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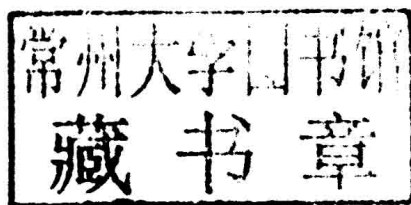
MULTIPLE STABLE STATES IN NATURAL ECOSYSTEMS

PETER PETRAITIS

Multiple Stable States in Natural Ecosystems

PETER PETRAITIS

Professor of Biology, University of Pennsylvania



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Multiple Stable States in Natural Ecosystems

For Carol, who has been with me for each step,
“no me sostiene el pan, el alba me desquicia
busco el sonido líquido de tus pies en el día”
(Sonnet XI, Pablo Neruda)

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

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Introduction

One of the most interesting and vexing problems in ecology is how natural ecosystems can appear to be so persistent and yet seem so susceptible to catastrophic change. This duality of persistence and susceptibility is observed in a wide variety of ecosystems, from coral reefs that are suddenly replaced with seaweeds to semi-arid grasslands that are shifted to shrub forests. Often the shifts are not only quite dramatic and occur without warning but also are very difficult to reverse. How can these communities appear to be so persistent for long periods, but then small shifts in environmental conditions cause an unexpected tipping of the system?

Ecologists are especially interested in these sudden shifts for both conceptual and practical reasons. On the conceptual side, these characteristics are often seen as indicators of an ecosystem with multiple stable states (e.g. de Young et al. 2004) while on the practical side, the unpredictable nature of the shifts and the inability to reverse changes can cause serious management problems (e.g. Bestelmeyer 2006, Groffman et al. 2006, Huggett 2005, Suding and Hobbs 2009, Thrush et al. 2009).

Both these characteristics—sudden and dramatic shifts in species composition and difficulty in reversing the shift—are considered hallmarks of multiple stable states, and so the theory of multiple stable states is often offered as an explanation for these sudden and unexpected shifts in the species composition of ecosystems. Again and again, natural communities that have undergone abrupt and difficult to reverse changes are put forward as examples of ecosystems with multiple stable states. Yet there are few clear guidelines about what constitutes good evidence for multiple stable states. How do we know if a sudden shift in species composition is evidence for multiple stable states, and more importantly, how do we define terms such as “sudden,” “abrupt,” “persistent,” and “irreversible,” which are so often used to discuss multiple stable states in natural communities?

1.1 Two examples of sudden irreversible shifts

Many of these abrupt and nearly irreversible changes have been due to the activities of humans. Yet while humans have been transforming the landscape and causing dramatic shifts in natural communities for hundreds, if not thousands, of years, in many cases it is not known if these shifts represent multiple stable states. The clearing of

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southern Australia and the demise of the passenger pigeon in North America provide compelling examples in which it is clear that the system has undergone irreversible changes that are likely to have some of the hallmarks of systems with multiple states.

Unlike many of the better known examples, the transformation of southern Australia is well documented. When Europeans began settling southern Australia, in the 1860s, they were confronted with vast expanses of wet eucalypt-dominated jungle that extended eastward across the Gippsland Plains and into the Strzelecki Ranges. Today this region, which is near Melbourne, is mostly a mixture of pasture, eucalypt savanna, and meadows of bracken fern and blackberries, which are nonnative species. The original forest was home to the world's largest flowering plant, *Eucalyptus regnans*, the Australian mountain ash, which can reach heights in excess of 100 m. Tarra-Bulga National Park contains one of the few remaining patches of mountain ash forest and gives one a sense of what settlers faced throughout the entire Gippsland Plains. The remaining trees of mountain ash in Tarra-Bulga tower over an understory of other large species such as blue gum (*Eucalyptus globulus*), and myrtle beech (*Nothofagus cunninghamii*). Tree ferns reach 20 m in height, and the wet ground is blanketed with smaller ferns and is home to the giant Gippsland earthworm, *Megascolides australis*, which can reach 3 m in length.

When settlers began to clear the forest for pasture, they did so with remarkable efficiency. On the plains, the trunk of each large tree was cut and girdled, cutting off the flow of sap from the roots to the crown, and low-hanging branches were cut from the trunk. Long, narrow planks, called springboards, were pounded into notches in the trunk and provided a series of stairs so that settlers could climb and cut the higher limbs. During the dry period of summer, the settlers organized community-wide burns to clear out the cut limbs and the dead trunks, and the resulting fires would often burn out of control for weeks.

The steep slopes were cleared with even greater ease: "A spectacular and economic felling method was quickly developed in the hilly country. Work would start from an already cleared pack track at the top of a ridge. Trees all the way down to the bottom of the gully would be 'nicked' on the up hill side. Then a few big trees high up the slope would be felled with care and accuracy to start an avalanche of spars (trunks), which bounced and crashed and roared down hill." (Daley 1960, p. 97).

