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BRIDGES

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Thresholds, breakpoints, and nonlinearity in freshwaters as related to management

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Abstract. Nonlinear ecological responses to anthropogenic forcing are common, and in some cases, the ecosystem responds by assuming a new stable state. This article is an overview and serves as the introduction to several articles in this *BRIDGES* cluster that are directed toward managers interested in dealing with nonlinear responses in freshwaters, particularly streams. A threshold or breakpoint occurs where the system responds rapidly to a relatively small change in a driver. The existence of a threshold can signal a change in system configuration to an alternative stable state, although such a change does not occur with all thresholds. In general, a mechanistic understanding of ecological dynamics is required to predict thresholds, where they will occur, and if they are associated with the occurrence of alternative stable states. Thresholds are difficult to predict, although a variety of univariate methods has been used to indicate thresholds in ecological data. When we applied several methods to one type of response variable, the resulting threshold values varied 3-fold, indicating that more research on detection methods is necessary. Numerous case studies suggest that the threshold concept is important in all ecosystems. Managers should be aware that human actions might result in undesirable rapid changes and potentially an unwanted alternative stable state, and that recovery from that state might require far more resources and time than avoiding entering the state in the first place would have required. Given the difficulties in predicting thresholds and alternative states, the precautionary approach to ecosystem management is probably the most prudent.

Key words: threshold, breakpoint, management, stable state.

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The scientific and popular literature are full of examples of rapid and sometimes catastrophic ecological change caused by what initially were thought to be benign and relatively small change(s) in the environment. Internal feedbacks can lead to multiple

stable states in ecosystems (Dent et al. 2002, Wootton 2010), and often these state changes are caused by anthropogenic factors. Examples include major changes in community structure and biogeochemistry of lakes subjected to nutrient pollution (Carpenter 2003), strong but delayed responses to nutrient addition in an arctic river (Slavik et al. 2004), decades-long lags in stream macroinvertebrate responses to watershed disturbance (Harding et al. 1998), shift to vegetation stabilization of substrates in streams following removal of terrestrial grazing pressure (Heffernan 2008), and shift to a flood-resistant algal and macroinvertebrate community following restoration of natural flood conditions (Robinson and Uehlinger 2008).

The ideas of potential instability and catastrophic change have existed in biological (Thom 1972) and ecological thought (e.g., May 1977) for decades. However, the concept of abrupt changes to alternative stable states has received considerable and warranted attention recently. A paper by Scheffer et al. (2001) on catastrophic shifts in ecosystems had been cited >1000 times by mid 2009. Analysis of Institute of Scientific Information (ISI) Web of Science citations indicates that the number of papers using the topics “ecological threshold” or “alternative stable state” coupled with “ecolo*” has climbed sharply every 5-y period since 1990 until the writing of this article (Fig. 1A). The percentage increase was substantially greater than the increase in articles with the topic “ecolo*” alone (Fig. 1B). This simple analysis indicates that the ideas of ecological thresholds and alternative stable states are receiving strong research interest and that managers might be helped by information on this relevant and rapidly developing area of ecology.

Predicting thresholds is important because they can influence ecosystem goods and services that people value (Martin et al. 2009). Recovery from a shift to an alternative stable state might not occur until stressor levels are reduced significantly (Bellwood et al. 2004, Hughes et al. 2005). Thus, identifying potential thresholds is an important aspect of managing ecological systems. Predictive understanding is central to applying ecology (Dodds 2009). Unfortunately, we cannot predict such changes well enough to manage many ecosystems adequately (Scheffer et al. 2009). How are managers of freshwater ecosystems to deal with the idea that systems can change abruptly in ways that do not mirror past patterns? Groffman et al. (2006) acknowledged that such abrupt changes are of interest to all ecologists, that the concept can be useful, but that much is not understood about how to apply the idea of abrupt change to management. For

