Introduction

Why do ecological systems (populations, communities, and ecosystems) change suddenly in response to seemingly gradual environmental change, or fail to recover from large disturbances? Why do ecological systems in seemingly similar settings exhibit markedly different ecological structure and patterns of change over time? The theory of multiple stable states in ecological systems provides one potential explanation for such observations. In ecological systems with multiple stable states (or equilibria), two or more configurations of an ecosystem are self-maintaining under a given set of conditions because of feedbacks among biota or between biota and the physical and chemical environment. The resulting multiple different states may occur as different types or compositions of vegetation or animal communities; as different densities, biomass, and spatial arrangement; and as distinct abiotic environments created by the distinct ecological communities. Alternative states are maintained by the combined effects of positive (or amplifying) feedbacks and negative (or stabilizing feedbacks). While stabilizing feedbacks reinforce each state, positive feedbacks are what allow two or more states to be stable. Thresholds between states arise from the interaction of these positive and negative feedbacks, and define the basins of attraction of the alternative states. These feedbacks and thresholds may operate over whole ecosystems or give rise to self-organized spatial structure. The combined effect of these feedbacks is also what gives rise to ecological resilience, which is the capacity of ecological systems to absorb environmental perturbations while maintaining their basic structure and function. Understanding these complex behaviors is important for managing ecological systems and their responses to environmental change.

General Overviews

In this article, we trace the history of the concept of multiple (or alternative) stable states, highlight important controversies and touch points in its development, and select focal ecosystem studies that represent the range of ecological systems and approaches to the investigation of alternative stable states. The first half of this list focuses on studies with the broadest application across diverse ecological systems. We present conceptual underpinnings in the study of multiple-state ecological systems, beginning with the introduction of the concept and ending with recent efforts to understand why some ecological systems may be more likely to possess multiple stable states. We then proceed to studies that have developed novel and widely applicable approaches to the evaluation of multiple stable state hypotheses and examine how different subdisciplines of ecology have approached inference of multiple stable states. The subsequent sections describe how theoretical and conceptual discussion of the nature of resilience in ecological and socio-ecological systems has deeply informed the development of modern approaches to adaptive management. In the second half of this article, we focus on the development of system-specific understanding of multiple stable states. Within each section, we focus on the first introductions of stable state hypotheses in each system and then trace major system-specific theoretical and empirical advances. We have made an effort to include series of papers that present competing hypotheses, observations, and interpretations, as such controversies are common in the study of multiple stable states. In assembling this article, we have included a range of approaches and
scales, and tried to fairly represent disagreements over the interpretation of theory, observation, and experiment. Our article begins with the earliest explicit descriptions of multiple stable states and extends to several emerging frontiers in the study of complex ecological systems. Space limitations have prevented the inclusion of many worthy ecological studies. We encourage readers to use this article as a starting point for the wider exploration of the study of complex systems in ecology and affiliated fields such as physics, geomorphology, economics, and sociology. We also encourage readers to pursue foundational and recent studies in the areas of disturbance ecology and stability theory; a complete overview of these areas is beyond the scope of this collection. These literatures will help readers appreciate the connections of multiple stable state studies to other important topics in ecological theory and research.

**Theoretical Basis for Alternative Stable States**

The idea that ecological systems have alternative stable state originated from the understanding of theoretical population and community dynamics, but has been applied widely through the development and testing of theory across virtually every type of terrestrial and aquatic habitat. Lewontin 1969 introduces the qualitative argument that the importance of history in ecological systems arises from the presence of multiple stable configurations of ecological communities. Holling 1973 introduces the concept of resilience as the persistence of any particular state and argues that the ubiquity of feedbacks and variability in ecological systems invalidates the expectation of a single equilibrium. Early case studies provided important conceptual advances: Sutherland 1974 examines biofouling communities in one of the first system specific examinations of the potential presence of alternative stable states, while Noy-Meir 1975 applies predator-prey models to rangeland systems and finds evidence for possible alternative states. Indeed, a wide range of classic ecological models can exhibit more than one stable state, as demonstrated in May 1977. Wilson and Agnew 1992 synthesizes a variety of mechanisms by which interactions between vegetation and the environment produce the types of positive feedbacks loops that are necessary for the presence of alternative stable states. Scheffer, et al. 2001 synthesizes the emerging evidence for multiple stable states in ecological systems and links the presence of multiple states to rapid and major (i.e., catastrophic) transitions in ecological systems. An as-yet unresolved question is why some systems exhibit alternative stable states and others appear not to. Didham, et al. 2005 proposes that multiple stable states are more likely in systems subject to abiotic stressors, while Kéfi, et al. 2016 explores the types and strength of positive interactions that are necessary to produce multiple stable states.


Didham and colleagues propose a general theory for why some ecosystems have alternative stable states while others seem not to. Specifically, they argue that communities experiencing stressful abiotic conditions or disturbance regimes are more likely to exhibit nonrandom trait under-dispersion. Specific, narrow, and distinct assemblages result, transitions between which are more likely to be sudden or catastrophic shifts in community structure than in assemblages weakly structured by environmental adversity.


Holling argues that variability is an inherent feature of ecological systems and therefore that the persistence of populations and communities and their interrelationships, rather than their equilibrium abundances, is the important measure of ecological stability. Holling defines this persistence as “resilience.” “Stability” is the degree to which disturbances displace systems from an equilibrium state. He argues that these properties are independent, and potentially antagonistic, and presents a theoretical framework for their measurement.

**Kéfi, S., M. Holmgren, and M. Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems?**
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Kéfi and colleagues addressed the question: When can positive interactions cause alternative stable states in ecosystems? Positive interactions may contribute to creating a positive feedback, and a positive feedback is a necessary condition for the emergence of alternative stable states at the community level. The key knowledge gap is translating from the individual-level positive interactions to community and the ecosystem scale positive feedback loops, and thereby alternative stable states.


Lewontin distinguishes proximate and ultimate explanations in ecology and links these to system dynamics. Proximate explanations relate the present state of natural communities solely to contemporary conditions, which presumes those conditions set a single and specific equilibrium of community composition. Ultimate explanations invoke history to explain the present state of communities and ask why a community occupies one of many possible stable points.


