Ecological Thresholds and Regime Shifts: from theory to operation

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Abstract

There is an apparent gap between the prominence of present theoretical frameworks involving ecological thresholds and regime shifts, and the paucity of efforts to conduct simple tests and quantitative inferences on the actual appearance of such phenomena in ecological data. There is a wide range of statistical methods and analytical techniques now available that render these questions tractable, some of them even dating half a century back. Yet, their application has been sparse and confined within a narrow subset of cases of ecological regime shifts. Our objective is to raise awareness on the range of techniques available, and to their principles and limitations, in order to promote a more operational approach to the analysis of ecological thresholds and regime shifts.

Regime Shifts in Ecology

The observation that managed ecosystems often fail to respond smoothly to changing pressures has generated perplexity and eventually lead researchers to draw parallels between the behaviour of ecological systems and other complex systems with non-linear dynamics, such as the global climate, the human immune system, and the world economy (cf. [1] for a popular account). Initial reports of kelp forest disturbance and recovery [2], freshwater ecosystem shifts engineered by beavers [3], and vegetation shifts affected by fire [4] have lead on to an ever-growing research effort on ECOLOGICAL THRESHOLDS and REGIME SHIFTS (see Glossary), whose underlying theoretical framework [5, 6] (Box 1) has been shown to be applicable to a broad range of ecosystems from coral reefs to forests and lakes [7,8]. These concepts are now also making their way into the minds and discussions of policy makers and might soon be translated into legislative frameworks [9].

Ecological regime shifts can be defined as abrupt changes on several trophic levels [10], leading to rapid ecosystem reconfiguration between alternative states. These shifts are generally thought to be driven by external perturbations (e.g. climatic fluctuations, overexploitation, eutrophication, and invasive species), but the exact mechanism is often unclear. The subject has become a fast growing scientific discipline, manifested by a 12-fold increase in publications between 1991 and 2006, twice as fast as the growth rate of research effort in ecology as a whole (7.7 % year^{-1}, ISI Web of Science). Most of the reported cases of ecological regime shifts are inferred from time series of monitoring data, while direct evidence by controlled experiments of the existence of alternative states is difficult to find [11]. Surprisingly, the general techniques available to test for regime shifts and thresholds have only to a limited extent been applied to these data sets. As formal tests of regime shifts have a long history in the context of climate change research (e.g. [12]) it is not surprising that formal statistical tests for ecological regime shifts have mostly been restricted to the effects of climate change on marine communities [13]. These observations suggest that there is a need to increase the awareness of ecologists on the availability and diversity of approaches allowing inferential analyses of ecological regime shifts and thresholds, helping this important research field to move to a more operational phase.

Here, after exploring research efforts in several fields we provide a review of methods for regime shift and threshold detection relevant to ecosystems, including both informal EXPLORATORY DATA ANALYSIS and formal HYPOTHESIS TESTING approaches, with the aim of encouraging a more quantitative approach to the study of these phenomena. Finally, we provide an operational summary of available software that can be useful for investigating abrupt changes in ecological data sets. As some of the terms are used differently among different research traditions, a glossary is provided.

Detecting thresholds and regime shifts in ecological data

Figure 1 shows that there are at least three ways by which an ecological system might exhibit abrupt changes over time; two which are reversible in response to changes in environmental drivers, while a third (Figure 1C) and most undesirable one is not [14]. Thus the existence of an abrupt CHANGE-POINT is a necessary but not sufficient condition for demonstrating BISTABILITY and HYSTERESIS (Box 1), as it might actually derive from sudden changes in the main drivers of the systems. It should also be kept in mind that while most ecological regime shifts are inferred from abrupt changes over time, time itself is never the actual underlying driver. Identification of the environmental driver(s) is complicated by the general interrelatedness of different social and environmental factors, and often also by the lack of data. Identification of a change-point in time is therefore the natural first step towards identifying a potential driver, which again is the first step towards identifying a regime shift mechanism that might eventually be relevant for policy-making.

There is an abundance of methods for identifying abrupt changes in time series, most of them developed in scientific fields other than ecology. The basic change-point problem, i.e. detecting a step change in the mean value in a sequence of random variables, has a long history in statistical inference (Box 2). The general scientific literature contains a bewildering diversity of methods that in a widest sense correspond to change-point detection, either in time or space (Box 3). In this review we contend that terms like regime shift [10,14], abrupt change [15], break- or change-point [16], STRUCTURAL CHANGE [17], ecological threshold [18], tipping point [19], and observational inhomogeneity [20], basically address the same problem and that methods developed for their analysis should have general relevance for the study of ecological regime shifts. The rapid growth of this literature already makes it hard to maintain an overview, and increases risk of unnecessary reinvention. For example, one of the threshold detection methods proposed in Ref. [21] is basically a rediscovery of the basic change-point problem presented a half a century earlier in Ref. [22] (Box 2).

Exploratory data analysis

A substantial part of the literature on ecological thresholds and regime shifts follows an explorative approach where data are pre-processed in various ways that render the presence of thresholds or jumps more evident to heuristic inspection, but usually without any statistical significance tests. The AVERAGE STANDARD DEVIATES (ASD) compositing method [23] is a rather popular representative based on simple heuristics rather than an underlying statistical model. The ASD was for example used to propose the occurrence of regime shifts in the North-Pacific in 1977 and 1989 [24] (Box 4). It has however been demonstrated that the ASD method is prone to false positives for AUTOCORRELATED time series, that is, to detect a regime shift when in fact there is none [25]. We recommend therefore that ASD, despite its popularity, is replaced by methods presented below for inference on regime shifts in ecology.

