Catastrophic shifts in ecosystems

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All ecosystems are exposed to gradual changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. Nature is usually assumed to respond to gradual change in a smooth way. However, studies on lakes, coral reefs, oceans, forests and arid lands have shown that smooth change can be interrupted by sudden drastic switches to a contrasting state. Although diverse events can trigger such shifts, recent studies show that a loss of resilience usually paves the way for a switch to an alternative state. This suggests that strategies for sustainable management of such ecosystems should focus on maintaining resilience.

The notion that ecosystems may switch abruptly to a contrasting alternative stable state emerged from work on theoretical models[1,2]. Although this provided an inspiring search image for ecologists, the first experimental examples that were proposed were criticized strongly[3]. Indeed, it seemed easier to demonstrate shifts between alternative stable states in models than in the real world. In particular, unravelling the mechanisms governing the behaviour of spatially extensive ecosystems is notoriously difficult, because it requires the interfacing of phenomena that occur on very different scales of space, time and ecological organization[4]. Nonetheless, recent studies have provided a strong case for the existence of alternative stability domains in various important ecosystems[5–8]. Here, we do not address brief switches to alternative states such as described for pest outbreaks[9]. Also, we do not fully cover the extensive work on positive feedbacks and multiple stable states in ecological systems. Instead, we concentrate on observed large-scale shifts in major ecosystems and their explanations. After sketching the theoretical framework, we present an overview of results from different ecosystems, highlight emerging patterns, and discuss how these insights may contribute to improved management.

Theoretical framework

Ecosystem response to gradually changing conditions

External conditions to ecosystems such as climate, inputs of nutrients or toxic chemicals, groundwater reduction, habitat fragmentation, harvest or loss of species diversity often change gradually, even linearly, with time[10,11]. The state of some ecosystems may respond in a smooth, continuous way to such trends (Fig. 1a). Others may be quite inert over certain ranges of conditions, responding more strongly when conditions approach a certain critical level (Fig. 1b). A crucially different situation arises when the ecosystem response curve is 'folded' backwards (Fig. 1c). This implies that, for certain environmental conditions, the ecosystem has two alternative stable states, separated by an unstable equilibrium that marks the border between the 'basins of attraction' of the states.

The presence of alternative stable states has profound implications for the response to environmental change (Fig. 2a). When the ecosystem is in a state on the upper branch of the folded curve, it can not pass to the lower branch smoothly. Instead, when conditions change sufficiently to pass the threshold ('saddle-node' or 'fold' bifurcation, F_2), a 'catastrophic' transition to the lower branch occurs. Note that when one monitors the system on a stable branch before a switch, little change in its state is observed. Indeed, such catastrophic shifts

occur typically quite unannounced, and 'early-warning signals' of approaching catastrophic change are difficult to obtain. Another important feature is that to induce a switch back to the upper branch, it is not sufficient to restore the environmental conditions of before the collapse (F_2). Instead, one needs to go back further, beyond the other switch point (F_1), where the system recovers by shifting back to the upper branch. This pattern, in which the forward and backward switches occur at different critical conditions, is known as hysteresis. The degree of hysteresis may vary strongly even in the same kind of ecosystem. For instance, shallow lakes can have a pronounced hysteresis in response to nutrient loading (Fig. 1c), whereas deeper lakes may react smoothly (Fig. 1b)[12]. A range of mathematical models of specific ecological systems with alternative stable states has been published. Box 1 shows an example of a simple model that can be thought of as describing desertification or lake eutrophication.

Effects of stochastic events

In the real world, conditions are never constant. Stochastic events such as weather extremes, fires or pest outbreaks can cause fluctuations in the conditioning factors (horizontal axis) but often affect the state (vertical axis) directly, for example, by wiping out parts of populations. If there is only one basin of attraction, the system will settle back to essentially the same state after such events. However, if there are alternative stable states, a sufficiently severe perturbation of the ecosystem state may bring the system into the basin of attraction of another state (Fig. 2b). The likelihood of this depends not only on the perturbation, but also on the size of the attraction basin. In terms of stability landscapes (Fig. 3), if the valley is small, a small perturbation may be enough to displace the ball far enough to push it over the hill, resulting in a shift to the alternative stable state. Following Holling[1], we here use the term 'resilience' to refer the size of the valley, or basin of attraction, around a state, which corresponds to the maximum perturbation that can be taken without causing a shift to an alternative stable state.