May applied the idea of multiple stable states of communities to simple one- and two-species systems. The author reviewed a variety of mathematical models for ecological systems, and each of these models showed the potential for two alternative stable states, so that continuous variation in a control variable can produce discontinuous behaviors. May’s work was the first robust theoretical indication that alternative stable states might be common features of ecological systems.


Noy-Meir applies predator-prey models to grazing systems in arid lands. By comparing model parameters that generate multiple stable states (MSS) to real variation in grazing rates and vegetation growth across grazing systems, he concludes that such complex behaviors are plausible or even likely, and that both theoretical ecology and resource management would benefit from greater integration. The paper serves as an accessible introduction to graphical interpretation of stability of simple ecological models.


Scheffer and colleagues argue for the generality of abrupt changes in ecological systems (which they label “catastrophic transitions”) and link these changes to the presence of alternative stable states. The authors present and explain a variety of examples of observed large-scale abrupt shifts in major ecosystems, arguing on an empirical basis that alternative stable states and resulting catastrophic shifts might be widespread under major anthropogenic environmental change. They propose that the loss of resilience paves the way for a switch to an alternative state.


Sutherland further developed the idea of multiple stable points in natural communities, originally proposed in Lewontin 1969. The paper presents empirical examples from various ecosystem types to show the existence of multiple stable points in ecosystems and to show the importance of historical events in determining the state of a community.

Wilson and Agnew describe the various classes of vegetation-environment feedbacks that can occur (termed “switches” in the paper) in terms of the nature of relationships among the interacting species and characteristics of their environment. They argue qualitatively that these switches can produce divergent and stable ecological communities, and they present an extensive list of plausible feedback mechanisms in vegetation-environment interactions.

**Spatial Processes**

As Levin 1974 shows, consideration of spatial processes creates the potential for a wider range of complex behaviors in ecological systems. Shurin, et al. 2004 examines how local and regional variability in species interactions and environmental conditions affect the persistence of competing species that produce alternative stable states. Rietkerk, et al. 2004 provides an overview of patterned landscapes and argues that the feedbacks that create pattern also favor the occurrence of multiple stable states at the landscape scale. Rietkerk and van de Koppel 2008 identifies scale-dependent feedbacks as a general mechanism that can create regular spatial pattern. Sheffer, et al. 2013 demonstrates how the scale of heterogeneity interacts with and interferes with pattern-forming feedbacks.


Levin introduces spatial processes into predator-prey and other population models. Among the results of this analysis, he demonstrates that when the dispersal rate of prey is sufficiently greater than that of predators, the steady-state solution of predator and prey populations is not stable. The implication is that spatial variation in the abundance of predators and prey will arise spontaneously. Such instabilities are the basis for pattern formation and other nonlinear processes.


This paper reviews self-organized patchiness and patterned landscapes. The authors go through various ecosystems, but also review the "string" or "maze" patterns of peatlands. The paper links self-organized spatial structure to the occurrence of multiple stable states (patchy and homogenous) at the landscape scale.


The authors review the evidence for the mechanisms behind pattern formation in ecosystems. They outline the importance of scale dependent feedbacks—long-distance inhibition with short-distance facilitation—as the general mechanism for the formation of regular pattern.


Sheffer et al. developed a unifying framework for the understanding of spatial vegetation patterns in heterogeneous landscape for the
first time. Combining a numerical simulation and field study, they suggested that real landscapes are generally mixtures of template-induced and self-organized patchiness.


This study evaluates the regional dynamics that allow persistence of competitors whose interactions produce priority effects and thus alternative stable states. Using a meta-community model, they show that abiotic heterogeneity can allow persistence of competing species and interactions that produce local alternative stable states, while homogeneous conditions favor regional competition with multiple stable outcomes.

**Inference of Multiple Stable States**

Although feedbacks are common, even ubiquitous, in ecological systems, demonstrating that a particular system has multiple stable states is a theoretical and empirical challenge. In general, community ecologists, presented in works such as Connell and Sousa 1983, have applied stricter criteria to judge whether ecological system have alternative stable states, whereas ecosystem ecologists, such as in Scheffer and Carpenter 2003, have argued for a weight-of-evidence approach. Beisner, et al. 2003 identifies another distinguishing view of community and ecosystem perspectives as whether abiotic factors and feedbacks are rightly viewed as internal or external to the system. Andersen, et al. 2009 reviews approaches to testing for regime shifts, which includes both true alternative stable states and threshold responses to external drivers. Applying the criteria of Connell and Sousa, Schröder, et al. 2005 reviews experimental tests of multiple stable states (MSS) and finds few field studies that support the MSS hypothesis. Van de Koppel, et al. 2001 shows how simple models may be coupled to field observations to test multiple state hypotheses, and Ives, et al. 2008 extends this approach to include a larger number of potential dynamic regimes. Seekell, et al. 2013 infers the presence of multiple stable states from a whole-lake experiment.


Anderson et al. review methods for the inference of regime shifts. Examples focus on marine systems where researchers commonly use multivariate analyses such as ordination to characterize covarying community and ecosystem structure.


This paper discusses the mismatch between ecosystem and community ecology in those disciplines’ acceptance of evidence of multiple stable states. The key difference arises from the different theoretical treatment of the abiotic environment. In community ecology, the view of abiotic environmental factors as external to the system of interest creates a narrower interpretation of alternative stable states. From an ecosystem perspective, changing drivers help inform rather than limit inference of multiple states.


Connell and Sousa propose persistence of populations over multiple generations and resistance to and recovery from disturbance as
criteria for deeming natural populations or communities stable or persistent. To infer that multiple communities are stable, these criteria must hold for more than one community under exactly the same environmental conditions.


Ives et al. use time series analysis of midge population densities in lakes to demonstrate the occurrence of multiple attractors with different temporal patterns. They observed populations with stable, cyclical, and chaotic dynamics, and showed that transitions between these were abrupt and discontinuous.


