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Catastrophic regime shifts in ecosystems: linking theory to observation

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Catastrophic regime shifts in ecosystems: linking theory to observation

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Occasionally, surprisingly large shifts occur in ecosystems. Theory suggests that such shifts can be attributed to alternative stable states. Verifying this diagnosis is important because it implies a radically different view on management options, and on the potential effects of global change on such ecosystems. For instance, it implies that gradual changes in temperature or other factors might have little effect until a threshold is reached at which a large shift occurs that might be difficult to reverse. Strategies to assess whether alternative stable states are present are now converging in fields as disparate as desertification, limnology, oceanography and climatology. Here, we review emerging ways to link theory to observation, and conclude that although, field observations can provide hints of alternative stable states, experiments and models are essential for a good diagnosis.

The usual state of affairs in nature is one of populations fluctuating around some trend or stable average. Occasionally, however, this scenario is interrupted by an abrupt shift to a dramatically different regime [1]. For instance, after a long period in which vegetation cover fluctuated around a gradually declining trend of vegetation cover, the Sahara region collapsed suddenly into a desert in ancient times (Figure 1). A recent example, illustrating how such changes can take us by surprise, is the shift in Caribbean coral reefs [2,3]. For decades, specialists from the Smithsonian Institute in Panama and other research teams had been studying the reefs. Although some aspects of these ecosystems became increasingly well understood, not one researcher foresaw the sudden dramatic shift of the vast majority of the reefs into an algal encrusted state. Only with hindsight were the probable mechanisms unraveled. Increased nutrient loading as a result of changed land use had promoted algal growth, but this result did not show as long as herbivorous fish suppressed the algae. With time, intensive fishing reduced the numbers of fish, but, in response, the sea urchin *Diadema antilliarum* became abundant and took the role of key herbivore. Finally, when a pathogen hit the dense *D. antilliarum* populations, algae were released from grazer control and the reefs became overgrown rapidly.

Similar dramatic regime shifts are now documented for a range of ecosystems, including the open ocean in which numerous populations jump suddenly to different abundances in synchrony [4,5], standing waters that can become overgrown by floating plants [6], savannahs that become encroached suddenly by bushes [7,8] and lakes that shift from clear to turbid [9,10].

The obvious intuitive explanation for a sudden dramatic change in nature is the occurrence of a sudden large external impact. However, theoreticians have long stressed that this need not be the case. Even a tiny incremental change in conditions can trigger a large shift in some systems if a critical threshold known as ‘catastrophic bifurcation’ is passed [11]. This phenomenon has many intuitive examples, such as the tipping over of an overloaded boat when too many people move to one side, the occurrence of earthquakes when tension builds up in the Earth’s crust and the legendary straw that breaks the camel’s back. Nevertheless, with respect to ecosystems, the concept remains counterintuitive to many, and there is a risk of a divide between believers and skeptics. This review is intended to help avoid this trap. We first review briefly the theory of alternative stable states and discuss fundamental aspects of ecosystems that cannot be captured by the commonly used simple models. Subsequently, we review approaches to find out if an ecosystem really has

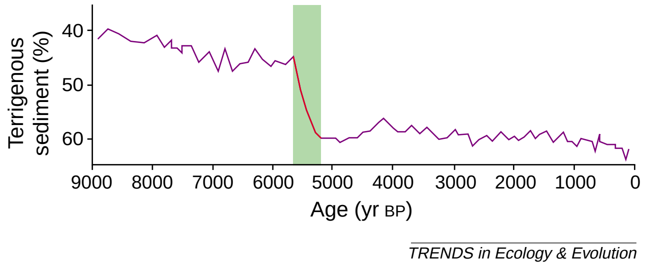

Figure 1. The collapse of Saharan vegetation as an example of an ancient regime shift. After millennia of fluctuations around a smoothly decreasing trend of vegetation cover, an abrupt collapse over the Sahara occurred between 5000 and 6000 years ago, as reflected in the contribution of terrigenous dust (axis reversed) to oceanic sediment at a sample site near the African coast. Modified with permission from [61].

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Box 1. A graphical model of a vegetation-water feedback

Although plants generally compete for resources, this competition can be overruled sometimes by facilitation [64] because the vegetation ameliorates certain critical conditions. For instance, submerged plants can enhance water clarity, thus improving the light for their underwater growth [65]. Similarly, terrestrial vegetation in dry regions can enhance soil moisture and microclimatic conditions [64] and rainfall [38,66]. This leads to a positive feedback (Figure I). The potential stability consequences can be illustrated by a simple graphical model (Figure II) that is based on three assumptions; (i) precipitation in the absence of vegetation is driven by the external climate system; (ii) vegetation has a positive effect on local rainfall; and (iii) vegetation disappears when precipitation falls below a certain critical level. In view of the first two assumptions, precipitation can be drawn as two different functions of the global climatically imposed situation: one for a situation without vegetation and one for a vegetated situation. Above a critical precipitation level, vegetation will be present, in which case the upper equilibrium line is the relevant one; below this precipitation level, the lower equilibrium curve applies. As a result, if the general climatic state tends to rather wet conditions, only the plant-dominated equilibrium exists, whereas at the driest overall climatic conditions, there is only a vegetationless equilibrium. Over a range of intermediate climatic situations, two alternative equilibria exist – one with vegetation and one without – separated by a (dashed) unstable equilibrium. The arrows indicate the direction of change if the system is not on one of the equilibrium lines. It can be seen from these arrows that the dashed middle line is unstable, because a small deviation from the line will make the system move further away to one of the (solid) stable equilibrium lines. An analogous model has been used earlier to explain the occurrence of alternative stable states in shallow lakes [65].

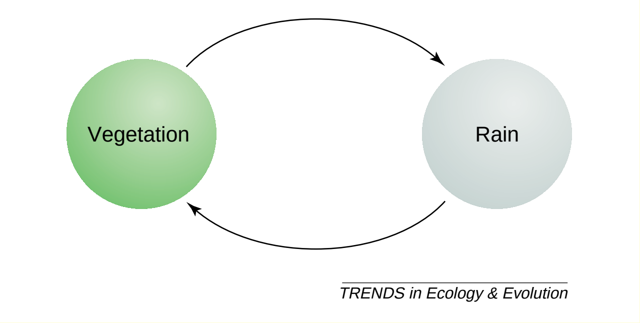

Figure I. A positive feedback can arise between vegetation cover and local rainfall in dry regions. Modified with permission from [67].

