



# Ecological Transitions: Regime Shifts, Thresholds and Tipping Points. Oxford Bibliographies in Environmental Science

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## **ECOLOGICAL TRANSITIONS: REGIME SHIFTS, THRESHOLDS AND TIPPING POINTS**

### **INTRODUCTION**

Regime shifts, ecological thresholds, and tipping points are increasingly used in environmental sciences to describe abrupt ecological transitions ranging from population collapse to community reorganization, and even shifts at the whole ecosystem scale. Although all are intuitively understood, they sometimes remain contested and often loosely defined terms. Regime shifts describe persistent changes at population, community, or ecosystem level. Ecological thresholds are related to a strong nonlinear response in ecosystem state at a critical level of an environmental driver. Tipping points mark the onset of self-sustained responses that lead to strong changes in ecosystem state. All terms are related to the concepts of critical transitions, \*Catastrophe Theory\*, multiple stable states, and resilience. Ecological transitions are usually used with an alarmist notion even though they can refer to positive transitions (e.g., ecosystem restoration). They are often used in mixed ways: to represent a threshold in environmental conditions, to highlight the potential risk of abrupt shifts between \*Alternative States\*, or even as a metaphor for rapid anthropogenic changes at the level of the biosphere. There is a rich literature on understanding potential mechanisms behind the occurrence of ecological transitions and tools for their identification and timely detection. Most work is theoretical but with increasing empirical examples, as experimentation and long-term ecological data are becoming available. Due to their generic properties, regime shifts, thresholds, and tipping points are actively researched across scientific disciplines other than ecology for understanding the dynamics on systemic transitions in general.

## GENERAL OVERVIEWS

Regime shifts are intricately related to the concept of \*Ecological Resilience\* (see the *Oxford Bibliographies in Environmental Science* article “\*Resilience[obo-9780199363445-0048]\*” by Craig Allen, Ahjond S. Garmestani, and David Angeler), which was introduced in [Holling 1973](#) to describe the possibility of shifting between alternative ecological states at the crossing of thresholds. Resilience and multiple states refer to properties of the stability of an ecological system ([Grimm and Wissel 1997](#), cited under \*[Historical Overview](#)\*) and were formally summarized in mathematical models of consumer-resource interactions ([May 1977](#), cited under \*[Definition](#)\*, and [Noy-Meir 1975](#), cited under \*[Alternative States](#)\*). The first observations of multiple states were described at the level of communities based on species differences in community composition before and after a disturbance ([Sutherland 1974](#), cited under \*[Alternative States](#)\*). Later, the notion of multiple alternative states was expanded to describe shifts at the level of ecosystems, and gained a lot of focus in rangelands ([Bestelmeyer 2006](#)) and marine ecosystems ([de Young, et al. 2008](#)). In a comprehensive survey, [Muradian 2001](#) lists five prominent ecological thresholds related to anthropogenic stress. Based on long-term data and experimental manipulations, the review by [Scheffer, et al. 2001](#) argued for the importance and ubiquity of threshold behavior between (potential) alternative states in a variety of ecosystems. Scheffer’s review combined [Holling 1973](#) ideas of ecological resilience with the mathematics of \*Catastrophe Theory\* in [Thom 1976](#) (cited under \*[Textbooks](#)\*), and triggered a search for thresholds and the mechanisms of alternative states in ecology ([Beisner, et al. 2003](#) cited under \*[Alternative States](#)\*). Thereafter, regime shifts between alternative states and resilience were suggested as novel ways to approach ecosystem management under global environmental change ([Folke, et al. 2004](#)), the idea being that natural systems are not responding always linearly to changing conditions but occasionally abruptly and irreversibly. A useful overview of multistability in different fields and between different dynamical behaviors can be found in [Feudel 2008](#). Thresholds and regime shifts have been increasingly replaced in the ecological literature by the term “tipping point,” as explained in [Lenton 2013](#) to describe threshold behavior in the Earth’s climate systems. Recent work suggests the existence of tipping points at the global biosphere ([Barnosky, et al. 2012](#)), and summarizes new approaches for \*Anticipating Ecological Transitions\* in advance ([Scheffer, et al. 2012](#); [Clements and Ozgul 2018](#)).

Barnosky, A. D., E. A. Hadly, J. Bascompte, et al. 2012. Approaching a state shift in Earth's biosphere. *Nature* 486.7401: 52–58.

[This review suggests that global scale tipping points may be possible to occur at the scale of the biosphere.](#)

Bestelmeyer, B. T. 2006. Threshold concepts and their use in range management and restoration: The good, the bad, and the insidious. *Restoration Ecology* 14.3: 325–329.

[A review of the application of thresholds in rangeland management with specific emphasis on irreversible \(insidious\) thresholds.](#)

Clements, C. F., and A. Ozgul. 2018. Indicators of transitions in biological systems. *Ecology Letters* 21.6: 905–919.

[A review of different indicators used as early-warning signals for ecological transitions.](#)

de Young, B., M. Barange, G. Beaugrand, et al. 2008. Regime shifts in marine ecosystems: Detection, prediction and management. *Trends in Ecology & Evolution* 23.7: 402–409.

[An overview of theory and issues in understanding and detecting regime shifts for marine ecosystems.](#)

Folke, C., S. Carpenter, B. Walker, et al. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology and Systematics* 35:557–581.

[A highly cited work on the conceptualization of how biodiversity affects resilience and its link to regime shifts in ecosystems.](#)

Feudel, U. 2008. Complex dynamics in multistable systems. *International Journal of Bifurcation and Chaos* 18.6: 1607–1626.

[A useful overview of multistability in different fields apart from ecology, including different dynamical types of attractors.](#)

Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.

[The prominent paper of Holling that triggered the development of the field of resilience, beyond the classical concept of local stability. This work was influential in studying thresholds, applying catastrophe theory to ecology, and even leading to a broader sense of system resilience in socioecological systems and from local to global scales.](#)

Lenton, T. M. 2013. Environmental tipping points. *Annual Review of Environment and Resources* 38:1–29.

This review is a complete treatment on the *\*Definition\**, origin, mechanism, and detection of tipping points. It summarizes past Earth tipping points and highlights future ones, while it also discusses ideas on promoting favorable tipping points next to avoiding unfavorable ones.

Muradian, R. 2001. Ecological thresholds: A survey. *Ecological Economics* 38.1: 7–24.

A nice review of thresholds in ecology with a historical overview from a perspective of an economist.

Scheffer, M., S. R. Carpenter, T. M. Lenton, et al. 2012. Anticipating critical transitions. *Science* 338.6105: 344–348.

An overview of tools and studies on detecting tipping points in advance. It offers a list of modeling and empirical work on indicators of tipping points and highlights open questions in understanding tipping points in complex networks.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413.6856: 591–596.

A most influential review on catastrophic shifts in ecosystems with *\*Alternative States\**. It re-emphasized the connection of catastrophe theory with regime shifts and the identification of multiple states and it is considered a classic read regarding ecosystem thresholds and tipping points.

## TEXTBOOKS

**Scheffer 2009** is a general dynamic theory book that focuses on the particular class of tipping points that are associated with catastrophic bifurcations. It describes the dynamics that give rise to *\*Alternative States\** and transitions between them in a variety of ecological systems. The original mathematical work on catastrophes is developed in **Thom 1976**. Thom's book is a challenging read, but a more focused mathematical treatment of bifurcations and catastrophes can be found in **Arnold 1992**. A practical textbook on catastrophes and their mathematics is **Gilmore 1981**. **Petraitis 2013** provides an excellent summary of the theory and practical identification of multiple stable states in ecosystems with a detailed historical background. Although not a formal textbook, **Gladwell 2000** popularized the term 'tipping point' by describing some interesting social dynamical behaviors, which however cannot be accurately defined as transitions between alternative states.

Arnol'd, V. I. 1992. *Catastrophe theory*. New York: Springer-Verlag. [ISBN: 9780387548111]

A mathematical treatment of bifurcations, singularities, and catastrophes.

Gilmore, R. 1981. *Catastrophe theory for scientists and engineers*. New York: John Wiley & Sons. [ISBN: 9780471050643]

This book is a complete treatment of the mathematics of catastrophes with examples and applications. It includes a set of catastrophe flags that are typically used and identified in a variety of ecological papers as hallmarks of transitions.

- Gladwell, M. 2000. *The tipping point*. New York: Little, Brown and Co Little, Brown; 1st edition (February 29, 2000) 288 pages **ISBN-10:** 9780316316965

A popular science book that popularized the notion ‘tipping point’ and offers a great story to get an intuition into the dynamics of runaway changes.