Scheffer and Carpenter identify sudden change over time, multimodal distributions, hysteresis, and sensitivity to initial conditions as the empirical observations and experimental results that indicate multiple stable states at the ecosystem level. They note that each of their proposed lines of evidence has alternative explanations. Combining multiple lines of evidence from different approaches, including models and experiments, provides the strongest evidence for the presence of alternative stable states.


Schröder and colleagues reviewed direct evidence for alternative stable states from manipulation experiments. Based on an extensive literature search, only thirteen of thirty-five experiments directly demonstrated the existence of alternative stable states. They found a bias toward laboratory experiments compared to field experiments in demonstrating bistability. Meanwhile, they did not find any clear pattern of the distribution of alternative stable states over experimental systems, habitat types, or involved organisms.


Seekell et al. analyzed results from a whole-lake experiment, in which the gradual increase in a top predator induced changes in other trophic levels. The authors use several statistical approaches to show that these changes are not linear, but rather reflect the presence of multiple attractors within the ecological system.


Van de Koppel et al. introduce an approach that couples simple mathematical models with field observations to infer the presence of multiple stable states in a benthic estuarine system. This work highlights the value of integrated theoretical and empirical approaches in an explicit hypothesis-testing framework when evaluating the presence of multiple stable states.

**Defining Resilience**
Resilience in the most general sense is usually meant to convey the ability of a system to recover to its prior state. Gunderson 2000 distinguishes between resilience concepts that assume the presence of a single global equilibrium ("engineering resilience") and those that assume the presence of multiple equilibria ("ecological resilience"). Holling 2001 integrates the concept of resilience with a hierarchical concept of adaptive cycles. Carpenter, et al. 2001 argues that measurable resilience must apply to specific perturbations and response variables. Ives and Carpenter 2007 demonstrates that the link between diversity and stability (and thus resilience) depends heavily on both the mechanisms and definitions of stability. Walker, et al. 2004 adds the concept of transformability as an aspect of socio-ecological resilience. Rist, et al. 2014 applies the resilience concept to production ecosystems and argues that human subsidies represent a form of coerced, and ultimately brittle, resilience.


Carpenter and colleagues addressed the issue of how to quantify resilience for socio-ecological systems (SES), and argue that measures of resilience require specifying both the response and the stressor. They explored the possibilities and limitations of measurable operational definitions of resilience for socio-ecological systems, using two contrasting SES: lake districts and rangelands.


Gunderson distinguishes between engineering resilience, defined as the rate of recovery to a pre-disturbance state, and ecological resilience, defined as the magnitude of change from which recovery can still occur. He argues for a hierarchical model of ecological resilience, integrating finer, faster scales with slower processes that create “memory.” Keystone structuring processes that link these scales are essential components of resilience and thus useful targets for management.


Holling introduces the concept of panarchy, which links adaptive cycles within scales (exploitation, conservation, release, reorganization) to the resilience of ecosystems across scales. The hierarchal structure of panarchy protects the other levels of structure from collapse during experimentation or adaptation. Holling presents this concept as framework for sustainable development and management, and increasing the adaptive capacity of a system.


Ives and Carpenter discussed the relationship between stability and diversity. They listed a number of different definitions for stability, which reflected different properties of ecosystems. These multiple definitions of stability necessarily result in varied diversity-stability relationships in theoretical models. They reviewed published studies on diversity-stability, and showed that existing empirical studies emphasized only a few types of stability, and rarely uncovered the mechanisms for stability.


This paper applies concepts of resilience to production ecosystems such as harvested forests, aquaculture, and croplands. They argue that subsidies provided to these ecosystems to enhance their productivity are a form of coerced resilience.

The authors use theory of nonlinear stability to clarify, explain, and diagnose known examples of regional development, poverty, and sustainability. They define resilience, adaptability, and transformability in the context of social ecological systems, and they discuss the implications of these concepts for understanding dynamics of social-ecological systems.

Managing Complex Systems

The potential occurrence of multiple states is not only important for our basic understanding of how ecological communities and ecosystems work, but for how decision makers at a range of scales manage and plan for environmental change. Modern approaches to environmental management owe their origins in large part to Walters and Holling 1990, which recognized that the difficulty of predicting nonlinear ecological systems required an experimental and flexible management approach. As argued in Holling and Meffe 1996, attempts to tightly control ecological systems can have the unintended consequence of undermining their resilience to environmental variability. As argued in Folke, et al. 2004, maintaining biodiversity is one approach to fostering the ability of ecological systems to respond to and accommodate variability and disturbance. Suding and Hobbs 2009 describes how resilience and multiple stable state concepts can be practically incorporated into ecological restoration. Rockström, et al. 2009 identifies global-scale thresholds for sustainability. Pahl-Wostl, et al. 2008 describes how models of adaptive management have continued to evolve, incorporating shared learning and stakeholder engagement in goal-setting and assessment stages of adaptive management. A few studies have begun to explore how decision-making processes themselves can introduce new dynamics to adaptive management. A few studies have begun to explore how decision-making processes themselves can introduce new dynamics to adaptive management. A few studies have begun to explore how decision-making processes themselves can introduce new dynamics to adaptive management.


In this study, the authors use an agent-based model of agricultural ecosystems and decision making to evaluate how these socio-ecological systems respond to disturbance (as climate variability). Their results indicate the potential for alternative stable states to arise from interactions among biophysical processes, economic dynamics, and land-use decisions.


This review discusses maintaining resilience in ecosystems. The authors propose that loss of biodiversity and functional diversity may decrease the resilience of the system and increase the likelihood of regime shift. Adaptive management and maintenance of resilience are required to keep ecosystems in a desirable state or improve degraded systems.


This paper discusses top-down management of ecosystems where managers try to control an ecosystem from direct control. This type of control can cause surprising behavior and consequences through the loss of ecosystem resilience. The authors propose other approaches to sustaining resilience in ecosystems.

Application of adaptive management principals to ecosystems can take different forms. In water resources, this shift from command and control to adaptive management is taking the form of engineering traditions versus social learning. Historically, engineering solutions focused on technical solutions to manage risks. This paper introduces social learning, an iterative learning process between community members, to find solutions as an alternative to engineering solutions.


