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ECOSYSTEMS

MINI REVIEW

Ecological Thresholds: The Key to Successful Environmental Management or an Important Concept with No Practical Application?

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ABSTRACT

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 responses in the ecosystem. Analysis of thresholds is complicated by nonlinear dynamics and by multiple factor controls that operate at diverse spatial and temporal scales. These complexities have challenged the use and utility of threshold concepts in environmental management despite great concern about preventing dramatic state changes in valued ecosystems, the need for determining critical pollutant loads and the ubiquity of other threshold-based environmental problems. In this paper we define the scope of the thresholds concept in ecological science and discuss methods for identifying and investigating thresholds using a variety of examples from terrestrial and aquatic environments, at ecosystem, landscape and regional scales. We end with a discussion of key research needs in this area.

Key words: thresholds; multiple stable states; critical loads; panarchy; ecological surprises; ecological modeling.

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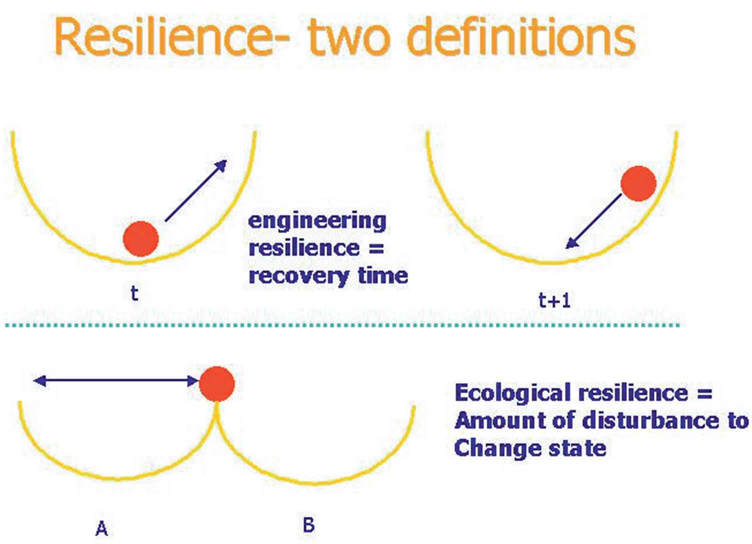

Figure 1. Definitions of resilience have changed over the last two decades from an ''engineering resilience'' concept based on how quickly a system recovers from disturbance (*top*), to an ''ecological resilience'' that considers the amount of disturbance necessary to change the state of an ecosystem, pushing it over the ''ecological threshold'' from state A to state B. From Gunderson (2000).

Introduction

There is great interest in identifying ecological thresholds, defined as the point at which there is an abrupt change in a quality (for example, wood production, the maintenance of a particular species), property or phenomenon or where small changes in a driver (for example, pollutant input, landscape fragmentation) may produce large responses in the ecosystem. The concept of ecological thresholds emerged in the 1970's from the idea that ecosystems often exhibit multiple ''stable'' states, depending on environmental conditions (Holling 1973; Beisner and others 2003). Initial interest in multiple states arose from theoretical models and from empirical observations of dramatic changes in ecosystems (for example, shifts from clear to turbid waters, grassland to shrubland) (May 1977; Scheffer and others 2001). Ecosystems were envisioned to exist in ''valleys of stability'' where the depth of the valley represented the systems' ''resistance'' to disturbance and the steepness of the valley sides represented the systems' ''resilience,'' or the speed at which it would return to its stable state (Figure 1). Given enough disturbance, the system can be pushed over the hill (threshold), into another valley or state.

Although the scientific community has generally accepted the concepts of both thresholds and multiple stable states, identifying specific examples of multiple states in ecosystems, and applying these concepts to environmental management has been limited (Connell and Sousa 1983; Scheffer and others 2001; Scheffer and Carpenter 2003; Walker and Meyers 2004). The difficulty in application raises the question of whether consideration of ecological thresholds is a useful theoretical concept that can help us to think about how ecosystems function (or cease to function), but does not have practical value in environmental management and problem solving.

Recently, interest in application of the ecological threshold concept has increased with the popularity of ''adaptive management'' as a tool for approaching environmental problems. In adaptive management, solutions to problems are proposed and implemented, but prescriptions are constantly re-evaluated based on actual ecosystem response to management (Holling 1978; Walters 1986). If we believe that we can use measurements in the environment as a motivation for management decisions, then we must be able to define specific ecological thresholds that, once crossed, move the system away from the 'desired state.' Adaptive management becomes a far easier process if those ecological processes that are likely to have nonlinear behaviors and/or threshold responses to changes in drivers can be identified. Understanding the conditions under which thresholds are likely to be crossed and what mechanisms underlie threshold behavior is critical. We also need to be able to identify specific ecosystems/landscapes that are on the brink of crossing a threshold. Thresholds greatly complicate our ability to make predictions about ecosystems; necessitating a shift from a ''steady state'', ''single-equilibrium view'' to a complex adaptive ecosystems perspective in environmental management.