Petraitis, P. S. 2013. *Multiple stable states in natural ecosystems*. Oxford: Oxford Univ. Press. [ISBN: 9780199569342]

This book is an excellent overview of the theory and \*Empirical Studies\* of \*Alternative States\*. It provides explanations of misuses and misconceptions of the theory and makes useful connection between models and data. It is written for an ecological audience in mind and is accessible and complete in covering the literature.

Scheffer, M. 2009. *Critical transitions in nature and society*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691122045]

An easy to read book on dynamics of critical transitions that combines both theory and examples. The book has two parts and can be read either from a theoretician’s or an empiricist’s perspective. Perhaps the best textbook on tipping points for the ecosystem scientist.

Thom, R. 1976. *Structural stability and morphogenesis*. Translated by D. H. Fowler. Reading MA: W. A. Benjamin. [ISBN: 9780805392791]

Originally *Stabilité Structurelle et Morphogenese* (1973) The reference book on catastrophes and structural stability that is better suited for a mathematics-oriented reader.

## JOURNALS

A variety of ecological journals are publishing articles on the topic of tipping points, regime shifts, ecological thresholds, or critical transitions (see section \*[Related Terms and Concepts](#)\*).

In particular, the journals *Ecosystems*, *Ecology and Society*, and *Global Change Biology* focus on ecosystem-wide studies and resilience theory. Occasionally, special issues are published on various aspects of thresholds, like Washington-Allen, et al. 2010 in *Ecology and Society*; Dakos and Hastings 2013 in *Theoretical Ecology*; Möllmann, et al. 2015 in *Philosophical Transactions B*; or articles in a special issues, such as Osman, Munguia, and Zajac 2010 in *Marine Ecology Progress Series*.

Dakos, V., and A. Hastings, eds. 2013. *Special issue: Regime shifts and tipping points in ecology. Theoretical Ecology* 6.3: 253–254.

This issue presents examples of applying *Leading Indicators* in ecological and climate systems predominantly in simulation and modeling settings.

*Ecology and Society*[<https://www.ecologyandsociety.org>]. 1997–. [class:periodical]

This is an open-access journal supported by the Resilience Alliance that focuses on thresholds and resilience of social-ecological systems.

*Ecosystems*[<https://link.springer.com/journal/10021>]. 1998–. [class:periodical]

This journal focuses on ecosystem-based studies, but also a social-ecological system.

*Global Environmental Change*[<https://www.journals.elsevier.com/global-environmental-change>]. 1990–. [class:periodical]

This journal often publishes paper on resilience and regime shifts.

Möllmann, C., C. Folke, M. Edwards, and A. Conversi, eds. 2015. *Special issue: Marine regime shifts around the globe: Theory, drivers and impacts. Philosophical Transactions of the Royal Society B: Biological Sciences* 370.1659. [doi:10.1098/rstb.2013.0260]

A diverse set of papers on theory, meta-analysis, and novel approaches to the drivers and mechanisms of regime shifts.

Osman, R. W., P. Munguia, and R. N. Zajac. 2010. Ecological thresholds in marine communities: Theory, experiments and management. *Marine Ecology Progress Series* 413:185–187.

A series of empirical, conceptual, and synthesis papers on thresholds in the marine environment, with emphasis on coastal communities.

Washington-Allen, R. A., D. D. Briske, H. H. Shugart, and L. F. Salo. 2010. Introduction. In *Special feature on catastrophic thresholds, perspectives, definitions, and applications*. Edited



by R. A. Washington-Allen, D. D. Briske, H. H. Shugart, and L. F. Salo. *Ecology and Society* 15.3: 38.

In this issue, the authors present conceptual and operational applications for understanding nonlinear behavior of complex systems with various ecological criteria at unique levels of organization.

## DEFINITION

In the early work by May 1977, discontinuous jumps in the equilibrium state of variables in response to continuous smooth changes are defined as thresholds. The Resilience Alliance, a collective of research scientists from social and ecological disciplines, defines ecological thresholds as “points between alternate regimes in ecological or social-ecological systems. When a threshold along a controlling variable in a system is passed, the nature and extent of feedbacks change, such that there is a change in the direction in which the system moves”; see also Walker and Meyers 2004. Regime shifts generally describe breakpoints and transitions in ecological states (Folke, et al. 2004, cited under \*General Overviews\*). Nowadays, regime shifts are defined in a broader context as large, persistent changes in the structure and function of social-ecological systems, with substantive impacts on the suite of ecosystem services provided by these systems; see Folke 2016. The term tipping point comes from the notion of “little things can make a big difference” as expressed in the original title of Gladwell 2000, cited under \*Textbooks\*. Van Nes, et al. 2016 suggests defining tipping points as cases where a small perturbation leads to a self-propagating change that eventually causes the system to change to a qualitatively new state. It is this characteristic self-propagated change caused by the existence of a strong positive feedback (see \*Positive Feedbacks\*) that determines the nature of environmental tipping points; see Lenton 2013, cited under \*General Overviews\*. In general, regime shifts, ecological thresholds, and tipping points refer to the situation where external conditions (e.g. a stressor, disturbance) cross a critical value causing an ecological system to respond in a nonlinear way. Similar definitions can be found in several reviews, including Briske, et al. 2010; Groffman, et al. 2006; Huggett 2005; Lenton 2013; May 1977; and Scheffer, et al. 2001 cited under \*General Overviews\*. However, there are occasionally misconceptions in their use and definition; see Petraitis 2013, cited under \*Textbooks\*.

Briske, D. D., R. A. Washington-Allen, C. R. Johnson, et al. 2010. Catastrophic thresholds: A synthesis of concepts, perspectives, and applications. *Ecology and Society* 15.3.

[A review paper on thresholds from the perspective of rangeland ecology.](#)

Folke, C. 2016. Resilience (Republished). *Ecology and Society* 21.4: 44.

[A fine summary of the development of Resilience science. Republished from the \*Oxford Research Encyclopedia of Environmental Science\*.](#)

[\[doi:10.1093/acrefore/9780199389414.013.8\]](https://doi.org/10.1093/acrefore/9780199389414.013.8)

Groffman, P. M., J. S. Baron, T. Blett, et al. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems* 9.1: 1–13.

[This review discusses the use of thresholds in environmental management and calls for a critical consideration of the concept.](#)

Huggett, A. J. 2005. Concept and utility of ‘ecological thresholds’ in biodiversity conservation. *Biological Conservation* 124.3: 301–310.

[This review discusses concepts, applications, contested views, and issues of the use of threshold for biodiversity conservation.](#)

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269.5628: 471–477.

[A pioneering work on formalizing the notion of thresholds and shifts between \\*Alternative States\\* in models of overgrazing, pest outbreaks, and parasite infections.](#)

van Nes, E. H., B. M. S. Arani, A. Staal, et al. 2016. What do you mean, ‘tipping point’? *Trends in Ecology & Evolution* 31.12: 902–904.

[This short communication intends to provide a structured definition to this loosely used term.](#)

Walker, B., and J. Meyers. 2004. Thresholds in ecological and social–ecological systems: A developing database. *Ecology and Society* 9.2: 3.

[This work presents the ongoing project of gathering evidence on ecological thresholds and developing a database of cases. Available](#)

[\\*online\[https://www.ecologyandsociety.org/vol9/iss2/art3/\]\\*.](https://www.ecologyandsociety.org/vol9/iss2/art3/)

## ***Historical Overviews***

The study of thresholds is closely related to the departure from the static equilibrium view that dominated ecological theory in the 1970s, summarized in [Briske, et al. 2005](#). Among the multiple concepts of stability summarized in [Grimm and Wissel 1997](#), stable equilibrium concepts have been dominant for understanding ecological dynamics. Early work on \*Ecological Resilience\* and breakpoints, including [Holling 1973](#), cited under \*[General Overviews](#)\*, and [May 1977](#), cited under \*[Definition](#)\*, demonstrated how ecological systems are not static nor globally stable, but they can experience threshold behavior that leads to local alternative equilibria ([Lewontin 1969](#); [Sutherland 1974](#), both cited under \*[Alternative States](#)\*). At the same period, the catastrophe theory of René Thom ([Thom 1976](#), cited under \*[Textbooks](#)\*), was popularized in [Zeeman 1976](#) (cited under \*[Historical Overviews: Catastrophe Theory](#)\*). [Zeeman 1976](#) also attempted to provide a universal explanation for the discontinuous behavior across a range of phenomena (see \*[Catastrophe Theory](#)\*). Although ecological thresholds and catastrophes shared common properties, the two concepts followed mostly separate paths until they were reemphasized in the early 2000s—see [Scheffer, et al. 2001](#), cited under \*[General Overviews](#)\*. The term ‘regime shift’ first appeared in oceanography to describe abrupt changes in time in the abundance of an ecosystem component (often a fish species—see [Lluch-Belda, et al. 1989](#), cited under \*[Related Terms and Concepts](#)\*). The term ‘tip point’ was first used in social sciences to describe segregation dynamics in white and black neighborhoods in [Grodzins’s 1957](#) study (found in [Lenton 2013](#), cited under \*[General Overviews](#)\*), in which a critical value of new nonwhite inhabitants was found to trigger a switch to a total black neighborhood. This critical threshold idea was popularized in [Gladwell 2000](#), cited under \*[Textbooks](#)\*, in a book detailing “how little things can make a big difference”. The book introduced an epidemiological perspective on social phenomena where behaviors spread rapidly through populations to lead to shifts in patterns and states in rather unexpected ways. Although, the type of dynamics described in [Gladwell 2000](#) is different from the mathematical underpinnings of catastrophe theory, the two concepts are used to a great extent interchangeably. The term “tipping point” was first introduced in the climate science discourse in [2005](#), as a metaphor that transformed climate change communication—see [Russill and Nyssa 2009](#). It was later adapted in the fifth IPCC assessment report, until [Lenton, et al. 2007](#) provided a structured definition for identifying tipping elements in the Earth’s climate. Afterwards, the term “tipped” to environmental sciences as it was closely

related to the concepts of ecosystem resilience ([Holling 1973](#), cited under *\*General Overviews\**), and catastrophic shifts ([Scheffer, et al. 2001](#), cited under *\*General Overviews\**).