The authors demonstrate how conventional versions of ecosystem management can lead to ecosystem collapse through a model of a two-state lake (oligotrophic and eutrophic). The typical methods of ecosystem management can lead to a cycle of collapse and recovery. This result suggests that alternative methods of management are necessary, and the authors present management approaches that could help prevent tipping to a new state.


This paper identifies sustainability thresholds for major aspects of global change, with the goal of identifying a safe operating space for humanity. Some of these targets are proposed as true thresholds in the sense that crossing them may induce sudden or irreversible change, but in most cases, and as the authors acknowledge, the magnitude of change and the nature of global responses to these drivers remain poorly understood.


Threshold concepts are being applied to conservation and management, but in many cases without evaluation. The authors introduce a framework for incorporating threshold models into restoration that emphasizes evaluation, decision making, and management.


Walters and Holling use agricultural systems to illustrate the inherent problems and unpredictable behaviors that systems can exhibit with management. They propose experimentation and adaptive management as solutions to unpredictable and nonlinear nature of systems.

**Leading Indicators**

Leading indicators, or early warning signals, of regime shifts provide the hope that scientists and managers can foresee the onset of regime shifts and proactively intervene to prevent them. Scheffer, et al. 2009 introduces the theory of generic early warning indicators and demonstrates their occurrence in a wide range of ecological and other systems. A broad class of generic indicators such as rising variance, flickering between states (Guttal and Jayaprakash 2008), critical slowing down (Dakos, et al. 2008), and changes in spatial auto correlation have the potential to warn of pending regime shifts, even when and where mechanistic understanding is poorly developed. These indicators have been validated in both field (Carpenter, et al. 2011) and laboratory experiments (Dai, et al. 2012), and
applied to remotely sensed data over whole continents (Verbesselt, et al. 2016). The rapid growth of the literature around leading indicators has also prompted critical analysis of their generality, timeliness, and utility (Boettiger, et al. 2013) and efforts to understand their limitations and timescales (Contamin and Ellison 2009).


The authors present a review of leading indicators, including their limitations and areas for development of new methods. They conclude that detection of these signals through statistics is difficult and not all systems exhibit leading indicators.


The authors present a whole ecosystem experiment where top predators in a lake were added to a lake to destabilize the food web. Comparing with a reference system, they monitored various components of the food web and measure the variance and skewness of the data. They found that the trophic levels show evidence of regime shift a year before the manipulation was complete.


The authors applied leading indicators to a model of lake eutrophication to determine which tests gave adequate advanced warning. They found that high-frequency signal in spectral density of a time series is the best leading indicator of regime shifts. The authors also discuss what amount of time is enough for advanced warning and what factors change that time period.


In this experimental study, authors use yeast colonies to test existing theories about critical slowing down. They found that population density increased in variation when nearing a tipping point. They conclude that this experiment supports theories of critical slowing down as an indicator of coming regime shifts.


Using climate data, authors try to determine if critical slowing down could have predicted historical climate shift. They found that eight historical climate shifts were preceded by slowing down of fluctuations. They conclude that critical slowing down could be used across many systems to predict regime shift.


The authors introduce skewness in time series data, showing asymmetry or flickering, as a possible warning signal of future regime
shifts. They use model simulations to test the ability of this method to predict impending shifts.

This paper reviews the early warning signals that scientists have purposed for ecosystems. The authors present a concise review of the theory and application of indicators of critical transitions. They introduce critical slowing down, or when a system begins to recovery more slowly from perturbations. They also discuss the theory and symptoms of flickering, or when a system moves between two basins of attraction.

This paper uses remote sensing to quantify temporal autocorrelation of tree recovery from drought. The study examines changes to autocorrelation in the Normalized Difference Vegetation Index (NDVI) with fluctuations to precipitation, temperature, or soil quality. The authors found that temporal autocorrelation increased as the precipitation reached the level that can be a tipping point for forest collapse.

Lakes
Early work in shallow lakes developed simple models of transitions in trophic state from clear water to phytoplankton-dominated turbid states. Sediment paleo-records such as Blindow, et al. 1993, and more recently Hargeby, et al. 2007, indicate clear shifts between these states. Experimental studies, including the mesocosm study Chase 2003 and whole-system interventions (Ibeling, et al. 2007), confirm that oligotrophic and eutrophic conditions can be alternative stable states. These transitions arise through a number of reinforcing feedbacks among trophic structure and sediment suspension (Zambrano, et al. 2001), and between phosphorus loading and phytoplankton productivity (Carpenter 2005). In tropical lakes, floating plants can also produce an alternative stable state (Scheffer, et al. 2003). More broadly, Scheffer and van Nes 2007 reviews the variety of stable states that are possible in lakes, depending on their setting, size, and other characteristics.

This paper presents empirical data from two Swedish lakes that have shifted several times between clear state with submerged vegetation and turbid state with almost the absence of submerged vegetation. They propose negative feedback mechanisms between submerged vegetation and light availability. They also discuss the role of piscivorous fish on the system.

This paper presents a model that looks at mechanism for persistent turbid, eutrophic lake state after reduction of nutrient inputs. Soil phosphorus can maintain the nutrient of level of a lake through slow flux of nutrients from the soil. They found that this state might be irreversible unless drastic steps are taken to reduce the amount of nutrients in the soil.

Experimental manipulations of grazers and nutrients indicate the presence of alternative eutrophic and oligotrophic states in pond mesocosms.


Hargeby et al. present a long-term empirical data set of shifts in two Swedish lakes. They found that changes in nutrient concentrations could have driven these shifts in the lakes over the decades and caused long-term destabilization of the clear water state.


This paper presents data from the restoration of Lake Veluwe, Netherlands, during and after a return to a clear state. They show hysteretic behavior of some variables during the restoration process. Unlike some other studies, they found that hysteretic behavior was not related to internal p-loading, but instead to light attenuation caused by sediment suspension caused by waves and benthivorous fish. In addition, reintroduction of zebra mussels (Dreissena) helped to push the lake back to a clear state.