PRINCIPAL COMPONENT ANALYSIS (PCA) and related techniques are known under a variety of names (EMPIRICAL ORTHOGONAL FUNCTIONS (EOF), SINGULAR SPECTRUM ANALYSIS (SSA), etc.). PCA is used to compress, by linear combinations, a large number of correlated time series into a small number of uncorrelated ones that contain as much as possible of the original total variance [26, 27]. The presence of threshold phenomena in the reduced set could become more evident to visual inspection, but further processing and statistical testing is recommended. Applications to regime shift detection include the reduction of 100 climatic and ecological time-series from the North-Pacific into just two variables [24] (Box 4) or the combination of different climatic indices related to Pacific fisheries into a single one [28]. The conclusions drawn from a PCA can be strengthened by combining it with other independent approaches to multivariate time series analysis, such as CHRONOLOGICAL CLUSTERING [29,30] (Box 4). For example, PCA and chronological clustering were found to yield comparable regime shift patterns in 78 time series from the North and Wadden Seas [31].

PCA methods have well known limitations [27], such as the inability to capture relationships that are not linear, and the possibility of the reduced variables being distorted by the requirement of linear independence. Variants of non-linear dimensionality reduction [32] have been developed independently and also partly based on very different underlying concepts, in for example cognitive psychology [33] and oceanography [34]. The ARTIFICIAL NEURAL NETWORK-based approach [34] is claimed to be able to reveal multimodality, which in principle would be very relevant for detecting regime shift mechanisms related to bistability and hysteresis loops. Unfortunately, it has also been shown that this approach [34] is prone to false positives, as it is reported to find multimodality even in data sets generated from a multivariate normal distribution [35], which, by definition, cannot be MULTIMODAL. Our opinion of the current state of this field is that non-linear dimensionality reduction methods should primarily be used if simpler methods such as PCA and chronological clustering have been documented to be incapable of capturing important variations in a data set. Conclusions will also in this case be strengthened if there is a general agreement between several independent methods.

Inferential statistics and hypothesis testing

In the search for ecological regime shifts there is always a risk for thresholds being detected in what is actually just random fluctuation. Statistical hypothesis testing aims at limiting this possibility to a predetermined fixed value, typically a significance level of 5%. If the time of the threshold event is known (e.g. introduction of an invasive species, change in management practice, deforestation event) the significance probability of the regime shift under a null hypothesis of no change can be analyzed using intervention methods from standard statistical textbooks [36]. While originally aimed at testing for a shift in a time series following a particular action, INTERVENTION ANALYSIS has also been applied to data where the change-point was not known a priori, but hypothesized following exploratory data analysis [37]. Classical intervention analysis cannot be used for situations with the change-point occurring at an a priori unknown time. This calls for sequential tests where the existence of a regime shift is tested for at every point in time, and which must be characterized by higher critical values of the test statistic than in classical statistical methods (cf. Box 2) due to the so-called type I error (false positive) inflation in multiple tests. The underlying principle of the sequential methods is to compare a test statistic with its distribution under the null hypothesis. Critical values at different significance levels are tabularized for regularly observed data points, typically time series [38], whereas critical values for irregularly spaced observations must be calculated case-by-case and therefore can be computationally costly, but the continuous increase in computing power has greatly alleviated this constraint. Sequential test methods have mainly been developed for univariate time series, particularly within econometrics [17, 39] (Box 3) and climate research [40, 41] (Box 3).

The most commonly investigated regime shift hypothesis is a step change in mean level using parametric [40, 42, 43] or non-parametric [44] methods. Regime shift detection methods involving changing variance, shift in the frequencies of fluctuations, or even simultaneous interrelated shifts in several ecosystem components at a particular point have also been proposed [45], but their application to practical data analysis has so far been limited. The computational burden increases exponentially with the number of change-points in the data set [17]. While methods intended for identifying only single thresholds can also be employed to the individual subsets separated by a significant change-point in a hierarchical fashion [46], this will normally be less efficient than a DYNAMIC PROGRAMMING approach [39]. As the goodness of fit will generally increase with the number of change-points, model selection procedures involving penalties for the number of model parameters are to be recommended [47].

One problem associated with the classical statistical framework for investigating regime shifts against a null hypothesis with no regime shift is the lack of STATISTICAL TEST POWER for robust inferences. Ecological time series displaying regime shifts are generally much shorter (typically 20-40 time steps, usually years) than the typical time series that has driven the development of threshold detection methods in econometrics and climate research (often > 100 time steps). As change-points occurring at the extremes of a time series do not lend much power to hypothesis testing, it is only those change-points located near the middle of the time series that can be detected with confidence. Moreover, since ecological data are typically also noisier than climatic or economic data, a null hypothesis of no change-point is unlikely to be rejected within a classical statistical testing framework.