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* 58.1: 1–10.

This paper summarizes the notions of state transitions, thresholds, and catastrophes that have early on gained ground in the field of rangeland ecology.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109.3: 323–334.

A reference paper that summarizes most notions of stability in ecology and attempts to suggest some rules in their use.

Lenton, T. M., H. Held, E. Kriegler, et al. 2007. Tipping elements in the Earth's climate system. *PNAS* 104.1: 1–10.

This work used models, paleoclimate data, and expert opinion to suggest potential elements of the climate system that are prone to tipping to a different state. It is an influential paper for popularizing the terms 'tipping point' and 'tipping elements.'

Russill, C., and Z. Nyssa. 2009. The tipping point trend in climate change communication. *Global Environmental Change* 19.3: 336–344.

An interesting read on the dynamics of the term 'tipping point' in the climate research discourse.

## RELATED TERMS AND CONCEPTS

A number of terms have been used to describe regime shifts and threshold and tipping point behavior. Some of these terms are used as synonyms whereas others are related concepts to characterize discontinuities in ecological state and properties. Occasionally, these terms are used interchangeably and create confusion—see [Dudgeon, et al. 2010](#), cited under *\*Alternative States\**. A few of the most common terms include: phase shifts, which usually refer to state transitions without alternative states ([Petraitis and Dudgeon 2004](#), cited under *\*Types of Ecological Transitions\**); catastrophic bifurcations, which are transitions related to the specific class of bifurcations described by *\*Catastrophe Theory\** ([Thom 1976](#), cited in *\*Textbooks\**); catastrophic shifts, which are related to abrupt shifts between alternative states ([Scheffer, et al.](#)

2001, cited under [\\*General Overviews\\*](#)); and critical transitions ([Scheffer 2009](#), cited under [\\*Leading Indicators\\*](#)), which is a generic term to describe abrupt transitions associated with bifurcation points that has been mathematically formalized (e.g., in [Kuehn 2011](#)). At the same time, the term ‘threshold’ has been used for different concepts. For instance, the extinction threshold in metapopulation models is defined as the critical level of habitat loss ([Hanski and Ovaskainen 2002](#)) that is also related to the critical fragmentation threshold at which landscapes become disconnected. On the other hand, a percolation threshold defines the threshold in the connectivity of the landscape for a disturbance (e.g., fire or disease) to propagate, as described in [Pascual and Guichard 2005](#). Analogous threshold concepts in physics are the first-order (discontinuous), and second-order (continuous) phase transitions summarized in [Solé, et al. 1996](#). When it comes to ecosystem management, [Mumby, et al. 2011](#) notes that ecological thresholds can be broken down to degradation and physiological thresholds, where the latter have been suggested to explain tipping points propagating from organismal to community and ecosystem level ([Monaco and Helmuth 2011](#)). In rangelands, these ideas are complemented by notions of restoration and intervention thresholds—see [Bestelmeyer 2006](#), cited under [\\*General Overviews\\*](#). Lately, thresholds at the scale of the Earth have been defined as planetary boundaries in [Rockström, et al. 2009](#), a hypothesis that is hotly debated, as discussed in [Brook, et al. 2013](#).

Brook, B. W., E. C. Ellis, M. P. Perring, A. W. Mackay, and L. Blomqvist. 2013. Does the terrestrial biosphere have planetary tipping points? *Trends in Ecology & Evolution* 28.7: 396–401.

[An opinion paper on the highly debated hypothesis of the existence of planetary tipping points.](#)

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16.3: 666–673.

[A classic paper that describes how habitat characteristics can delay extinction even when the extinction threshold is crossed in a metapopulation.](#)

Kuehn, C. 2011. A mathematical framework for critical transitions: Bifurcations, fast-slow systems and stochastic dynamics. *Physica D: Nonlinear Phenomena* 240.12: 1020–1035.

[A rigorous mathematical formalization of critical transitions based on slow-fast systems and their consequences in the presence of stochasticity.](#)

Lluch-Belda, D., R. J. M. Crawford, T. Kawasaks, et al. 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. *South African Journal of Marine Science* 8:195–205.

[A description of wax-and-wane dynamics of fish stocks and their characterization as regime shifts due to climatic factors.](#)

Monaco, C. J., and B. Helmuth. 2011. Tipping points, thresholds, and the keystone role of physiology in marine climate change research. *Advances in Marine Biology* 60:123–160. Elsevier.

[This work is revisiting tipping points from a physiological point of view and suggests a missing link in physiological constraints that can be connected to ecosystem-wide tipping points.](#)

Mumby, P. J., R. Iglesias-Prieto, A. J. Hooten, et al. 2011. Revisiting climate thresholds and ecosystem collapse. *Frontiers in Ecology and the Environment* 9.2: 94–96.

[This short communication aims at policymakers and managers by proposing a splitting of the notion of threshold into multiple components.](#)

Pascual, M., and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. *Trends in Ecology & Evolution* 20.2: 88–95.

[A review paper explains how self-organized criticality can lead to phase transition in spatial explicit models incorporating disturbance.](#)

Rockström, J., W. Steffen, K. Noone, et al. 2009. A safe operating space for humanity. *Nature* 461.7263: 472–475.

[This highly debated paper suggests the idea of the existence of thresholds at the planet level \(planetary boundaries\) and provides evidence for having crossed some of them already.](#)

Solé, R. V., S. C. Manrubia, B. Luque, J. Delgado, and J. Bascompte. 1996. Phase transitions and complex systems. *Complexity* 1.4: 13–26.

[An accessible physicist primer on characterizing different types of transitions: first-order, second-order, and noise-induced transitions.](#)

## **CATASTROPHE THEORY**

Most of the dynamical features of ecological transitions, especially tipping points, are mathematically rooted in catastrophe theory. Catastrophe theory drew great attention in the

1970s from [Zeeman 1976](#), who popularized the work of [Thom 1976](#), cited under [\\*Textbooks\\*](#), but also created skepticism, a summary of which can be found in [Deakin 1990](#). [Thom 1976](#) had developed a theory of catastrophe topologies that related to the notion of structural stability: discontinuities in the present system form caused by smooth changes in a parameter. [Gilmore 1981](#), cited under [\\*Textbooks\\*](#), provides a practical mathematical description of Thom's work and in particular gives a list of catastrophe flags that are used to identify catastrophic transitions, some of which are presented in [\\*Features of Ecological Transitions\\*](#) and [\\*Detection of Ecological Transitions\\*](#). Thom's catastrophes can be found in a variety of ecological models summarized in [Loehle 1989](#) and [Petraitis 2013](#) (cited under [\\*Textbooks\\*](#)). The cusp (and its degenerate fold [or saddle-node]) is the catastrophic bifurcation most broadly used to describe thresholds and [\\*Alternative States\\*](#) in ecology ([Lockwood and Lockwood 1993](#)). Although the fold is still the most predominantly described catastrophic bifurcation in ecological models with thresholds ([Scheffer, et al. 2001](#), cited under [\\*General Overviews\\*](#)), [Rinaldi and Scheffer 2000](#) provides a number of bifurcations that can also result in abrupt shifts between attractors that are not strictly a fold. A list of local and global bifurcations that can be catastrophic can be found in [Thompson and Sieber 2011](#).

Deakin, M. A. B. 1990. Catastrophe modelling in the biological sciences. *Acta Biotheoretica* 38.1: 3–22.

[This work provides a mathematical review of catastrophe models together with examples from biology.](#)

Lockwood, J. A., and D. R. Lockwood. 1993. Catastrophe theory: A unified paradigm for rangeland ecosystem dynamics. *Journal of Range Management* 46.4: 282–288.

