July 10, 2015

Book proposal for the Princeton Monographs in Population Biology series

Historical Contingency in Community Assembly

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Overall topic and scope and why timely and important

The goal of this book is to present a new "historical theory" of community assembly. This theory is aimed at predicting the conditions under which the structure and function of ecological communities are sensitive to the past history of species immigration and, conversely, those under which they are robust to historical contingency.

To give a bit of historical background to explain why this theory is needed, ecological communities were once thought to tend toward a single climax state. This state is characterized by a deterministic composition of species that can be predicted from local environmental conditions. More recently, there is increasing realization that priority effects are crucial: even under the same environmental conditions and the same set of potential colonists, the way species affect one another in communities and their consequences for species composition and diversity can depend on the order and timing in which species immigrate.

The extent of historical contingency due to priority effects is difficult to quantify because it is rarely possible to reconstruct immigration history in sufficient detail. Yet, experiments that manipulate immigration history during community assembly reveal that priority effects can be strong enough to shape major patterns of biodiversity at multiple spatial and temporal scales. These patterns include species-area relationships, productivity-diversity relationships, local-regional richness relationships, and boom-and-bust patterns of evolutionary diversification.

Moreover, priority effects are directly relevant to urgent environmental and medical issues. For example, knowledge of historical contingency informs the restoration of biodiversity and ecosystem functioning in the face of habitat fragmentation, biological invasion, and the phenological and distributional shifts induced by climate change. Likewise, in medicine, this knowledge can be essential for the maintenance of healthy gut microbiome after antibiotic treatment or fecal transplantation.

Despite its basic and applied importance, historical contingency has remained a fairly minor part of the community assembly literature over the past two decades. This minor status is in contrast to the growing general interest in community assembly during the same period and the rapid increase in the relative number of papers on related topics such as functional traits and phylogenetic structure within this literature.

I believe there are two likely reasons for this trend in the literature, one practical and one philosophical. Practically, data on species traits and phylogenies are more readily available than historical data on community assembly, resulting in more papers on these more easily accessible topics. Philosophically, the vagaries of history tend to be viewed as an obstacle that hinders advances in community ecology as a predictive science. Historical idiosyncrasies can easily make each instance of community assembly appear unique and not understandable within a general framework. In my book, I will argue that this view is misguided and offer an alternative way forward that embraces, rather than ignores, historical contingency.

Four major conceptual shifts are beginning to emerge in the study of community assembly, and I will integrate new advances in these areas of research in the historical theory of community assembly that I will develop in the book. First, community assembly research has traditionally assumed that regional species pools function as stable reservoirs of species that constantly supply immigrants to local communities. However, as some authors have recently emphasized, regional species pools are more dynamic than usually assumed, changing over time and interacting with local communities. I will devote much of the book on the generation and maintenance of species pools as an issue fundamental to understanding historical contingency.

Second, community assembly has traditionally been studied as either an ecological phenomenon (ecological succession) or an evolutionary one (lineage diversification), but recent research on eco-evolutionary dynamics suggests a wider array of the mechanisms by which priority effects cause historical contingency than previously recognized. I will discuss community assembly as an eco-evolutionary phenomenon, where local adaptation and diversification interact with ecological competition and predation.

Third, historical contingency in community assembly has traditionally been studied with respect to species composition. However, growing evidence indicates that immigration history also influences the ecosystem-level functional properties of communities, such as total biomass, decomposition, and nutrient and energy flow. Changes in community function can in turn affect community structure, creating function-structure feedback. I will consider this feedback throughout the book.

Finally, the traditional focus on equilibrium, represented by the popular concept of alternative stable states, has begun to be challenged by studies indicating the importance of long-term transient dynamics of community assembly. I will consider not only alternative stable states, but also alternative successional trajectories as well as cyclic assembly trajectories, to broaden the scope of the book.

Table of contents

The book will be organized as follows. Preface and Chapters 1 and 2 will introduce the topic of the book by presenting the historical background and significance of historical contingency. Chapters 3 to 6 will be the core of the book, and will develop a set of general predictions about the conditions for historical contingency, beginning with local processes and progressively moving up to larger geographical and phylogenetic scales. Chapters 7 and 8 will illustrate the applied values of these predictions, highlighting medical issues concerning host-associated microbiome and infectious disease and environmental issues concerning global change factors and ecosystem management. Chapter 9 will synthesize Chapters 3 to 8 to draw general conclusions.