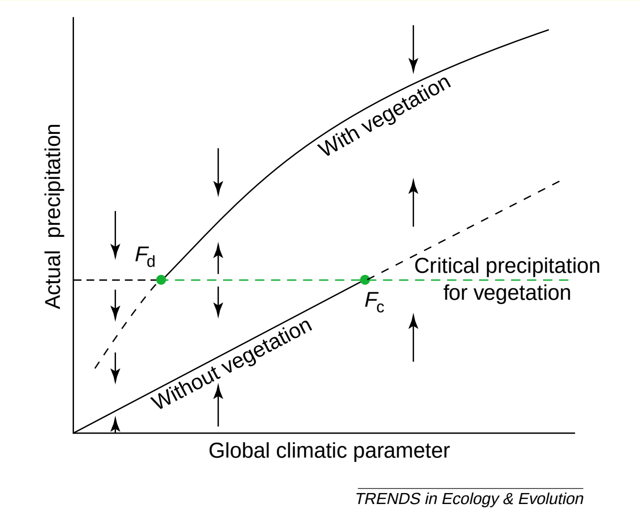

Figure II. A graphical model showing how alternative attractors might be caused by a positive feedback between vegetation and local precipitation. Modified with permission from [67].

alternative stable states and discuss key problems to be resolved.

From simple models to complex reality

Alternative stable states can arise, under some conditions, from a positive feedback in a system. To obtain an intuitive grasp of how this can happen, consider the graphical model of positive effects of plants on their growing conditions presented in Box 1. More sophisticated models of this and other problems suggest that the response of ecosystems to changing conditions (e.g. temperature, exploitation pressure or nutrient load) can vary from smooth to discontinuous (Figure 2). The occurrence of alternative stable states is just part of the spectrum of possibilities one should expect, but has profound implications for the way in which systems respond to variation in conditions (Box 2). Although the theory seems straightforward, there are aspects that are not explicit in these simple models, but clearly need to be addressed if we wish to relate them to the real world. In this section, we address the main gaps

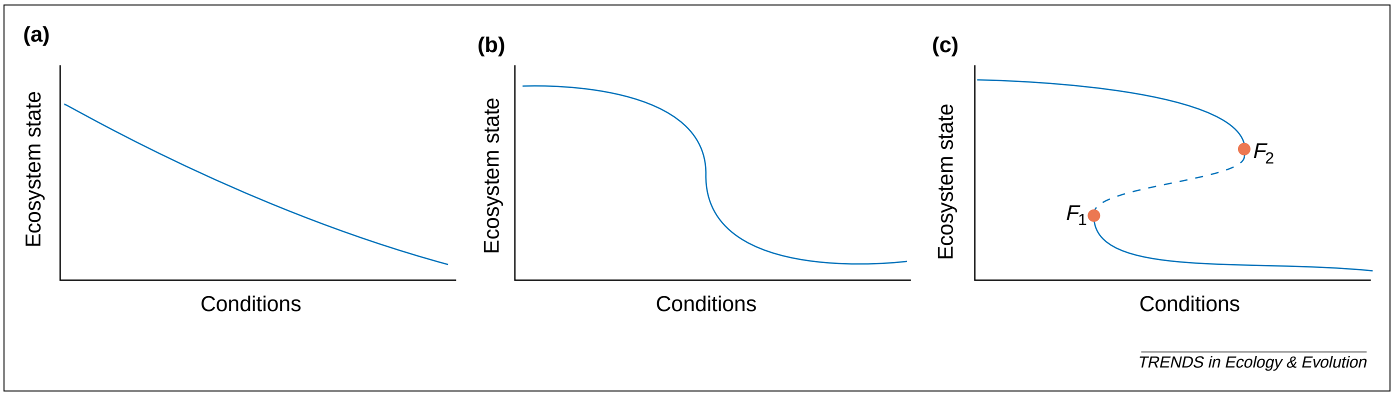

Figure 2. Different ways in which an ecosystem can respond to change in conditions. Although dynamic systems can respond smoothly to change in external conditions (a), they can sometimes change profoundly when conditions approach a critical level (b) or have more than one stable state over a range of conditions (hysteresis) (c). Although some systems tend to respond in a more non-linear way than do others, the response is not a fixed property of a system. For instance, depending on the depth of the lake, its turbidity can respond in either way to increased nutrient loading. Modified with permission from [1].

Box 2. Basic theory and terminology

The implications of alternative stable states (Figure 2c in main text) can be made intuitively clear by means of 'landscapes' representing the stability properties at different external conditions (Figure I). The ball (representing the state of the ecosystem) tends to settle in the valleys, which correspond to stable equilibria. The hilltops correspond to the dashed line, which represents unstable equilibria, and marks the border between the alternative valleys (also called 'basins of attraction').

Change in external conditions affects the stability landscape. This leads usually to minor changes in the position of the bottom of a valley (the equilibrium). However, the valley can shrink, and when it disappears eventually (this is a bifurcation; e.g. F_2) a 'catastrophic transition' to another valley occurs. To induce a switch back to the original valley, it is not sufficient to restore the environmental conditions present before the collapse. Instead, one needs to go back beyond another bifurcation point (F_1), where the system shifts back. The difference between forward and backward switches is known as hysteresis.

For conditions in which alternative equilibria exist, the initial state (i.e. place in the landscape) determines the equilibrium to which the system will settle. This has been called 'path dependency' and implies, among other things, that a sufficiently severe perturbation (e.g. fire eliminating part of the biomass) can induce a shift to another stable state. Obviously, a system is kicked more easily into an alternative state if the basin of attraction around the current state is small. The size of the basin of attraction is also called resilience. Note that change in external conditions can reduce resilience without affecting the equilibrium state much. This implies that the system appears unaltered, but has become brittle in the sense that increasingly small perturbations can induce a shift to the other state (Figure II).