Ultimately, environmental managers have a pressing need for information about ecosystem thresholds because of the potentially high-stakes consequences of exceeding them, which may limit future management actions, force policy choices, and in some circumstances be non-reversible. Consequently, managers are keen to have empirical information available that will help them assess the existence of ecological thresholds and when they are being approached, and to have predictive tools available that can assist them in evaluating the future consequences of when they are exceeded.

Given the potential usefulness of ecological thresholds in environmental management, and the difficulty in determining specific thresholds for real problems in particular ecosystems, the US Environmental Protection Agency, Office of Research and Development, in collaboration with the Woodrow Wilson Center for International Scholars, convened a conference on ecological thresholds in Washington, DC, on November 4–5, 2002, to articulate key research questions and needs in this area. Conference objectives were to (1) define the scope of the topic of ecological thresholds, and (2) lay out the key research questions that need to be addressed to convert this interesting basic science concept into a useful applied science tool in environmental management. In this paper we (1) define the scope of ecological threshold analysis using examples from terrestrial and aquatic ecosystems; (2) review methods for studying thresholds in spatial, temporal and human dimensions; and (3) discuss topics that need to be addressed in future research.

The Scope of Ecological Threshold Analysis

There are three main ways that threshold concepts have been applied in ecology: (1) analysis of dramatic and surprising ''shifts in ecosystem state,'' where a small change in a driver causes a marked change in ecosystem condition; (2) the determination of ''critical loads,'' which represent the amount of pollutant that an ecosystem can safely absorb before there is a change in ecosystem state and/or in a particular ecosystem function; and (3) analysis of ''extrinsic factor thresholds,'' where changes in a variable at a large scale alter relationships between drivers and responses at a small scale. In this section, we illustrate each of these applications to define the scope of ecological threshold analysis. It is important to note that although there are major differences in the types of threshold analyses discussed below, there is much overlap and interaction among them, for example, pollutants considered in critical loads analysis are often the drivers that cause marked changes in ecosystem condition.

Shifts in Ecosystem State

A common use of the ecological thresholds concept is in analysis of surprising and dramatic changes in the state of ecological systems (Scheffer and Carpenter 2003). An excellent example of such a shift is Florida Bay, a 2,200 km^2 shallow estuary at the southern tip of Florida, which changed abruptly from an oligotrophic clear water system in which primary production was dominated by seagrasses (rooted aquatic plants) to a more turbid system in which production became dominated by phytoplankton blooms in the early 1990's (Gunderson and Holling 2002).

The shift in Florida Bay illustrates three key aspects and challenges of the ecological thresholds concept. First, there was a non-linear response in ecosystem state to environmental change, with dramatic changes in several parameters (water clarity, primary production, nutrient cycling, food webs) once a threshold was crossed. Second, multiple anthropogenic and natural causes were potentially linked to the shift, including nutrient input from septic systems, sea level change, a lack of hurricanes, drought, water diversions and removal of grazers. Understanding the shift required identifying key response variables in the systems, that is, seagrass and phytoplankton, and the key disturbances that influenced these variables, that is, salinity, hurricanes, grazing, nutrients. Third, the driver and response variables operated at different time scales, with a mix of variables that respond to perturbation quickly (for example, algal production, water clarity) and some that respond slowly (sea level change, removal of grazers). Ongoing work is oriented toward establishing quantitative thresholds for human-influenced factors (salinity, nutrients), with an eye towards ensuring resilience in the face of variables that cannot be controlled (hurricanes).

Although the concept of ecological resilience has been around for over 30 years, there has been increased discussion and enhancement of its use in the last decade (Ludwig and others 1997; Gunderson 2000). Some authors define resilience as the time it takes for a system to recover from a disturbance, which Holling (1996) defines as engineering resilience. In contrast, the amount of disturbance necessary to change the state of an ecosystem is known as ecological resilience (Figure 1; Holling 1973, 1996). Ecological resilience emerges from the interaction of the functional diversity, response diversity, and cross-scale diversity of an ecosystem (Peterson and others 1998; Lundberg and Moberg 2003; Elmqvist and others 2003). Consequently, the ecological resilience of a system can be changed by shifts in the areas surrounding that ecosystem. In the Florida Bay example, the dynamics of seagrass and phytoplankton were strongly affected by delivery of water from larger surrounding areas, which were affected by human activities and climate. Human activities that attempt to stabilize a system in one particular state by removing natural disturbances often reduce resilience by eliminating mechanisms that allow the system to adapt to external change, making them more likely to pass thresholds and undergo dramatic shifts in state. For example, the placement of dams on riverine systems removes natural flow variability and along with that the ability of many plant and animal populations to recover from external disturbances, for example, floods (Graf 2003). The loss of these populations, and their various functions, reduces the response diversity, functional diversity, and ultimately, the resilience of the system (Elmqvist and others 2003; Lundberg and Moberg 2003).