Scheffer et al. model the invasion of mats of free-floating plants in tropical lakes after nutrient enrichment. These mats cause dark, anoxic conditions that can lead to state change. They use a model to show that free-floating plants can be a self-stabilizing state. They also present evidence from field data for alternative stable states between free-floating mats and clear lake states.


This review discusses the advances in theory and examples beyond the original clear/turbid case of multiple stable states in shallow lakes. They look at how nutrients affect shallow lakes and the possible changes to shallow lakes with climate change. In addition, they discuss other possible alternative states in lakes, such as free-floating plants and cyanobacteria.


Fish can alter the trophic web of a lake ecosystem and shift lake states. In this paper, the authors explore the effects of introducing benthivorous common carp on lake state through a simple model of carp density, invertebrates, and sediment resuspension. At a certain density threshold, fish overexploit the benthic invertebrate population until collapse, resulting in increased turbidity caused by prey searching of fish. They found this pattern was more significant for turbidity in shallow lakes than deeper lakes.
Open Oceans

Because biota have limited ability to influence large-scale climatic and circulation patterns, open-ocean scientists have adopted the term "regime shift" rather than "alternative stable states" to describe sudden shifts from one community or ecosystem state to another. Conversi, et al. 2014 proposes that open ocean and near-shore marine systems differ in the importance of physical versus ecological processes as drivers of regime shifts. Methods to determine if a regime shift has occurred are complex and must take into account our limitations when sampling the open ocean (Mantua 2004). Regime shifts may be triggered by overharvesting by fisheries (Myers, et al. 1997); by shifts in ocean circulation patterns (Beaugrand 2004); or, in near-shore environments, by changes in salinity and nutrients (Petersen, et al. 2008). Regardless of the driver, changes in physical conditions or trophic structure can cascade up and down food webs with consequences for community structure and biogeochemical processes (Chavez, et al. 2003; Litzow and Ciannelli 2007). Other studies have pointed to climatic shifts in the open ocean that can change the structure of organisms in the ecosystem (Beaugrand 2004).


Beaugrand discusses the regime shift in the 1980s in the North Sea. He attributes the regime shift to climate and oceanic forcing, including increased sea surface temperature and changing wind direction and intensity. Using plankton data and fish recruitment, Beaugrand found shifts in the biological data matching the shifts in the physical conditions.


Anchovies and sardines abundance have switched in several areas in the Pacific Ocean. Authors related changes to marine food webs (zooplankton and primary production) to physical changes (thermocline, sea surface temperature, currents) in the ocean causing the shifts between sardines and anchovies.


This paper highlights gaps in the theory of marine regime shifts and proposes a framework for investigating the relative importance of physical and ecological processes driving regime shifts across different near-shore and open-ocean ecosystems.


Litzow et al. use a thirty-four-year time series of Pacific cod and five prey species data to explore the drivers of trophic control. They found that warming caused shifts between top-down and bottom-up control.


Review paper outlining the methods for detecting regime shifts in marine environments and the strengths of each approach using

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Mantua also recommends combining empirical and modeling approaches to detect a marine regime shift.


The authors argue that virtual population analysis depict lower recruitment levels of cod than survey-based analysis of fishery stock. They found that high juvenile mortality was most likely due to discarding young fish in fishing practices, leading to catch misreporting and an overestimation of abundance. They conclude that overexploitation, not juvenile recruitment, was the cause of the fishery collapse.


This study documents a major shift in the structure of a coastal ecosystem that arises from the interaction between nutrient enrichment and salinity. The paper documents a cascade of interactions from changes in benthic filter feeders to water clarity and the structure of primary producers, and ultimately to waterfowl.

Coral Reefs

The coral reef literature provides a clear example where different lines of evidence support different conclusions about the occurrence of multiple stable states. The core feedback in coral reef multiple state models is the depletion of grazers that leads to overgrowth of reefs by macro-algae, which in turn inhibit colonization by corals (Knowlton 1992). While the importance of grazer algae interactions is widely recognized, the transitions from coral to macro-algae have also been hypothesized as a simple threshold or phase shift (Dudgeon, et al. 2010). Theoretical models suggest that coral reefs only have alternative stable states (ASS) under a limited set of conditions (Fung, et al. 2011), and large-scale surveys have failed to detect clear modes of coral and algal extent (Żychaluk, et al. 2012). On the other hand, grazer dynamics interact with hurricanes to influence the probability of state changes (Mumby, et al. 2007); the combination of these drivers could obscure the local effects of multiple stable states. A recent, novel approach combining field experiments and modeling supported the presence of alternative stable states (Muthukrishnan, et al. 2016).


This paper challenges the view that coral reefs have macro-algal assemblages alternative states. Dudgeon et al. differentiate between multiple stable state (bistable) and phase-shift (or threshold) hypotheses and argue that evidence supports the phase-shift hypothesis in coral reefs.


Fung et al. use dynamic models to show that with or without anthropogenic stress (i.e., sedimentation, fishing, eutrophication), coral
Reefs can exhibit ASS. They also found that discontinuous phase shifts only occurred in the models where coral characteristics were at the extremes of the empirically determined ranges.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–682. Knowlton details the theoretical framework in which multiple stable states of coral and algae can persist in a single environmental regime. This early paper describes the conditions necessary to produce multiple stable communities in coral reef ecosystems.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101. Mumby et al. used a fully parameterized simulation model, as well as a simple analytical model, to analyze an urchin mortality event in the Caribbean coral reefs. They found thresholds of urchin and parrotfish grazing that lead to hysteretic return to high coral cover after disturbance. The authors also calculated resilience of the coral ecosystem to disturbance based on amount of grazing.

Muthukrishnan, R., J. O. Lloyd-Smith, and P. Fong. 2016. Mechanisms of resilience: Empirically quantified positive feedbacks produce alternate stable states dynamics in a model of a tropical reef. *Journal of Ecology* 104:1662–1672. This paper uses both empirical data and a simulation model to measure feedbacks and assess ASS in the coral reefs of the Eastern Tropical Pacific. Through the use of bioassays, they identified feedbacks on algal growth: herbivore grazing activity and nutrients. Using these feedbacks in a simulation model, they found the feedbacks were necessary for hysteresis and bistability. Their modeling results were complemented by empirical data set.