Preface
The preface explains the goal, scope, and organization of the book, with a brief introduction to each chapter.

Chapter 1. Historical contingency: obstacle or opportunity?
This chapter will briefly describe the history of the study of historical contingency in community assembly and how this study contributes to explaining patterns and mechanisms governing biodiversity, in particular beta diversity, the variation in species composition among local

communities. I will then point out that historical contingency is a neglected major source of beta diversity and may be as important, if not more important, as the two other, more obvious and better studied sources of beta diversity, environmental heterogeneity and dispersal limitation. I will discuss why historical contingency has been overlooked by community ecologists and why now is a good time to reverse this trend and regard historical contingency as an opportunity, rather than an obstacle, for advancing community ecology.

Chapter 2. Mechanisms and consequences of priority effects
This chapter will summarize current knowledge on the mechanisms and long-term consequences of priority effects that cause historical contingency, which will form the basis of the arguments developed in Chapters 3-6. Mechanisms of priority effects will be grouped into niche preemption and niche modification, each with different implications for the structure and functional properties of communities. Long-term consequences will be classified into three types, alternative stable states, alternative transient states, and compositional cycles. The conditions that allow each type to be realized are often different, which will be discussed in the following four chapters.

Chapter 3. Rate of local population dynamics
For community assembly to be historically contingent, two requirements need to be satisfied. First, local population dynamics must occur rapidly enough for early-arriving species to preempt or modify niches before other species arrive. Second, the regional species pool must contain species that can together yield priority effects. The first requirement will be dealt with in Chapter 3, and the second in Chapters 4-6. In Chapter 3, I will synthesize studies that looked at the effects of local conditions such as nutrient availability and environmental variability and regional conditions such as habitat connectivity and landscape configuration on how readily priority effects happen. These factors are conceptually of the same kind in that they all affect the strength of priority effects by determining the rate of local population dynamics relative to immigration and disturbance frequency. Eco-evolutionary dynamics (e.g., the rate of local adaptation as affected by the genetic diversity of immigrants) will also be considered.

Chapter 4. Formation of local species pools
This chapter focuses on the local species pool shaped by environmental conditions and dispersal limitation. On a regional scale, we can envision a set of species that have the potential to disperse to a local habitat patch. This is the regional species pool. However, the physical and chemical conditions of the local habitat patches as well as the location of the patches within the region will determine the so-called effective local species pool, i.e., the subset of the species in the larger, regional species pool that can actually arrive and survive in a given local patch. For priority effects to cause historical contingency, the environmental and dispersal filtering shaping the effective local species pool has to select for species that together yield priority effects when they interact in local communities. Chapter 4 will explore the ecological and evolutionary conditions under which such particular filtering occurs.

Chapter 5. Maintenance of regional species pools
The majority of community assembly studies thus far have assumed that the species pool is a static external reservoir that constantly supplies immigrants to local communities, as in MacArthur and Wilson's mainland-island model. In reality, however, species pools rarely exist externally. In many cases, local communities contribute to shaping the regional species pool, so there is a feedback between local communities and the species pool, making the species pool internal, as in the metacommunity model of community assembly. When we have such an internal pool, inhibitory priority effects within local communities can scale up to result in regional dominance by a few species, making the regional maintenance of local priority effects difficult.

Chapter 5 discusses mechanisms that facilitate this regional maintenance, with special attention paid to eco-evolutionary feedbacks affecting the local and regional species abundances as well as the species traits responsible for priority effects.

Chapter 6. Generation of regional species pools
The issues considered in Chapter 5 concern the regional maintenance of species over eco-evolutionary time. Ultimately, we also need to understand how species pools are generated over longer macroevolutionary time at large geographical spatial scales in order to know why the regional pools have the set of species they do. For example, inferring how species have come together by lineage diversification occurring at these large scales may help to explain when to expect many competitively equivalent species in the same local species pool, which would increase the chance of priority effects by niche preemption. Chapter 6 will focus on the generation of the regional species pool as a result of macroevolutionary and macroecological dynamics at regional and global scales.

Chapter 7. Host-associated microbiome
To illustrate the utility of concepts developed in Chapters 2-6 beyond intellectual curiosity, Chapters 7 and 8 will apply the concepts to two timely issues that involve management of ecological systems. Chapter 7 considers the medical ecology of host-associated microbiome, with a focus on management of pathogenic microbes. Recent evidence shows that the transmission and within-host abundance of microbial pathogens, such as strains of *Borrelia burgdorferi* that cause Lyme disease and strains of *Salmonella enterica* that cause diarrhea and typhoid fever, can be strongly influenced by priority effects within hosts. I will discuss how eco-evolutionary concepts on historical contingency can be applied to prevent and cure these and other infectious diseases.