Coupled human-natural systems can be viewed as a ''panarchy''; an interacting set of adaptive cycles that reflect the dynamic nature of human and natural structures across time and space (Gunderson and Holling 2002). Just as natural disturbances, for example, hurricanes, cause a re-organization and re-development of an ecosystem (Bormann and Likens 1979), sudden shifts in ecosystem state motivate changes in human understanding of the way that systems need to be managed and these changes, in turn, may alter the institutions that carry out that management.

Although system regime shifts such as the one described in Florida Bay above are well documented in aquatic and marine systems (for example, Steele 1998), there is evidence that regime shifts are also characteristic of terrestrial ecosystems, for example, shifts from grass- to shrub-dominated communities in the Chihuahuan Desert (Brown and others 1997), ''wet'' and ''dry'' Sahel regimes that persist for decades at a time (Foley and others 2003), the presence of ''two-phase'' mosaics in semiarid rangelands (Montaña 1992), and the multiple ''wet'' and ''dry'' states of tundra during the Holocene (Zimov and others 1995). Although most examples involve external drivers (for example, nutrient overloading in lakes, shifts in precipitation, overgrazing by domestic cattle) some systems appear to undergo major shifts without an external driver (Hartvigsen and others 1998). Even single species populations may undergo dramatic shifts in their spatial patterns despite environmental homogeneity simply due to intrinsic dynamics such as local dispersal coupled with predator-prey interactions (Harrison 1997).

Critical Loads

A second common application of the concept of ecological thresholds is that of critical loads: the determination of the quantity of pollutant inputs that an ecosystem can safely assimilate before there is a change in ecosystem state and/or in a particular ecosystem function. Critical loads, or critical thresholds as they are now called, are used in the development of abatement strategies to control emissions of air pollutants in Europe (see the convention of long-range transboundary air pollution (LTRAP) of the UNEC, http://www.unece.org/env/lrtap/). For these strategies, a critical load is defined as ''a quantitative estimate of an exposure to one or more pollutants (nitrogen (N) and sulfur (S), for example) below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge.'' Given that controlling emissions, which are a by-product of fossil fuel combustion, is expensive, there is a strong need for quantitative, critical loads, based on a scientifically defensible understanding of ecological thresholds.

The actual determination of critical loads for acids and nutrients for particular ecosystems is complicated by the great spatial and temporal variation in the nature and extent of loading and system responses (for example, Weathers and others 2000) and system thresholds that vary with abiotic (climate, geology) and biotic factors (type of vegetation, disturbance history, management regime) (Figure 2). In Europe, critical loads for S and N deposition have been set for different ecosystems based on specific changes in ecosystem function associated with quantitative thresholds. For example thresholds for calcareous forests are set at approximately 15–20 kg N ha^{-1} $year^{-1}$ based on concerns about changes in ground flora, whereas thresholds for mesotrophic fens are set at approximately 20–30 kg N ha^{-1} $year^{-1}$ based on concerns about loss of plant diversity (Emmett and Reynolds 2003).

Extrinsic Factor Thresholds

A third application of the threshold concept is the consideration of where extrinsic factors constrain the structure and function of ecosystems. As the level or intensity of an extrinsic factor reaches a threshold, the nature of ecosystem structure, the rate of an ecological process, or the level of eco-