Sometimes, models do not settle into a stable state (or equilibrium), but instead converge to an oscillating pattern (e.g. a predator–prey cycle) or a pattern of erratic fluctuations. All regimes to which a system moves asymptotically are known as 'attractors' (e.g. a point attractor, a cycle or a strange attractor). By contrast, unstable structures, be they points, cycles or other structures, are known as 'repellers'.

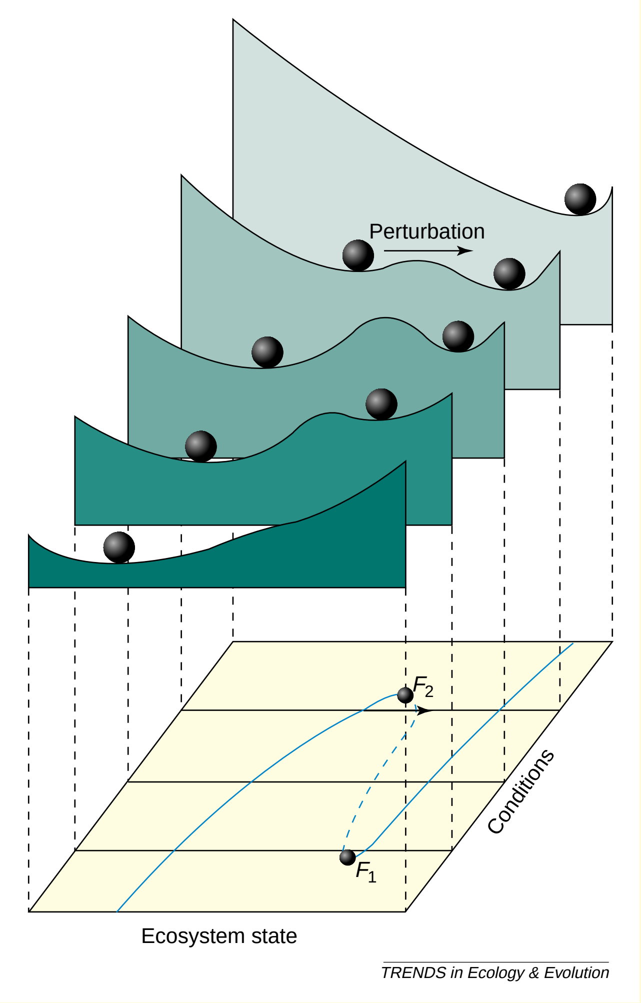

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Figure I. Stability landscapes illustrating how external conditions can affect the resilience of equilibria. Modified with permission from [1].

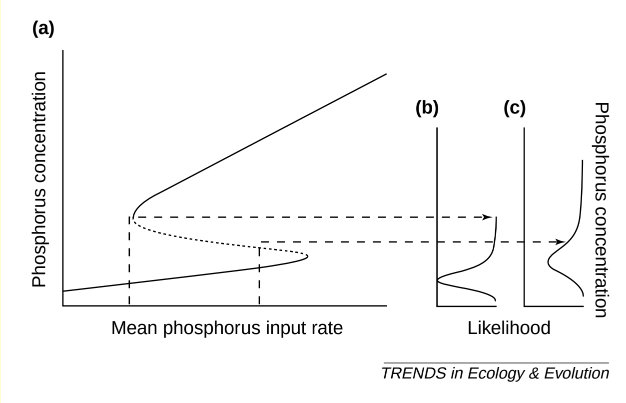

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Figure II. Example of how reduced resilience makes the system vulnerable to a shift. Resilience of the low phosphorus state is the distance from the lower solid line to the dashed line measured parallel to the y-axis (a). Note that the probability of crossing the threshold at a low input rate (b) is negligible, whereas, at a higher input rates (c), the chance of crossing the threshold is larger.

between simple models and complex reality, and attempt to clarify points that have caused confusion in scientific discussion.

Stable states are really dynamic regimes

Ecosystems are obviously never stable in the sense that they do not change. First, there are always slow trends. For instance, lakes fill up with sediment to eventually become land and species evolve. Second, natural populations always fluctuate. This is in part because of seasonality and fluctuations in weather. However, even if environmental conditions were constant, populations would probably still fluctuate. This is suggested by some experimental work in microcosms [12] and by the fact that models of interacting populations often converge to cycles or chaotic dynamics rather than stable states [11,13–15]. Although intrinsically generated dynamics and the effect of external forces remain difficult to unravel [16,17], fluctuations rather than stable states are obviously the rule. Therefore, it might be more appropriate to use words such as 'regimes' or 'attractors' instead of terms such as 'stable states' or 'equilibria' that seem to exclude dynamics [18]. The term 'regime shifts', which is also used in oceanography [19–21], describes aptly sudden shifts in ecosystems.

Multiple causality is the rule in regime shifts

The fact that fluctuations in natural populations are due to an intricate mix of internal processes and external forces also sheds a different light on the idea that a 'perturbation'

(Box 2) can trigger a regime shift. In models, a shift to a different attractor can be triggered by purely internally-generated fluctuations, such as predator–prey cycles or more complex dynamics. Such events are called 'non-local bifurcations' or 'basin boundary collisions' [11,14]. In practice, it will always be a blend of internal processes and external forces that generates fluctuations [17]. Overall, the way in which dynamic systems respond to environmental fluctuations – the 'noisy clockwork' [16] – is still poorly explored. One clearly important aspect to tackle is the question of how the frequency of environmental 'noise' affects the probability that the ecosystem will shift to another attractor [21,22]. A final important caveat with respect to interpreting causality of shifts is the tendency for researchers to neglect the factors that undermine resilience slowly, such as eutrophication or global warming [1,23]. Regime shifts are attributed all too easily to obvious stochastic events such as hurricanes [24] or species invasions [25].