Shallow and Intertidal Marine Systems

As in coral reefs, studies of alternative community states in kelp forests and intertidal zones has revolved around distinguishing true alternative stable states from phase shifts driven by broader-scale biotic (predation) or physical drivers (current and salinity). Simenstad, et al. 1978 first proposed that kelp forests might exhibit alternative stable state dynamics, based on long records of diet from Aleut archaeological sites. Konar and Estes 2003 shows experimentally that the physical structure of kelp blades creates a feedback through exclusion of urchin grazers. Filbee-Dexter and Scheibling 2014 reviews evidence of alternative stable states across many kelp forest sites. Along rocky coasts, distinct communities can be maintained by difference in predator abundance, leading Bertness, et al. 2002 to argue that these are not self-maintained alternative stable states. However, Menge, et al. 2017 shows that experimentally established communities can persist for decades. Paitritis, et al. 2009 demonstrates the importance of scale to the establishment of alternative stable communities following major disturbance events, and Paine and Trimble 2004 illustrates how size dependence of predator-prey interactions can stabilize newly established communities.
This study uses experimental manipulations to evaluate whether mussel beds and macro-algae represent alternative stable states in the rocky intertidal zone. Comparison of cleared plots with and without consumers indicates that the distinct communities are deterministic outcomes of environmental conditions and trophic interactions rather than metastable communities.

This paper reviews and synthesizes studies of transitions between kelp beds and sea urchin barrens. Hysteresis and documented feedback mechanisms lead the authors to conclude that these transitions generally represent true alternative, but can also occur in response to changes in broader-scale oceanic drivers.

This experimental study evaluates feedbacks that maintain sharp and stable boundaries between kelp beds and nearby barrens. They conclude that that physical motion of kelp is an important mechanism inhibiting urchin invasion, and that this feedback may maintain alternative stable states.

Resampling of a long-abandoned field experiment shows the persistence of artificially established communities, indicating strong and long-lasting priority effects that are consistent with an alternative stable state hypothesis.

This study links long-term records of mussel and seaweed abundance with experimental demonstrations that mussels can achieve size refuges from starfish predation. This escape size favors the establishment of alternative stable states depending on disturbance regime.

This study integrates statistical analysis of broad-scale and long-term observations with experimental manipulations of rocky intertidal communities. The authors conclude that algal and mussel communities are true alternative stable states, and that transitions between these states require relatively large disturbance events that reset colonization dynamics.

This study uses deposits from Aleut communities to reconstruct the history of near-shore marine communities. Sharp shifts in diet composition are uncorrelated with changing oceanic conditions, leading the authors to hypothesize that nearshore communities exhibit alternative stable states.

Wetlands

In low-relief wetlands, biota can exert strong effects on soil development and micro-topography, through effects on accrual of organic and inorganic material, which in turn feed back on vegetation abundance and composition by affecting hydrologic and biogeochemical conditions. Such interactions can create two or more local associations of elevation and vegetation, and these mosaics can occur in a wide range of striking spatial patterns. In peatlands, Eppinga, et al. 2008 uses spatial patterns of nutrients and hydrologic conditions to evaluate nutrient accumulation and anoxia feedbacks as possible mechanisms of maze pattern formation in peatlands. Marani, et al. 2013 shows that the physiological and morphological characteristics differences between species generate distinct elevation equilibria and patterns of tidal wetland zonation. In the Everglades, Larsen and Harvey 2010 shows how the spatial pattern of distinct ridges and sloughs arise from the coupling of peat accumulation and transport of flocculent organic matter. In carbonate landscapes, Watts, et al. 2014 argues that regularly sized and spaced depressional wetlands may arise from the coupling of hydrologic conditions, vegetation productivity, and bedrock dissolution. Where erosive energy is particularly high, the persistence of a wetland of any kind may depend on vegetation feedbacks that resist that erosion, as demonstrated in Heffernan 2008 in desert streams. Dong, et al. 2015 shows that the distribution and persistence of wetlands in desert drainages depends on how vegetation-erosion feedbacks interact with hydrologic variability over time and the geomorphic template of river corridors. Coastal wetlands can similarly constitute an alternative stable state maintained by vertical accretion or sediment erosion feedbacks (Kirwan and Murray 2007, Mariotti and Fagherazzi 2013). In other low-relief settings, fire-driven regime shifts from forests to wetlands may be reinforced by changes in landscape-scale water balance (Fletcher, et al. 2014).


Dong et al. examined the response of the spatial pattern and distribution of riverine wetlands in a desert stream to interannual variation in the hydrologic regime. They found that the geomorphic setting of the wetlands provided more explanatory power in dry years than wet years. Additionally, the geomorphic setting constrained areas with low vegetation cover, whereas the density dependent feedback stabilized areas with high vegetation cover.


Peatlands can exhibit patterning in the form of hummocks and hollows (elevation differences). This empirical study tested the mechanistic theory (scale dependent feedbacks) behind these patterns. They found that the nutrients, hydrology, and hydrochemistry of the landscape fell within the predicted pattern and were consistent with the scale-dependent feedback theory.


Fletcher et al. used pollen records to show a shift between forest and wetland in Australia. A catastrophic fire drove an irreversible shift from forested Cyperaceae-*Sphagnum* wetland to a non-forested Restionaceae wetland at c. 7000 calibrated yr. BP. Reduced
interception and transpiration of the non-forest state resulted in local waterlogging, presenting an eco-hydrological barrier to forest reestablishment over the past seven thousand years.

Development of ciénegas (riparian wetlands in desert drainages) was studied in a desert drainage in Arizona after the reestablishment of wetlands. Using a model, Heffernan shows that a density-dependent vegetation mechanism stabilizes the channel substrate in the face of flooding and scour. Empirical data from Sycamore Creek supports model results with bimodal distribution of vegetation cover and nonlinear, negative relationships between herbaceous biomass and aboveground biomass prior to flood.