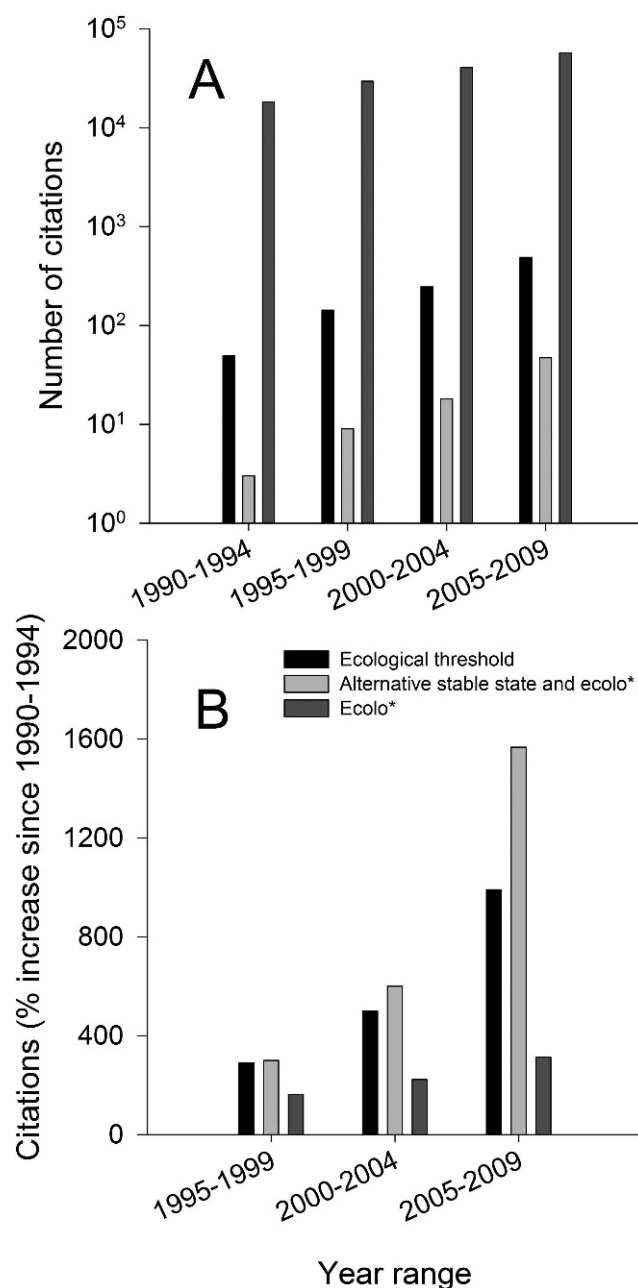


FIG. 1. Search results of number of citations from Institute of Scientific Information (ISI) Web of Science for the 3 topics: 1) ecological threshold, 2) alternative stable state and ecolo* and 3) ecolo*, where the * represents a character string wildcard. A.—Searching defined ranges of years for the 3 topics. B.—Results presented as a percentage of 1990 to 1994 citations to control for the increase in general ecology articles (ecolo*). Note the search was conducted in July 2009, so the last range of dates is truncated.

example, feedbacks leading to alternate states might be more common in lakes than in rivers (Dent et al. 2002), but this hypothesis has not been tested, and poor management decisions could arise from the

TABLE 1. Definitions of overarching terms associated with ecological thresholds used in this paper.

Term	Definition	Comments
Ecological state	Ecosystem structure and function	Ecosystem refers to all communities and populations as well as their relationships to each other and the abiotic environment in a region
Driver	Abiotic or a biotic change over time or space that influences ecological state	
Threshold	The point at which there is an abrupt change in an ecological quality, property, or phenomenon or where small changes in a driver can produce large responses in the ecosystem (Groffman et al. 2006)	In our paper, we assume the driver can be an ecological gradient or a biotic change (e.g., the addition or loss of an individual species)
Breakpoint	Generally refers to a place where one functional relationship between a driver and a response variable changes to another; not clearly different from threshold in the ecological literature	The term is often used to denote a discontinuous relationship, and can include a step function; alternatively referred to as a changepoint
Nonlinear relationship	Functions that are not 1 st - or 0 th -order polynomials (e.g., exponential, hyperbolic)	Not to be confused with mathematical definition of linearity
Alternative stable state	The fundamental configuration of the ecological state of the system changes; stable against normal environmental variation	
Regime shift	Abrupt changes on several trophic levels leading to rapid ecosystem reconfiguration between alternative states	Mayer and Rietkerk 2004, Andersen et al. 2009

assumption that the statement is an accurate generalization (not the intent of the paper by Dent et al. 2002). The papers in this *BRIDGES* cluster (Clements et al. 2010, Hilderbrand et al. 2010, King and Baker 2010) and another paper in this issue (Gido et al. 2010) illustrate advances in detecting thresholds and their consequences in streams.