[This work explicitly intends to recast rangeland dynamics into a catastrophe theory framework.](#)

Loehle, C. 1989. Catastrophe theory in ecology: A critical review and an example of the butterfly catastrophe. *Ecological Modelling* 49.1–2: 125–152.

[This paper is another early discussion of the controversy that arose from the application of catastrophe theory across various cases.](#)

Rinaldi, S., and M. Scheffer. 2000. Geometric analysis of ecological models with slow and fast processes. *Ecosystems* 3.6: 507–521.

[A graphical treatment of ecological models where dynamics can lead to a series of threshold behaviors with temporary shifts across different regimes.](#)

Thompson, J. M. T., and J. Sieber. 2011. Predicting climate tipping as a noisy bifurcation: A review. *International Journal of Bifurcation and Chaos* 21.2: 399–423.

[A mathematical overview of safe, explosive, and catastrophic local and global bifurcations.](#)

Zeeman, E. C. 1976. Catastrophe theory. *Scientific American* 234:65–83.

[The notorious work that popularized catastrophe theory from René Thom and applied it to a series of different examples from physiology to sociology.](#)

## TYPES OF ECOLOGICAL TRANSITIONS

Abrupt transitions in the state of an ecological system can occur in time or in space. [Andersen, et al. 2009](#) describes three types of threshold behavior: driver threshold where a jump change in the driver causes a jump change in the state of the ecosystem; state threshold where a continuous change in the driver causes a jump change in the state of the ecosystem; and driver state hysteresis where continuous changes in the driver cause jumps in the state of the ecosystem among alternative states. The same three types of responses are also used to differentiate between linear, nonlinear but continuous, and nonlinear but discontinuous responding ecological systems (see [Collie, et al. 2004](#), cited under [\\*Detection of Ecological Transitions\\*](#); [Scheffer, et al. 2001](#), cited under [\\*General Overviews\\*](#)). All types can be characterized as regime shifts, but the first type is not considered either as ecological threshold or tipping point. On the other hand, both the nonlinear continuous and discontinuous transitions exhibit the characteristic discontinuous response to a smooth change in environmental conditions, although it is difficult to distinguish between the two as they require the presence of alternative stable states, explained in [Petraitis and Dudgeon 2004](#) (see also [\\*Alternative States\\*](#) and [\\*Discontinuity\\*](#)). In that case the tipping point is related to a catastrophic bifurcation (see [\\*Catastrophe Theory\\*](#)) and the transitions can be characterized as bifurcation-type tipping; see [Ashwin, et al. 2011](#).

Alternatively, [Scheffer, et al. 2001](#) (cited under [\\*General Overviews\\*](#)) notes a tipping point can also occur when external disturbances force the state variable to shift to the alternative state by crossing the threshold that divides the basins of attraction of the alternative states (see also [\\*Alternative States\\*](#) and [\\*Discontinuity\\*](#)) [Ashwin, et al. 2011](#) has termed this case as noise-induced tipping in addition to a third type of tipping—rate-dependent tipping—which occurs when the external forcing exceeds a critical rate that makes the system leave its present attractor even though the stability of the attractor is not affected (as explained in [Siteur, et al. 2016](#)).



These types are only formalisms; in reality regime shifts and threshold behavior can be a mix of all the above processes.

Andersen, T., J. Carstensen, E. Hernández-García, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: Approaches to identification. *Trends in Ecology & Evolution* 24.1: 49–57.

A prominent review that categorizes types of threshold behavior and offers a list of tools for *\*Identifying Discontinuities\** in time series data.

Ashwin, P., S. Wieczorek, R. Vitolo, and P. Cox. 2011. Tipping points in open systems: Bifurcation, noise-induced and rate-dependent examples in the climate system. *Philosophical Transactions of the Royal Society A* 370.1962: 1166–1184.

This work formalizes three types of tipping points using climate models as examples.

Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. *Journal Of Experimental Marine Biology And Ecology* 300.1–2: 343–371.

This paper emphasizes the difference between phase shifts and shifts between alternative states and reviews examples from marine systems that may fall under either type.

Siteur, K., M. B. Eppinga, A. Doelman, E. Siero, and M. Rietkerk. 2016. Ecosystems off-track: Rate-induced critical transitions in ecological models. *Oikos* 125.12: 1689–1699.

In this paper, the authors explain the features and dynamics of rate-induced tipping points in ecological models and discuss their consequences.

## FEATURES OF ECOLOGICAL TRANSITIONS

A series of features have been described to be a cause, phenology, or consequence of ecological transitions, especially the ones that are associated with tipping points and catastrophic shifts. The most prominent ones are summarized in the next paragraphs.

### *Positive Feedbacks*

Escaping a present state to an alternative state was early on related to the existence of positive feedbacks (Holling 1973, cited under *\*General Overviews\**; Peterson 1984, cited under *\*Experimental Approaches\**). Generally, positive feedbacks are destabilizing and tend to amplify small deviations, while negative feedbacks are stabilizing and buffer deviations (DeAngelis, et al. 1986). For a tipping point to take place, these positive feedbacks need to create strong loops, where a small disturbance will be strongly self-amplified and will lead through a runaway

process to an alternative attractor. Positive feedback loops can emerge due to biotic-abiotic interactions (e.g., biogeochemical, biogeomorphological, biogeophysical) as explained in [Lenton 2013](#), cited under [\\*General Overviews\\*](#); or biotic (ecological) interactions (e.g., facilitation, Allee effects [or depensation] competition)—see [Kéfi, et al. 2016](#); [Knowlton 1992](#); and [Wilson and Agnew 1992](#). [Jones, et al. 1994](#) shows how the emergence of positive feedback loops could be the workings of ecosystem engineers (e.g., seagrass meadows that can promote their existence by modifying hydrodynamics and nutrients in the water column as described in [van der Heide, et al. 2007](#)). [Didham, et al. 2005](#) has also hypothesized that the emergence of positive feedbacks gives rise to alternative states that may be enhanced under strong abiotic conditions. Nonetheless, [Petraitis and Hoffman 2010](#) notes that positive feedbacks, ecosystem engineers, or strong abiotic conditions are not sufficient condition for the existence of multiple states and thresholds in ecological systems.

DeAngelis, D. L., C. C. Travis, and W. M. Post. 1986. *Positive feedback in natural systems*. New York and Berlin: Springer-Verlag. [ISBN: 9780387159423]

[A must-read book on describing positive and negative feedbacks in ecological systems to understand homeostasis and stability from an organismal to the ecosystem level.](#)

Didham, R. K., C. H. Watts, and D. A. Norton. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? *Oikos* 110.2: 409–416.

[This idea paper intends to identify conditions that would increase the probability of \\*Alternative States\\* and suggests the existence of harsh abiotic conditions as a potential mechanism leading to alternative states along the trajectory of community assembly.](#)

Kéfi, S., M. Holmgren, and M. Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology* 30.1: 88–97.

[An excellent review of how positive feedbacks can create alternative states with specific emphasis on facilitation.](#)

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32.6: 674–682.

[One classic early work of understanding the dynamics behind thresholds and potential multiple states in coral reef communities.](#)

Petraitis, P. S., and C. Hoffman. 2010. Multiple stable states and relationship between thresholds in processes and states. *Marine Ecology Progress Series* 413.1: 189–200.

This work aims to clarify the relationship between thresholds and the existence of alternative states using simple mathematical models.

van der Heide, T., E. H. van Nes, G. W. Geerling, A. J. P. Smolders, T. J. Bouma, and M. M. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems* 10.8: 1311–1322.

An example of understanding and discovering the consequences of a feedback mechanism in promoting seagrass meadows.

Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23:263–336.

A classical work on four types of positive feedbacks in plant communities that can lead to compositional shifts.

### ***Alternative States***

The prominent feature often related to ecological transitions is the existence of multiple states that represent alternative local attractors, separated by their own basins of attraction. The idea of such locally stable equilibria was identified in the early 1970s in the works of [Holling 1973](#), cited under [\\*General Overviews\\*](#); [Lewontin 1969](#); and [Sutherland 1974](#) (see [\\*Historical Overviews\\*](#)), and was formalized in mathematical models with alternative stable states ranging from single population models of exploitation in [Noy-Meir 1975](#), to consumer-resource models of pest outbreaks by [Ludwig, et al. 1978](#); stage- and size-structured models with trophic collapses (e.g. [De Roos and Persson 2002](#)); and assembly models with alternative end state communities as in [Law and Morton 1993](#). Empirically, it has been always difficult to prove the existence of alternative states in natural systems ([Connell and Sousa 1983](#); [Beisner, et al. 2003](#) and this challenge remains until today ([Petraitis 2013](#), cited under [\\*Textbooks\\*](#))—see also [\\*Detection of Ecological Transitions\\*](#).