In systems with multiple stable states, gradually changing conditions may have little effect on the state of the ecosystem, but nevertheless reduce the size of the attraction basin (Fig. 3). This loss of resilience makes the system more fragile in the sense that can easily be tipped into a contrasting state by stochastic events. Such stochastic fluctuations may often be driven externally; however, they can also result from internal system dynamics. The latter can happen if the alternative

attractors are 'cycles' or 'strange attractors', rather than equilibria. A system that moves along a strange attractor fluctuates chaotically even in the absence of an external stochastic forcing. These fluctuations can lead to a collision with the boundary of the basin of attraction, and consequently induce a switch to an alternative state. Models indicate that such 'non-local bifurcations'[13] or 'basin boundary collisions'[14] may occur in ocean-climate systems[15] as well as various ecosystems[9]. In practice, it will often be a blend of internal processes and external forcing that generates fluctuations[16] that can induce a state shift by bringing systems with reduced resilience over the boundary of an attraction basin. In view of these permanent fluctuations, the term 'stable state' is hardly appropriate for any ecosystem. Nonetheless, for the sake of clarity we use 'state' rather than the more correct term 'dynamic regime'.

Examples

Lakes

Shifts between alternative stable states occur in lakes[12,17]. One of the best-studied and most dramatic state shifts is the sudden loss of transparency and vegetation observed in shallow lakes subject to human-induced eutrophication[5,18]. The pristine state of most shallow lakes is probably one of clear water and a rich submerged vegetation. Nutrient loading has changed this situation in many cases. Remarkably, water clarity often seems to be hardly affected by increased nutrient concentrations until a critical threshold is passed, at which the lake shifts abruptly from clear to turbid. With this increase in turbidity, submerged plants largely disappear. Associated loss of animal diversity and reduction of the high algal biomass makes this state undesired. Reduction of nutrient concentrations is often insufficient to restore the vegetated clear state. Indeed, the restoration of clear water happens at substantially lower nutrient levels than those at which the collapse of the vegetation occurred (Fig. 4). Experimental work suggests that plants increase water clarity, thereby enhancing their own growing conditions[5]. This causes the clear state to be a self-stabilizing alternative to the turbid situation (Fig. 5). The reduction of phytoplankton biomass and turbidity by vegetation involves a suite of mechanisms, including reduction of nutrients in the water column, protection of phytoplankton grazers such as *Daphnia* against fish predation, and prevention of sediment resuspension. In contrast, fish are central in maintaining the turbid state, because they control *Daphnia* in the absence of plants. Also, in search for benthic food they resuspend sediments, adding to turbidity. Whole-lake experiments show that a temporary strong reduction of fish biomass as 'shock therapy' can bring such lakes back into a permanent clear state if the nutrient level is not too high[19].
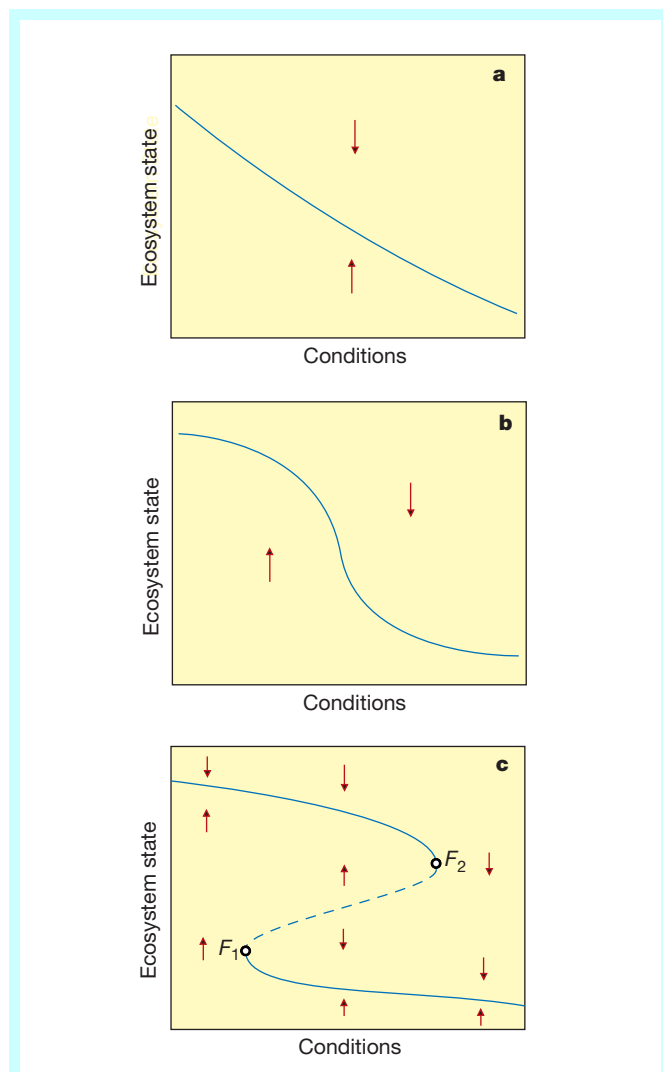