The aims of our paper are to: 1) define and organize common terms, 2) collate and apply some methods with promise for identifying thresholds, 3) review illustrative examples of thresholds and alternative stable states from aquatic systems, and 4) establish how mechanistic understanding coupled with detection of thresholds could be of use to managers. This paper also serves as an introduction to the *BRIDGES* cluster, which aims to demonstrate different analytical methods to detect thresholds, highlight evidence of degradation and recovery thresholds in streams, and discuss implications of nonlinear response patterns to management of aquatic ecosystems.

Definition of Terms Related to Thresholds and Alternative Stable States

Groffman et al. (2006) defined an *ecological threshold* as the point at which an abrupt change occurs in an ecological quality, property, or phenomenon or where small changes in a driver produce large responses in the ecosystem (see Table 1 for a list of definitions of relevant terms used in our paper). Here, we assume the driver is an abiotic or biotic change over time or

space that influences ecological state. In some cases, time or space can be used as a proxy for the change in the driver and to account for lags in response to drivers. *Threshold* does not refer to the form of the function, which could be a step, an abrupt but continuous change in a functional relationship to a different equation, or a property of a single equation. *Breakpoint* often is used interchangeably with threshold, but usually refers to a place or time at which a sharp jump occurs from one function to another (a step function).

Species area curves, N saturation of rivers, fragmentation of stream networks (Fagan et al. 2002), patch size and extinction risk, biotic responses to contaminants, and altered thermal regimes are all examples of nonlinear responses. However, nonlinearity does not necessarily indicate that a specific threshold exists. Nonlinearities can be difficult to distinguish from thresholds in real-world data, but thresholds can indicate movement to an alternative stable state and a specific point of which managers should be aware, whereas many nonlinear relationships yield no specific natural breakpoint or threshold.

We provide 2 examples of nonlinearity that are not profitably viewed as a threshold. First, consider regular oscillations of an ecosystem property, perhaps approximated by a sine wave. If we observe only a single trough and peak, we could assume a threshold shift. A longer time series would reveal the regular oscillations. Second, consider the example of the