Patterns depend on spatial scale

Implications of spatial heterogeneity for alternative attractors have been studied poorly so far. Nonetheless, some patterns emerge from the scarce studies. Clearly, alternative states can coexist side-by-side. For instance, a clear and a turbid state can coexist even in a single lake [26], and landscapes often comprise a mosaic of patches with different alternative stable vegetation types that remain unaltered for decades until an extreme event triggers a shift in the pattern [27–29]. Models suggest that in spatially heterogeneous landscapes, a local tendency to alternative stable states tends to smooth out on a larger scale. For instance, if the climate becomes drier, forest will be lost on the dry sites, whereas relatively fertile and moist sites remain vegetated much longer [30]. In spite of this smoothing effect on 'catastrophic' transitions, hysteresis (i.e. the condition of more than one stable state) can be preserved on the larger scale in the sense that the system follows a different path in its response to an increase and decrease in a control factor [31]. A special situation occurs if patches in one state benefit from the neighbouring area in the alternative state. In arid systems, for example, vegetated 'islands of fertility' trap runoff water and nutrients from the surrounding unvegetated land [32]. This tends to lead to pronounced self-organising spatial patterns (e.g. 'tiger bush'), and can cause the system to have alternative attractors on a landscape scale, even if this does not occur on a local scale [33].

External conditions should be independent or slow

The theory of alternative attractors (Box 2) describes the response of the system to some external condition. We consider the system to have alternative attractors if it can be in more than one 'stable state' for the same value of such an external condition. It is important that this condition is really external, in the sense that it is not an interactive part of the system. Reasonable examples are the effect of nutrient load on a lake or the effect of the Earth's orbit on solar radiation in the Sahara. A common misconception is the idea that all abiotic conditions are 'external'. This neglect of the view of an ecosystem as an interactive biotic-abiotic entity [34] has caused the idea that situations in which local abiotic conditions are different in the alternative states should not be considered 'proper' alternative stable states [35]. This view would exclude the examples of plants promoting local water availability (Box 1) and many other important cases of alternative stable states known today [1].

The requirement that the external condition under study is not affected by the system becomes less important if change in this condition is very slow relative to the rates of change in the system under study. For simplicity, we can then treat the slow variable as an independent control parameter [15]. Note that it is the relative difference in rates that matters, not the absolute rates. For instance, lake plankton dynamics are fast relative to changes in fish biomass [36,37], but the collapse of vegetation in the Sahara (even if it took a century) was fast compared with the driving change in the Earth's orbit [38,39]. In some systems, fast and slow components affect each other mutually in a way that leads to cycles [15]. Recurrent pest outbreaks are a well-known example. Such slow-fast cycles can also be understood by considering the processes at the slow and the fast time scales separately (Box 3).

Hints from field data

Although is not easy to demonstrate the existence of alternative attractors in real ecosystems, several lines of evidence have been proposed [18]. We review three indicators of alternative stable regimes that can be obtained from field data, and in the following sections discuss ways to check the alternative stable states hypothesis by means of experiments and models.

Jumps in time series (Figure 3a)

There are many ways of determining whether a shift in a time series can be explained by chance [4,40,41]. Importantly, a significant jump in a time series does not necessarily imply alternative attractors. Sudden shifts might be simply a result of a stepwise change in an important control parameter (e.g. a sudden change in temperature), or to the fact that a control parameter has passed a critical threshold that is not related to bifurcation (Figure 2b). There is a statistical approach to infer whether or not alternative attractors are involved in a shift [42], based on the principle that all attractor shifts imply a phase in which the system is speeding up as it is diverging from a repeller (see Box 2). Another approach is to compare the fit of contrasting models with and without attractor shifts [43,44] or compute the probability distribution of a bifurcation parameter [43]. All available tests require extensive time series containing many shifts [23].

Massive colonisation events deserve special mention. These happen, for instance, in marine fouling communities [45] that, once established, can be very persistent and hard to replace until the cohort simply dies of old age. It seems inappropriate to relate such shifts to alternative stable regimes [35], unless the new state can persist through more generations by rejuvenating itself. The latter might be the case, for instance, in dry-forests, where adult plant cover is essential for survival of juveniles except in very rare wet years, which trigger initial massive seedling establishment [46].

Box 3. Cyclic regime shifts

Outbreaks of pests are typically sharp transitions that have much in common with regime shifts, but tend to recur in an almost cyclic fashion. This is basically because of the interaction of a slow variable with a fast one. A classic example is the spruce-budworm cycle [68,69]. Dynamics of budworms that can dramatically defoliate spruce trees during outbreaks are much faster than the regrowth of spruce tree foliage on which they forage. This results in a time series with sharp transitions, rather than a smooth predator–prey cycle.

Recurrent regime shifts such as this can occur if the slow ‘control’ variable (s) interacts with a variable (f) of a fast system with alternative attractors in a particular way. In terms of the catastrophe-fold diagram (Figure I), such a ‘slow-fast limit cycle’ arises if there is a zero-growth isocline of the slow variable $(\dot{s} = (\dot{s} - 0))$ that separates the two stable branches of the bifurcation diagram of the fast system, such that in either of the two alternative stable states, the system moves slowly to the corresponding bifurcation point at which the switch to the other state is inevitable. Such systems converge to a cycle (Figure Ia) from every initial state (e.g. 1). The time series representation (Figure Ib) illustrates that the cycle is characterised by periods of relatively little change separated by rapid dramatic transitions.