Within a very short time, the landscape was transformed—cleared of forest and converted into pasture. The Gippsland Plains and the western areas of the Strzelecki Ranges were cleared by the 1890s. Many areas, particularly in the eastern Strzelecki Ranges, proved to be too steep for pasture and were abandoned only to be taken over by bracken fern and blackberries.

The loss of the forest has completely altered the evapotranspiration regime of the region. The cool wet forest with its boggy soil is now open dry land. Gippsland's giant earthworm is rare although honored in the annual worm festival in Korumburra, Victoria. Bracken fern and blackberries are a constant problem, even in Tarra-Bulga National Park. The mountain ash has not recovered and is unlikely to do so. Unlike many eucalypt species, mountain ash can be killed by severe fires and does not have the

capacity to regenerate after fire. The species depends on seed for regeneration, and the near perfect clearing of the forest has not only cut off the input of seeds but also created an environment in which germination is difficult. The shift from forest to pasture, bracken, and blackberries has been swift and has proven difficult to reverse.

The difficulty in reversing this trend is likely to be a combination of several factors (Lindenmayer et al. 2011). Specifically addressing mountain ash, Lindenmayer et al. suggest that landscape-level processes are important, and include climatic effects that have altered life-history patterns. Interestingly, they coin a new phrase for this—landscape traps—and assert that these are fundamentally different from multiple stable states. In fact, their conceptual model looks strikingly similar to models of multiple stable states that have been proposed for semi-arid rangelands and coral reefs.

The disappearance of the passenger pigeon (*Ectopistes migratorius*) was just as dramatic. In a span of 100 years, the passenger pigeon was driven from being the most abundant and common bird in North America to extinction. At the time of the arrival of Europeans in North America, the population of passenger pigeons was estimated to be between 3 and 5 billion (10^9), possibly accounting for 25 to 40% of all the birds in North America (Schorger 1955). Passenger pigeons ranged as far west as Texas, south to northern Florida, and into southern Canada. Nesting grounds were confined to southern New England and the US states surrounding the Great Lakes. The appellation “passenger” refers to the bird’s migratory behavior and likely from the French adjective *passager* which means passing.

Audubon’s description of the massive numbers of passenger pigeons around 1830 is almost unbelievable (Sanders 1986). Audubon, who is well known for his exquisite paintings of North American birds, described traveling by horseback for 3 days and over a distance of 90 km and having the sky filled with birds the entire time. The birds were so numerous that the sky was darkened as during an eclipse and droppings fell like snow.

Passenger pigeons formed large communal roosts at night and for breeding. Nesting pairs produced one egg, and both parents produced “milk” which was regurgitated from the crop (Schorger 1955). A nesting roost in Michigan in 1879 covered approximately 26 000 hectares (Halliday 1980). Pehr Kalm, who was a student of Linnaeus and was in North America in the 1740s, wrote that it was dangerous to walk through a forest during nesting (Kalm and Gronberger 1911). The weight of roosting birds could be so great that tree limbs the “size of a man’s thigh” could break off and whole trees were often uprooted. Droppings could be 0.3–0.4 m thick on the ground.

Passenger pigeons ate the fruits and nuts of at least 29 species (Webb 1986). Their diet varied with season, and during the spring could include insects. Schorger (1955) mentions that birds would dis-engage food if they found a more desirable item, and Webb (1986) suggests the range expansion of trees with large seeds after the retreat of the Wisconsin ice sheet 10 000 to 15 000 years ago was facilitated by passenger pigeons.

The impact of their feeding must have been enormous. Passenger pigeons weighed between 340 and 400 g and based on estimated field metabolic rates, they would have

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required between 550 and 620 kJ per day per bird (Nagy 2005). Large flocks were capable of stripping oak forests of nearly all acorns during mast years, and it should not be surprising that early settlers feared the impact of passenger pigeons on their crops (Schorger 1955).

Given the ease of capturing and killing passenger pigeons, they were exploited as food. Birds were shot—a single discharge of a shotgun was capable of killing up to 100 birds. Audubon said that it was often not possible to hear the discharge over the cooing of the birds. Trapping was done using captive birds, which were tethered to platforms and attracted other birds. These tethered birds were known as “stool pigeons.” Given the ease of capture, the industry included wholesale dealers who would provide information about roosting sites and helped spur the construction of railroads near roosting sites to lower the costs of shipping.

By the early 1890s, passenger pigeons were nearly gone. Conservation efforts failed to slow the decline. Schorger (1955) provides a listing of reported sightings of a few birds here and there during final decade, and stated in 1900 the last bird in the wild was killed in Ohio. A few birds survived in the Cincinnati Zoo but never bred successively, and the last bird, named Martha after Martha Washington, died in 1914.

