Chapter 2—Ecological Thresholds

2.1 Introduction

Temperature, precipitation, and related climate variables are fundamental regulators of biological processes and it is reasonable to expect that significant changes in the climate system may alter linkages and feedbacks between ecosystems and regional climate systems. Increasing focus is being placed on the existence and likelihood of abrupt state changes or threshold responses in the structure and functioning of ecosystems (Holling, 1986; Schefferet al., 2001; Higginset al.et al. 2002; Foleyet al.et al. 2003; Schneider, 2004; Burkettet al.et al. 2005; Hsiehet al.et al. 2005). Various interrelated terms are employed in the scientific literature to characterize these types of discontinuous and rapid changes in ecosystems, including ecosystem tipping points, regime shifts, threshold responses, alternative or multiple stable states, and abrupt state changes. Our current understanding of thresholds and ecosystem responses makes it *unlikely* that we can predict such discontinuities in ecosystems, and these discontinuties are *likely* to result in profound changes to natural resources that are sensitive to climate changes, as well as to human societies that depend on ecosystem goods and services, this assessment, based on the literature and the synthesis teams' expertise, indicates that thresholds are *likely* to represent large-scale risk and uncertainty and can *likely* be a major challenge to natural resource managers.

Abrupt transitions have occurred in numerous ecosystems where incremental increases in global temperature have produced sudden and dramatic changes in the state of and the dynamics governing these systems (Anderson et al. 2008). These thresholds of magnified ecological change are a consequence of the underlying nonlinear nature of ecosystems and are *very likely* critical to adaptation strategies for managing natural resources in a rapidly changing world. Sudden, unanticipated shifts in ecosystem dynamics are a major source of risk and uncertainty for managers and make planning and preparation difficult. One of the primary objectives of this report (SAP 4.2) is to enhance the understanding and ability of managers to predict and forecast the effects of climate change on ecosystems.

As discussed elsewhere in this chapter, the occurrence of threshold, or abrupt changes in ecosystems, is suggested by current ecological theory and models, and is documented with laboratory and field examples and even in the paleoecological record. However, on a predictive level, thresholds remain poorly understood, particularly in terms of the underlying causal mechanisms and the general factors that predispose systems to threshold effects. For example, it is unclear under what circumstances climate change, both in its mean state and in its variance in space and time, including occurrence of extreme weather events, might cause ecosystem threshold shifts, instead of more gradual, continuous changes in ecosystems and species. Further, it is not known what the resulting effects of climate thresholds on ecosystems will be. Thus, while the phenomenology of rapid transitions in ecosystems is clear, reaching a level of understanding that enables one to anticipate or actually predict threshold effects is the main bottleneck to producing results useful to managers (Muradian, 2001; Bestelmeyer, 2006; Groffmanet al.et al. 2006; Kinziget al.et al. 2006).

2.2 Early Development

The concepts of ecological thresholds, multiple stable states, and regime shifts originated in early theoretical work on the stability or persistence of ecosystems

(Margalef, 1963; Lewontin, 1969; Odum, 1969; Holling, 1973; May 1973, 1977). The two key components of stability were considered to be the system's "resilience," or the speed at which it would return to its current "stable equilibrium" , and its "resistance," or ability to maintain its current "stable" state in the face of disturbance of a given magnitude. According to this early thinking, given enough disturbance, systems could be pushed into alternative stable states. This theoretical work was complemented (however sparsely) with early empirical demonstrations of multiple stable states in marine experimental systems (Sutherland, 1974) and with field data combined with model analysis for terrestrial ecosystems (Ludwiget al.et al. 1978).

"Stability" as a well-defined mathematical concept was central to these early theoretical discussions of thresholds. Lewontin (1969) reviewed mathematical models of stability and discussed the forces required to move an ecosystem out of a basin of attraction or stable state. May (1973) presented a precise definition of stability and a crater and ball analogy to illustrate the concepts and later (1977) focused attention on the existence of alternative stable states and multiple equilibrium points with an emphasis on the thresholds between them. Holling (1973) drew attention to the ability of ecosystems to absorb and respond to disturbance and introduced the concept of robustness (although he used the term resilience). Again, robustness focuses on dynamics far from equilibrium and was used to measure the magnitude of perturbations from which recovery of a system was no longer possible.