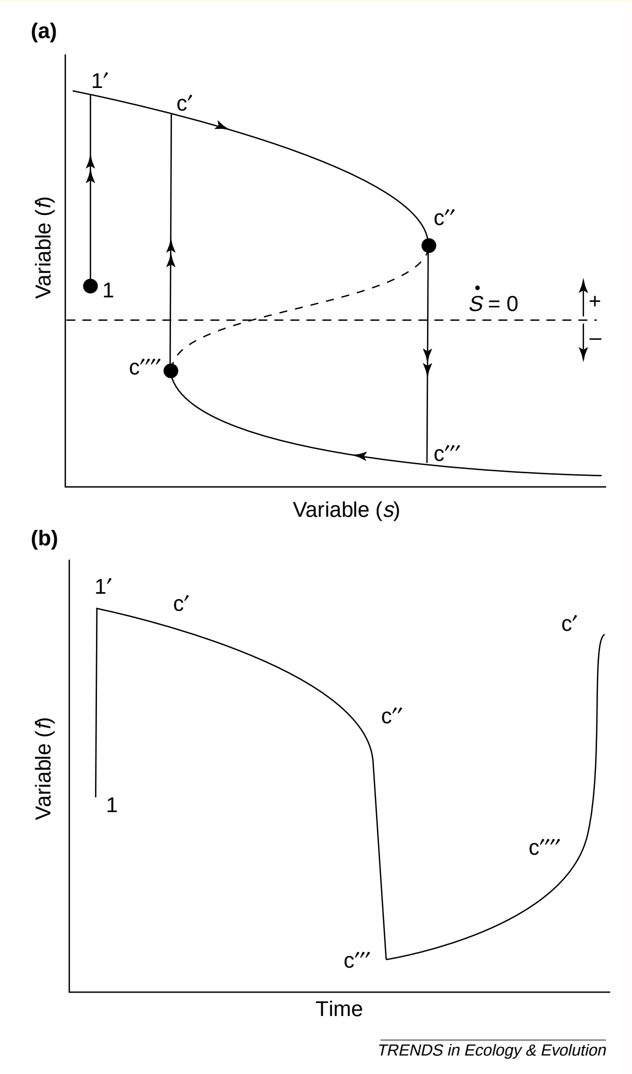

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Figure I. An example of how interaction between a fast variable, f, and a slow one, s, can lead to cycles (a) that show recurrent sharp transitions when plotted as a time series (b). Reproduced, with permission, from [15]

Multimodality of the frequency distribution of states (Figure 3b)

The spatial analogue to jumps in time series is the occurrence of sharp boundaries between contrasting states as found in kelp forests [47], or segregation of distinct units such as lakes into contrasting classes [48]. Statistically, the frequency distributions of key variables should be multimodal if there are alternative attractors. Sophisticated tests are available for multimodality [49], but these require rich datasets [50] and have low power for the limited datasets often available for ecological studies. Therefore, there is a good chance of concluding that one mode is sufficient even when the data are truly multimodal. Importantly, significant multimodality does not necessarily imply alternative attractors. As in the case of regime shifts, alternative explanations are a multimodal distribution of a driving factor, or a threshold response of the system that is not related to a bifurcation (e.g. Figure 2b).

Dual relationship to control factors (Figure 3c)

Tests for multimodality do not address the relationship of state variables to control factors. Thus, it might be more informative to test whether the response of the system to a control factor is best described by two separate functions rather than one single regression. Tests for multiplicity of regression models are conducted easily using likelihood ratios, the extra sum of squares principle, or information statistics [51]. Dual relationships can be suggestive of an underlying hysteresis curve (Figure 2c), although, again, the same alternative explanations as with multimodality should be kept in mind.

In conclusion, one can obtain good indications for the existence of alternative attractors from field data, but they can never be conclusive. There is always the possibility that discontinuities in time series or spatial patterns are due to discontinuities in some environmental factor. Alternatively, the system might simply have a threshold response (Figure 2b). In addition to their practical importance, thresholds suggest that under different conditions true alternative attractors could arise in the same system.

Experimental evidence

Although experiments can be difficult to perform on relevant scales in ecosystems, they are easier to interpret than field patterns [18]. We discuss three major ways in which experiments can provide evidence for the existence of alternative attractors.

Different initial states lead to different final states (Figure 4a)

Systems with more than one basin of attraction will converge to different attracting regimes depending on the initial state. Many field observations suggest this phenomenon. For instance, excavated gravel pit lakes in the same area of the UK stabilised in either a clear or a turbid state in which they persisted for decades depending on the excavation method [52]. In field situations, there might be

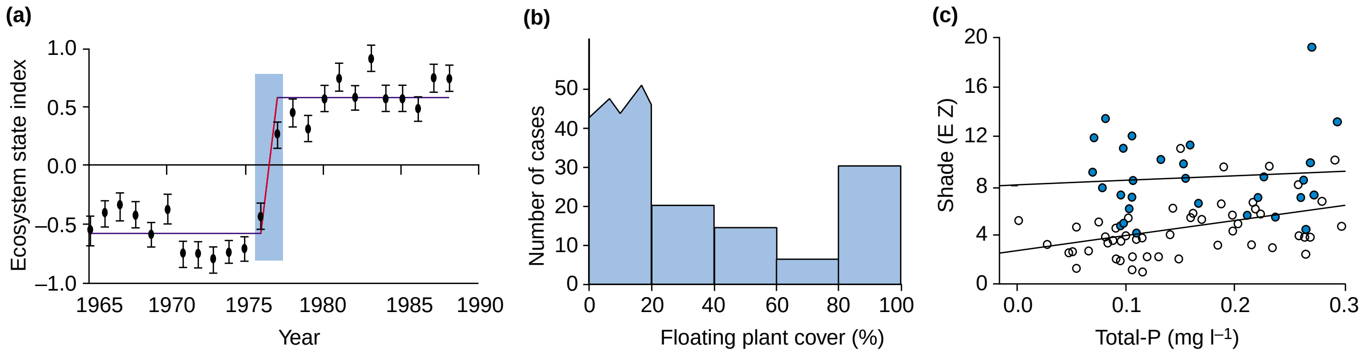

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Figure 3. Three types of hints of the existence of alternative attractors from field data: (a) shift in a time series, (b) multimodal distribution of states, and (c) dual relationship to a control factor. The specific examples are (a) regime shift in the Pacific Ocean ecosystem (shaded) (modified with permission from [4]), (b) bimodal frequency distribution of free floating plants in a set of 158 Dutch ditches (modified with permission from [6]), and (c) different relationships between underwater shade and the total phosphorus concentration for shallow lakes dominated by Cyanobacteria (blue circles) and lakes dominated by other algae (open circles) (modified with permission from [62]).

various alternative explanations for convergence to different endpoints. However, path dependency can be explored experimentally. For instance, different orders of colonisation from a common species pool have been shown to result in alternative endpoint communities that are all stable in the sense that they are resistant against colonisation by other species from the pool [53].