The decline of the mountain ash and loss of the passenger pigeon contain features that are often associated with multiple stable states. For the mountain ash it is clear that there are two states—forests with the tree and more savanna-like systems without it. The alternative state for passenger pigeons is a “state” in the sense the bird no longer exists. In both cases, there appears to have been a point of no return at which decline in the system cannot be reversed. For animals, this is known as the Allee effect. Allee (1931) suggested that there can be a beneficial result of social interactions—for example group behavior that lowers the per-capita death rate due to predation. This effect, however, can be reduced if population levels fall too low, and thus is one of the common explanations for the decline of passenger pigeons. Communal roosts became too small to support successful breeding. While Allee was primarily interested in social interactions, any plausible ecological process that gives rise to a nonlinear function for either births or deaths has the potential for creating a system with multiple equilibrium points. The case of mountain ash is also an Allee effect in that recruitment of seedlings fails at low densities of adult trees.

Tied to the point of no return is the phenomenon of hysteresis, which is the existence of sudden and difficult to reverse shifts. The term was coined in 1890 by Sir James Alfred Ewing, from the ancient Greek word for deficiency or lagging behind, during his studies of the magnetization of metals induced by electric currents. Ewing noted that when he reversed the direction of an electric current the reversal of the polarity of induced magnetic field in metals was not instantaneous and lagged behind the change in current direction. This lag is due to a nonlinear response in the system—Ewing hypothesized that individual metal particles retained a memory of the electric field and resisted reversals in current. Formal development of the mathematics of hysteresis in nonlinear systems was carried out in the 1970s by a group of Russian mathematicians

led by the Ukrainian Mark Krasnosel'skii (Krasnosel'skii and Pokrovskii 1989). Currently the term hysteresis is more broadly used for any system in which the response to an object, a material, or a system lags behind the force applied to it. However, the underlying mathematics of all examples contains some sort of nonlinearity.

1.2 Making the connections between observations and theory

Are the changes from mountain ash forests to pasture and the extinction of the passenger pigeon reflections of the fact that these systems contain multiple stable states? And more importantly, how would we know? These questions require us to examine what we can learn from the theory of multiple stable states and how theory can be used to guide us in developing critical experimental tests and in identifying key observations. We must also come to terms on how we translate the terminology of models—parameters, state variables, and stability—into useable concepts for experimental ecology.

Nearly 40 years ago, theorists provided plausible mathematical models to explain how different communities could arise in the same environment (Lewontin 1969, May 1977, Noy-Meir 1975). Lewontin (1969) asked, "Can there be more than one stable community composition in a given habitat?" His answer was yes, and he along with others (Knowlton 1992, May 1977) went on to suggest that small environmental perturbations can produce large, discontinuous, and irreversible changes in natural communities. The switch between different communities is often sudden and occurs at a critical environmental threshold with a rapid transition in species composition.

Models of multiple stable states are easy to construct. The simplest and most often cited example in ecology is the unstable coexistence of two competing species in the Lotka–Volterra model of competition. In this case, each species, once established, can resist the invasion by the other, and these alternative conditions represent the two stable points of the system. Past history matters, and the first species that arrives and becomes established will be able to prevent any attempts by the other to invade. If both species arrive at the same time, then the relative abundance of the species upon arrival and their characteristics (i.e. the r s and K s and competition coefficients) will determine which species wins. This situation is often described as two bowls or valleys separated by a ridge. The two stable equilibrium points are at the bottom of the bowls and on the ridge there is a third equilibrium point that is unstable. This pattern was described by Lotka (1956, p. 147), who wrote, "it is clear that two pits of [stable equilibrium points] . . . cannot occur without some other type of singular point between them, just as it is physically impossible for two mountains to rise from a landscape without some kind of a valley between", although he warned this analogy was "purely qualitative." Almost as an aside, Lotka mentions that the reader can find a more complete discussion of the mathematics involved and cites references as early as 1891. While Lotka seems to have mixed his metaphor of pits with mountains, ecologists now visualize multiple stable states as valleys separated by a ridge.

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The possibility of more complex models for multiple stable states in ecosystems first came to the attention of ecologists with the publication of Lewontin's article "The meaning of stability" in 1969, but it was May's 1977 review article in *Nature* that brought the notion of multiple stable states to the forefront of ecology. May developed a series of models that showed how ecological systems could undergo abrupt and dramatic changes, and paraphrasing a 1660 saying by Pascal, May suggested these changes were as if the "hinge of history turn[ed] on the length of Cleopatra's nose...." May used dynamical models to explore catastrophic shifts in budworm outbreaks on spruce, crashes in harvesting in commercial fisheries, and transmission of malaria and schistosomiasis, and his demonstration that relatively simple models could give rise to complex and unexpected outcomes captured the imagination of ecologists. In contrast, Lewontin (1969) saw the possibility of catastrophic shifts as a serious problem for developing predictive theory in ecology and added, "[I]t must be hoped that such structural instabilities will prove to be the exception."