Testing the existence of hysteresis poses a statistical challenge even greater than threshold identification, because modelling hysteresis requires a memory effect to be included into the model formulation such that the present regime becomes dependent on previous states. Statistical inference must therefore be based on comparing the observations with the output of a dynamical model. In THRESHOLD AUTOREGRESSIVE (TAR) models the dynamics can switch between different linear autoregressive models depending on a linear function of the previous state relative to a threshold value [48]. The classical Canadian lynx population data could be modelled with a TAR model having two regimes, representing the increasing and declining phases of the lynx population cycle [49]. Otherwise, quantitative statistical studies of regime shifts with hysteresis in ecology are remarkably few. Needless to say, data requirements are high, as several transitions are needed to identify hysteresis effects (e.g. typically >10 transitions in the Canadian lynx data sets [49]). Additional complications caused by to missing values, measurement errors, and non-stationarity could also contribute to the paucity of applications of these analyses.

Although most of the threshold testing procedures described in the literature are univariate, they can naturally be expanded to include multiple variables. The advantage of multivariate analyses is that the power of testing increases provided that all variables show similar trends and have interactions that can be accounted for in the analysis. However, if only a subset of the variables shows a threshold response, the power of the test decreases and the outcome can become less clear. Simultaneous estimation of changes in the community interaction matrix (i.e. the density-dependent effects of a population both on itself and on other populations) has been suggested [50], but this approach will usually inflate the number of parameters such that the data requirements will be beyond what is realistic for ecological time series. Consequently, parsimonious consideration of the variables to be included in a multivariate test is recommended.

Available software for analysing regime shifts

Most of the statistical methods discussed in this review are implemented in available software packages (Table 1). Table 1 is not an exhaustive list of relevant software, but rather a selection of possible starting points for scientists interested exploring different approaches to quantitative regime shift detection. The list contains both tools requiring little background knowledge, such as standalone products or Excel add-ins, as well as toolboxes or packages for some of the major statistical computing environments such as R, Matlab, and O-matrix. The emphasis in Table 1 is on inferential tools for hypothesis testing, but some of the software listed also implements exploratory analysis methods.

Conclusions and future perspectives

The remarkable paucity of inferential analyses of ecological regime shifts and thresholds in the literature is at odds with the vigorous growth of this research direction, and could be attributable to the perception that these techniques are so data-demanding that only exceptionally few long-term ecological data sets would meet the requirements. However, the impressive impetus to the development and implementation of observational platforms across a broad range of ecosystems over the past two decades (e.g. the US NSF Long term ecological research (LTER) network and the EU Water framework directive (WFD) monitoring system) has already and will continue to deliver a wealth of data sets that could meet the requirements of even the more demanding of the techniques available. Lack of awareness on available techniques or misperceived data requirements should not keep ecologists from applying statistical techniques for threshold detection.

As human pressures on ecosystems continue to increase worldwide, the need for analytical approaches allowing the detection of ecological thresholds and regime shifts becomes a matter of urgency. Particularly, the impacts of climate change on biodiversity and ecosystems are currently assumed to be smooth, involving a continuous increase in impacts and extinctions as global temperature rises [51]. Well-documented fisheries statistics have shown that even relatively smooth climatic changes might lead to strong regime shifts in ocean ecosystems [13], increasing the likelihood of more prevalent and abrupt regime shifts as the planet warms beyond ecological thresholds for a growing fraction of species and ecosystems. Ecologists should increasingly contribute quantitative evidence of ecological thresholds for the future environmental policy making.

This review has documented a diversity of approaches, differing in complexity, power and requirements, which we hope will stimulate the transition from a phenomenological assessment of ecological regime shifts and thresholds to an operational one. All of the exploratory and inferential techniques covered here require that the threshold has to be crossed in order to be detected, which means that they cannot directly be used to prevent abrupt changes in ecosystems [1]. However, the accumulation of a broad empirical basis on the presence of ecological threshold and regime shifts in response to key pressures, such as increased nutrient inputs, ecosystem fragmentation or climate change, will certainly help develop a predictive framework to be used to anticipate and avoid changes associated with loss of essential ecosystem functionality. The accumulating knowledge base of ecological thresholds across different ecosystems should be accompanied by developing quantitative methods that allow confident extrapolation of thresholds for ecosystems that have not yet experienced, in particular irreversible, regime shifts.

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Glossary

Artificial neural network: a mathematical model where input signals are processed through one or more layers of interconnected computational nodes resembling biological neurons

Autocorrelation: the smoothness of a time series expressed as the correlation between its successive values

Autoregressive model: a linear regression model that uses past values to predict the present value of a time series variable

Average standard deviates (ASD): a regime shift detection method for multiple time series where the individual variables are forced to have the same sign on the same side of a change-point; known to have unacceptable false positive rate on autocorrelated data

Bifurcation: a qualitative change in the behaviour of a dynamical system resulting from a small change in a system parameter

Bistability: the existence of more than one locally stable stationary state in a dynamical system

Brownian bridge: a Brownian motion (random walk) where both ends are clamped to zero

Change-point: a step change in the mean value, or more generally, the distribution of a time series variable

Chronological clustering: a hierarchical grouping of successive steps in a multivariate time series according to a dissimilarity measure, also called constrained or stratigraphic clustering

CUSUM: cumulative sum of scaled deviations from a target value, such as the mean of a time series

Dissimilarity measure: a single numerical value expressing a distance between two multivariate objects, such that identical objects have 0 dissimilarity

Dynamic programming: a computationally efficient method for solving sequential decision problems by recursion