Disturbance can trigger a shift to another permanent state (Figure 4b)

The presence of alternative attractors also implies that a single stochastic event might push the system to another basin of attraction from where it converges to an alternative persistent regime. Field manipulations can show this rather convincingly. For instance, a temporary reduction in the fish stock (biomanipulation) of one of the turbid English gravel pits mentioned above has induced a shift to a long-term clear state [52]. Lasting effects of single disturbances have also been studied in ecotoxicological research, where the inability of the system to recover to the original state after a brief toxic shock has been referred to as ‘community conditioning’ [54]. Such experiments should be interpreted cautiously. The return of the original species should not be prevented by isolation of the community. Another problem is the potentially long return time to equilibrium, which can suggest an alternative stable regime even if it is just a transitional phase. For instance, the biomanipulated Lake Zwemlust (the Netherlands) remained clear and vegetated for six years until it started slipping back to the turbid state [55].

Hysteresis in response to forward and backward changes in conditions (Figure 4c)

Demonstration of a full hysteresis in response to a slow increase and subsequent decrease in a control factor also comes close to proving the existence of alternative attractors. Examples of hysteresis are seen in lakes recovering from acidification [56] or eutrophication (M.L. Meijer, PhD Thesis, Wageningen University, 2000; [10]), and in hemlock-hardwoods forests responding to change in

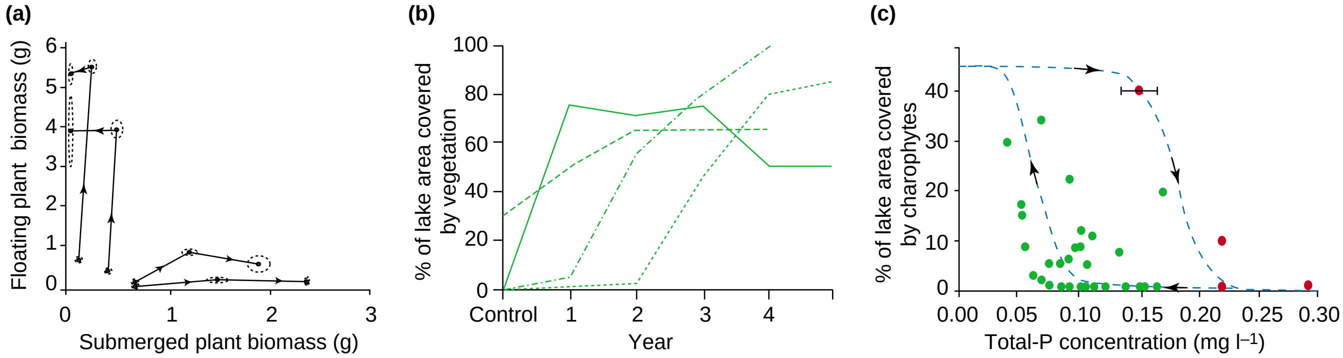

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Figure 4. Three types of experimental evidence for alternative attractors: (a) different initial states leading to different final states, (b) disturbance triggering a shift to another permanent state, and (c) hysteresis in response to forward and backward change in conditions. The specific examples are (a) path dependency in growth trajectories from competition experiments of a submerged plant (*Elodea*) and a floating plant (*Lemna*). Different lines represent the development of the two species in the experiments run under identical conditions, but starting from, different initial plant densities (reproduced with permission from [6]); (b) shifts of shallow lakes to a vegetation-dominated state triggered by temporary reduction of the fish stock. Each line represents a different experimental lake (modified with permission from [63]); (c) hysteresis in the response of charophyte vegetation in the shallow Lake Veluwe (the Netherlands) to an increase and subsequent decrease in the phosphorus concentration (modified, with permission, from M.L. Meijer, PhD Thesis, Wageningen University, 2000).

disturbance intensity [28]. However, a hysteretic pattern might not indicate alternative attractors if the response of the system is not fast enough relative to the rate of change in the control factor. Indeed, one will always see some hysteresis-like pattern unless the system response is much faster than the change in the control variable.

In conclusion, experiments can be a powerful way to show that a system has alternative attractors. There are obvious limitations to exploring large spatial scales and long time spans. However, small and fast systems, which are more tractable experimentally, can help us to infer what might happen in larger and slower ones.

The contribution of models

In addition to field data and experiments, models remain a central ingredient of most of the work on alternative attractors. Discussion of the long history of confusion over the question of what models can tell us exactly is beyond the scope of this review, but we highlight some crucial points of interest.

Qualitative reasoning

Alternative attractors require positive feedbacks, and change among attractors implies a shift in dominant controlling feedbacks. For instance, in stratified lakes, a clear-water state prevents anoxic phosphorus recycling from the sediments, which, in turn, limits phytoplankton growth. By contrast, in a turbid state, high algal biomass boosts anoxic phosphate recycling, promoting more algal growth [10]. Positive feedbacks are sometimes interpreted as being almost synonymous with the possibility of switches between alternative attractors [57]. Although this might seem reasonable intuitively, positive feedbacks only lead to alternative attractors if they are sufficiently strong. Thus, qualitative reasoning is not sufficient to infer alternative attractors from observed feedback loops.

Simple mathematical models

Mathematical models provide a much more powerful tool than qualitative reasoning for showing that certain mechanisms can lead to phenomena of interest such as alternative attractors. Most models in the literature are so-called minimal models that focus on a minimal set of mechanisms needed to produce a certain behaviour [58]. Such models have been useful for exploring mechanisms that are too intricate to grasp from common sense alone, and also serve well for exploring the fundamental implications of important aspects such as spatial heterogeneity [30,31,33] and environmental fluctuations [16,17,22].

Large simulation models

A drawback of simple models is that they necessarily leave out many potentially important aspects. This has invoked the development of much criticised [58] big simulation models intended to provide quantitative predictions. Although true validation of such predictive models is simply impossible [59], they remain very important. One simply cannot do appropriate experiments with large important systems, such as oceans and the atmosphere. In these situations, our best hope is a combination of multi-interpretable records of past behaviour with ‘plausible models’ of the system.

In conclusion, different models have different strengths and weaknesses, and the best strategy is obviously to use different models in parallel. Each model is a ‘lie’ in the sense that it is an imperfect representation of reality. However, if various independent models coincide in predicting alternative attractors, then one can adopt the philosophy that ‘the truth is the intersection of independent lies’ [60].