Figure 1 Possible ways in which ecosystem equilibrium states can vary with conditions such as nutrient loading, exploitation or temperature rise. In **a** and **b**, only one equilibrium exists for each condition. However, if the equilibrium curve is folded backwards (**c**), three equilibria can exist for a given condition. It can be seen from the arrows indicating the direction of change that in this case equilibria on the dashed middle section are unstable and represent the border between the basins of attraction of the two alternative stable states on the upper and lower branches. Modified from ref. 58.
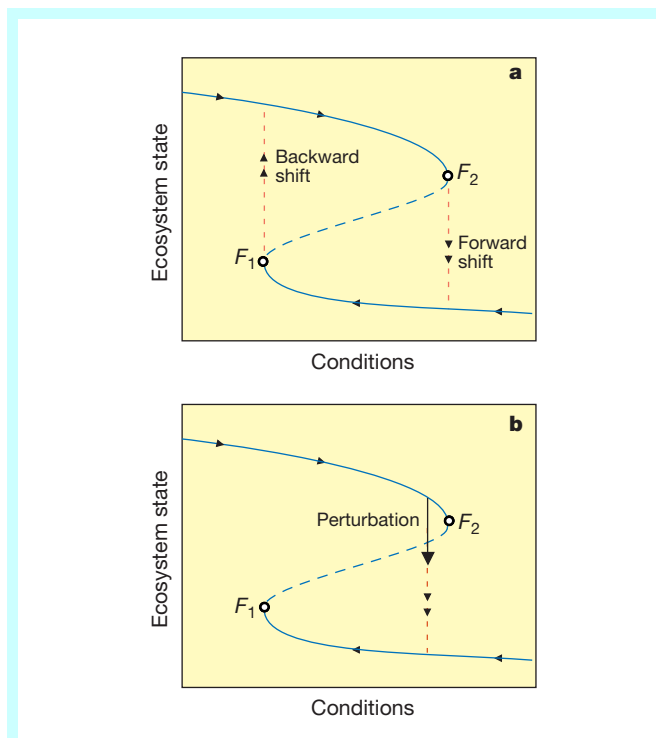

Figure 2 Two ways to shift between alternative stable states. **a**, If the system is on the upper branch, but close to the bifurcation point F_2, a slight incremental change in conditions may bring it beyond the bifurcation and induce a catastrophic shift to the lower alternative stable state ('forward shift'). If one tries to restore the state on the upper branch by means of reversing the conditions, the system shows hysteresis. A backward shift occurs only if conditions are reversed far enough to reach the other bifurcation point, F_1. **b**, A perturbation (arrow) may also induce a shift to the alternative stable state, if it is sufficiently large to bring the system over the border of the attraction basin (see also Fig. 3).