Ecological regime shift: a sudden shift in ecosystem status caused by passing a threshold where core ecosystem functions, structures, and processes of are fundamentally changed

Ecological threshold: the critical value of an environmental driver for which small changes can produce an ecological regime shift

Ecotone: a transitional area between two adjacent ecological communities

Empirical orthogonal function (EOF): a principal component decomposition of a multivariate time series

Exploratory data analysis: the analysis of data for the purpose of formulating hypotheses worth testing, thus complementing the conventional statistical tools for hypothesis testing

Hypothesis testing: making statistical decisions about data by asking a hypothetical question formulated as a null hypothesis

Hysteresis: a property of systems that can follow different paths when increasing and when relaxing a perturbation

Intervention analysis: a test of the hypothesis that an event at a known time caused a change in an autoregressive time series model

Likelihood ratio: the relative probabilities of an observed data set under two alternative hypotheses

Matrix decomposition: expressing a matrix as a product of (usually) simpler matrices

Multimodal distribution: a probability distribution with more than one peak

Principal component analysis (PCA): an orthogonal MATRIX DECOMPOSITION of the covariance or correlation matrix of a multivariate data set to reduce the dimensionality of interrelated variables

Recursive processing: a computational method for processing new data incrementally as they arrive, instead of processing them all in a single batch

Singular spectrum analysis (SSA): a technique for estimating the frequency components of a time series through a principal component decomposition of its autocorrelation matrix

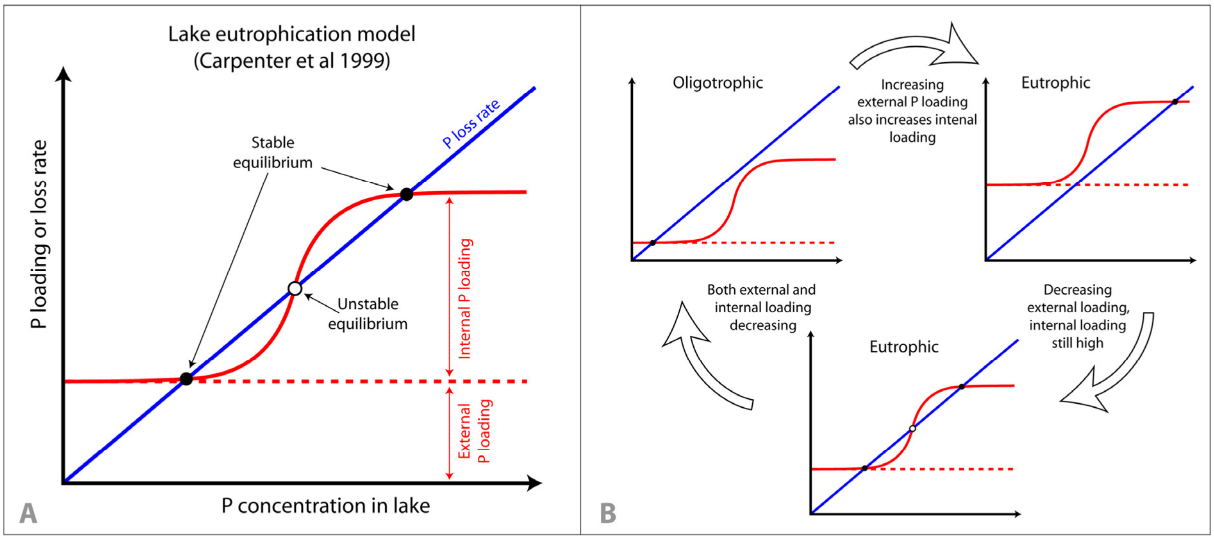
Statistical test power: the probability that a statistical test will reject a false null hypothesis; the sensitivity of the test

Structural change: a change-point with a step change in the parameters of the generating model for a time series

Threshold autoregressive model: a time series model that can change structurally depending on the past values of the series (rather than at a particular change-point in time)