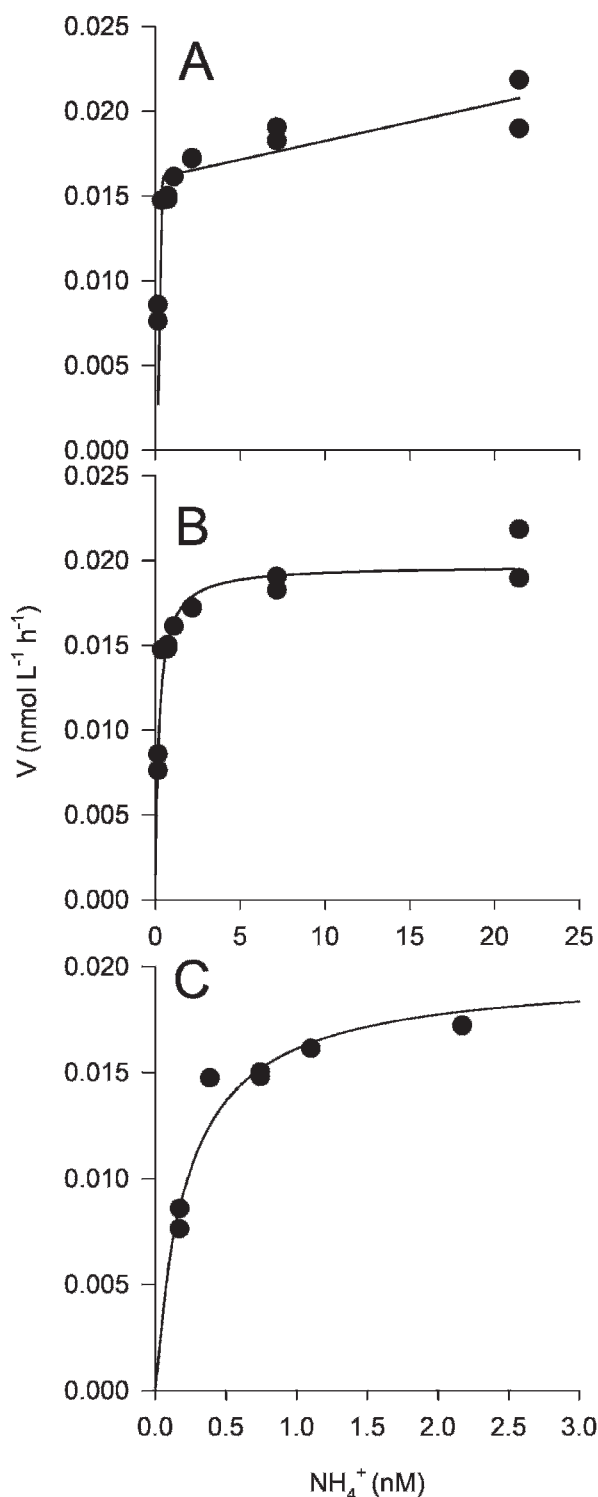


FIG. 2. Relationship between NH_4^+ concentration and uptake for Flathead Lake phytoplankton based on piecewise linear fit (adjusted $r^2 = 0.92$) (A), Michaelis-Menten fit (adjusted $r^2 = 0.92$) (B), and the lower portion of the Michaelis-Menten curve expanded (C). Data from Dodds et al. (1991).

Michaelis-Menten relationship for enzyme activity (Dodds et al. 1991). The function can roughly describe mechanism of nutrient uptake of microbial assemblages (Williams 1973). When data from this equation are viewed graphically, they could be equally well represented by 2 straight lines or by the Michaelis-Menten function (Fig. 2A vs 2B). However, the continuous nature of these data becomes more obvious at lower nutrient concentrations ($\sim 0.6 \text{ nM NH}_4^+$) (Fig. 2C). In both these examples, defining the nonlinear pattern as a threshold incorrectly characterizes the known nature of the systems.

Thresholds or breakpoints often are linked to *alternative stable states*. However, the existence of a threshold does not dictate the presence of mechanisms that would maintain an alternative stable state after the threshold is crossed. Stable states can be defined mathematically (e.g., community matrices where all eigenvalues have negative real parts, Lyapunov stability; May 1973) or conceptually (under conditions where strict mathematical definition is difficult, not possible, or not necessary).

The concept of an alternative stable state can be presented simply (e.g., a ball on a 2- or 3-dimensional landscape with local minima; Gunderson 2000). However, the actuality of stable states in ecological systems is more complex (Pawlowski 2006), and establishing their existence in the context of ecological management can be difficult and can depend on temporal and spatial scale. For example, alternative stable states exist when shallow lakes or ponds can be dominated by either macrophytes or phytoplankton (Carpenter 2003), but both of these states are ephemeral with respect to the fact that the pond will fill over geological time scales. Movement of a system from one state to another also has been defined as a *regime shift* (Andersen et al. 2009). *Ecological regime* has been defined as synonymous to alternative stable state (Mayer and Rietkerk 2004), but the definition of ecological regime provided by Anderson et al. (2009) does not specifically require that the alternative state be stable. Here, we use the term alternative state and indicate if it is a stable state, and we avoid referring to ecological regimes.

Methods for Fitting Nonlinear Ecological Relationships

Numerous methods can be used to find thresholds and characterize nonlinearity between a variable describing ecological state and a driver gradient or temporal trend (e.g., Brenden et al. 2008, Andersen et al. 2009; Table 2). Some thresholds, such as losing a species to extinction, paving a meadow, or drying a

TABLE 2. Some methods for identifying nonlinear and threshold relationships. D_1 = detection limit of the method, T_{95} = region with 95% certainty of change.