Prospects

Clearly, we have advanced much over the past decade in bridging the gap between abstract theory and ecosystem dynamics observed in the field. Field data are explored with more powerful techniques, and models are being used to address implications of important aspects such as environmental fluctuations and spatial complexity. Because neither field patterns nor models alone can be conclusive, it is also crucial that well-designed experiments are being used now to demonstrate alternative attractors. Still, although strong cases have been made, it remains remarkably difficult to prove the existence of alternative attractors in the field. This is perhaps not surprising in view of the historical difficulties in demonstrating the general importance of virtually all important mechanisms (e.g. competition, chaos or density dependence) in ecology. However, in view of the formidable consequences of alternative attractors for conservation

Box 4. Outstanding challenges

Obtaining better clues from field data

There is a wealth of ecological time-series and cross-systems data that remain to be explored. Finding hints of alternative attractors requires the use of novel techniques [18]. Perhaps even more challenging is the question of how we can obtain early warning signals of regime shifts from time-series data [18]. Foreseeing shifts is probably very difficult [1], but it has been suggested that subtle changes in the fluctuation pattern such as ‘reddening’ can serve as a clue of an upcoming collapse [70].

Building more realism into simple models

Theory has so far been restricted largely to the easiest case of a few species interacting in a spatially homogeneous (‘well mixed’) and constant environment. It seems important to pursue crucial aspects that have been largely neglected such as spatial heterogeneity [30,31,33], seasonality [31,36] and environmental fluctuations [16,17,21,22]. Also, empirical relationships can be linked into simple models to give transparent quantitative predictions.

Performing crucial experiments

Controlled experiments are obviously the most powerful way to demonstrate alternative attractors and to reveal underlying mechanisms. A real challenge here lies in experiments on realistic spatial and temporal scales [71]. Small-scale experiments can be very helpful in explaining large-scale patterns [6,47], but this has been poorly explored.

Designing smart restoration strategies

Insight into alternative attractors can be used to design unconventional restoration methods [72,73]. In particular, the idea of taking advantage of climatic extremes such as El Niño events to induce a shift to a desired regime [27] is an exciting, novel development.

and management [1], it seems urgent to make more headway soon. Several obvious challenges stand out (Box 4).

A more philosophical question to address is what our null model should really be. In the light of current theory, it would be remarkable if ecosystems did not have alternative attractors. Thus, one could argue that instead of focusing on proving that a system does have alternative attractors, it might be better to attempt to falsify this hypothesis; in other words, to prove that the system has only one attractor. Clearly, the absence of hints of alternative attractors in field data (Figure 3) does not imply that they do not exist. The only way to falsify the existence of alternative attractors is to demonstrate that the system settles eventually to the same regime from every initial condition. Obviously, this is very difficult in practice. However, one can question where the burden of proof should be. Assuming that multiple attractors are absent when they are actually present could lead to dangerous false assumptions, such as the idea that pollution effects can be reversed easily, that an endangered population cannot vanish, or that a harvested population cannot collapse.

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References

1 Scheffer, M. *et al.* (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596

2 Nystrom, M. *et al.* (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* 15, 413–417

3 McCook, L.J. (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reef* 18, 357–367

4 Hare, S.R. *et al.* (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progr. Oceanogr.* 47, 103–145

5 Reid, P.C. *et al.* (1998) Phytoplankton change in the North Atlantic. *Nature* 391, 546–546

6 Scheffer, M. *et al.* (2003) Floating plant dominance as a stable state. *Proc. Natl. Acad. Sci. U. S. A.* 100, 4040–4045

7 Ludwig, D. *et al.* (1997) Sustainability, stability, and resilience. *Conserv. Ecol.* 1 http://www.consecol.org/vol1/iss1/art7

8 Walker, B.H. (1993) Rangeland ecology: understanding and managing change. *Ambio* 22, 2–3

9 Scheffer, M. (1998) *Ecology of Shallow Lakes*, Chapman & Hall

10 Carpenter, S.R. *et al.* (1999) Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9, 751–771

11 Kuznetsov, Y.A. (1995) *Elements of Applied Bifurcation Theory*, Springer-Verlag

12 Kersting, K. (1985) Properties of an aquatic micro-ecosystem V. Ten years of observations of the prototype. *Verhand. Int. Verein. Theor. Ang. Limnol.* 22, 3040–3045

13 Huisman, J. *et al.* (1999) Biodiversity of plankton by species oscillations and chaos. *Nature* 402, 407–410

14 Vandermeer, J. *et al.* (1999) Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology* 80, 1817–1827

15 Rinaldi, S. *et al.* (2000) Geometric analysis of ecological models with slow and fast processes. *Ecosystems* 3, 507–521

16 Bjornstad, O.N. *et al.* (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293, 638–643

17 Ellner, S. *et al.* (1995) Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Nat.* 145, 343–375

18 Carpenter, S.R. (2003) *Regime Shifts in Lake Ecosystems: Pattern and Variation [Excellence in Ecology Series (Vol. 15]*, Ecology Institute

19 Anderson, P.J. *et al.* (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* 189, 117–123

20 Mantua, N.J. *et al.* (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78, 1069–1079

21 Steele, J.H. (1998) Regime shifts in marine ecosystems. *Ecol. Appl.* 8, S33–S36

22 Steele, J.H. *et al.* (1994) Coupling between physical and biological scales. *Philos. Trans. R. Soc. London.B* 343, 5–9

23 Carpenter, S.R. (2001) Alternate states of ecosystems: evidence and some implications. In *Ecology: Achievement and Challenge* (Press, M.C. *et al.*, eds), pp. 357–381, Blackwell

24 Schelske, C.L. *et al.* (1992) Can Lake Apopka be restored? In *Restoration of Aquatic Ecosystems* (Maurizi, S. *et al.*, eds), pp. 393–398, National Academic Press

25 Paine, R.T. *et al.* (1998) Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545

26 Van den Berg, M.S. *et al.* (1998) Clear water associated with a dense Chara vegetation in the shallow and turbid Lake Veluwemeer, the Netherlands. In *Structuring Role of Submerged Macrophytes in Lakes* (Jeppesen, E. *et al.*, eds), pp. 339–352, Springer-Verlag