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1.7: 376–382.

An early review paper on the [\\*Definition\\*](#) and ideas behind alternative states and thresholds in ecology

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121.6: 789–824.

A critical paper on the existence of alternative states, part of the early debate on multiple states in nature.

De Roos, A. M., and L. Persson. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences of the United States of America* 99.20: 12907–12912.

This theoretical study belongs to a set of models where size- or age-structure can create growth feedbacks that give rise to catastrophic shifts in natural populations.

Dudgeon, S., R. Aronson, J. Bruno, and W. Precht. 2010. Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series* 413 (August): 201–216.

This paper criticized the problems in properly defining and discriminating phase shifts (reversible) from shifts between alternative states.

Law, R., and R. D. Morton. 1993. Alternative permanent states of ecological communities. *Ecology* 74.5: 1347–1361.

This paper refers to a body of literature studying alternative states in Lotka-Volterra models along the process of community assembly.

Lewontin, R. C. 1969. The meaning of stability: In *Special issue: Diversity and stability in ecological systems, report of a symposium held 26–28 May. Brookhaven Symposia in Biology* 22:13–24.

This influential contribution introduced the potential of multiple states in ecological systems and challenged the prevailing ideas of global stability.

Ludwig, D., D. D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *Journal Of Animal Ecology* 47.1: 315–332.

One of the first modeling studies describing abrupt transitions of pest outbreaks and alternative states of forest health.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator-prey graphs. *Journal of Ecology* 63.2: 459–481.

The classic model of Noy–Meir that described overexploitation with multiple equilibria and threshold responses.

Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* 108.964: 859–873.

Another classic work on the early work and debate over the existence of alternative states using evidence from historical trajectories of community dynamics.

### ***Discontinuity***

A jump in the state of an ecosystem in response to changes in environmental conditions is to a great extent the most pronounced feature of a tipping point ([Gilmore 1981](#), cited under [\\*Textbooks\\*](#); [Scheffer, et al. 2001](#), cited under [\\*General Overviews\\*](#)). Nonetheless, as [Dudgeon, et al. 2010](#) explains (cited under [\\*Alternative States\\*](#)) a discontinuity may not imply the existence of alternative states but merely a phase (or regime) shift (see also [\\*Related Terms and Concepts\\*](#)). Typically, discontinuities are identified along a temporal trajectory of an ecosystem (see [\\*Identifying Discontinuities\\*](#)). But such trajectories may also be gradual.

[Hughes, et al. 2013](#) shows that inherently slowly changing ecological systems will exhibit time lags and slow responses that will not appear discontinuous or catastrophic despite the existence of thresholds. Theoretical models have shown that tipping points between alternative states can be gradual, depending on the level of heterogeneity in the landscape (see [van Nes and Scheffer 2005](#)) Also [Bel, et al. 2012](#) shows how gradual shifts can be found in spatial models of vegetation when conditions pass the so-called Maxwell point—at this point a local disturbance will slowly propagate in the landscape and gradually tip the ecosystem to an alternative state.

Bel, G., A. Hagberg, and E. Meron. 2012. Gradual regime shifts in spatially extended ecosystems. *Theoretical Ecology* 5.4: 591–604.

A theoretical paper that exemplifies the effect of the Maxwell point: a critical point beyond which transitions to an alternative state occur in a gradual (noncatastrophic) way due to the expansion of a front.

Hughes, T. P., C. Linares, V. Dakos, I. A. van de Leemput, and E. H. van Nes. 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology & Evolution* 28.3: 149–155.

The main point in this work is to emphasize the importance of time lags and slow responding ecosystems to stress that may hide already trespassed thresholds and tipping points.

van Nes, E. H., and M. Scheffer. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* 86.7: 1797–1807.

This paper presents the consequences of spatial heterogeneity on the threshold responses of spatial extended ecosystems with alternative states.

### ***Irreversibility***

The typical shift from one state to another occurs after a small change in external conditions, a bifurcation-type tipping; see [\\*Types of Ecological Transitions\\*](#). If [\\*Alternative States\\*](#) exist, restoring conditions does not guarantee the reversal to the previous state ([Gilmore 1981](#), cited under [\\*Textbooks\\*](#); [Scheffer, et al. 2001](#), cited under [\\*General Overviews\\*](#)). Such irreversibility is termed ‘hysteresis’: a common property of models with alternative states—see also [\\*Catastrophe Theory\\*](#). The term was coined by Alfred Ewing coming from the Greek word of ‘lagging behind’ (cited in [Petraitis 2013](#) in [\\*Textbooks\\*](#)). Hysteretic effects can have important consequences on the management of ecological system, as has been highlighted in [Bestelmeyer 2006](#), cited under [\\*General Overviews\\*](#), and [Suding and Hobbs 2009](#).

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: A developing framework. *Trends in Ecology & Evolution* 24.5: 271–279.

This work is making a link between threshold models and irreversibility to the management implications of terrestrial systems especially when it comes to their potential for restoration.

### ***Ecological Resilience***

Ecological resilience refers to the amount of disturbance an ecological system can receive without shifting to an alternative state, as first defined in [Holling 1973](#) (cited under [\\*General Overviews\\*](#)). Usually, threshold and tipping points are associated with the loss of ecological resilience ([Scheffer, et al. 2015](#), cited under [\\*Detection of Ecological Transitions\\*](#)). It is distinguished from engineering resilience that refers to the time needed for a system to return back to equilibrium after a perturbation; see [Pimm 1984](#). [Carpenter, et al. 2001](#) reviews how the notion of resilience has considerably evolved (see also *Oxford Bibliographies in Environmental Science* article “[\\*Resilience\[obo-9780199363445-0048\]\\*](#)” by Craig Allen, Ahjond S. Garmestani, and David Angeler), but in terms of thresholds and tipping points, ecological resilience is still understood as the size of the basin of attraction of the present system state—the larger a disturbance needed to shift the system out of its present state, the more resilient the system is.

Carpenter, S. R., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4.8: 765–781.

A mini-review that intends to clarify the different facets of resilience and asks for a proper problem *\*Definition\** in terms of the point of measure and the type of disturbance.

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307.5949: 321–326.

A classic paper on the relationship between complexity and stability of ecological systems.

## DETECTION OF ECOLOGICAL TRANSITIONS

Detecting ecological transitions refers to identifying critical values toin external conditions where a shift occurs. However, as the identification of actual critical values is an ominous task, detection is usually related to identifying the possibility of alternative states in an ecological system (see section *\*Alternative States\**). This means identifying mechanisms and patterns that are related to the existence of alternative states and transitions between them (e.g., [de Young, et al. 2008](#), cited under *\*General Overviews\**). In catastrophe theory, [Gilmore 1981](#) (cited under *\*Textbooks\**) refers to these patterns as catastrophe flags (see also *\*Catastrophe Theory\**).

Alternatively, these flags can be used as criteria for diagnosing catastrophic regime shifts as explained in [Collie, et al. 2004](#), and [Scheffer and Carpenter 2003](#). Recently, [Ratajczak, et al. 2018](#) has summarized how the type and nature of disturbance can affect the inference and diagnosis of ecological transitions especially in terrestrial ecosystems. Moreover, there has been renewed interest in developing leading indicators (or early-warning signals) for anticipating tipping points as reviewed in [Scheffer, et al. 2009](#), cited under *\*Leading Indicators\**. Detection methods follow in general either a structural (models, experiments) or a statistical (pattern recognition) approach ([Lenton 2013](#), cited under *\*General Overviews\**). A complete review can be found in [Scheffer, et al. 2015](#).

Collie, J. S., K. Richardson, and J. H. Steele. 2004. Regime shifts: Can ecological theory illuminate the mechanisms? *Progress in Oceanography* 60.2–4: 281–302.

This paper revises the mechanisms behind different types of regime shifts that are typically encountered in the marine environment and proposes a set of criteria for diagnosing what type of threshold behavior is encountered.

Ratajczak, Z., S. R. Carpenter, A. R. Ives, et al. 2018. Abrupt change in ecological systems: Inference and diagnosis. *Trends in Ecology & Evolution* 33.7: 513–526.

This paper reviews approaches in understanding regime shifts in field observations and experiments in the light of multiple types of disturbances.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution* 18.12: 648–656.  
[doi:10.1016/j.tree.2003.09.002]

A well-known review that is written as a guide for avoiding misconceptions on identifying thresholds between \*Alternative States\*. It provides a guideline for studying regime shifts and identifying their mechanisms and their potential underlying alternative states.

Scheffer, M., S. R. Carpenter, V. Dakos, and E. H. van Nes. 2015. Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics* 46:145–167.