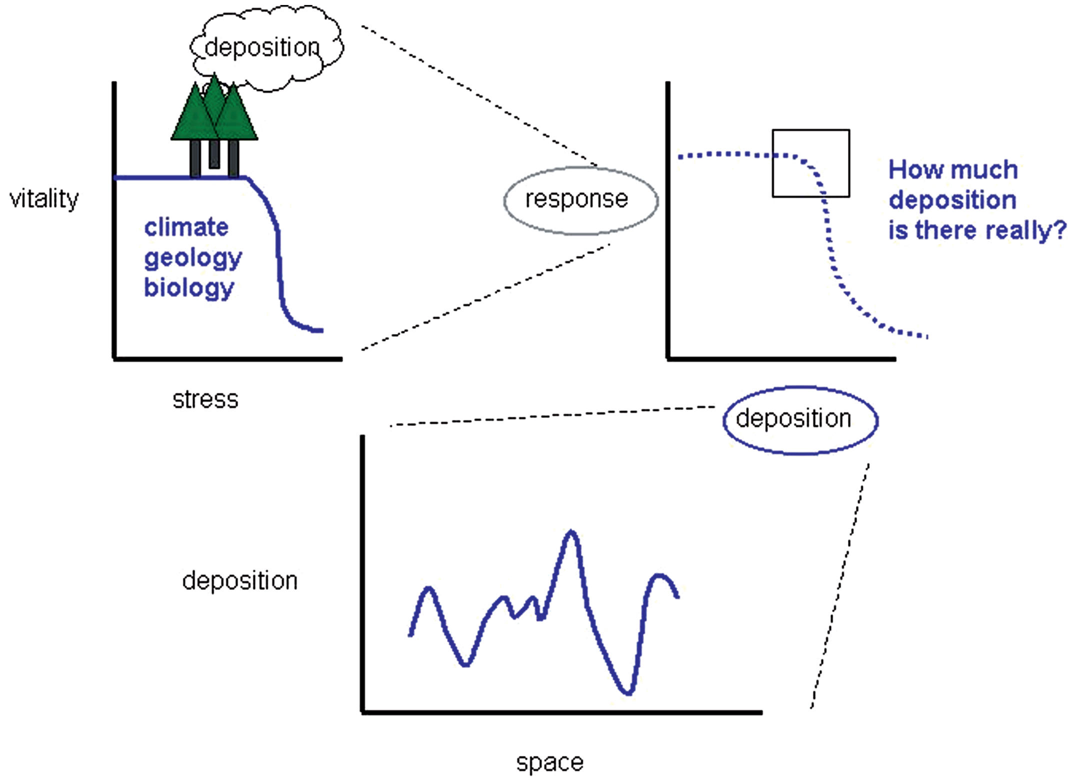

Figure 2. As the ''stress'' of atmospheric deposition increases past a threshold, ecosystem ''vitality'' markedly declines. Determining thresholds and critical loads for atmospheric deposition is complicated by variation in deposition over space and in system response, which varies with physical, chemical and biological factors. From Weathers and others in press.

system function/service that can be attained is altered. Extrinsic factor thresholds are readily observed in rivers, where hydrology and geomorphology function to constrain the structure and function of riverine ecosystems, and in urban ecosystems, where thresholds in the environmental impacts associated with the amount of impervious surface constrain the structure and function of stream and riparian ecosystems.

Riverine ecosystems are strongly influenced by extrinsic factors, operating at a variety of scales. Establishing thresholds for these systems requires identification of the key extrinsic drivers, for example regimes of streamflow, sediment, temperature, and chemicals or nutrients and the key structural and functional response variables (for example, stream morphology, biotic communities). Although there have been many studies of relationships between individual drivers and response variables, we lack an integrated understanding of how drivers interact to regulate ecological processes and whether threshold levels of individual or combined drivers occur.

Some examples of physical thresholds are well established. For example, movement of streambed particles (habitat for benthic organisms) during high flows is often considered in terms of a threshold of incipient movement for these particles (Leopold and others 1964; Parker and others 1982). Such disturbances play an important role in mediating species interactions and community structure. Another obvious threshold occurs when rivers attain sufficient flows to spill over their banks and inundate lateral floodplains. Many riparian tree populations, such as cottonwood (*Populus* spp.) in the western US, are dependent on this periodic inundation and, in its absence, will senesce and be displaced by upland species (Scott and others 1996). Indeed, there is some suggestion that the invasion of exotic salt cedar (*Tamarix* spp.) in rivers of the western US where overbanking flows have been removed, creates a positive geomorphic feedback, contributing to a raising of the floodplain height and subsequent further isolation from overbanking flows (Dent and others 2002).

In recent years, much has been much written about putative thresholds between the degree of impervious surface in watersheds and indices of aquatic biological health. Impervious surface increases rates of rainfall runoff and reduces sediment supply to receiving streams, greatly altering energy dissipation. Several scientists have suggested that once a ''threshold'' of 10–15% impervious watershed surface is attained, stream ecological ''health'' may decline precipitously (Klein 1979; Paul and Meyer 2001); however, sufficient empirical data that can be used to rigorously test this idea are only now surfacing. Many studies are showing strictly linear declines in species richness as imperviousness increases (Morley and Karr 2002; A. Moore and MA. Palmer, submitted) supporting earlier assertions that the threshold generalization does not hold up (Karr and Chu 2000; Bledsoe and Watson 2001). Allan (2004, in press) concluded that the response of streams to urbanization is too complex for a single threshold to apply because impervious surface is often associated with many other stressors that may or may not be important at a particular site (for example, oil or salt run-off from roads, stormwater outflows, and so on).

Methods for Investigating Thresholds

Given the variability in the types of threshold analyses discussed above, we need to develop approaches for identifying thresholds in specific ecosystems: what are they or do they exist at all? Where are they? And can we determine them in advance? The concept of ecological services, that defines specific ecosystem functions that are valued by humans (Daily and others 1997; Carpenter and Turner 2000), is useful for directing these efforts. One approach is to focus on an ecosystem service(s), identify the key aspects of ecosystem structure and function that influence that service and then identify key factors that could influence, or alter, those aspects. We can then ask (and, with luck and skill, then measure) if these factors, and their interactions, exhibit threshold responses. Further, if they do, the next question is whether there are general statements to be made about threshold behaviors for different physical, chemical and/or biological functions, and/or if there are critical processes or structural attributes that indicate that whole suites of functions are about to change. The latter – critical attributes/changes – could be structural (for example, impervious surface, fragmentation) or functional (for example, hydrologic residence time). Further, because stakeholders may be involved in setting acceptable 'levels' of ecosystem services, science can be brought to bear on identifying levels of these attributes or functions that will maintain the service at the desired level. This is particularly attractive for systems that do not readily exhibit dramatic regime shifts until they are ''too far gone.'' In such cases, stakeholders are essentially defining the thresholds that will be used for management.