While the theory of these systems is well understood, whether multiple stable states actually exist in nature has remained a hotly debated subject, and the translation of theory into experimental tests has not been easy. The phrase "multiple stable states" has a very precise meaning in theory, but not in practice. Lewontin stressed that random events and historical accidents blur what stability, equilibrium, and habitat mean in nature. While stability is well defined by theorists, there is little agreement on how stability should be measured in nature (Grimm and Wissel 1997). The modifiers used to describe shifts in species composition add to the problem. Labeling shifts in species composition as "dramatic," "sudden," or "unexpected" is akin to Shakespeare asking, "Shall I compare thee to a summer's day?" (Sonnet 18). How big must a shift be to be called dramatic, or how fast to be sudden? Is it only the lack of information that causes us to be surprised by unexpected changes in species composition? Differences in terminology among subdisciplines also present serious problems. The idea that multiple stable states underlie the observation of sudden and nearly irreversible shifts in natural communities has been elaborated in several different areas of ecology, with each subdiscipline using different terms for the same phenomena, or worse, the same term for different phenomena. To add to the confusion, several conceptual ideas—most notably, state and transition models and regime shifts—have been broadened to include multiple stable states. Yet systems with regime shifts or models using states and transitions do not always have multiple stable states. Finally, while reviews of the literature tend to agree that the experimental evidence is conflicting, the same experiment may be cited as supporting opposing views (Connell and Sousa 1983, Didham et al. 2005, Peterson 1984, Scheffer et al. 2001, Schröder et al. 2005, Sousa and Connell 1985).

Part of the difficulty is how we make the links between theory, observation, and experiments. Bob May, in his seminal paper on multiple stable states (May 1977), even commented that "empirical observations remain largely anecdotal, and... theory remains metaphorical." I would suggest that even today May's observation is apropos

for almost all areas of ecology, and I believe making the link between anecdotes and metaphors remains one of the biggest challenges facing ecologists. At best, ecological theory provides ideas about how to organize observations of natural phenomena and guides research by providing testable predictions. The utility of a particular theory in ecology depends not only on how well the theory “works” but also the assumptions we make in order to create the theory. The use of simplifying assumptions means that ecological theory will always be only a metaphor or a map for reality. Not all metaphors or maps are equally useful, and a trivial but compelling example is the fact that a subway map for New York City is not useful for driving in Manhattan.

If theory provides us with maps then the usefulness of a particular map depends on what the map is meant to represent, how well it does so, and an implicit agreement between the mapmaker and the map reader about the representation. A New York subway map is a beautifully drawn representation, but not all maps are as well drawn. Even in this day and age of Google maps, most of us have suffered from the fate of relying on a map hastily drawn by a well-intentioned friend with directions to a party. Our friend’s sense of distance, important landmarks and even sense of direction may not match our own, and so we missed a critical turn and ended up arriving late.

Not all theoreticians are skilled mapmakers and not all experimentalists are adept at reading maps or using them to navigate. For example a misreading of the map for competition that was formulated by Lotka and Volterra led ecologists on a long detour about competitive exclusion. The mathematical model of two-species competition developed by Volterra and Lotka indicated that range of parameter values that allowed for stable coexistence of both species was small, and species with similar requirements could not coexist. The clearest and most precise statement of this finding is “Complete competitors cannot coexist” (Hardin 1960). However, many ecologists used Gause’s reading of Lotka and Volterra’s map. Gause showed how difficult it was to maintain coexistence in a series of experiments on competition between two species of *Paramecium*, and in his book *The struggle for existence*, which was published when he was 24, he stated that two species could not share the same niche (Gause 1934). This interpretation is often called Gause’s principle of competitive exclusion, even though several people stated the principle before him, which Gause himself acknowledged. Today, Grinnell is often cited as the earliest reference (Hardin 1960) although Johnson clearly stated the same idea in 1910 (Gaffney 1975). The interpretation by Gause, Grinnell, and Johnson of the map provided by Lotka and Volterra led ecologists on a 50-year expedition to understand why so many species appear to coexist in systems that seem to have very few niches or types of resources. Yet the problem is two-fold: the map was poorly drawn and the reading was imprecise. By the 1980s, theoreticians had shown that the number of coexisting species at stability could far exceed the number of resource classes in closed systems (e.g. Armstrong and McGehee 1980) if two key assumptions of the Lotka–Volterra model were relaxed. First, allow population growth to be a curvilinear function of densities, and second, consider nonpoint equilibria. If these