Box 1: Theoretical and mechanistic approaches to regime shifts

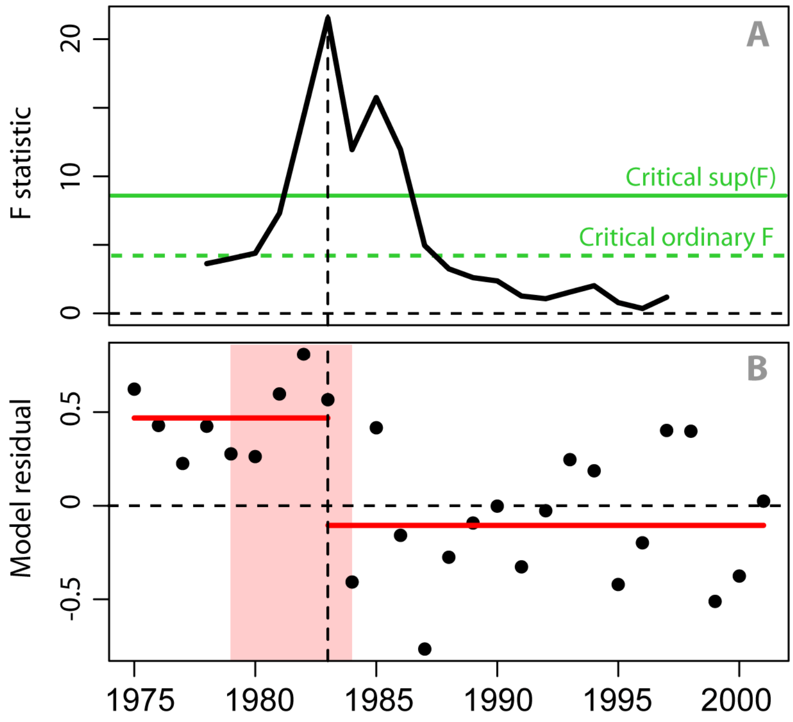
An abrupt jump in a system indicator when changing continuously a driver is an example of the class of phenomena known as bifurcations. In general, a BIFURCATION is a qualitative change in system state, including appearance and disappearance of available regimes or alteration of their stability, as drivers exceed specific threshold values. Bifurcation theory [52] is the branch of mathematics which studies them, identifying a broad catalogue of possible types of transitions: from steady to cyclic regimes, to irregular (chaotic) fluctuations, etc. Ecological analyses have been restricted mainly to transitions between two steady states. In the typical case there is a range of driver values for which two steady stable states are possible (for example high and low internal phosphorus (P) loading in a lake at the same rate of external P supply [53], as illustrated in panel A). This phenomenon, known as bistability, makes the actual system state depend on a hysteresis loop of past history (panel B; see also Figure 1, column C).



Regime shifts and bifurcations occur even in rather simple ecosystems; for example, models of food chains with only 3 trophic levels can display virtually any of the known bifurcation types [54]. Attaining reliable predictive power from realistic complex models, however, faces the difficulty of constraining model parameters from the relatively short and noisy time series typically available in ecology. As a consequence mechanistic models can rarely be used to predict accurately non-linear phenomena in ecological systems, but they can still give qualitative predictions that could be useful to interpret observations. For example, simplified models of grazing interactions [5] or of desertification [7] allow understanding the availability of multiple stable states for ecosystems in terms of the classical image of a marble rolling down a rugged landscape [5], for which the final rest state varies with the initial condition. They also reveal that system indicators will tend to change more slowly when approaching a regime change (this is called "critical slowing down" [52]). This and other features have led to propose indicators that should in principle enable detection of an approaching threshold before crossing it: rising variance [55], spectrum reddening (i.e. the relative increase of fluctuations of low frequency) [56], increasing return time from perturbations [57, 58], growing skewness [59]. Unfortunately, all these methods are very data demanding, and thus of restricted applicability to the analysis of real ecological time series.

Box 2: The basic change-point problem

The simplest case of threshold detection is identical to what statisticians have called the change-point problem: to estimate the change-point $i=k$ in a sequence $\{x_i\}$ of independent random variables with constant variance, such that the expectation of x_i is μ if $i \leq k$ and $\mu + \alpha$ otherwise. Quandt [22] showed already in 1958 that the change-point can be estimated by finding the index value k that maximizes a LIKELIHOOD RATIO, which in the case of normally distributed variables corresponds to the ratio of the residual sum of squares for the alternative hypothesis (a change-point at k with $\alpha \neq 0$) to that of the null hypothesis (no change-point, $\alpha = 0$). As this likelihood ratio would be F-distributed in the normal case, Quandt's test statistic would be the maximum or supremum of F (sup(F)). Still, it was evident that a test for the existence of a change-point could not be made from critical values of the F statistic, due to the well-known inflation of p-values in multiple tests (n-1 in this case, since an F value can in theory be computed for every $1 \leq k < n$). The asymptotic distribution of Sup(F) under the null hypothesis of $\alpha = 0$ was not worked out until 16 years later when MacNeill [60] showed that it could be constructed from moments of a BROWNIAN BRIDGE process. Extensions of these results are used for computation of confidence limits of Sup(F) and for general change-point hypothesis testing in software products such as the strucchange package for R [39] (Table 1).



We illustrate the use of this method on a data set [61] where a temporal pattern suggestive of a change point was found in the residuals of a multiple regression model for bottom-water oxygen concentrations in the Danish straits (panel B). The change-point F statistic (A) shows a distinct peak in 1983 and a smaller one in 1985, both higher than the 95% probability level for the sup(F) statistic under the null hypothesis (green line). Notice that the critical level for the sup(F) statistic is about twice that of the corresponding ordinary 2-sample F test (dashed green line). The fitted linear model (B; red line) indicates a 0.5 mg O_2 L^{-1} drop in the model residuals after 1983, although the 95% confidence interval for the change-point runs from 1979 to 1984 (red shaded area). This step change was interpreted as a consequence of the first major hypoxia event in the region, leading to a major restructuring of the zoobenthos community with repercussions on the system's susceptibility to new hypoxia events [61].

Box 3: What can be learned from other scientific disciplines?

The literature is enriched with a diversity of statistical methods for detecting thresholds, originating from other disciplines than ecology. Ecologists should adopt these methods rather than re-inventing new ways for analysing regime shifts.

The goal of statistical process control, dating back to the 1930s [62], is to detect systematic deviations in the mean value of a time series of some quality measure, for example the yield of an industrial process. Parameter estimates of the process or specific statistic, such as the cumulative sums of scaled residuals (CUSUM), are updated, in a RECURSIVE fashion, as new observations arrive. These tools could be applied to ecosystem monitoring programs as early warning indicators of a potential regime shift.