Studying Threshold Behaviors in Time

There is a critical need for development of parameters and monitoring strategies to determine if an ecosystem is approaching a threshold. For example, a major challenge in estuarine and coastal research and management is to link land use and aquatic responses, with an eye towards establishing thresholds for nutrient inputs to prevent dramatic shifts in ecosystem state such as that observed in Florida Bay (NRC 2000). Although developing these relationships is inherently a site or ecosystem-specific enterprise, there is great interest in developing broadly applicable thresholds and land use guidelines.

Research in the Neuse River Estuary in North Carolina has focused on using microbes as broad-scale indicators of thresholds and change. Extensive research has quantified how specific changes in algal groups are related to hydrology and water residence time, the input and output of taxa and internal processes and drivers. Microbial indicators have proven to be broadly applicable for showing the dynamic nature of nutrient-production linkages and thresholds within and between water bodies (Paerl and others 2002, 2003). Microbial-based monitoring programs have been developed for particular water bodies to evaluate specific land management schemes and to formulate and validate water quality models aimed at predicting nutrient-productivity and algal bloom thresholds. This system has recently experienced extreme, unpredictable events, including three large hurricanes in one season (1999) (Paerl and others 2001). The great challenge for the monitoring programs and associated modeling efforts is to encompass both acute (hurricanes) as well as chronic (seasonal runoff) hydrologic and nutrient perturbations (www.marine.unc.edu/neuse/modmon).

Identifying and characterizing the behavior of thresholds is more difficult in terrestrial ecosystems than in aquatic systems because the main components of the system change more slowly. For example, perennial terrestrial primary producers turn over much more slowly than phytoplankton. Similarly soil substrates turn over very slowly in comparison to the relatively rapid residence time of water. Terrestrial arid ecosystems appear to be particularly sensitive to threshold behaviors in response to changes in climate and human management as shown by work in the Serengeti (Dublin and others

1990), with acacia woodlands in the Southwestern US (Brown and others 1999) and in Kruger National Park in South Africa (Rogers and Biggs 1999). These examples highlight the nonlinear behavior of ecosystems as a product of interactions between diverse ecological factors (for example, the life span of the acacias, the number of wildebeest), human activities (for example, cattle grazing, fire setting) and climate (for example, spatial and temporal variability in precipitation). Furthermore, these interactions are constantly being modified by naturally occurring stochastic events (pest outbreaks, fires, droughts) and anthropogenic stressors (for example, habitat fragmentation, loss of species diversity) that operate at different spatial and temporal scales, and in a historical context defined by previous sequences of events. Identifying thresholds in these ecosystems requires monitoring a broad series of variables and their spatial distribution to provide a more comprehensive indication of an approaching threshold. A good example of such an approach is in Kruger National Park, where scientists and managers have defined a series of ''thresholds of probable concern'' that represent a range of spatially and temporally bounded indicators of ecosystem response to the main potential agents of change (Rogers and Biggs 1999). Alternatively, the development of readily measured integrative indictors of threshold behavior for terrestrial ecosystems, similar to the microbial indicators developed for use in the Neuse Estuary, would be a great aid.

Studying Thresholds in Space

Several approaches have been useful for investigating thresholds in spatial connectivity in landscapes. Percolation theory (Stauffer 1985; Stauffer and Anharony 1992) and neutral landscape models (NLM) (Gardner and others 1987; Turner and others 1989; With and King 1997) have been particularly useful for relating spatial patterns to ecological processes. Analyses from NLMs have proven to be extremely rich; one of the most important insights is the importance of critical thresholds in habitat abundance above or below which ecological processes are qualitatively different. Thus, changes in habitat abundance that occur near the critical threshold may produce large, surprising changes in the system because the habitat can suddenly become connected or disconnected. Below the thresholds, patches are small and isolated; above the threshold, patches are large and well connected. The numerical value of critical thresholds is dependent upon the particular process and landscape, but the occurrence of the threshold is not.

Empirical studies support the existence of critical thresholds in habitat abundance for bird and mammal populations, although the actual values may vary (Andren 1994; Bissonette 1997). The spatial spread of disturbances such as fire may exhibit threshold responses (Turner and others 1989; Turner and Romme 1994). For example, the spread of fire depends on the presence, distribution and connectivity of flammable fuels across a landscape. Below the critical thresholds, fire extent depends on the frequency of initiation, because fire cannot spread without adequate spatial connectivity of fuel. Above the critical threshold, fire extent depends on the probability of spread; with well-connected fuel, even a single ignition can affect the entire susceptible area. The NLM methods also allow for exploration of how thresholds might be altered by changes in environmental conditions, for example, fire may respond to landscape pattern differently depending on the weather (Figure 3). The important concept for critical thresholds is that the change between states occurs at a threshold of habitat abundance. For an organism, this influences the ability to move around a landscape and to locate suitable sites for establishment, foraging, nesting, or dispersal. For disturbance, it determines whether spread is constrained spatially or not. For flows of material (for example, nutrients), it influences the balance between sources and sinks.