This paper presents a 3-D model of tidal marsh building and channel network progression. In particular, this model develops feedbacks between vegetation and sediment deposition/transport on the marsh platform. Vegetation determines the sediment deposition, creek bank slumping, and the rate of sea-level rise under which the marsh is able to persist. They find that the feedback between vegetation and sediment dynamics creates a metastable equilibrium of marsh platform elevation even under increasing rates of sea-level rise.

This paper explores patterning that is parallel to flow, such as the pattern found in the ridge and slough landscape of the Everglades National Park, Florida. The authors modeled feedbacks between vegetation, hydrology, and sediment transport. They found that flow on the landscape that is just enough to redistribute sediment was necessary for pattern formation; flow greater or less than this condition resulted in different vegetation and open-water areas.

Vegetation zonation with sharp boundaries is a frequently observed feature of salt marshes. In this paper, Marani et al. model a transect along the marsh platform to determine the drivers of zonation. They found that vegetation can build elevation that is suitable for a species’ adaptive range, effectively engineering the ecosystem and creating multiple stable states. They support their findings with field data from Venice Lagoon, Italy.

In this paper, Mariotti et al. integrate the lateral controls on salt marsh area to a model that accounts for both lateral migration and vertical building processes. They find that at a threshold width of tidal flat and fetch, marshes erode to a low wetland area equilibrium. This state is reinforced by a feedback between increasing fetch and increased erosion. They also find that sediment concentration, not sea level rise or wind regime, explains the variability in the critical width threshold. The results of this study suggest that there could be two alternative stable states of marsh extent: fringing and extensive.

The authors evaluated the spatial pattern of depressional wetlands in the carbonate landscape of Big Cypress National Preserve, Florida. Forested cypress domes (which are actually depressions) are evenly sized and evenly spaced. This spatial pattern is proposed to arise through feedbacks among micro-topography, hydrology, vegetation density and productivity, and dissolution rates.

**Patterned Drylands**

Dryland vegetation provides some of most visible examples of self-organized pattern formation. Greig-Smith 1979 was among the first works to describe and attempt to explain these patterns, and Klausmeier 1999 provides among the first process-based explanation of these patterns. Barbier, et al. 2006 uses remotely sensed estimates of vegetation cover to show the transition from continuous to patchy, spatially patterned vegetation with increasing aridity. Kéfi, et al. 2007 shows that shifts in patch-size distribution may reflect the near onset of desertification. Stewart, et al. 2014 challenges the underlying mechanism of scale-dependent feedbacks as drivers of vegetation pattern, and d’Odorico, et al. 2006 shows that pattern formation can arise from stochastic climate variability and may therefore not reflect the presence of landscape-scale alternative stable states.


Barbier et al. used remotely sensed data taken at either end of a forty-year interval in Southern Niger and presented broad-scale empirical evidence of regime shift from homogenous vegetation cover to regularly spotted patterns in response to increasing aridity in the region.


This paper challenges the link between pattern formation and the occurrence of landscape-scale alternative stable states. Using a model with stochastic climate variability, the authors show that patterns can form in response to temporal variability, and that this pattern does not exhibit alternative stable state dynamics as suggested by deterministic Turing instability models.


This is one of the earliest studies to describe vegetation patterns and to try to understand the mechanisms giving rise to the patterning.


The authors document changes in the size distribution of vegetation patches along a gradient of grazing pressure in three Mediterranean landscapes, and they demonstrate theoretically that this pattern change is indicative of desertification.

Klausmeier developed a mechanism-based model, as opposed to phenomenological models in the past, with feedback between plant biomass and water availability to explain vegetation stripes in dryland.


Stewart et al. reviewed and criticized the existing problems with the Turing-instability-type model used to generate dryland vegetation patchiness. They argue that previous models did not consider the inherent patchiness in the vegetation or were developed to generate patterns with little consideration of dynamics. The authors developed a new modeling framework rooted in landscape connectivity to consider the temporal changes of vegetation patterns in drylands.

**Grassland-Shrubland Transitions**

Shrubland invasion is a widespread but still imperfectly understood transition in many arid and semiarid grasslands. Van Auken 2000 identifies a variety of mechanisms as potential drivers of this transition and as feedbacks that maintain it: changes in material distribution and transport (resource heterogeneity, length of pathway, and erosion), fire-biomass feedbacks, or others have been proposed. Van de Koppel and Rietkerk 2000 uses a model to demonstrate that this transition and its irreversibility could arise from overgrazing. Okin, et al. 2009 presents an alternative model that invokes erosion feedbacks as drivers of shrubland transitions. Ratajczak, et al. 2014 uses a long-term observation record to demonstrate the nonlinearity of grassland-shrubland transition and its dependence on fire frequency. D’Odorico, et al. 2012 reviews more recent evidence with respect to these hypotheses. Whether shrub invasion indicates desertification may depend on the climatic setting, as demonstrated in Maestre, et al. 2009. Peters, et al. 2012 shows that reversal of transitions to shrubland may require sustained wet climate conditions that permit grassland re-establishment.


The authors review evidence for four major feedbacks for shrub encroachment in arid grasslands: (1) fire-grass feedback, (2) erosion-vegetation feedback, (3) small mammals grazing—grass biomass, and (4) shrub encroachment—surface energy balance.


This study argues that woody encroachment is not necessarily a sign of desertification. The impact of shrub invasion shifts from negative to positive as climate becomes wetter—it is a function of the biological trait of actual shrub species under consideration.


Okin and colleagues used a model to investigate the cause of irreversibility and alternative stable states between grassland and shrubland. They found that a potential cause is the grass biomass and soil erosion feedback, not the advantage of shrub over grasses or fire-biomass feedbacks.

This study presents and evaluates long-term responses of grassland and shrubland ecosystems to precipitation variability, using vegetation maps to describe century-scale change and more recent field studies to document climate responses of diversity and productivity. The authors conclude that multiple wet years are necessary for recruitment of grasses that could reverse desertification.


Used a twenty-eight-year data with annual resolution on mesic grassland and provided the first empirical evidence that the transition between mesic grasslands and shrublands was nonlinear, representing regime shift between alternative attractors. Their data showed that shrub cover was correlated with distinct threshold of fire and grass cover.