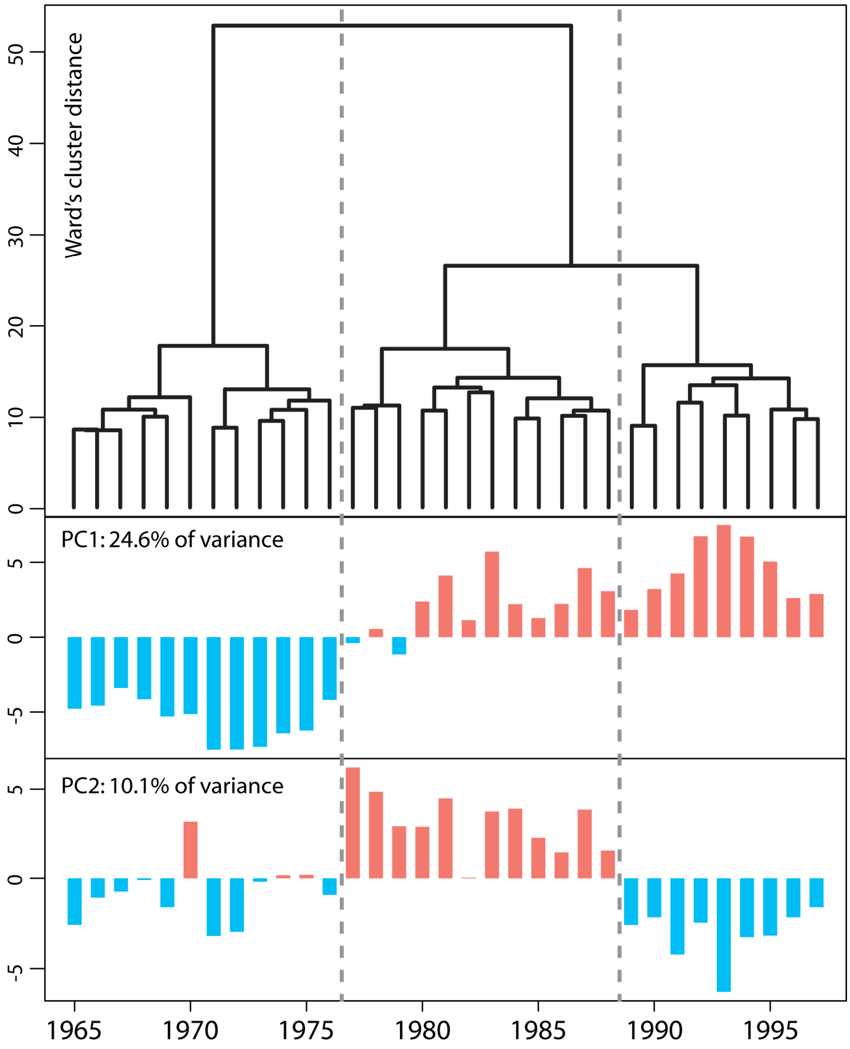
Econometry deals with time series that can be rich in abrupt changes due to both external interventions (e.g. policy options) and internal dynamics (e.g. consumer behaviour or different phases of economic cycles). Econometricians have developed a range of tools for detecting step changes in linear time series models, typically called structural changes or breaks in the econometric literature (see [63] for a recent review). These methods could be readily employed in ecology to obtain statistical evidence of regime shifts.

Climatologists also have a long tradition of investigating regime shift phenomena [12, 40, 41], however, with the concern that some sudden step changes in climate time series might be artefacts of the measurement system, for example due to a change in the measurement method or a relocation of a meteorological station. Therefore, climatologists have developed so-called homogenization methods to account for measurement artefacts [20, 64], and embedded this approach into general procedures for simultaneous detection of climate change and observational bias [65]. Techniques developed in climatology appear particularly suitable for ecological research, due to the similarities in both the studied phenomena and in the observational problems.