Coral reefs

Coral reefs are known for their high biodiversity. However, many reefs around the world have degraded. A major problem is that corals are overgrown by fleshy macroalgae. Reef ecosystems seem to shift between alternative stable states, rather than responding in a smooth way to changing conditions[20–22]. The shift to algae in Caribbean reefs is the result of a combination of factors that make the system vulnerable to events that trigger the actual shift[8]. These factors presumably include increased nutrient loading as a result of changed land-use and intensive fishing, which reduced the numbers of large fish and subsequently of the smaller herbivorous species. Consequently, the sea urchin *Diadema antilliarum*, which competes with the herbivorous fish for algal food, increased in numbers. In 1981 a hurricane caused extensive damage to the reefs, but despite high nutrient levels, algae invading the open areas were controlled by *Diadema*, allowing coral to recolonize. However, in subsequent years, populations of *Diadema* were dramatically reduced by a pathogen. Because herbivorous fish had also become rare, algae were released from the control of grazers and the reefs rapidly became overgrown by fleshy brown algae. This switch is thought to be difficult to reverse because adult algae are less palatable to herbivores and the algae prevent settlement of coral larvae.

Woodlands

Many studies indicate that woodlands and a grassy open landscape can be alternative stable states. Landscapes can be kept open by herbivores (often in combination with fires) because seedlings of woody plants, unlike adult trees, are easily eliminated by herbivores. Conversely, woodlands, once established, are stable because adult trees can not be destroyed by herbivores and shading reduces grass cover so that fires can not spread. Well analysed examples are African woodland dynamics in Botswana[23] and Tanzania[24], where regeneration of woodlands occurred for a few decades from the 1890s because of low herbivore numbers due to a combination of rinderpest epidemic and elephant hunting. Once established, these woodlands could not be eliminated by grazers. However, the current destruction of woodlands by humans and high densities of elephants is probably irreversible in these regions

unless herbivore numbers are again reduced (which is unlikely given the focus of the national parks' policy on attracting tourists)[23].

In dry areas, conditions in the absence of cover by adult trees may be too desiccating to allow the seedlings to survive, even in the absence of herbivores, implying a more severe irreversibility of woodland loss, as illustrated by mattoral woodlands in the drier parts of Mediterranean central Chile[25]. This implies that only rare combinations of wet years and repressed herbivore populations may allow recovery of these diverse woodlands, which once covered extensive areas. Another case of irreversible loss of trees is that of cloud forests[26]. Condensation of water from clouds in the canopy supplies moisture for a rich ecosystem. If the trees are cut, this water input stops and the resulting conditions can be too dry for recovery of the forest.

In savannahs, sparse trees with a grass layer are the natural state. A shift to a dense woody state (known as 'bush encroachment') can result from a combination of change in fire and grazing regimes. Occasional natural fires reduce the woody plant cover and favour development of the grass layer. However, excessive grazing by livestock reduces grass and hence fuel for fire. In the absence of fire, cohorts of shrubs establish during wet years and can suppress grass cover, thereby inhibiting the spread of fire. The system stays in this thicket state until trees begin to die, thereby allowing grass cover to attain levels that will carry an effective fire[27,28].