Van Auken hypothesized the drivers involved in woody plant encroachment to arid grasslands, including climatic warming, high level of herbivory by domestic animals, and fires.


Van de Koppel and Rietkerk used theoretical models to show that irreversible vegetation change may occur when herbivore numbers are independent of the vegetation.

**Dryland Climate Feedbacks**

At broad scales, whole regions or biomes have an important influence on climate, but considerable debate has centered on whether these feedbacks are strong enough to produce regional-scale alternative stable states. Claussen and Gayler 1997 presents a model of vegetation-climate feedbacks that generate abrupt switches from arid to humid climates in the Sahara, while Foley, et al. 2003 links these longer-term dynamics with more recent drought. Kröpelin, et al. 2008 uses paleo-environmental reconstruction to suggest that the transition from green to arid Sahara was gradual, while Claussen, et al. 2013 argues that transition rate is not indicative of feedback strength. Lenton, et al. 2008 reviews how possible tipping points at regional-scales (including the Sahara, Sahel, and Amazon) may influence or even produce global-scale feedbacks in the climate system. D’Odorico and Porporato 2004 provides theoretical and empirical evidence of climate-soil moisture feedbacks in the Midwestern United States.


Claussen et al. argued that whether it is a gradual or an abrupt shift does not inform us the strength of vegetation-climate feedbacks. A
strong vegetation-climate feedback could also have gradual shift, if we consider the biodiversity of plant species and functional types.

Claussen and Gayler built a coupled vegetation–atmosphere model to explain the greening of the Sahara during the mid-Holocene.

This paper generates and tests a model of soil-moisture atmosphere feedbacks, which are supported by the observation of distinct modes of soil moisture in the central United States.

Foley et al. discussed broadly two regime shifts at two time scales: first is the abrupt from “green Sahara” to “desert Sahara” about five thousand years ago, and another is the persistent severe drought since the late 20th century in Sahel.

This study uses paleo-environmental reconstruction to demonstrate the transition from a humid and green Sahara to a desert Sahara in North Africa is ecosystem succession driven by gradual climate changes. The transition was gradual, not abrupt, suggesting that the vegetation-climate feedback is weak.

Lenton reviews evidence for regional-scale tipping points in the global climate system, arguing that each creates a threshold beyond which forcing by that system feeds back into global climatic change.

Forest Savannah Transitions

Forests and savannas co-occur in tropical regions, and extensive study has attempted to understand the ecological and climate feedbacks that may explain their distribution. Nepstad, et al. 1999 called early attention to the scale of deforestation and landscape change in the Amazon and the potential for feedbacks to reinforce this change. Moreira 2000 shows experimentally that fire can control tree abundance in savanna, and Beckage, et al. 2009 demonstrates that this can produce multiple stable states in tree cover. Hirota, et al. 2011 and Staver, et al. 2011 simultaneously found that tree cover across the tropics is multimodal, with peaks corresponding to desert, savanna, and forest. Hanan, et al. 2014 shows that this pattern could arise from artifacts in statistical estimation of tree canopy, but Dantas, et al. 2016 shows that multimodal tree cover distributions are also evident in field data. Malhi, et al. 2009 shows that fire drought interactions could promote transitions from forest to savanna in the Amazon, and Brando, et al. 2014 provides experimental...
evidence in support of this mechanism. Higgins and Scheiter 2012 evaluates the scale of potential transitions induced by atmospheric CO2 enrichment, and finds that transitions are likely to be local rather than regional in scale.


Beckage et al. included vegetation-fire feedback in their model. They found that positive feedback between fire frequency and savanna trees, alone or together with grasses, can stabilize savannas, blocking the conversion of savanna to forests.


Brando et al. presented the first experimental evidence of tipping point in Amazon forests due to altered fire regime. Based on results of a large-scale, long-term experiment with annual and triennial burn regimes in the Amazon, they found abrupt increase in fire-induced tree mortality during a severe drought event. Their results show that extreme drought event, coupled with forest fragmentation and anthropogenic ignition sources, are already causing widespread fire-induced tree mortality and forest degradation cross Amazon forests.


Dantas et al. used meta-analysis and provided the first example using empirical field data—instead of satellite data—to show that savanna and forest are indeed distinct modes of tree cover and thus likely alternative stable states.


Hanan et al. argue that satellite-derived tree-cover data may contain artifacts that mimic multimodal patterns predicted by alternative stable state theory, and urge caution in their interpretation.


Higgins and Scheiter showed that large-scale vegetation systems can tip into alternative states via vegetation-climate feedbacks. Increasing CO2 concentration would force the transitions of tropical grassland, savanna, and forest ecosystems to vegetation states characterized by higher biomass and/or wood-plant dominance. The timing of these shifts will not coincident at the continental scale.


Hirota et al. (as well in Staver, et al. 2011) analyzed satellite data on the distribution of tree cover in Africa, Australia, and South America and provided empirical evidence of tropical forest and savanna as alternative stable states. Hirota et al. use relationships of
tree cover with precipitation to estimate the spatial distribution of forest resilience.


Malhi et al. explore potential climate-change-induced dieback of the Amazon rainforest in global climate models. Their analysis suggested that dry-season water stress is likely to increase in the East Amazon over the 21st century, and Amazon forest will transition to a seasonal forest. Further, the spread of fire ignition associated with advancing deforestation, logging, and fragmentation may act as nucleation points that trigger the transition of these seasonal forests into fire-dominated, low-biomass forests.


Moreira provided experimental evidence on the effect of fire on tree abundance in savanna. It suggested that fire protection increased the abundance of woody plants and favored fire-sensitive species. Shrub tends to be less affected by fire than trees.


Nepstad et al. called attention to the severe decline of forest cover in Amazon. They found that present estimates of annual deforestation for Brazilian Amazonia captured less than half of the forest area that is impoverished each year, and even less during years of severe drought.


Staver et al. (as well in Hirota, et al. 2011) analyzed satellite data on the distribution of tree cover in Africa, Australia, and South America and provided empirical evidence of tropical forest and savanna as alternative stable states. The authors link these stable states to shifts in fire regime.