Thresholds can occur in a variety of driving variables across landscapes. For example, effects of patch size, originally introduced in island biogeography theory, may also exhibit thresholds. Some organisms require patches of a minimum size for persistence, although the generality of this has been debated (Bowers and Matter 1997). The size and shape of habitat patches influences the ability of animals to persist in a landscape (Lindenmeyer and others 1999), and patch size can also influence nutrient dynamics (Ludwig and others 2000). Thresholds in patch size may also be related to patch shape and the underlying drivers of pattern (Krummel and others 1987).

At very large spatial and temporal scales, the application of multiple approaches such as surveys, experimental manipulations, paleoecological reconstructions and models can be used to assess if small changes in a driver can cause dramatic and surprising shifts in ecosystem state. For example, analysis of the chemistry of 597 lakes in the Western Lake Survey (Landers and others 1987), coupled with paleo-ecological analysis of change in phytoplankton communities (Wolfe and others 2001; Nydick 2002), lake mesocosm studies and terrestrial fertilization and gradient (Rueth and

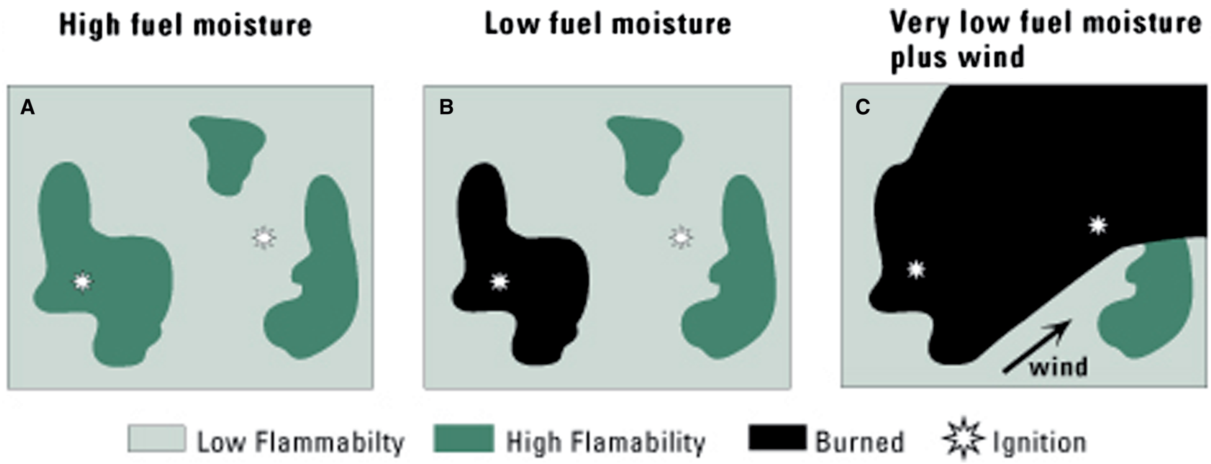

Figure 3. The distribution of patch types and environmental conditions influence the spread of disturbance in the landscape. Spatial thresholds that influence contagion, connectivity and percolation of animals and disturbance in the landscape vary with climate. From Turner and others 2001, based on Turner and Romme 1994.

Baron 2002) studies shows how small changes in deposition may lead to dramatic changes in the structure and function of both terrestrial and aquatic ecosystems in the western US, a region not generally considered to be at risk from N deposition (Baron and others 2000a, b; Williams and Tonnessen 2000).

Methods to Bring Humans into the Equation

Perhaps the greatest challenges in applying thresholds concepts to environmental problems arise from difficulties in incorporating human decision-making and behavior into our evaluation framework and methods. Humans control the ecosystem attributes that are valued, they are often the source of stressors that push systems toward and over thresholds, and they institute management schemes to achieve a variety of goals. New methods for modeling ecosystem dynamics that include humans in their development and application are emerging as important tools for establishing thresholds for environmental management.

One example of these new modeling approaches is work done to manage rare longleaf pine (*Pinus palustris*) forests at Eglin Air Force base in Florida (Peterson 1999; Hardesty and others 2000; Peterson 2002). On the sandy, well-drained soils of northern Florida, forests can be dominated by either longleaf pines or various hardwood species, primarily oaks. Fire suppression by humans leads to a decrease in pine and development of a fire-suppressant oak-scrub forest (Rebertus and others 1989). To address concerns about declines in the pine ecosystem, land managers of the base, in collaboration with The Nature Conservancy, initiated an adaptive management program to learn how to better use fire to manage the longleaf pine forest (Hardesty and others 2000).

Ecosystem modeling is a key aspect of adaptive management (Walters 1986). In adaptive management, modeling is used as a process for managers and ecologists to reflect upon what aspects of an ecosystem are critical for their management activities. At Eglin, a fire management model was iteratively developed through a series of workshops with forest managers. This process led to the development of a model that captured the dynamics of past landscape change and passed peer-review by an external set of longleaf pine ecologists. This model was then used to develop and test management options. This process had three main conclusions. First, restoring the historical wildfire regime would be insufficient to restore the landscape, due to changes in the spatial pattern of Eglin's forest. Second, it showed that a massive increase in prescribed fire was needed to prevent the continued slow loss of longleaf pine savanna. Finally, new fire management practices that considered ecological thresholds in fire frequency and spatial pattern could restore longleaf pine savanna on Eglin with far less fire.