Although mathematically tractable and well defined in static engineering contexts, "stability" and the implication of "equilibrium" in ecological systems began gradually to give way in the 1990s to growing evidence that real ecological systems are not static nor even well approximated, as such. Notions of stable equilibrium, which continue to dominate much of our thinking and research to date (for example, Maximum Sustainable Yield as written into the 2006 reauthorization of the Magnusson-Stevens Act), are based on models and controlled experiments (for example, on paramecia and flour beetles) from the middle of the last century where singular static equilibrium was the ideal. Cracks in the equilibrium view began to appear as quantitative evidence mounted from natural systems, that “change” rather than “constancy” is the rule, and that nonlinear instability, thresholds, and chaos can be ubiquitous in nature (Dublinet al.et al. 1990; Sugihara and May, 1990; Tilman and Wedin, 1991; Grenfell, 1992; Knowlton, 1992; Hanskiet al.et al. 1993; and Sugihara 1994). The possibility that so-called “pathological” nonequilibrium, nonlinear behaviors seen in theoretical treatments could be the rule in nature as opposed to a mathematical curiosity, opened the door for credible studies of thresholds. Indeed, now threshold changes appear to be everywhere. Recognition and documentation of sudden, not readily reversible changes in ecosystem structure and function have become a major research focus during the past 10 to 20 years (Schefferet al.et al. 2001; Scheffer and Carpenter, 2003).

Perhaps the most important driver of the current interest in nonlinear ecosystem behavior and, in particular, threshold effects has been the recognition of the importance of indirect effects of climate change. Although much climate change research has focused on the direct effects of long-term changes in climate on the structure and function of ecosystems, there has been increasing recognition that the most dramatic consequences of climate change may occur as a result of indirect effects, including threshold changes (Vitousek, 1994; Carpenter, 2002; Schneider, 2004).

2.3 Current Discussions of Threshold Phenomena

As ecologists were exploring the existence of alternative stable states in ecosystems, oceanographers were documenting the impacts of major climatic events on the North Atlantic Ocean (Steele and Henderson, 1984), North Pacific Ocean, and Bering Sea ecosystems. They eventually used the term "regime shift" to describe the sudden shifts in biota that are driven by ocean climate events (Steele, 1996; Hare and Mantua, 2000). More recently, for the California Current Ecosystem (CCE), regime shifts in the biota have been distinguished from random excursions in the ocean climate based on the nonlinear signature of the time series (Hsiehet al.et al. 2006). The main idea here is that regimes represent different rules governing local dynamics (that is, they depend on environmental context), and that nonlinear instabilities (latent positive feedbacks) drive the system across thresholds into different dynamical domains. Thus, regime shifts in marine ecosystems are an amplified biological response to ocean climate variation (mainly temperature variation) rather than a simple tracking of environmental variation (Andersonet al.et al. 2008). On the other hand, ocean climate for the CCE in the 20th century did not have this nonlinear signature insofar as the dynamical rules were the same in both warm and cold periods. Hsieh and others (2006) and Anderson and others (2008) suggest nonlinear forecasting methods as a rigorous way to make this distinction that avoids the circularities of statistical methods for detecting regimes and thresholds. The dynamics of regime shifts are considered to be the essential fingerprint. Current interest in regime shifts and thresholds in marine science have focused on understanding the factors that determine thresholds and on ways of extracting dynamics from observational data to make predictions.

Muradian (2001) and Walkers and Meyers (2004) used a definition of regime shift developed by Sheffer and Carpenter (2003) emphasizing changes in the threshold level of a controlling variable in a system, such that the nature and extent of feedbacks change and result in a change in the system itself (which was based on Rene Thom's (1975) fold catastrophe model). Scheffer and Carpenter (2003) built on work in shallow lakes to demonstrate empirically the concept of threshold-like hysteric change and used these examples to further reinforce the idea that ecosystems are never stable but are dynamic and that fluctuations (in populations, environmental conditions, or ecosystems) are more the rule than not.

Given the move in thinking among many ecologists toward nonequilibrium and unstable dynamics, the broader technical concept that may eventually replace "equilibrium" in this context is a more general notion concept that includes equilibrium, stable limit cycles, and nonequilibrium dynamics or chaos (Sugihara and May, 1990; Hsiehet al.et al. 2006). Depending on whether the control variable is thought of as part of the system (an intrinsic coordinate of the state space) or as external to the system (an extrinsic variable), threshold behavior may be thought of as a ridge of instability that separates control variables. From a more descriptive point of view, the idea suggests that there are particular states or characteristic combinations of species (grasslands, chapparel, oak-hickory forests, and so forth) that make up the biological component, and that ecosystem thresholds can be identified in the physical part of the system. Part of the nonlinearity or nonequilibrium nature of ecosystems comes from the fact that the biology (especially the dynamics) of the system is contingent on its own particular state (suite and abundance of species), as well as on the physical context in which it resides.