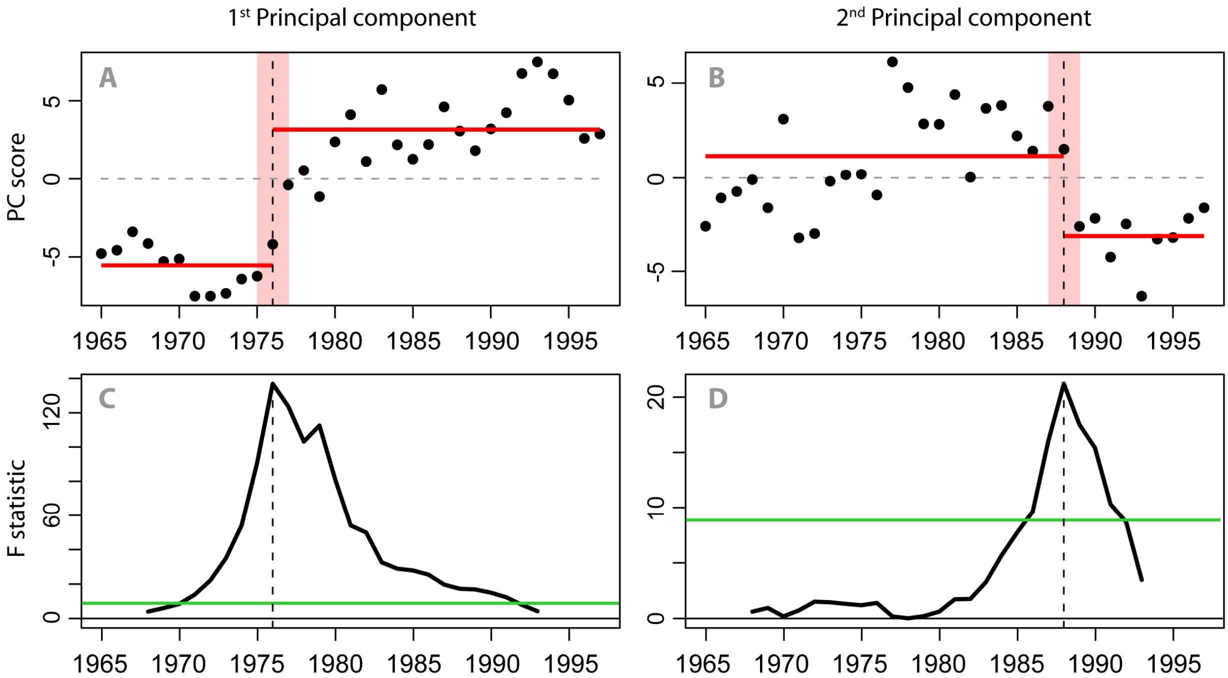
Vegetation ecologists have a range of methods for detecting change-points or discontinuities in the spatial extent of plant communities (reviewed in [66] and [67], among others). Such spatial discontinuities, called ECOTONES, are detected in multivariate data ordered in one dimension through comparisons of DISSIMILARITY MEASURES computed between the two halves of all sequential groups of samples [68]. The vegetation analysis approach is inherently multivariate, but otherwise displays similarities to the sliding window methods used for univariate time series by e.g. econometricians and climatologists. The potential of these methods for detecting regime shifts in multivariate ecological time series [69] deserves to be explored further.

Box 4. Regime shift detection in practice

Here we illustrate the analysis of a particular data set with some of the methods described in the main text. Hare and Mantua [24] (hereafter HM) compiled 100 time series from the North Pacific Ocean and the Bering Sea, covering a 33-year period from 1965 to 1997 (http://www.iphc.washington.edu/Staff/hare/html/decadal/post1977/100ts.xls). 31 of the time series were indicators of atmospheric and oceanic processes while the remaining were biological data, mostly catch and recruitment from commercially important fish stocks, but also some from lower trophic levels. As a first exploratory approach, we perform a Principal Component decomposition of the data set. Several of the time series have missing data which are filled with the mean of the series. The first 2 principal components (PC) of the HM data set contain about 35% of the total variance. As pointed out in the original publication [24], visual inspection of PC1 and PC2 (see figure) suggests abrupt changes around 1976-77 and 1988-89. While HM further analyzed the series with the ASD method, we show instead the use of two different methodologies: First, following within the exploratory approach, we perform chronological clustering [29] of the same 100 time series data, using Ward's linkage method on an Euclidean distance matrix (similar dendrograms are produced by other methods like complete or average linkage). The temporal grouping of three main regimes is consistent with the visual impression of the first two PCs.



Altogether, two reasonably independent exploratory methods both indicate regime shifts in 1976-77 and 1988-89 in the area covered by the HM data set. We now move to the inferential methodology by using the sup(F) statistic described in Box 2 to show that the existence of change-points in the 2 first PCs is statistically well supported. Nevertheless the magnitudes of the F statistics indicate that the statistical support for the 1976-77 change-point is stronger than for the 1988-89 one. It has been proposed [24] that the different change-points in the two PCs could be interpreted as the regime shift in 1988-89 not just being a flip back to pre 1977 conditions, but rather a transition to an altogether new regime.

1 

1st Principal component
2nd Principal component
A
B
C
D
PC score
F statistic

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Table 1. Software for regime shift detection

A selection of available software products with relevance to detection of thresholds and regime shifts in ecological data sets

Program	Methods	Approach	Availability	Authors	URL
Brodgar	Chronological clustering, dynamical factor analysis, min/max autocorrelation factor analysis, etc.	Inferential	Commercial, standalone with R interface, Windows	A. F. Zuur [30]	www.brodgar.com/brodgar.htm
Change Point Analyzer	CUSUM charts, bootstrap tests	Inferential	Shareware, standalone + Excel add-in, Windows	W. Taylor	www.variation.com/cpa/
Caterpillar-SSA	Singular spectrum analysis, structural change detection	Exploratory	Commercial, standalone, Windows	N. Golyandina, V. Nekrutkin, A. Zhigljavsky [34]	www.gistatgroup.com/cat/index.html
DCPC	Detection of changes using a penalized contrast	Inferential	Freeware, Matlab scripts, multiple OS	M. Lavielle	www.math.u-psud.fr/~lavielle/programs/
Dimensionality Reduction toolbox	Linear (PCA, etc) and non-linear dimensionality reduction methods	Exploratory	Freeware, Matlab scripts, multiple OS	L. van der Maarten [32]	http://www.cs.unimaas.nl/l.vandermaaten/Laurens_van_der_Maaten/Matlab_Toolbox_for_Dimensionality_Reduction.html
Palaeo	Chronological clustering	Exploratory	Freeware, R package, multiple OS	S. Juggins	http://www.campus.ncl.ac.uk/staff/Stephen.Juggins/analysis.htm
Regime Shift Detection	Sequential t-tests, pre-whitening option for auto-correlated data	Inferential	Freeware, Excel add-in, Windows	S. Rodionov [42]	www.beringclimate.noaa.gov/regimes/
STSA - Time Series Analysis Toolbox	Dynamical linear models, TAR models, Singular spectrum analysis, etc.	Inferential	Commercial, O-matrix toolbox, Windows	D. D. Thomakos	www.omatrix.com/stsa.html
Strucchange	Multiple change-points, F-tests, empirical fluctuation processes, etc.	Inferential	Freeware, R package, multiple OS	A. Zeileis, F. Leisch, B. Hansen, K. Hornik, C. Kleiber [39]	cran.r-project.org/src/contrib/Descriptions/strucchange.html
ThEnhancer	Nonlinear diffusion filtering	Exploratory	Freeware, standalone, multiple OS	A. Jacobo, P. Colet, E. Hernandez-Garcia	ifisc.uib.es/ThEnhancer/