Deserts

Desertification—the loss of perennial vegetation in arid and semi-arid regions—is often cited as one of the main ecological threats facing the world today[29], although the pace at which it proceeds in the Sahara region may be less than previously
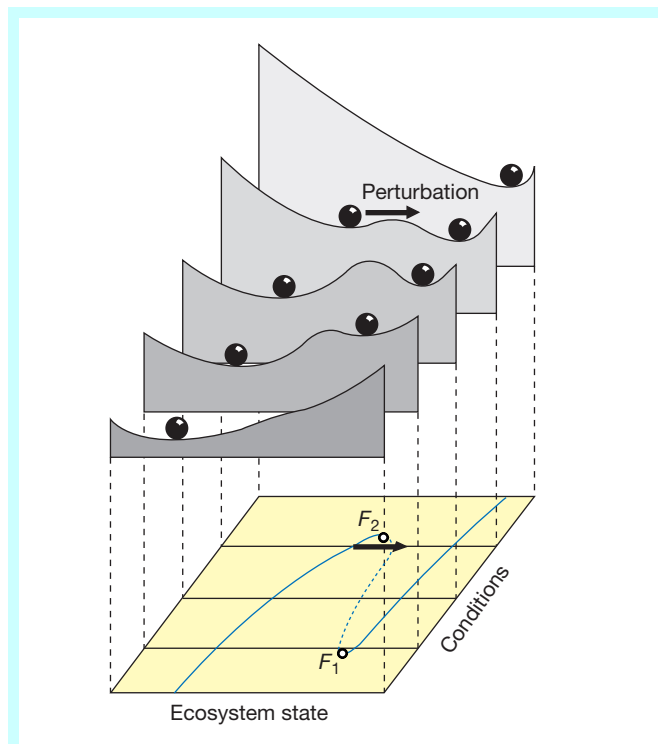
Figure 3 External conditions affect the resilience of multi-stable ecosystems to perturbation. The bottom plane shows the equilibrium curve as in Fig. 2. The stability landscapes depict the equilibria and their basins of attraction at five different conditions. Stable equilibria correspond to valleys; the unstable middle section of the folded equilibrium curve corresponds to a hill. If the size of the attraction basin is small, resilience is small and even a moderate perturbation may bring the system into the alternative basin of attraction.
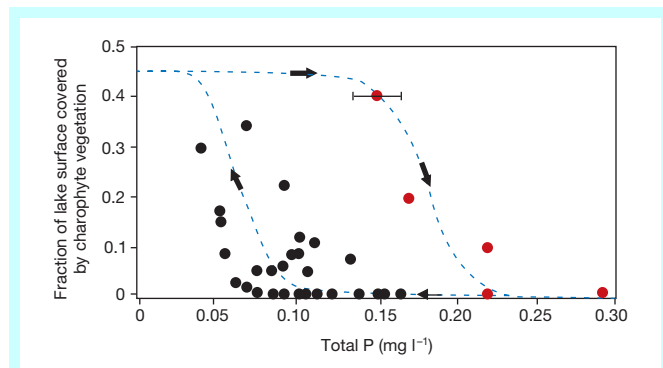

Box 1
A minimal mathematical model

A minimal model of an ecosystem showing hysteresis describes the change over time of an 'unwanted' ecosystem property x:

$$dx/dt = a - bx + rf(x) \qquad (1)$$

The parameter a represents an environmental factor that promotes x. The remainder of the equation describes the internal dynamics: b represents the rate at which x decays in the system, whereas r is the rate at which x recovers again as a function f of x. For lakes, one can think of x as nutrients suspended in phytoplankton causing turbidity, of a as nutrient loading, of b as nutrient removal rate and of r as internal nutrient recycling[12]. For desertification, one could interpret x as barren soil, a as vegetation destruction, b as recolonization of barren soil by plants and r as erosion by wind and runoff[58].

For $r = 0$, the model has a single equilibrium at $x = a/b$. The last term, however, can cause alternative stable states, for example, if $f(x)$ is a function that increases steeply at a threshold h, as in the case of the Hill function:

$$f(x) = x^p/(x^p + h^p)$$

where the exponent p determines the steepness of the switch occurring around h. Notice that (1) can have multiple stable states only if the maximum $\{rf'(x)\} > b$. Thus, steeper Hill functions (resulting from higher p values) create stronger hysteresis.

Figure 4 Hysteresis in the response of charophyte vegetation in the shallow Lake Veluwe to increase and subsequent decrease of the phosphorus concentration. Red dots represent years of the forward switch in the late 1960s and early 1970s. Black dots show the effect of gradual reduction of the nutrient loading leading eventually to the backward switch in the 1990s. From ref. 59.

thought[30]. Various lines of evidence indicate that vegetated and desert situations may represent alternative stable states. Local soil–plant interactions are important in determining the stability of perennial plant cover[6,31]. Perennial vegetation allows precipitation to be absorbed by the topsoil and to become available for uptake by plants. When vegetation cover is lost, runoff increases, and water entering the soil quickly disappears to deeper layers where it cannot be reached by most plants. Wind and runoff also erode fertile remains of the topsoil, making the desert state even more hostile for recolonizing seedlings. As a result, the desert state can be too harsh to be recolonized by perennial plants, even though a perennial vegetation may persist once it is present, owing to the enhancement of soil conditions.