The field of range science has a parallel and largely independent literature on thresholds, resilience, regime shifts, and alternative stable states that has engendered a lively debate over how these terms are used in that field. Bestelmeyer (2006) argued that there is a lack of clarity in the use of the term “threshold” and its application to state-and-transition models (STMs) used in range management. STM’s describe alternative states and the nature of thresholds between states. Bestelmeyer’s argument reflects a broad lack of consensus or understanding among range scientists about how best to define and use the threshold concept. Watson and others (1996) criticized a focus on the consequences of threshold shifts at the expense of the processes that precede them. Many definitions of threshold phenomena emphasize relatively rapid, discontinuous phenomena (for example, Wissel, 1984, and Denoel and Ficetola, 2007). Others emphasize the points of instability at which systems collapse (Radfordet al.et al. 2005), or the point at which even small changes in environmental conditions lead to large changes in state variables (Sudinget al.et al. 2004). Still other definitions emphasize changes in controlling variables. According to Walker and Meyers (2004), “a regime shift involving alternative stable states occurs when a threshold level of a controlling variable in a system is passed.”

There is clearly a need in range science for more rigorous and consistent use and application of the ecological threshold concept and its associated terminology. One point of consensus underlying both the theoretical and empirical approaches to the topic of thresholds is that changes from one ecological condition to another take place around specific points or boundaries. But further advancement and agreement is limited by the small number of empirical studies that address this topic. Some believe that further advancement will depend on rigorous statistical testing for reliable identification of thresholds across different systems (Huggett, 2005), while many in fields outside of range science see the danger of circularity in such arguments and suggest dynamic tests for determining threshold behavior (Hsiehet al.et al. 2005).

2.4 Ecological Thresholds Defined for SAP 4.2

Because of the variety of ways that the concept of thresholds has been developed, this assessment (SAP 4.2) uses the following general definition of ecological thresholds: *An ecological threshold is the point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in an environmental driver produce large, persistent responses in an ecosystem.* Fundamental to this definition is the idea that positive feedbacks or nonlinear instabilities drive the domino-like propagation of change that is potentially irreversible.

In line with this definition, threshold phenomena are particular nonlinear behaviors that involve a rapid shift from one ecosystem state (or dynamic regime) to another that is the result of (or that provokes) instability in any ecosystem quality, property, or phenomenon. Such instability always involves nonlinear amplification (positive feedback in some form) and is often the result of the particular structure of the interactions or the complex web of interactions. This definition distinguishes thresholds from other biological changes that are simple responses to external environmental change. Thus, bifurcation cascades (the point in which events take one of two possible directions with important final consequences, making dynamical systems evolve in a non-linear way with successive disruptions/divergences/breaks from previous trends), nonlinear amplification (Dixonet al.et al. 1999), hysteresis, and the propagation of positive feedback (instabilities) through complex webs of interactions are all interrelated attributes that fit our general working definition of threshold phenomena.

"Systemic" risk, or risk that affects the whole ecosystem rather than just isolated parts of the system provides a useful analogy. Systemic risk corresponds to widespread change in an ecosystem characterized by a break from previous trends in the overall state of the system. Runaway changes are propagated by positive feedbacks (nonlinear instabilities) that are often hidden in the complex web of interconnected parts. The changes may be hysteretic in the sense that recovery may be much slower to achieve than the collapse, and they may be irreversible in that the original state may not be fully recoverable (Chapin et al. 1995).

Other specific examples of threshold crossings or transitions that illustrate this definition are (following Groffman, 2006)—

1. The interactions of drought and overgrazing that trigger runaway desertification.
2. The exceeding of some critical load, as with the toxicity limit of a contaminant or elimination of a keystone species by grazing, so that when one component of the system fails, it provokes a domino-like cascade of instability that substantially alters the rest of the system.

These and other examples are discussed in more detail in the case studies presented in Chapter 3.

These simplistic metaphors for our concept of threshold transitions include so-called bifurcation cascades where, for example, small changes in a controlling variable, such that the nature and extent of feedbacks change, leads to a sudden destabilization of the system, which follows the classic fold-catastrophe model as first described by Rene

Thom (1975). Thus our operational notion of ecological threshold covers sudden changes of state and sudden changes in the dynamical behavior of ecosystems. The overriding theme of interest for natural resource mangers is the uncertainty and lack of predictability that surrounds such large-scale system-wide changes.

