

Preface

The notion of multiple or alternative community states has captured the imagination of ecologists for over 50 years, and this book is only a snapshot of what has been done by so many researchers. Multiple stable states has been discussed and tested by researchers across many subdisciplines in ecology and unfortunately without much exchange of ideas across the borders. The idea of multiple stable states in ecosystems has been discovered with near independence or invented anew by researchers studying lakes, coral reefs, and semi-arid rangelands. There has been some cross-fertilization, but not as much as we might hope.

A casual glance at the citations of five of the most influential and seminal papers as of August 2012 easily makes lack of cross-fertilization clear (e.g. Lewontin 1969, May 1977, Noy-Meir 1975, Scheffer et al. 2001, Westoby et al. 1989). The ends of the spectrum are Lewontin's paper, which has been cited about 150 times, and Scheffer et al.'s paper, which has been cited over 1450 times. I suspect the frequency of citation is a reflection of the ease of access and the rise of reference databases and software. Lewontin's paper was published in a symposium volume, which is still relatively difficult to obtain. In between are Noy-Meir's paper with just over 400 citations, May's paper with almost 550, and Westoby et al.'s paper with about 750. It is interesting that the rank correlation between the number of citations and the date of publication is perfectly negative (i.e. -1.0). Far more troubling is the lack of overlap in citations. May's paper introduced the idea of multiple stable states to a broader audience, and Westoby et al.'s paper lays the groundwork for state-and-transition models and is the touchstone for nearly all models of multiple stable states of grazing in grasslands and rangelands. May's and Scheffer et al.'s papers are most often cited by researchers not working in rangelands; researchers of rangeland systems rarely cite May or Scheffer et al. There are only about 40 papers in which both Westoby et al. and Scheffer et al. are cited and another 40 papers that cite both May and Westoby et al. Out of roughly 2,300 unique citations among these three papers, only ten or about 0.4% cite all three.

As a result, I have had to make a number of tough decisions given the overwhelming span of papers about multiple stable states, and for the most part, I have attempted to cite only the earliest and more relevant literature. I have, indeed, left many citations out for various reasons.¹ As Oscar Wilde said, "I am not young enough to know everything."

This book has had a long gestation, and I am indebted to many people and organizations that have supported me during the process of writing. The beginnings of the book

¹ References can be overlooked for a variety of reasons, both pro and con. Failure to cite someone may reflect an unwillingness to cite poor, but "important" work as well as overlooking of important but obscure research. The h-index may tell us more about a Matthew effect than anything else.

took place during my sabbatical in Chile, and I am especially grateful for the support from the Fulbright Foundation and Pontificia Universidad Católica de Chile while on sabbatical. Much of the earlier work on the book could not have been accomplished without the warm and generous support of my friend and host, Juan Carlos Castilla in Chile. I also would like to thank the US National Science Foundation for its support of my research on multiple stable states. I am grateful for the patience of Ian Sherman, Lucy Nash, Helen Eaton, and the rest of the staff of Oxford University Press for seeing me through to the end. I also thank Mike Angilletta for suggesting that Oxford University Press might be a good home for this book. Parts of several sections in Chapters 2, 4, 8, and 9 have been re-worked from parts of published papers (Petraitis and Dudgeon 2004, Petraitis and Hoffman 2010, Petraitis et al. 2009).

There are many people who have pushed me along on this path. My mentors played an important role in my development as an ecologist and in how I think about ecology, and I am indebted to Tom Ebert, Jeff Levinton, and Fred Grassle. My early speculations about multiple stable states were fueled by conversations with Roger Latham and Peter Fairweather in the early 1990s. Roger and Peter have continued to provide insightful comments. Almost all of my research on multiple stable states has been done in collaboration with Steve Dudgeon, and I am especially grateful for his constant stream of encouragement, comments, and help over the last 15 years. Jon Fisher (Memorial University, Newfoundland), B. Boldgiv (National University of Mongolia), Mike Sears (Clemson University), and Mike Russell (Villanova University) have also provided many insights as have the students and faculty of the ecology and evolution group in the Department of Biology of the University of Pennsylvania. Much of my work in the field, which allowed me to think more deeply about multiple stable states, could not have been done without help from Erika Rhile, B. Boldgiv, Jon Fisher, Steve Dudgeon, Catharine Hoffman, Lisa Methratta, Nick Vidargas, Annalise Paaby, and the many students from Cheverus High School who were brought to Swan's Island by their teacher, Erika Rhile.

The writing of the book occurred in short bursts over many years, and I must thank some of my friends who provided me with places to write. This includes not only many nice desks at various universities in the USA, Chile, Australia, and Mongolia but also the occasional kitchen table in the homes of friends. For providing me this collection of quiet places, I would like to thank Peter Fairweather and Gillian Naiper (Adelaide, Australia), Tony Underwood and Gee Chapman (Spain), Jim and Wendy Hunt (San Diego, California), Bob Steneck and Rick Wahle (Darling Center, University of Maine), Gary and Mimi Rainford (Swan's Island, Maine), B. Boldgiv (National University of Mongolia), Juan Carlos Castilla (Pontificia Universidad Católica de Chile), Sergio Navarrete (Estación Costera de Investigaciones Marinas in Las Cruces, Chile), Ricardo Guíñez (Universidad de Antofagasta, Chile), Martin Thiel and Carlos Gaymer (Universidad Católica del Norte, Coquimbo, Chile), and Alvaro Palma (Quintay, Chile).

I could not have written this book without the love, support, and encouragement of my family. Carol, Dan, and Rob have always kept me grounded and reminded me that

doing an experiment in ecology is but a small slice of a world that includes bigger things such as making music, creating art, and working for human rights. Thank you for keeping me focused on the truly important things in life.

Peter Petraitis
27 August 2012
Swan's Island, Maine

1. Introduction	
1.1 Two examples of sudden, irreversible shifts	1
1.2 Making the connections between observations and theory	2
1.3 Overview of the book	3
2. What theory actually tells us about multiple stable states	11
2.1 Models, state variables, parameters, and equilibrium	11
2.2 Allee or discontinuous effects and multiple stable states for a single species	14
2.3 Consumer models with one, two, and three competitors	15
2.4 Competition models	20
2.5 Conclusions	21
3. Detection of multiple stable states	32
3.1 Signs for multiple basins of attraction: persistence, alternation	32
3.2 Mutual invasibility and basins of attraction for two stable states	33
3.3 Demonstration of hysteresis	34
4. Experimental evidence	37
4.1 Morley's comments on the badger and deer	37
4.2 Church's experiment	38
4.3 Rocky intertidal shores and the red alga	39
4.4 Concluding remarks	40
5. Catastrophe theory	41
5.1 René Thom and an introduction to catastrophe theory	41
5.2 Ecological examples	42
6. Hallmarks of catastrophes	43
6.1 Time conventions	43
6.2 The flags of catastrophe	44
7. Other modeling approaches	45
7.1 New and variation models and other conceptual approaches	45
7.2 Functional approaches	46
7.2.1 Weakly dissipative systems	46
7.2.2 Weakly dissipative systems with fast state variables	47
7.2.3 Examples of weakly dissipative systems with fast state variables	48
7.2.4 Coupled systems	49