Method	Description	Citation
Breakpoint regression (piecewise regression)	Statistical determination if 2 relationships (usually linear) fit data better than one; also called piecewise regression	Common in modern statistical packages
Cumulative frequency distributions	Detects changes in expected distributions, can be combined with analytical methods to determine differences among distributions (e.g., D_1) and acceptable levels of change (e.g., T_{95})	Paul and McDonald 2005, Utz et al. 2009, Hilderbrand et al. 2010
Nonlinear curve fitting	Search methods used to fit a user-defined equation	Common in modern statistical packages
Nonparametric changepoint analysis	A test for change in variance, closely related to 2-dimensional Kolmogorov–Smirnov test; adapted to calculate empirical confidence intervals	Qian et al. 2003, King and Richardson 2003
Quantile regression	Characterization of changes in variance; includes quantile regression trees and quantile regression splines	Chaudhuri and Loh 2002, Cade and Noon 2003, Anderson 2008
Recursive partitioning (regression tree)	Predictors can be categorical or continuous; response can be univariate (classification and regression tree [CART]) or multivariate (multivariate regression tree [MRT]); referred to as regression tree analysis	Breiman et al. 1984, De'ath and Fabricius 2000, De'ath 2002
Regime shift detection	Find shifts in temporal data series	Rodionov 2004, Gal and Anderson 2010
Significant zero crossings (SiZer)	Derivative-based nonparametric approach using a smoothing function	Sonderegger et al. 2009
Threshold Indicator Taxa Analysis (TITAN)	Indicates changes in community structure across a gradient, a form of nonparametric changepoint analysis combined with indicator species analysis	Baker and King 2010
Two-dimensional Kolmogorov–Smirnov test	A nonparametric test for changes in variance; predicts a threshold in the driver and the response variable	Garvey et al. 1998

stream channel, are so obvious that no statistics are needed. In other cases, graphing the data is a good first step and is useful for checking statistical results (Brenden et al. 2008). We know of only 2 published studies in which suitability of various methods was tested by application to the same data. Results from 2-dimensional Kolmogorov–Smirnov testing and breakpoint regression were in general agreement on thresholds in a very limited study of the relationship between stream nutrients and benthic algal biomass (Dodds et al. 2002). Brenden et al. (2008) used simulated univariate response data to test for thresholds in a step function, a decrease, and a data wedge. They found that a quantile piecewise linear approach (a form of regression tree analysis) was the most robust method, but they did not evaluate uncertainty (e.g., confidence limits around thresholds, variability, and capture rate of simulated thresholds).

We subjected data on the relationship between total P and stream macroinvertebrate richness to additional methods (see references in Table 2 for analytical details). All methods agreed that a threshold concentration of nutrients existed above which macroinvertebrate diversity declined less rapidly. The concentra-

tion of total P at which the threshold occurred was similar across methods, but some methods differed as much as 3-fold in their threshold estimates (Table 3, Figs 3A, 4A–C). Because some methods lacked confidence limits or other measures of uncertainty, threshold estimates could not be compared rigorously among methods. A more extensive approach, such as that applied by Brenden et al. (2008), but using a greater variety of methods and measures of uncertainty with real and simulated data would be necessary to evaluate which method works best on specific types of data.

Some methods are better suited for specific data types. Time series are particularly important in understanding thresholds (Andersen et al. 2009). For example, responses of state variables can be expressed as a function of time since restoration of a system. Sonderegger et al. (2009) developed a derivative-based, nonparametric approach to detect ecological thresholds in long-term data sets. The significant zero crossings (SiZer) approach was used to quantify recovery of benthic communities following improvements in water quality (Clements et al. 2010) and was useful to distinguish long-term (11 y) recovery threshold from shorter-term climatic variation.

TABLE 3. Breakpoints or thresholds in the relationship between macroinvertebrate richness and total P determined using various methods applied to data presented in Figs 3A, 4A–C. For reference to method used, see Table 2. Confidence interval in piecewise regression was Bonferroni corrected. – indicates method unable to calculate parameter. SiZer = significant zero crossings.