On a much larger scale, a feedback between vegetation and climate may also lead to alternative stable states. The Sahel region seems to shift back and forth between a stable dry and a stable moister climatic regime. For example, every year since 1970 has been anomalously dry, whereas every year of the 1950s was unusually wet; in other parts of the world, runs of wet or
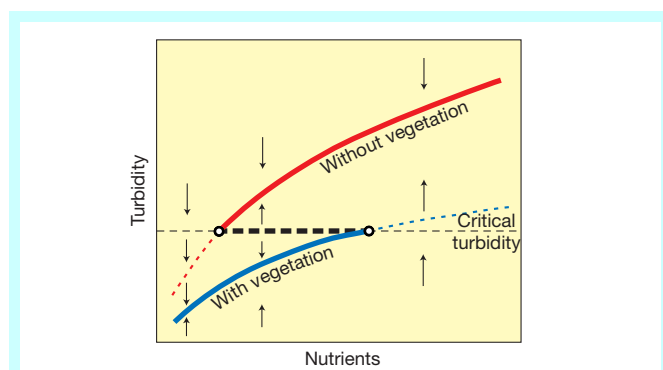
dry years typically do not exceed 2–5 years[32]. Many studies have addressed the question of why this system shifts between distinct modes, instead of drifting through a series of intermediate conditions. A new generation of coupled climate–ecosystem models[33–35] demonstrates that Sahel vegetation itself may have a role in the drought dynamics, especially in maintaining long periods of wet or dry conditions. The mechanism is one of positive feedback: vegetation promotes precipitation and vice versa, leading to alternative states.

Intriguing evidence for alternative stable states in the Sahel and Sahara desert systems comes from ancient abrupt shifts at a large scale between desert and vegetated states, coupled to climatic change in North Africa. During the early and middle Holocene—about 10,000 to 5,000 years before present—much of the Sahara was wetter than it is today, with extensive vegetation cover and lakes and wetlands[36,37]. Then, some time around 5,000 years before present, an abrupt switch to desert-like conditions occurred[38]. By means of combined atmosphere–ocean–biosphere models, it has been shown that feedbacks causing alternative stable states could indeed explain such an abrupt switch, even when the climate system is being driven by slow gradual change in insolation resulting from subtle variations in the Earth's orbit (Fig. 6)[38,39].

The timescales in this example are rather long. Nonetheless, it illustrates the same phenomenon of alternative stability domains that underlies the dynamics found in the other examples. An important implication here is that small environmental changes, such as overgrazing[40], increased dust loading[32], or changes in nearby ocean temperatures[33], may potentially cause a total state shift for the entire area once a certain critical threshold is passed.

Oceans

Time series of fish catches, oyster condition, plankton abundance and other marine ecosystem properties indicate conspicuous jumps from one rather stable condition to another (Fig. 7). These puzzling events have been termed 'regime shifts'[41]. The implications of oceanic regime shifts for fisheries and oceanic CO_2 uptake[42] are profound, but the cause of the shifts is poorly understood[41]. In view of the overriding importance of sea currents on these ecosystems, changes in the oceanic circulation or weather pattern can reasonably be
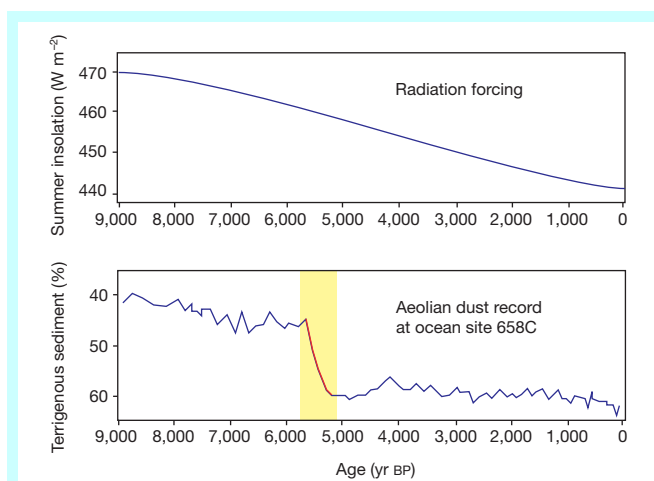