This is a quite complete review on indicators of resilience (a.k.a \*Leading Indicators\* or early-warning signals). It summarizes mechanisms of these indicators, reviews studies and methodologies, suggests types of use, and highlights new approaches for quantifying loss of resilience and the risk of upcoming tipping points.

### ***Building Models***

Detection (and understanding) of ecological transitions begins with qualitative reasoning on identifying key factors that influence ecosystem functions and can exhibit threshold behavior (Groffman, et al. 2006, cited under \*Definition\*). This approach most often goes hand in hand with identifying the mechanisms that produce relevant positive feedbacks that could potentially lead to a runaway shift between \*Alternative States\* explained in Kéfi, et al. 2016, cited under \*Positive Feedbacks\*. Scheffer and Carpenter 2003, cited under \*Detection of Ecological Transitions\*, highlights how such qualitative reasoning can be complemented by minimal mechanistic models in understanding threshold behavior. Most of such models involve a minimum set of mechanisms to describe the ecological transition and usually assume a certain threshold in a process (May 1977, cited under \*Definition\*; Scheffer, et al. 2001, cited under \*General Overviews\*), although Petraitis and Hoffman 2010, cited under \*Positive Feedbacks\*, shows that this does not need to be necessarily the case. Combining data with such models helps to identify potential critical values of environmental thresholds, like the critical phosphorus load causing lake eutrophication in Carpenter and Lathrop 2008. Other modeling approaches involve



models of higher complexity that account for a complete set of mechanisms (e.g., PCLake [Janse 1997]), or are conceptual, like the state-and-transition models that have been a powerful tools to describe discontinuous vegetation transitions in rangelands (Westoby 1980). Overall, there have been a great number of different model types that describe tipping points in lakes (Carpenter 2002), drylands (Rietkerk and van de Koppel 1997), or coral reefs (Mumby, et al. 2007), to name a few representative examples.

Carpenter, S. R. 2002. *Regime shifts in lake ecosystems: Pattern and variation*. Excellence in Ecology 15. Oldendorf/Luhe, Germany: International Ecology Institute.

This is a notable book on threshold dynamics of lakes, especially on trophic cascades and eutrophication with a close link between data and mechanistic models.

Carpenter, S. R., and R. C. Lathrop. 2008. Probabilistic estimate of a threshold for eutrophication. *Ecosystems* 11.4: 601–613.

This modeling paper develops a way of realistically estimate a threshold critical value of phosphorus load using a mechanistic model of lake eutrophication.

Janse, J. H. 1997. A model of nutrient dynamics in shallow lakes in relation to multiple stable states. *Hydrobiologia* 342:1–8.

This work highlights the developments of a highly complex model that describes most of the physical, chemical, and biological variables and parameters in a shallow lake and exhibits threshold behavior.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450.7166: 98–101.

This modeling work refers to one of the most cited models for describing coral reef transitions to algae overgrowth.

Rietkerk, M., and J. van de Koppel. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79.1: 69–76.

A modeling paper that showed how \*Positive Feedbacks\* between plants and water availability can give rise to thresholds and \*Alternative States\* in semiarid ecosystems under stress.

Westoby, M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany* 28.3–4: 169–194.

This work refers to classical state-and-transition models that have been used to describe successional patterns in rangelands. Although these models do not per se refer to alternative states they have been strong conceptually for understanding threshold dynamics. cited.

### ***Experimental Approaches***

The existence of a discontinuity (see section [\\*Discontinuity\\*](#)) is the first diagnostic of a potential threshold. However, this does not guarantee the existence of alternative states and feedbacks triggering shifts between them. [Connell and Sousa 1983](#), cited under [\\*Alternative States\\*](#), early on requested experimental evidence for the existence of alternative states. [Peterson 1984](#) proposed four criteria that need to be fulfilled when experiments for testing alternative states are conducted. [Scheffer and Carpenter 2003](#), cited under [\\*Detection of Ecological Transitions\\*](#), suggest three criteria: different initial states leading to different end states, disturbance triggering a shift to the alternative state, and hysteresis in back-and-forward changes in environmental conditions. These criteria are what [Gilmore 1981](#) names catastrophe flags, cited under [\\*Textbooks\\*](#): namely divergence, inaccessibility, and hysteresis (see also [\\*Catastrophe Theory\\*](#)). [Schroder, et al. 2005](#) showed, however, that only a few studies have conclusively demonstrated the existence of alternative states. Some of the problems lie in the misconception of how to define basic notions of threshold behavior and equilibrium states. [Scheffer and Carpenter 2003](#) argue that alternative stable states are better described as dynamic regimes rather than equilibria, whereas their temporal and spatial scale dependencies plague their proper [\\*Definition\\*](#) and thus the identification of tipping points and thresholds. [Petraitis 2013](#), cited under [\\*Textbooks\\*](#), provides a detailed account on difficulties arising from implementing conditions and criteria set in the literature, and proposes a “before and after control and impact” experimental design for robust identification of alternative states based on a long history of experimentation in rocky intertidal communities.

Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist* 124.1: 127–133.

[Peterson’s note provided a set of four criteria for clarifying the existence of \[\\\*Alternative States\\\*\]\(#\) and it is part of the early debate on the study of multiple states in nature.](#)

Petraitis, P. S., E. T. Methratta, E. C. Rhile, N. A. Vidargas, and S. R. Dudgeon. 2009. Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia* 161:139–148.

One of the most complete experimental tests of alternative states in a marine community.

Schroder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: A review. *Oikos* 110.1: 3–19.

This paper scrutinizes thirty-five experimental studies of alternative states to identify the strongest evidence for the true existence of alternative states while providing some clear conditions and criteria for deciding on the empirical detection of alternative states.

### ***Identifying Discontinuities***

Discontinuities (see section [\\*Discontinuity\\*](#)) are usually reflected as jumps in time-series data. They are the first place to look for identifying thresholds and tipping points from field studies ([Peterson 1984](#), cited under [\\*Experimental Approaches\\*](#); [Scheffer and Carpenter 2003](#), cited under [\\*Detection of Ecological Transitions\\*](#)). Usually these tests are performed post hoc using monitored univariate or multivariate time series of the relevant ecological state. [Andersen, et al. 2009](#), cited under [\\*Types of Ecological Transitions\\*](#), brilliantly summarizes tools that have been developed across different fields to address this also called break- or change-point analysis. Some of these tools have been predominantly developed in marine science ([Rodionov 2004](#)) for identifying regime shifts in multivariate data ([Beaugrand 2004](#)). A good example of a complete analysis of discontinuous shifts can be found in [Lindegren, et al. 2016](#). Other statistical techniques involve iterative methods of model selection ([Gröger, et al. 2011](#)), threshold autoregressive models ([Ives and Dakos 2012](#)), or off-of-the shelf R statistical packages for break-point analysis ([Verbesselt, et al. 2010](#)). Despite the fact that most of these techniques provide built-in significance testing, [Rudnick and Davis 2003](#) show that comparison to null models is desirable, because similar discontinuous patterns may be created by purely stochastic processes. Less frequently, when state variables and environmental conditions are available, their relationships could be fitted to normal forms of cusp catastrophes rather than simple regressions as explained in [Ouimet and Legendre 1988](#).

Beaugrand, G. 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60.2–4: 245–262.

A well-cited example of a marine regime shifts from long-term monitored data in the North Sea across spatial scales and analysis of discontinuities in multivariate data.

Gröger, J. P., M. Missong, and R. A. Rountree. 2011. Analyses of interventions and structural breaks in marine and fisheries time series: Detection of shifts using iterative methods. *Ecological Indicators* 11.5: 1084–1092.

This methodological work showcases a model-based approach with formal model selection criteria and significance testing to identify thresholds and regime shifts in time series.

Ives, A. R., and V. Dakos. 2012. Detecting dynamical changes in nonlinear time series using locally linear state-space models. *Ecosphere* 3.6: 1–15.

In this work, an application of threshold autoregressive models is presented for identifying potential \*Alternative States\* in flickering time series or for identifying breakpoints.

Lindgren, M., D. M. Checkley Jr., M. D. Ohman, J. A. Koslow, and R. Goericke. 2016. Resilience and stability of a pelagic marine ecosystem. *Proceedings of the Royal Society of London B* 283.1822:20151931. [doi: 10.1098/rspb.2015.1931]

An analysis of the threshold dynamics of a pelagic system with a toolbox classically used in regime shift studies and tipping points for marine studies.

Quimet, C., and P. Legendre. 1988. Practical aspects of modelling ecological phenomena using the cusp catastrophe. *Ecological Modelling* 42.3–4: 265–287.

One of the early works for fitting actual cusp catastrophe models onto ecological data.

Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31.9: 2–5. [doi:10.1029/2004GL019448]

This paper presents one of the most used statistics for identifying discontinuities, first developed for oceanographic studies.

