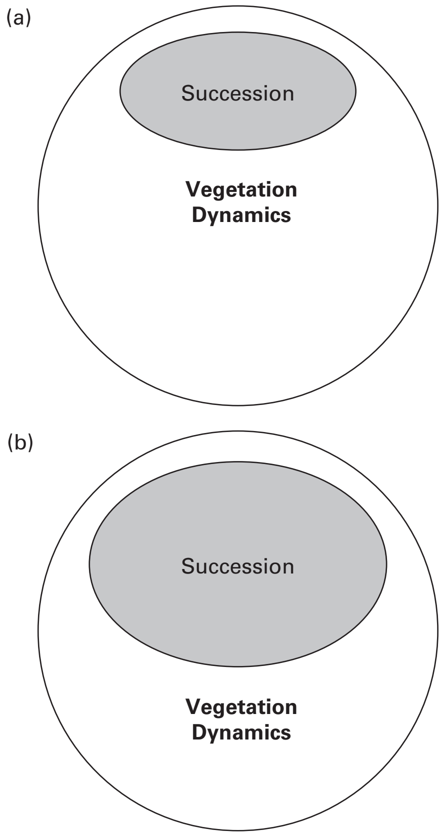

Figure 1.1 Conceptual representation of the relationship between succession and vegetation dynamics using a restrictive (A) and more broad (B) definition of succession. In all cases the dynamics represented by succession are a subset of vegetation dynamics as a whole. At the most extreme, succession and vegetation dynamics may be considered synonymous, with complete overlap. This illustrates the commonalities of mechanisms in succession and vegetation dynamics.

pulses in the mortality and regeneration of canopy trees. Furthermore, soil disturbances such as plowing may leave persistent legacies for up to centuries (Dupouey *et al*., 2002; Flinn and Marks, 2007; Walker *et al*., 2010). Operationally, it may be simplest to envision a gradual shift from successional to non-successional dynamics and abandon the notion of a definable endpoint because of its inherent artificiality (Figure 1.2).

The data

The core of this project is a unique data set from a series of permanent plots in abandoned agricultural land (Chapter 2). Following the initial abandonment treatments, these plots and fields have been left unmanipulated as the vegetation changes have been documented. The observational nature of the data have from time to time drawn criticism from

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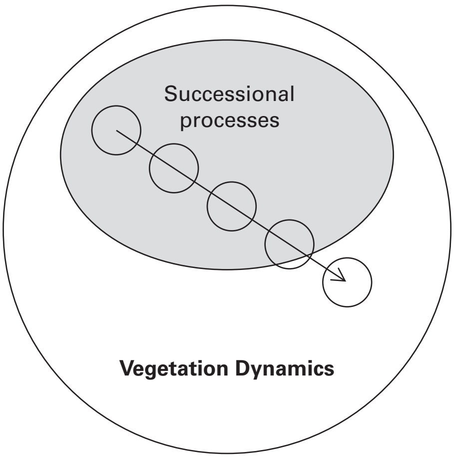

Figure 1.2 Representation of successional shifts in the processes that regulate dynamics within plant communities. Early in succession, dynamics are driven by the processes that initiated succession (e.g. disturbance). As succession proceeds, driving forces shift towards those not related to the initiation of the system, signaling the end of succession.

Figure 1.3 Diagrammatic representation of the parallel gradients of experimental to observational study and of mechanistic specificity in ecological studies. While the increased ability of manipulative studies to isolate mechanisms over observational studies is commonly noted, there is also a tradeoff in the broader applicability of such data. Highly manipulative studies provide direct and specific mechanistic tests, but sacrifice the ability to test the importance of other hypotheses, particularly the further those hypotheses lie from the original motivating question. Observational studies lack the ability to clearly isolate mechanisms, but data from these may be applied to a wide diversity of questions with little constraint.

reviewers and (unfairly!) from granting agencies. This criticism stems from the inability of such data sets to definitively link community dynamics to specific mechanisms. We believe that while reductionistic approaches have their merit, there is also real value in data derived from observational approaches (Austin, 1981).

Our logic behind this claim follows that of Levins' (1966) critique of population models. There is an inherent tradeoff between the generality of a model to a variety of systems and its accuracy in forming predictions within individual systems. We posit that there is a similar tradeoff between the level of manipulation and control imposed on a research system and the ability of a study's data to address questions beyond the original scope (Figure 1.3). The more controlled the experiment, the greater the ability to isolate the individual mechanisms that operate. However, this mechanistic specificity comes at

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a cost – the more limiting the controls on the system, the less utility the resulting data have to address other questions. Observational studies, in contrast, lack the strong mechanistic linkage that makes manipulative experiments desirable. However, there are also few limitations on how that data may be used to address additional hypotheses as there are no constraints on the data imposed by the experimental manipulation. Both approaches are important in ecology, providing complementarity in the results achieved. Observational studies provide an important context and reality check for manipulative studies that may overemphasize the role of individual drivers. Similarly, observational studies may suggest avenues for reductionist experimentation and may further the development of ecological theory (Austin, 1981).

For this book we exploit observational data following experimental variation in abandonment conditions. The original goal of the project was to focus on successional dynamics. We are not constrained by the original framing goal, allowing us to explore issues of assembly rules, biological invasions, heterogeneity and functional ecology. The long-term data pre-date these ideas in ecology, but can still be successfully used to explore them.

The organization of this book

This book is organized into four main sections, each building off the previous in a (hopefully) logical and clear manner. Each section has specific goals that constrain the material and approach within each. We have strived to make the progression of themes logical so that the reader will have all the pertinent information by the time a particular idea arises. This approach will be useful for someone reading the text in its entirety, but means that someone reading an individual chapter may need to skim back through previous sections to fully understand what is being presented. There would quite simply be too much repetition to fully develop each chapter as a stand-alone contribution. Indeed, had this been possible, there wouldn't really be a need to write an entire book. Our goals for each section are as follows:

Context – In this section we will provide the background for both the data that we will be presenting and the conceptual premise of the book. We will start with a history of the data and the site that forms the basis for this book. We will also provide a somewhat abbreviated history of successional thought, particularly focusing on linking ideas to show conceptual development and key advances over the years. From there we will build the conceptual framework that forms the guiding principle for this text – that although community dynamics are complex, there is a strong value in simply organizing drivers of community change hierarchically. Finally, we will briefly review the primary drivers of community dynamics and place them into our hierarchical conceptual framework.

Pattern – These chapters primarily deal with the long-term data and the dynamics seen within our system. They focus largely on ecological pattern rather than on developing a mechanistic understanding of temporal and spatial dynamics in plant communities. The specific purpose of these chapters is to set the stage for the hierarchical and mechanistic approach in the chapters that follow. This is not done to reduce the importance of these ideas, but rather to more quickly and efficiently move us on to the areas that we would like to address in more depth. This section will also address