Chapter 8. Global change phenomena
This chapter will look at the influence of global change phenomena on communities and ecosystems, with a focus on the phenological and distributional range shifts and the alteration of the local and regional species pools induced by climate change, biological invasion, and habitat fragmentation. I will use plant, animal, and microbial examples to illustrate how priority effects may be altered by these anthropogenic disturbances and how priority effects can be used to manage damaged ecosystems for species conservation and restoration.

Chapter 9. Historical theory of community assembly
This final chapter synthesizes Chapters 2-8 by considering the spatial grain and extent at which one wants to understand communities. Based on this synthesis, I will present a historical theory of community assembly, intended as a set of general, interrelated hypotheses for better explanation and management of biodiversity and ecosystem functioning.

Audience and comparison to existing books

The target audience is graduate (and upper-level undergraduate) students, postdocs, and more senior researchers who are interested in community ecology. The book will revolve around fundamental concepts, but illustrate them with ample use of natural history to enrich the concepts, making sure no taxonomic bias is introduced to the choice of examples (except Chapter 7, which will discuss symbiotic microbes). Therefore, the book should interest all community ecologists regardless of their particular taxonomic interest. In addition, because the book will use insights from other subfields related to community ecology, including population ecology, ecosystem ecology, biogeography, global change biology, and evolutionary ecology,

those who are interested in these subfields should also find the book of interest. I will also show how basic principles help solve problems in conservation (e.g., ecosystem restoration), agriculture (e.g., biological control), and medicine (e.g., management of host-associated microbiome). For this reason, the book should also be of interest to those interested in these applied issues.

Two related books were published recently: *Critical Transitions in Nature and Society* by Marten Scheffer (2009) and *Multiple Stable States in Natural Ecosystems* by Peter Petraitis (2013). My book will be different in four ways. First, Scheffer and Petraitis did not explicitly consider the maintenance or generation of the species pools, whereas this will be a central subject of my book. Second, Petraitis almost exclusively focused on ecological processes and Scheffer's evolutionary consideration mostly concerned macroevolution, whereas my book will emphasize eco-evolutionary feedbacks in addition to ecological and macroevolutionary processes. Third, both Scheffer and Petraitis were mainly interested in ecosystem properties, whereas my primary interest will be biodiversity and the feedback between community structure and ecosystem functioning. Fourth, Scheffer and Petraitis focused on multiple stable states and sudden shifts between them. I will present a more inclusive view, considering long-term transient dynamics and assembly cycles in addition to multiple stable states.

Many other books have been written on community ecology, but they are either general textbooks (e.g., *Community Ecology* by Peter Morin, 1999; *Community Ecology* by Gary Mittelbach, 2012) or more advanced books with a theme related but distinct from mine (e.g., *Ecological Niches* by Jonathan Chase and Mathew Leibold, 2003; *Metacommunities* edited by Marcel Holyoak *et al.*, 2005; *The Theory of Island Biogeography Revisited* edited by Jonathan Losos and Robert Ricklefs, 2010). Finally, my understanding is that two forthcoming books in the MPB series will have a similar focus to mine: *Metacommunities* by Mathew Leibold and Jonathan Chase, and *The Assembly of Ecological Communities* by Mark Vellend. However, I believe my emphasis on historical contingency will be unique.

Estimates

Book length: about 5,000 words per chapter x 9 chapters = 45,000 words total, with a total of about 300 references
Illustrations: about 5 figures per chapter x 9 chapters = 45 figures total
Completion date: December 2016

Author biography

Tadashi Fukami is an Assistant Professor (and will become a tenured Associate Professor in September 2016) in the Department of Biology at Stanford University. He has published more than 50 papers in community and ecosystem ecology, and has served on the editorial boards for *Ecology Letters*, *Oikos*, and *PLoS ONE*. He earned his undergraduate degree from Waseda University, a Master's degree from the University of Tokyo, and a Ph.D. in Ecology and Evolutionary Biology from the University of Tennessee, Knoxville. He was a postdoctoral fellow at Landcare Research in New Zealand and an Assistant Professor at the University of Hawaii at Manoa before moving to Stanford in 2008.