The collaborative process of model development changed the way managers thought about the forest. The computer modeling process allowed them to create a new mental model of the forest that led to new management policies that take into account the ecological thresholds in the balance between tree species that exist in longleaf pine forests. The ability to consider surprising outcomes, beyond past and current experience, is critical to the ability to predict, identify and manage thresholds. As such, model development and application of the type employed at Eglin Air Force Base is emerging as a key tool in threshold-based environmental management.

CROSS CUTTING ISSUES AND RESEARCH FRONTIERS

Thresholds for What? Where?

A major factor inhibiting the use of ecological threshold concepts in environmental management is a lack of general principles for applying these concepts to different kinds of response variables (what) and different kinds of ecosystems (where). Without these general principles, each stressor and ecosystem response must be evaluated independently, a process that often requires years of site specific research, for which funding or time before shift in ecosystem state occurs may not be available. Because thresholds have been considered in very diverse ways, from whole ecosystem shifts (for example, Florida Bay) to reductions in the areal coverage of specific species (for example, Longleaf pine) to changes in specific ecosystem functions (for example, N retention by forests) the lack of general principles is understandable. Research is needed to determine whether there are general principles for applying threshold concepts to different types of ecosystems (for example, rivers versus estuaries versus forests), ecosystem attributes (for example, biodiversity, biogeochemistry) or the provisioning of ecosystem services (for example, drinking water, carbon sequestration). Are there inherent differences in threshold behavior between humid and arid, temperate versus tropical, conifer versus deciduous regions? Conversely, we can ask if there are commonalties among ecosystems and their thresholds. For example one might investigate the slow versus fast variables for any given ecosystem type, and identify ecosystem attributes that span aquatic and terrestrial systems, such as primary production and residence times. Developing these principles and guidelines should be a major aid in making threshold concepts a central problem-solving tool in environmental science. Once general principles have been developed, adaptive management pilot studies may prove useful in providing relevant feedback to scientists and environmental managers regarding uses and limitations of these principles.

Reversibility and Hysteresis

Any discussion of alternative stable states for ecosystems, thresholds and environmental management necessarily raises questions about reversibility. Some changes appear to be reversible (for example, if we reduce phosphorus or sewage inputs into lakes and rivers, the system often returns to a clear water state from a eutrophic, turbid water state – Smith 1998; Carpenter and others 1999), whereas others do not (for example, if we reduce acid rain inputs to northeastern forests, stream acid neutralizing capacity may not recover to pre acid deposition levels – Likens and others 1996; Driscoll and others 2001). In some cases, changes are reversible, but the return path to the original state is different from the path taken in the original state change – a hysteretic response. It is critical to make some evaluation of reversibility before embarking on a program of management or remediation. In the Eglin Air Force base example, model analysis showed that just allowing fires to burn rather than suppressing them would not reverse the loss of longleaf pine in the landscape. Rather, more aggressive management of fire and vegetation was required. In this case, the consideration of threshold effects prevented implementation of an unsuccessful management strategy and stimulated the implementation of a novel strategy that considered threshold effects, preventing a host of problems.

One line of reasoning suggests that reversibility is controlled by the alteration (or lack of) of key structural or functional aspects of the system. For example, acid neutralizing capacity has not returned to some streams in the northeastern US in part because acid deposition reduced soil base saturation, an important controller of stream chemistry (Driscoll and others 2001). Simply restoring fire to Eglin Air Force Base would not reverse the loss of longleaf pine because changes in the distribution of vegetation patches had altered the ability of the landscape to transmit fire. In the southwestern US, removing shrubs does not restore grassland because the shrub invasion alters patterns of soil resources in ways that inhibit re-establishment of grass (Brown and others 1999). In addition to changes in fundamental structure and function, system changes may not be reversible if something external to the system such as climate, toxic chemical inputs, or sedimentation has changed. A final consideration is that multiple interacting stressors, for example, climate change accompanied by changes in fishing pressures, greatly complicate the interpretation and predictability of ecosystem-level threshold responses. Clearly, our ability to determine if dramatic environmental changes are reversible increases with our understanding of the key relationships between structure and function in the ecosystem in question, that is, basic ecological research.

Scale, Scale, Scale

Discussion of threshold behavior in ecosystems almost always ends up with anguished discussion of scale. Consistent scale-related problems that frequently emerge include feedbacks between local and more spatially extensive processes (for example, local conservation of fish habitat in a river can be hindered by upstream land use changes in the watershed) and between fast and slow processes (for example, rapid reductions in acid inputs result in slow improvement in stream acid neutralizing capacity). The result is that local, short-term thresholds, which are what we most commonly manage, are constantly shifting due to changes in the spatially extensive and/or slow variables. A key research need is to establish conceptual linkages between specific ecosystem services and the aspects of ecosystem structure and function that influence these services. The set of drivers must encompass the linkages between factors that operate over small and large scales, and on fast and slow time frames. Once a complete set of scale appropriate drivers has been established, threats to those drivers can be identified and managed. Panarchy, which views coupled human-natural systems as a cross-scale nested set of adaptive cycles that reflect the dynamic nature of human and natural structures in time and space, is developing as a powerful conceptual framework for addressing scale issues (Gunderson and Holling 2002; Redman and Kinzig 2003).