2.5 Factors That Influence Persistence, Resilience, and Robustness

At a general level, systems can be viewed as consisting of mixtures of positive and negative feedbacks, with positive feedbacks tending to alter the nature of the system, and negative feedbacks tending to minimize these changes (Chapinet al.et al. 1996). Changes that strengthen positive feedbacks (for example, the invasion and spread of highly flammable grass in a desert) can lead to a change in conditions (for example, the fire regime) that may exceed the tolerance of other components of the system. This, in turn, leads to destabilization and threshold changes. Thresholds occur when positive feedbacks amplify changes in system characteristics in ways that exceed the buffering capacity of negative feedbacks that tend to maintain the system in its current state or the current limits of the control variables.   Viewed from a management perspective, thresholds occur when changes in the system exceed the adaptive capacity of the system to adjust to change. Because systems are tuned to the natural variability experienced in the past, anything that disrupts that variability can make them vulnerable to further change and amplified instability (Walkeret al.et al. 2006; Folke, 2006).

The following is a partial list of factors that are believed to come into play in determining a system’s persistence, robustness, resilience, and sensitivity to threshold behavior (see also May and McLean, 2007):

1. A higher diversity of very weakly connected and substitutable components are thought to enhance robustness. Such arguments were made in the classic stability complexity debate (see reviews by Pimm 1984 and McCann 2000).

2. Compartmentalization of interactions into guilds is a way to make model ecosystems more robust to systemic events (Mayet al.et al. 2008). Compartmentalization acts as a fire-break that prevents the spread of a system's collapse.

3. A predominance of weak linkages in the system with a few strong linkages leads to relatively low connectance (McCann, 2000; Mayet al.et al. 2008) and is thought to increase resilience. Real ecological systems are thought to have a lognormal distribution of interaction strengths, which has been associated with increased resilience (Sala and Graham, 2002).

4. Ecosystems are robust by virtue of their existence. They are the selected survivors of billions of years of upheaval and perturbation (continental drift, meteor extinctions, and so forth), and show some remarkable constancy in structure that persists for hundreds of millions of years (for example, the constancy of predator/prey ratios). As such, enumerating the common attributes of these diverse naturally selected surviving systems could be of interest to understanding thresholds.

5. Higher measured nonlinearity (greater instability) in the dynamics that provoke an increase in boom and bust population variability (Andersonet al.et al. 2008) is directly associated with regime shifts. This is true in exploited marine fish populations, which show greater swings in abundance than their unexploited

6. In line with the so-called “paradox of enrichment” (Rosensweig, 1971), fertilizing a system to increase growth rates and carrying capacity can provoke a rapid loss of species to a much simpler state.
7. Increasing time lags involved in population regulatory responses can destabilize systems (May 1977), and this effect becomes more pronounced with higher growth rates. This is analogous to a large furnace (rapid growth) with a poor thermostat (regulatory delay), which tends to produce undershooting and overshooting of temperature in a way that predisposes the system to large-scale failure.
8. Reductions in variance, as might occur when managing systems for a stable flow of one particular good or service, tends to favor those species and components that are typical of this set of conditions at the expense of species that function more effectively under other conditions. Consequently the species as a whole remains stable under a narrower range of conditions.

2.6 The Bottom Line

To manage risks associated with ecological thresholds, it is essential to be able to forecast such events and to plan for and study alternative management scenarios. Better integration of existing monitoring information from the local to the largest possible spatial scales will be required to monitor and identify ecosystems that are approaching and undergoing critical transitions. Field research that focuses on ecosystems undergoing a threshold shift can help clarify the underlying processes at work. And natural resource managers may *very likely* have to adjust their goals for the desired states of resources away from historic benchmarks that may no longer be achievable in a nonequilibrium world that is continually changing and now being altered by climate change. Such changes in methods and outlook as the following may be required—

- Abandon classic management strategies that assume a constant world in equilibrium (for example, MSY-models, and mass-balance equilibrium models).
- Acknowledge in our management strategies and in our models that ecosystems are nonlinear, interdependent, and nonequilibrium systems.
- Use near-term forecasting tools, statistical and otherwise, that are appropriate to this class of system (for example, nonlinear time series prediction coupled with scenario models).
- Increase our understanding of the potential mechanisms involved both generically and on a case-by case basis.
- Continue to identify the characteristics of systems that make them more or less vulnerable.
- Continue to identify early warning signals of impending threshold changes (and to monitor for those signals).
- Survey and triage the major biomes to identify which systems might be most vulnerable to current climatic trends.
- Employ adaptive management strategies, such as skillful short-term forecasting methods coupled with scenario exploration models that are

capable of dealing with new successional scenarios and novel combinations of species.