1 · *Introduction*

Plant succession is the replacement of plant species and communities over time in response to a disturbance of either natural or human origin. It is a unifying concept of ecology, integrating temporal and spatial scales, abiotic and biotic disturbances, plant-soil and plant-animal interactions, plant life histories, biodiversity patterns, species interactions, and other fundamental ecological principles across a heterogeneous landscape. While we have a simple, intuitive grasp that plant communities change (e.g., abandoned pastures change to forests; vegetation recovers following damaged by fire), the actual drivers of such change are not fully understood, even after more than a century of formal study (Clements, 1916; Glenn-Lewin *et al.*, 1992; Meiners *et al.*, 2015a). One of the challenges is that most work on plant succession (henceforth "succession" because of the preponderance of plant-focused studies; but see heterotrophic succession, Walker & del Moral, 2003) has been specific to a given site or type of disturbance. Yet progress has been made in identifying certain ecological principles that are likely to be important in succession. In this book, we explore global-scale patterns of several key aspects of plant succession to discern at what level generalizations about succession are possible. For the first time, we systematically compare terrestrial successional processes following all major disturbances among all the world's biomes. This synthesis also provides a framework for aiding land managers attempting to manipulate succession through restoration (Prach & Walker, 2011).

The incomplete understanding of successional drivers is clearly a function of the complexity of interacting and continuously changing variables. For example, on a recent lava flow, there are many unpredictable factors, each with successional consequences. These variables include the stochastic nature of seed dispersal and germination; abiotic influences such as climate fluctuations, surface chemistry, and nutrient status; presence or absence of competing plants or hungry animals; and sequential colonists and plant communities that reinforce, displace, or have no effect

on the first plant colonists. These series of stochastic events therefore accumulate uncertainty over time. Moreover, humans change the whole surrounding landscape, including with the introduction of invasive alien species that can be particularly good invaders of new disturbances (e.g., on the lava flows in Hawaii; Vitousek *et al.*, 1987). Predicting detailed future plant communities on that patch of lava therefore becomes as complex as predicting the weather years in advance. And even when local successional patterns are discernible, how broadly they apply is still unclear. Despite these hesitations, we are convinced that certain successional traits can be predicted.

Three topics of successional studies became the basis for our global comparison of succession, in part because of their importance to understanding succession and in part because they were commonly measured and therefore provided a basis for comparison among studies. First, the focus of many successional studies has been on trajectories and rates of change. For example, if succession is directional, which community represents the final or relatively stable endpoint and how long and how many intermediate communities are needed to get there? Are there multiple pathways to the same endpoint or are their multiple endpoints? And to what degree does any eventual endpoint resemble the pre-disturbance or surrounding vegetation? These questions have important implications for establishing and achieving restoration goals. We used two aspects of this area of research in our comparisons: 1) the success of a sere (successional sequence) in achieving a resemblance to the natural vegetation, and 2) whether the trajectories in a given study were convergent, divergent, or neither.

A second area of inquiry in ecology has been on patterns and causes of biodiversity. This interest stems from both a theoretical interest in how species evolve in dynamic environments and a practical interest in conserving species in the face of natural and human disturbances. One factor affecting biodiversity is species interactions (among plants and among trophic levels). In succession, much effort has been focused on determining when positive (facilitative) or negative (competitive) interactions are most likely to drive succession. In our comparative studies, we examined patterns of change in species richness (an aspect of species diversity) during succession.

A third topic in ecology is the increasingly urgent concern about the influence of invasive alien species, introduced directly or indirectly by humans. The rapid spread of plant species around the world has resulted in many new communities with profound consequences for ecosystem

function and successional dynamics. Unfortunately, these consequences are poorly understood. We compared the degree to which invasive alien species affected succession in different biomes and after different disturbances.

Because of the great heterogeneity of data presented in studies on succession, and the frequent absence of primary data, we used only simple ordinal or categorical evaluations of the trends in successional trajectories, species richness, and importance of alien invasive species. This simplification enabled us to compare more studies than would have been possible with a more analytical and quantitative approach.

We wrote this book for several reasons. First, it was time for a global update on the steady output of successional studies. Recent book-length reviews addressing succession have tended to be more site-specific (Meiners *et al.*, 2015b), disturbance-specific (Cramer & Hobbs, 2007); or focused on disturbance (Johnson & Miyanishi, 2007; Walker, 2012; Wohlgemuth *et al.*, 2019) or restoration (Walker *et al.*, 2007) more than on succession. Second, the accumulation of site-specific studies challenges us to ask: Are we ready to make broad generalizations about succession, and if so, at what spatial scale? Third, although biomes and disturbances are a fundamental aspect of vegetation studies, no one has yet explicitly contrasted succession among biomes within a disturbance type or among disturbance types. Fourth, any theoretical implications from such comprehensive comparisons could potentially advance our still incomplete understanding of successional principles. Finally, practical implications will help guide managers who are trying to conserve still relatively pristine natural areas or to restore damaged lands. Generalizations, where possible, will help those in poorly studied biomes or disturbances glean strategies appropriate for their use.

One previous attempt to summarize succession by habitat (Burrows, 1990), and the most recent comprehensive book on succession in general (Walker & del Moral, 2003) are several decades old. Therefore, we hope that this book, with its comparative approach to studying succession by biomes and disturbance types, helps further our general understanding of temporal dynamics. We are encouraged by several recent papers (e.g., Peltzer *et al.*, 2010; Meiners *et al.*, 2015a) and a special feature (Chang & Turner, 2019) that focus on novel findings and future directions for successional research.

Our book is organized into three sections. Part I (Chapters 1–3) continues with an overview of how humans have interacted with and studied succession and an overview of the terrestrial biomes of the world.

Part II (Chapters 4–15) examines succession by disturbance type and includes 1) a description of the disturbance, 2) abiotic and biotic variables that affect succession following each disturbance, and the results of our comparative analyses, and 3) theoretical and practical implications of our findings. Details on how we chose certain studies for comparison are found in Chapter 4. Part III presents a synthesis of several prominent themes that emerged from Part II and a conclusion with future challenges for studies of succession. At the end of the book is Appendix 1, a glossary, and Appendix 2 containing the literature and search phrases used in our comparative analyses.