Method	Comment	Breakpoint on x-axis (mg/L TP)	Significance of breakpoint	Confidence interval of breakpoint (95%)
Breakpoint regression (Fig. 3A)		0.100	0.001	0.06879–0.131
Cumulative frequency (Fig. 4A)	Point where ½ of sites with >25 species had been reached	0.05	–	–
Quantile regression tree (Fig. 4B)	10%, 50% and 90% quantiles, respectively	0.041, 0.049, and 0.75	<0.001	–
Nonparametric changepoint analysis (Fig. 4C)		0.041	<0.001	0.040–0.075
Two-dimensional Kolmogorov–Smirnov		0.090	0.002	–
Regime shift detection	Total P substituted for time	0.05	<0.001	–
SiZer	Threshold estimated based on locally weighted polynomial regression using a bandwidth of $h = 0.06$	0.15	–	–

Methods that could detect thresholds before they are crossed would be most useful to managers. Prediction might be possible because thresholds are associated with a rise in variance as the threshold is approached (Carpenter et al. 2008), and an increase in autocorrelation between a response variable and a driver or time can occur (Scheffer et al. 2009). However, these ideas have not been broadly tested, and their use might be complicated because variance can increase with the length of the time series (Halley 1996). Knowledge of an impending threshold and resulting regime shift would be valuable for maintaining ecosystem condition, but the temptation could be to try to manage the system up to the threshold in an effort to optimize the system. Given uncertainties in our ability to estimate thresholds, this approach could provide a false sense of security that the system is below the ecological threshold.

The Importance of Defining Mechanism

In addition to the challenges associated with empirical methods used to detect thresholds, field methods, experiments, and models used to demonstrate the existence of alternative stable states are accompanied by challenges. Scheffer and Carpenter (2003) state that it is “remarkably difficult to prove the existence of alternative attractors in the field”. The challenges of predicting change are exacerbated by the fact that global geochemical, geophysical, and biolog-

ical changes are leading to unprecedented biotic (Fox 2007, Williams and Jackson 2007, Dodds 2008, Jelks et al. 2008) and hydrologic (Milly et al. 2008) conditions. Extrapolation from empirical relationships (e.g., Peters 1991) will be complicated because the context of these relationships will have changed.

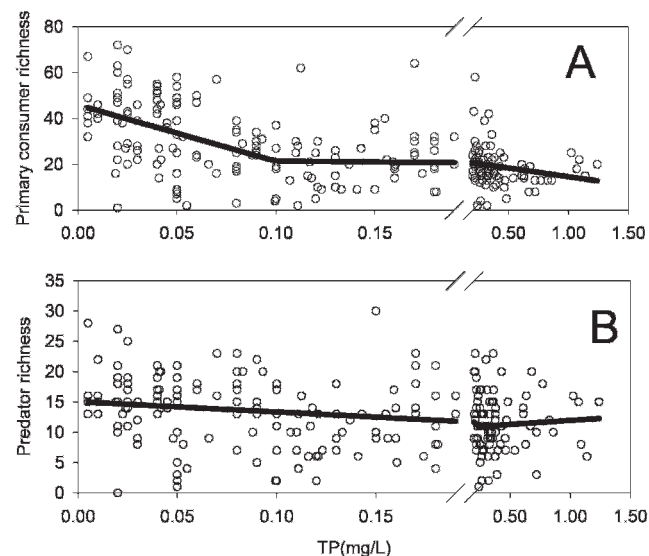


FIG. 3. Breakpoint regression analysis of macroinvertebrate consumer (A) and predator (B) richness as a function of water-column total P (TP) from 237 US Central Plains stream sites across Kansas, Nebraska, and Missouri in spring and autumn (data from Evans-White et al. 2009).