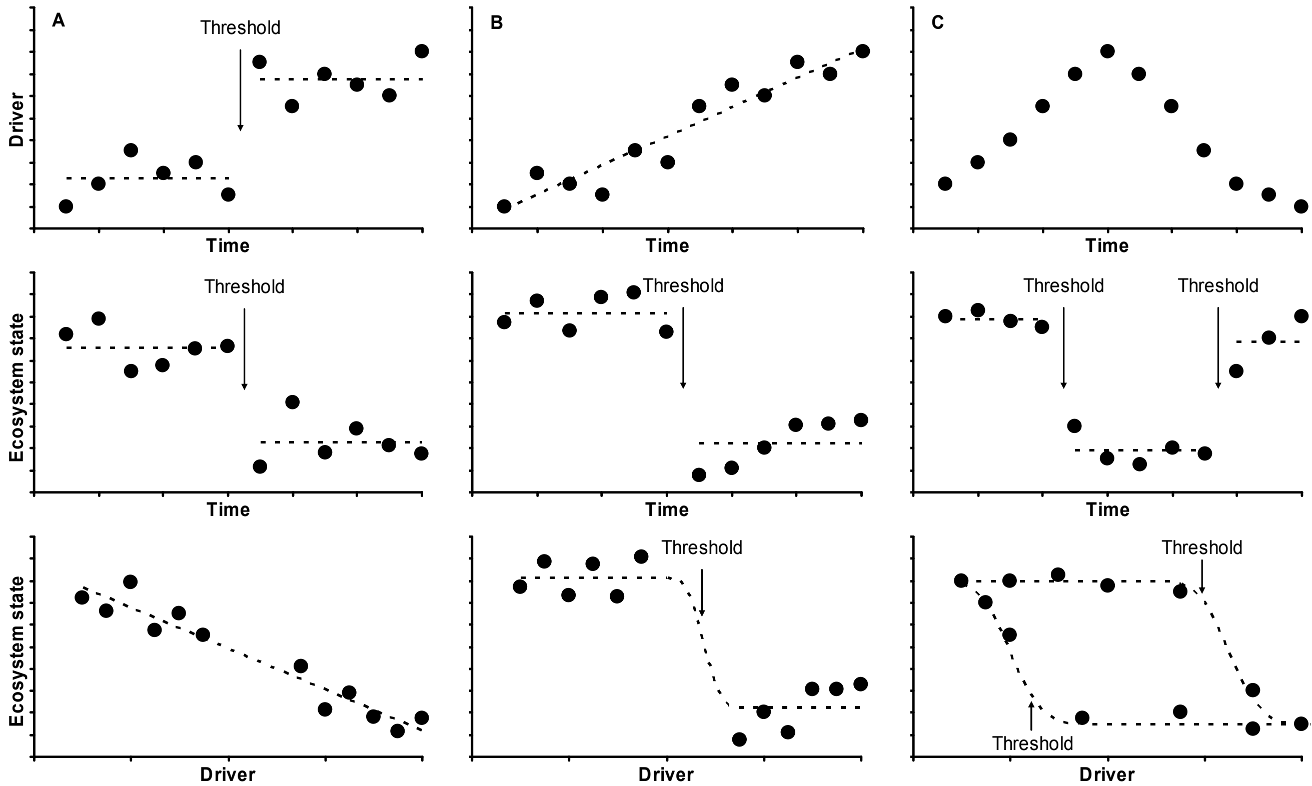

Figure 1. Three scenarios for regime shifts: Illustration of differences between regime shifts resulting from smooth pressure-status relationships, threshold-like responses, and bistable systems with hysteresis. The two top rows of graphs show time series of driver (e.g. nutrient inputs) and ecosystem state (e.g. phytoplankton biomass), and the lower row of graphs show the relationship between the driver and ecosystem state. Column A) Regime shift in driver linearly mediated to the ecosystem state. Jumps appear only in the time series. Column B) Regime shift in ecosystem state after driver exceeds a threshold. This is manifested through a jump in the time series of the ecosystem state. Column C) The hysteresis loop linking the ecosystem state to the environmental driver results in jumps between two alternative states when the driver is first slowly increased and then decreased again. Figure inspired by [70].