Rudnick, D. L., and R. E. Davis. 2003. Red noise and regime shifts. *Oceanographic Research Papers* 50 (July 2002): 691–699.

In this work, the authors show how classical identified regime shift and threshold behavior in marine data could be attributed to purely stochastic processes.

Verbesselt, J., R. Hyndman, A. Zeileis, and D. Culvenor. 2010. Phenological change detection while accounting for abrupt and gradual trends in satellite image time series. *Remote Sensing of Environment* 114.12: 2970–2980.

A methodological paper on breakpoint analysis that is also available to perform as an [\\*R package\[http://bfaster.r-forge.r-project.org\]\\*](http://bfaster.r-forge.r-project.org).

### ***Identifying Multimodality***

Multimodality (or more often bimodality in the specific case of two *\*Alternative States\**) refers to the existence of multiple states that can be estimated from frequency distributions of state variables. [Scheffer and Carpenter 2003](#) remarked that such identification is limited by the lack of available rich datasets, as cited under *\*Detection of Ecological Transitions\**. Advances in monitoring techniques have reduced this limitation. Vegetation data from satellite surveys have recently been used to identify multimodal distributions of tree cover in the tropics. Combined with precipitation data, [Hirota, et al. 2011](#) reconstructed stability landscapes to identify thresholds of tree cover between forest and savanna states. Reconstruction of stability landscapes can be performed not only from spatial data, but also from flickering time series ([Livina, et al. 2010](#)) in stochastically perturbed systems ([Nolting and Abbott 2016](#)). [Scheffer, et al. 2015](#), cited under *\*Detection of Ecological Transitions\**, have suggested to use this approach as a probabilistic measure of ecological resilience; see also *\*Ecological Resilience\** and *\*Leading Indicators\**.

Hirota, M., M. Holmgren, E. H. van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334:232–235.

[This paper uses satellite data to compare tree cover distributions across continents and to use these distributions to infer multimodality and thresholds in tropical forests and savannas.](#)

Livina, V. N., F. Kwasniok, and T. M. Lenton. 2010. Potential analysis reveals changing number of climate states during the last 60 kyr. *Climate of the Past* 6.1: 77–82.

[This work developed a methodology for reconstructing potential landscapes from time series that could be used to identify multiple states in a system.](#)

Nolting, B. C., and K. C. Abbott. 2016. Balls, cups, and quasi-potentials: Quantifying stability in stochastic systems. *Ecology* 97.4: 850–864.

[In this paper, the authors present an approach for reconstructing potential landscapes from stochastic time series and estimating steady state probability distributions and mean first passage times that could be used to infer ecosystem stability. It is also linked to an \[\\\*R\]\(#\)](#)

package[<https://journal.r-project.org/archive/2016/RJ-2016-031/RJ-2016-031.pdf>]\* for performing such analysis.

### ***Critical Slowing Down***

Critical slowing down is the mathematical phenomenon of increased slow recovery upon perturbation in the vicinity of local bifurcation points (Wissel 1984). Gilmore 1981, cited under \*Textbooks\*, considers it as one of the hallmarks of catastrophes, although it is not restricted to catastrophic bifurcations or to \*Alternative States\* (Kéfi, et al. 2013). Nonetheless, van Nes and Scheffer 2007 have suggested using the increased slow recovery from a disturbance as a potential indirect indicator of an ecosystem approaching a tipping point. Moreover, critical slowing down is linked to a number of signatures that have been developed to detect upcoming tipping points reviewed in Scheffer, et al. 2009, cited in \*Leading Indicators\*.

Kéfi, S., V. Dakos, M. Scheffer, E. H. van Nes, and M. Rietkerk. 2013. Early warning signals also precede non-catastrophic transitions. *Oikos* 122.5: 641–648.

This modeling paper emphasizes the fact that critical slowing down is not unique in systems with tipping points but it can precede non-catastrophic thresholds.

van Nes, E. H., and M. Scheffer. 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *The American Naturalist* 169.6: 738–747.

The authors used simple models to demonstrate how empirically one can measure critical slowing down as recovery rate upon disturbance to quantify the risk of an approaching threshold.

Wissel, C. 1984. A universal law of the characteristic return time near thresholds. *Oecologia* 65.1: 101–107.

A pioneering paper that studies critical slowing down close to thresholds in a variety of models and argues for its use as criterion of system stability.

### ***Leading Indicators***

Recently, there has been emphasis in anticipating tipping points and estimating the risk of an impending transition to a different state with the use of leading indicators (or early warning signals) summarized in Scheffer, et al. 2009. The majority of these indicators are related to critical slowing down (see section \*Critical Slowing Down\*) and they have been primarily developed and tested in ecological and climate studies (Scheffer, et al. 2012). The most

prominent is rising variance (Carpenter and Brock 2006), and increasing autocorrelation (Held and Kleinen 2004) in the temporal dynamics of a system. Other indicators are deviations in skewness (Guttal and Jayaprakash 2008), or characteristic changes in spatial patterns (Rietkerk, et al. 2004), and in patch size distributions before a tipping point (Kéfi, et al. 2007). Frameworks for estimating and interpreting leading indicators can be found in Dakos, et al. 2012 for time series and in Kéfi, et al. 2014 for spatial datasets. The fact that most of these indicators are quite generic has often led to misunderstandings in their appropriate use (Dakos, et al. 2015), and criticism in their ability for detecting tipping points (Ditlevsen and Johnsen 2010), as well as potential bias associated to applying them in cases where a threshold behavior has already been identified; see Boettiger and Hastings 2012. In combination with new approaches, a recent review demonstrates the utility of these indicators for ranking, monitoring, or probabilistically inferring resilience in an ecological system (see Scheffer, et al. 2015, cited in \*Detection of Ecological Transitions\*). An almost exhaustive list of proposed leading indicators can be also found in Clements and Ozgul 2018, cited in \*General Overviews\*.

Boettiger, C., and A. Hastings. 2012. Early warning signals and the prosecutor's fallacy.

*Proceedings of the Royal Society B: Biological Sciences* 279.1748: 4734–4739.

This paper discusses biases and issues of misidentification of leading indicators giving rise to false positive results.

Carpenter, S. R., and W. A. Brock. 2006. Rising variance: A leading indicator of ecological transition. *Ecology Letters* 9.3: 311–318.

This paper introduces increasing variance as leading indicator before a transition to an alternative state in a model of lake eutrophication.

Dakos, V., S. R. Carpenter, W. A. Brock, et al. 2012. \*Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data[<https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0041010>]\*. *PLoS One* 7.7: e41010–e41010.

A guide for applying and interpreting a suite of leading indicators when analyzing time-series for detecting tipping points. It also provides an \*R package[<https://github.com/earlywarningtoolbox>]\* for performing such analysis in.

Dakos, V., S. R. Carpenter, E. H. van Nes, and M. Scheffer. 2015. \*Resilience indicators: Prospects and limitations for early warnings of regime

shifts[<http://rstb.royalsocietypublishing.org/content/370/1659/20130263>]\*. *Philosophical Transactions of the Royal Society B-Biological Sciences* 370.1659: 20130263.

This work summarizes limitations and challenges in the application of leading indicators and set up a guardrail for their proper use.

Ditlevsen, P. D., and S. J. Johnsen. 2010. Tipping points: Early warning and wishful thinking. *Geophysical Research Letter* 37.19: L19703. [doi.org/10.1029/2010GL044486]

A more skeptical view of the utility of leading indicators in a climate dataset.

Guttal, V., and C. Jayaprakash. 2008. Changing skewness: An early warning signal of regime shifts in ecosystems. *Ecology Letters* 11.5: 450–460.

This modeling paper showed that asymmetries in the potential landscape of models with \*Alternative States\* can be reflected as changes in the skewness of the monitored state variable and serve as leading indicators of upcoming transitions.

Held, H., and T. Kleinen. 2004. Detection of climate system bifurcations by degenerate fingerprinting. *Geophysical Research Letters* 31.23: 1–4.

A climate study that proposed how changes in autocorrelation could signal the proximity to instability in a thermohaline circulation model.

Kéfi, S., V. Guttal, W. A. Brock, et al. 2014. \*Early warning signals of ecological transitions: Methods for spatial patterns[<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3962379/>]\*. Edited by Ricard V. Solé. *PLoS One* 9.3: e92097.

A guide for applying and interpreting a suite of leading indicators when analyzing spatial data for detecting tipping points. It also provides \*code[<https://github.com/earlywarningtoolbox/>]\* for performing such analysis in.

Kéfi, S., M. Rietkerk, C. L. Alados, et al. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449.7159: 213–217.

A study combining data and models to demonstrate how the loss of power law distributions of vegetation patch sizes can be used as indicator of degradation in drylands.

Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305.5692: 1926–1929.