27 Holmgren, M. *et al.* (2001) El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems* 4, 151–159

28 Augustine, D.J. *et al.* (1998) Evidence for two alternate stable states in an ungulate grazing system. *Ecol. Appl.* 8, 1260–1269

29 Peterson, G.D. (2002) Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5, 329–338

30 Sternberg, L.D. (2001) Savanna-forest hysteresis in the tropics. *Glob. Ecol. Biogeog.* 10, 369–378

31 van Nes, E.H. *et al.* (2002) Dominance of charophytes in eutrophic shallow lakes – when should we expect it to be an alternative stable state? *Aquat. Bot.* 72, 275–296

32 Schlesinger, W.H. *et al.* (1990) Biological feedbacks in global desertification. *Science* 247, 1043–1048

33 Rietkerk, M. *et al.* (2002) Self-organization of vegetation in arid ecosystems. *Am. Nat.* 160, 524–530

34 Peterson, C.H. (1984) Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *Am. Nat.* 124, 127–133

35 Connell, J.H. *et al.* (1983) On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121, 789–824

36 Scheffer, M. *et al.* (1997) Seasonal dynamics of *Daphnia* and algae explained as a periodically forced predator–prey system. *Oikos* 80, 519–532

37 Scheffer, M. *et al.* (2000) Effects of fish on plankton dynamics: a theoretical analysis. *Can. J. Fish. Aquat. Sci.* 57, 1208–1219

38 Brovkin, V. *et al.* (1998) On the stability of the atmosphere-vegetation system in the Sahara/Sahel region. *J. Geophys. Res. Atmos.* 103, 31613–31624

39 Claussen, M. *et al.* (1999) Simulation of an abrupt change in Saharan vegetation in the mid-Holocene. *Geophys. Res. Lett.* 26, 2037–2040

40 Box, G.E.P. *et al.* (1994) *Time Series Analysis: Forecasting and Control*, Prentice-Hall

41 Ives, A.R. *et al.* (2003) Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* 73, 301–330

42 Brock, W.A. *et al.* (1996) A test for independence based on the correlation dimension. *Econ. Rev.* 15, 197–235

43 Carpenter, S.R. and Pace, M.L. (1997) Dystrophy and eutrophy in lake ecosystems: implications of fluctuating inputs. *Oikos* 78, 3–14

44 Liermann, M. and Hilborn, R. (1997) Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* 54, 1976–1984

45 Sutherland, J.P. (1974) Multiple stable points in natural communities. *Am. Nat.* 108, 859–873

46 Holmgren, M. *et al.* (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* 16, 89–94

47 Konar, B. *et al.* (2003) The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84, 174–185

48 Van Geest, G.J. *et al.* (2003) Vegetation abundance in lowland flood plan lakes determined by surface area, age and connectivity. *Freshw. Biol.* 48, 440–454

49 Efron, B. *et al.* (1993) *An Introduction to the Bootstrap*, Chapman & Hall

50 Havlicek, T.D. *et al.* (2001) Pelagic species size distributions in lakes: are they discontinuous? *Limnol. Oceanogr.* 46, 1021–1033

51 Hilborn, R. *et al.* (1993) *The Ecological Detective*, Princeton University Press

52 Giles, N. (1992) *Wildlife after Gravel; Twenty Years of Practical Research by the Game Conservancy and ARC*, Game Conservancy

53 Drake, J.A. *et al.* (1996) Microcosms as models for generating and testing community theory. *Ecology* 77, 670–677

54 Matthews, R.A. *et al.* (1996) The community conditioning hypothesis and its application to environmental toxicology. *Environ. Toxicol. Chem.* 15, 597–603

55 van Donk, E. *et al.* (1995) Transition of a lake to turbid state six years after biomanipulation: mechanisms and pathways. *Water Sci. Technol.* 32 (4), 197–206

56 Frost, T.M. *et al.* (1995) Species compensation and complementarity in ecosystem function. In *Linking Species and Ecosystems* (Jones, C. *et al.*, eds), pp. 224–239, Chapman & Hall

57 Wilson, J.B. *et al.* (1992) Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23, 263–336

58 Scheffer, M. *et al.* (1994) Ecological models and the pitfalls of causality. *Hydrobiologia* 276, 115–124

59 Oreskes, N. *et al.* (1994) Verification, validation, and confirmation of numerical models in the earth sciences. *Science* 263, 641–646

60 Levins, R. (1966) The strategy of model building in population biology. *Am. Sci.* 54, 421–431

61 deMenocal, P. *et al.* (2000) Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. *Quat. Sci. Rev.* 19, 347–361

62 Scheffer, M. *et al.* (1997) On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* 78, 272–282

63 Meijer, M.L. *et al.* (1994) Long-term responses to fish-stock reduction in small shallow lakes – interpretation of five-year results of four biomanipulation cases in the Netherlands and Denmark. *Hydrobiologia* 276, 457–466

64 Holmgren, M. *et al.* (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78, 1966–1975

65 Scheffer, M. *et al.* (1993) Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275–279

66 Zeng, N. *et al.* (1999) Enhancement of interdecadal climate variability in the Sahel by vegetation interaction. *Science* 286, 1537–1540

67 Foley, J.A. *et al*. Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in Northern Africa. *Ecosystems* (in press)

68 Ludwig, D. *et al*. (1978) Qualitative analysis of insect outbreak systems the spruce–budworm and forest. *J. Anim. Ecol.* 47, 315–332.

69 Holling, C.S. (1988) Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Mem. Entomol. Soc. Can.* 0, 21–32

70 Kleinen, T. *et al*. (2003) The potential role of spectral properties in detecting thresholds in the Earth system; application to the thermohaline circulation. *Ocean Dynamics* 53, 53–63.

71 Carpenter, S.R. (1998) The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In *Successes, Limitations and Frontiers in Ecosystem Science* (Pace, M.L. *et al.*, eds), pp. 287–312, Springer-Verlag

72 Moss, B. *et al.* (1996) *A Guide to the Restoration of Nutrient-Enriched Shallow Lakes*, Broads Authority/Environment Agency

73 Hansson, L.A. *et al.* (1998) Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1, 558–574