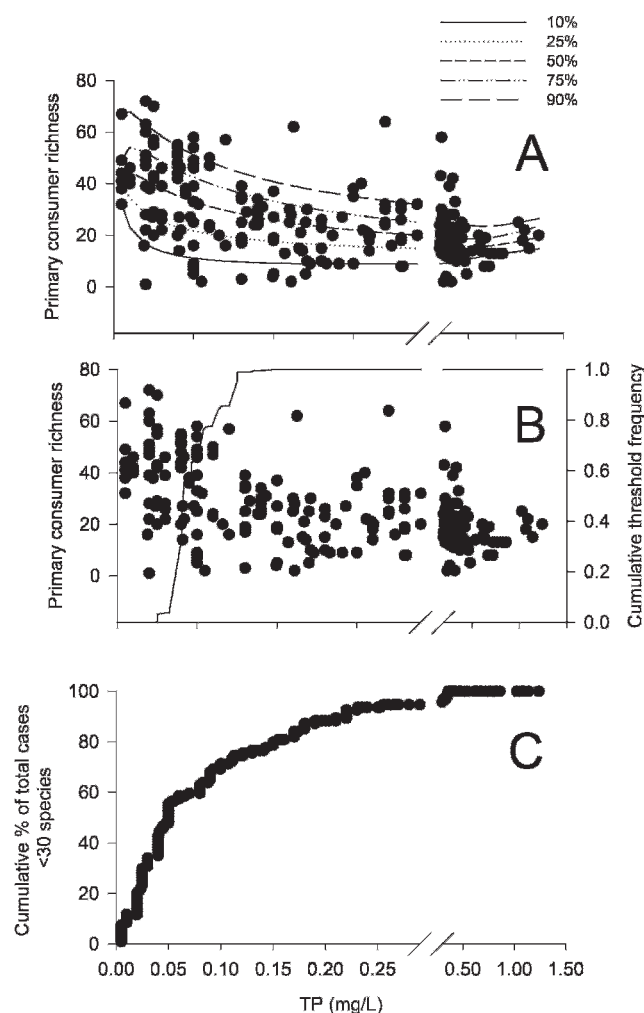


FIG. 4. Macroinvertebrate consumer richness represented as the cumulative percentage of cases with <30 primary consumer species (A), quantile regression splines (B), and nonparametric changepoint analysis cumulative threshold frequency (C) as a function of water-column total P (TP) from 237 US Central Plains stream sites across Kansas, Nebraska, and Missouri in spring and autumn (data from Evans-White et al. 2009).

Thus, understanding specific mechanisms that control the state of a system is essential to increase our ability to understand what would alter the system or return it to its initial state and to predict thresholds (Dodds 2009). Consider again the Michaelis–Menten relationship (Fig. 2A–C). The empirically fitted breakpoint offers no mechanism to predict the ability of microorganisms to take up NH_4^+ after chronic fertilization. However, our understanding of nutrient uptake by enzymes and biological tradeoffs suggests that maximum uptake should increase and uptake at lower concentrations should decrease. Our ability to predict the functional relationships among nutrient

loading, uptake, and retention depends on understanding the mechanisms driving nutrient uptake (O'Brien et al. 2007) and has specific relevance to managers concerned with ecosystem responses to chronic and acute nutrient pollution (O'Brien and Dodds 2010).

Two of the most commonly cited cases of thresholds and alternative stable states are found in lakes. In both cases, clear understanding of mechanisms aids in management. 1) Dissolution of iron phosphate in anoxic conditions that develop in hypolimnia of eutrophic lakes leads to high rates of internal P loading and a very stable eutrophic state that is insensitive to decreases in external nutrient loading (Carpenter et al. 1999). The chemical mechanism is well understood, and the implication for managers is that allowing a lake to become so eutrophic that anoxic conditions develop will make restoring the lake extremely difficult. 2) Shallow lakes can be dominated either by phytoplankton or macrophytes. Foodweb manipulation can reduce phytoplankton shading and increase macrophytes, and increased macrophytes can produce allelochemicals that reduce phytoplankton growth rates and maintain clear water (Dent et al. 2002). The mechanism is biotic and revolves around competition for light and ability of macrophytes to produce allelochemicals. The implication for management is that removing all macrophytes from a shallow lake could cause unwanted phytoplankton blooms.