A prominent review exhibiting changes in pattern formation in a variety of terrestrial ecosystems as indicators of stress and risk of collapse.



Scheffer, M., J. Bascompte, W. A. Brock, et al. 2009. Early-warning signals for critical transitions. *Nature* 461.7260: 53–59.

This is a seminal review that promoted ideas behind detecting upcoming transitions in ecological systems using statistical indicators from time series and spatial data. It has prompted a huge amount on theoretical and \*Empirical Studies\* on methods and applications across disciplines, but primarily in ecology and climate science.

## EMPIRICAL STUDIES

There is a big amount of work studying regime shifts and thresholds. For example, the [Resilience Alliance and Santa Fe Institute 2004](#) lists 103 empirical cases of ecological thresholds in their online database. Similarly, the [\\*\\*Regime Shifts Data Base\\*\\*](#) hosted by the Stockholm Resilience Center lists more than thirty types of regime shifts from more than 324 case studies that potentially represent systems with tipping points between alternative stable states. In the next two sections only a small fraction of this work is presented.

Resilience Alliance. 2004. \*Thresholds and Alternate States in Ecological and Social-Ecological Systems[<https://www.resalliance.org/thresholds-db>]\*. In *Resilience Alliance/ Santa Fe Institute*.

A database of thresholds and systems with potential \*Alternative States\* in coupled socioecological systems.

\*Regime Shifts DataBase [[www.regimeshifts.org](http://www.regimeshifts.org)]\*. [class:dataSet-database]

Perhaps the most complete, updated, and continuously growing list of regime shifts in coupled socioecological systems. Created by the Stockholm Resilience Center.

### *Identifying Ecological Transitions*

Empirical examples span aquatic and terrestrial ecosystems, at population, community, and ecosystem level; see [\\*General Overviews\\*](#). Among the most pronounced examples are lake eutrophication ([Carpenter, et al. 1999](#)); shifts between clear and turbid shallow lakes ([Scheffer, et al. 1993](#)); desertification of drylands ([Hardenberg, et al. 2001](#)); and shifts between savanna and forests ([Staver, et al. 2011](#)). Research in marine environments has greatly pioneered the study of the existence of thresholds across \*Alternative States\*, from early work in rocky intertidal communities by [Paine, et al. 1985](#); to the collapse of salt marsh vegetation in tidal flats as in [van de Koppel, et al. 2005](#); and to thresholds in marine hypoxia ([Conley, et al. 2009](#)). Examples of

threshold responses in relation to fishing and climate in the marine environment have been recently summarized in Möllmann and Diekmann 2012. In coral reefs, classical example of a threshold response includes the shift to algal overgrowth (Hughes 1994). In most cases, despite the existence of a threshold behavior, there is no clear evidence for the existence of alternative states behind such transitions; see Schroder, et al. 2005 cited in \*Experimental Approaches\*.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* 9.3: 751–771.

This eminent paper introduces a mechanistic model of lake eutrophication, fitted on data, and provides a thorough treatment of a list of factors that can affect the lake's threshold behavior along with scenarios of management implications.

Conley, D. J., J. Carstensen, R. Vaquer-Sunyer, and C. M. Duarte. 2009. Ecosystem thresholds with hypoxia. *Hydrobiologia* 629.1: 21–29.

This paper identifies the causes of hypoxia in three examples of coastal ecosystems and discusses their potential threshold behavior and \*Irreversibility\* under changing climate conditions.

Hardenberg, J. von, E. Meron, M. Shachak, and Y. Zarmi. 2001. Diversity of vegetation patterns and desertification. *Physical Review Letters* 87.19: 198101.  
[doi.org/10.1103/PhysRevLett.87.198101]

This modeling paper makes a link between changes in spatial patterns of vegetation in drylands and the collapse into desertification. Article available with authorization or by subscription.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265.5178: 1547–1551.

A well-known empirical study that demonstrated the phase shift of Jamaican coral reefs to macroalgae dominance, used as a flagship example of \*Alternative States\* in coral reefs.

Möllmann, C., and R. Diekmann. 2012. Marine ecosystem regime shifts induced by climate and overfishing: A review for the Northern Hemisphere. *Advances in Ecological Research* 47:303–347.

A review on the state-of-the-art techniques and understanding of marine regime shifts related to fishing and climate changes in the marine environment.

Paine, R. T., J. C. Castillo, and J. Cancino. 1985. Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington State. *The American Naturalist* 125.5: 679–691.

One of the first experimental studies for alternative states on coastal macroinvertebrate communities.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8.8: 275–279.

A review that combines models, mechanisms, and empirical data to support the existence of alternative states and shifts between clear and turbid water in the most pronounced example of an ecological tipping point in shallow lakes.

Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334.6053: 230–232.

This study combined tree cover data on continental scales to show the existence of discontinuities driven by tree-fire feedbacks that promote the existence of alternative states between forest and savanna.

van de Koppel, J., D. van der Wal, J. P. Bakker, and P. M. J. Herman. 2005. Self-organization and vegetation collapse in salt marsh ecosystems. *American Naturalist* 165.1: E1–12.

This study combined models and experimentation to suggest how *\*Positive Feedbacks\** between clay accumulation and plant growth can sustain salt marsh vegetation against erosion and can lead to collapse when wave stress increases.

### ***Anticipating Ecological Transitions***

The timely detection of thresholds to avoid undesirable shifts to possibly irreversible states has attracted increasing attention lately; see section *\*Leading Indicators\**. There is a growing number of studies that test the possibility of quantifying the risk of an upcoming transition in *\*Empirical Studies\**, mostly in hindsight. Table 1 in [Scheffer, et al. 2012](#) (cited in *\*General Overviews\**), highlights a number of empirical examples across scientific fields. Most work is based on laboratory experiments, like the collapse of yeast cultures ([Dai, et al. 2012](#)); extinction of zooplankton populations ([Drake and Griffen 2010](#)); and algae monocultures under stress ([Veraart, et al. 2012](#)). Field experiments are harder to conduct but few studies are already available from lake ecosystems, such as [Carpenter, et al. 2011](#), and coastal ecosystems, such as

Rindi, et al. 2017. More often detection is based on past or ongoing field observations, like changes in vegetation pattern formation (Rietkerk, et al. 2004, cited in \*Leading Indicators\*); patch size distribution in drylands (Kéfi, et al. 2007, also cited in \*Leading Indicators\*); or the retreat of vegetation in salt marshes (van Belzen, et al. 2017). Still, anticipating tipping points in advance remains a challenge as demonstrated by the mixed results obtained when analyzing abrupt transitions, even in cases where there is a strong conceptual basis for the existence of tipping points and alternative stable states; see Bestelmeyer, et al. 2011 and Gsell, et al. 2016. Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, et al. 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2.12: 1–26.

This study analyzed a number of abrupt transitions from terrestrial and marine systems using techniques of tipping point identification and detection to highlight the limitations and challenges of existing approaches.

Carpenter, S. R., J. J. Cole, M. L. Pace, et al. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. *Science* 332.6033: 1079–1082.

The biggest field experiment that aimed in identifying warnings of a trophic cascade in a whole lake.

Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336.6085: 1175–1177.

Perhaps the most complete experimental demonstration of a tipping point and its detection using \*Leading Indicators\* in a yeast population in the lab.

Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467.7314: 456–459.

A pioneering experimental study for demonstrating changes in variance and spatial correlation in zooplankton populations starved to extinction.

Gsell, A. S., U. Scharfenberger, D. Özkundakci ,et al. 2016. \*Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems[<http://www.pnas.org/content/113/50/E8089>]\*. *Proceedings of the National Academy of Sciences* 113.50: E8089–E8095.

A meta-analysis of observed regime shifts in a number of freshwater systems that revealed the challenge of measuring \*Leading Indicators\* despite the presence of complete records and well-understood mechanisms.

Rindi, L., M. Dal Bello., L. Dai, J. Gore, and L. Benedetti-Cecchi. 2017. Direct observation of increasing recovery length before collapse of a marine benthic ecosystem. *Nature Ecology & Evolution* 1:0153.

A field experiment showcasing how increasing recovery length can be used as an indicator of impending transition to dominance of algal turfs in a rocky intertidal system. Available by purchase or subscription.

van Belzen, J., J. van de Koppel, M. L. Kirwan, et al. 2017. \*Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation[<https://www.nature.com/articles/ncomms15811>]\*. *Nature Communications* 8:15811.

An empirical study, combining satellite images and experiments, that demonstrated critical slowing down in salt marshes.

Veraart, A. J., E. J. Faassen, V. Dakos, E. H. van Nes, M. Lürling, and M. Scheffer. 2012. Recovery rates reflect distance to a tipping point in a living system. *Nature* 481.7381: 357–359.

Perhaps the first study that directly measured critical slowing down prior to extinction of a phytoplankton monoculture due to light stress in the lab.