Prediction

As environmental science has matured as a problem-solving discipline since the 1960's, interest in ''early intervention,'' ''preventative management,'' and ''prediction'' has increased (Carpenter 2002). A variety of approaches have been used to address global environmental problems such as climate change, deforestation, and the destruction of the ozone layer, ranging from synthesis of current understanding [for example, the intergovernmental program on climate change (IPCC)] to the use of ''syndrome'' or scenario models that look at large-scale processes and key interactions (Alcamo and others 1998). Clark and others (2001) note that the process of predicting the state of ecosystems, ecosystem services, and natural capital must explicitly include estimates of uncertainty. Hence, scenario-based modeling can provide decision-makers with an idea of possibilities, instead of definitive probabilities, and will be extremely useful for integrating scientific knowledge from many different natural and social science disciplines to portray the consequences of human activities and to elucidate potential options for mitigating causes or adapting to negative impacts (Leemans 1999; Millenium Ecosystem Assessment 2003).

The usefulness of nonlinear models and statistics to represent behaviors of systems (including threshold behaviors and multiple states) has been of increasing interest among ecologists and theoretical biologists (Henson and others 2002; Scheffer and Carpenter 2003). With sufficient data, one may be able to model shifts between multiple ecosystem states with equations and then use the model to make management decisions. Dent and coworkers (2002) emphasized that it is important for us to begin to identify what factors determine when nonlinear models may be most appropriate to use (that is, when multiple states are likely to exist). They suggest that nonlinear responses may be expected when there is ''a capacity within the system for resource accumulation to be followed by a release from these resources, when there is a mix of slow and fast acting variables influencing system dynamics, or there are shifts of control between multiple drivers.'' More recently, Fath and others (2003) have applied Fisher Information theory to develop an index that is sensitive to transient behavior in ecosystems with the hope of distinguishing ''normal'' dynamics from fundamental changes in system state.

Implications for Environmental Monitoring

Incorporating threshold concepts into environmental modeling, monitoring and management would be a major advance in our ability to deal with ecological surprises. We should take advantage of our ability to observe current non-linear changes in ecosystems (for example, El Niño effects on production and community composition in arid rangelands, hydrologic input affects on lake, river and estuarine nutrient cycling and production) to change our monitoring protocols, models and policy structures. Monitoring is a key component of adaptive management, used to determine if management goals are being met. Major research challenges in this area include developing ecosystem monitoring techniques that would provide early warning that a system is approaching a threshold (for example, like the microbial indicators used in the Neuse Estuary), methods to determine if ecosystem resilience is improving, and approaches for identifying ecosystem shifts that are likely to be irreversible.

Final Thoughts

Are understanding and incorporating ecological thresholds the key to successful environmental management, or are they an important and appealing conceptual way of looking at ecosystems with no real potential for practical application? There is abundant evidence that threshold behaviors occur in many ecosystems, with important effects on multiple ecosystem services. There is also evidence that ecological threshold concepts are used in policy decisions (for example, critical loads for atmospheric deposition). Yet, this does not mean they exist in all systems and even for those in which they exist, it remains very difficult to identify thresholds in specific ecosystems and to incorporate their dynamics in management or predictive models (Scheffer and Carpenter 2003).

We suggest that progress in this area depends on both general and specific research. Detailed analysis of specific ecosystems, for example, longleaf pine forests on Eglin Air Force base, coupled with more general and conceptual research, for example, panarchy, non-linear modeling, is essential to bridging the gap between theory and application that exists in this field. These analyses must include many of the approaches and concepts discussed above. We need to broaden our conceptualization of ecosystems to consider longer time scales and ecological surprises as has been done in the Neuse River Estuary, and to consider spatial interactions between fire and vegetation as has been done at Eglin Air Force Base and in other sites with Neutral Landscape models. The work on N deposition effects on lakes in the western US has shown how regional scale analyses can illustrate how subtle changes in environmental drivers can cause major changes in ecosystem structure and function. These new conceptualizations of ecosystems need to be incorporated into our models–conceptually through the use of scenario approaches and with group modeling efforts as has been done at Eglin Air Force Base and quantitatively, for example with new non-linear modeling methods. Specific studies, using these new approaches, should allow us to make progress on some of the great challenges that thresholds present, such as reversibility and the practical and theoretical issues of dealing with different spatial and temporal scales. Indeed, we argue that the examples presented above suggest that we are poised for major advances in this area and that ecological thresholds will soon be commonly used in the analysis of environmental problems and will be important in improving the quality of environmental management and our ability to predict the behavior of ecosystems over the next 10–20 years.

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