In streams, the relationship between total P and macroinvertebrate diversity exhibits a threshold. Diversity decreases as P increases up to a point, and then decreases less rapidly above a breakpoint (Evans-White et al. 2009; Fig. 3A). The proposed mechanism for this threshold is that consumers that specialize on low-P food are less competitive when P is abundant in the water column. In contrast, predators meet their P requirement by consuming relatively P-rich animal prey and are less directly affected by water-column P. The fact that predators do not demonstrate a strongly defined P threshold (Fig. 3B) but consumers do (Fig. 3A) provides support for the mechanism. Whether macroinvertebrate diversity can recover with P control and whether this alternative state is stable are not known. The implication for management is that P should be kept below the threshold to maintain diversity.

Representative Case Studies From This Issue

The papers in this *BRIDGES* cluster (Clements et al. 2010, Hilderbrand et al. 2010, King and Baker 2010) or associated with the cluster (Gido et al. 2010) describe

cases of thresholds, some of which are characterized by alternative stable states.

An increase in impervious surfaces in watersheds can lead to abrupt changes in macroinvertebrate assemblages. Whether these changes represent an alternative stable state is not clear, but threshold data can be used to estimate effects of urbanization on regional macroinvertebrate biodiversity. Hilderbrand et al. (2010) described a series of species-specific thresholds at which extirpation occurs abruptly in response to increases in impervious cover, and they used these thresholds to predict the species of stream macroinvertebrates likely to be extirpated with increased urbanization. King and Baker (2010) used a newly developed technique to illustrate changes in entire communities across stress gradients. They used simulated data and data on impervious surfaces and macroinvertebrates as test cases to identify thresholds that were not apparent in analyses based on traditional community metrics.

Many species begin declining well before they have reached the point where they are destined for extinction or extirpation. The point at which a species begins to respond negatively to a stressor represents a subtle and difficult-to-identify threshold (King and Baker 2010). One way to detect early signs of decline and the point at which a species is effectively lost from the landscape is to compare cumulative frequency distributions of observed against expected distributions along gradients of potential stressors. Utz et al. (2009) used this technique to identify sensitivity of benthic macroinvertebrate taxa to land-use change and to test regional differences in sensitivity. This approach also can be used to forecast biodiversity loss in the face of changing landscapes (Hilderbrand et al. 2010). These tools for identifying thresholds early in a time series are useful to managers because they allow identification of species of concern in stressed landscapes.

Groundwater pumping and reservoir construction have shifted fish assemblages into alternative stable states. Streams in the Great Plains that rely on the Ogallala aquifer for base flow have experienced an abrupt change in the quantity and variability in stream flow since the 1960s when groundwater pumping rapidly increased. These changes coincided with construction of impoundments of various sizes and have strongly altered regional fish assemblages (Gido et al. 2010). These modifications abruptly altered the habitat of stream biota, but because stream networks are highly heterogeneous, many taxa maintained populations until recently (i.e., 10 y ago). Moreover, the distribution of invasive species in some areas expanded 10 to 20 y after reservoir

construction. In this system, time-lagged responses to environmental stressors were observed at large spatial and temporal scales. The mechanisms underlying the changes are species-specific responses caused by the interaction of life-history traits with physical habitat changes caused by reservoir construction and drying of small streams by groundwater withdrawal. The altered state is not stable over geological timescales, but is stable relative to generation times of the fishes.

Recovery over time in disturbed streams also can display nonlinear patterns. Clements et al. (2010) described a statistical technique that can be used to assess recovery trajectories and identify thresholds occurring over time. They found multiple thresholds in macroinvertebrate communities following restoration of part of a river damaged by mining waste. Their study illustrated the complex nonlinear nature of recovery and that managers should not assume that simple recovery trajectories will result from mitigation techniques.

Conclusions on Thresholds, Stable States, and Management

Detection of thresholds in advance might be possible, but the field is in its infancy (Scheffer et al. 2009). We lack enough ecological information in most systems to make a priori mechanistic predictions of where thresholds will occur, but thresholds can be identified empirically. If a threshold exists, it should be assumed (under the precautionary principle) that return will be difficult once the threshold is crossed because predicting whether the system has moved to an alternative stable state is difficult (Bellwood et al. 2004). Management decisions that might cause a system to approach an ecological threshold should be viewed with caution because the alternative state could be costly in terms of economic damages, lost opportunities, and restoration efforts.

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