Figure 5 A graphical model[60] of alternative stable states in shallow lakes on the basis of three assumptions: (1) turbidity of the water increases with the nutrient level; (2) submerged vegetation reduces turbidity; and (3) vegetation disappears when a critical turbidity is exceeded. In view of the first two assumptions, equilibrium turbidity can be drawn as two different functions of the nutrient level: one for a vegetation-dominated situation, and one for an unvegetated situation. Above a critical turbidity, vegetation will be absent, in which case the upper equilibrium line is the relevant one; below this turbidity the lower equilibrium curve applies. As a result, at lower nutrient levels, only the vegetation-dominated equilibrium exists, whereas at the highest nutrient levels, there is only an unvegetated equilibrium. Over a range of intermediate nutrient levels, two alternative equilibria exist: one with vegetation, and a more turbid one without vegetation, separated by a (dashed) unstable equilibrium.

Figure 6 Over the past 9,000 years, average Northern Hemisphere summer insolation (upper panel) has varied gradually owing to subtle variation in the Earth's orbit. About 5,000 years before present (yr BP), this change in solar radiation triggered an abrupt shift in climate and vegetation cover over the Sahara, as reflected in the contribution of terrigenous (land-eroded) dust to oceanic sediment at a sample site near the African coast (lower panel). Modified from ref. 61.
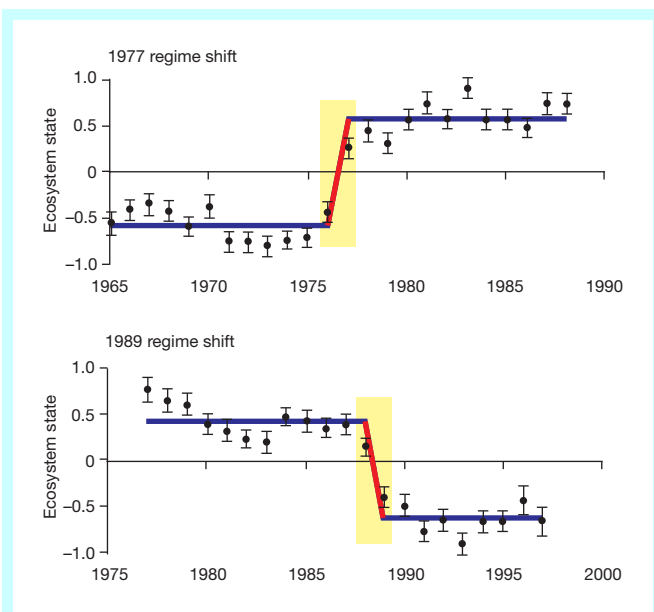
Figure 7 Distinct state shifts occurred in the Pacific Ocean ecosystem around 1977 and 1989. The compound indices of ecosystem state are obtained by averaging 31 climatic and 69 biological normalized time series. Modified from ref. 41.

expected to be the drivers of change. However, the state shifts are sometimes reflected more consistently by the biological data than by the physical indices, suggesting that biotic feedbacks could be stabilizing the community in a certain state, and that shifts to a different state are triggered merely by physical events[41].

It is becoming increasingly clear that competition and predation are much more important in driving oceanic community dynamics than previously thought[43]. It is therefore not surprising that fisheries can affect the entire food web, causing profound shifts in species abundance on various trophic levels[44–46]. Also, such tight biotic interactions imply that sensitivity of a single keystone species to subtle environmental change can cause major shifts in community composition[47]. Therefore, solving the puzzle of regime shifts in oceanic ecosystems may require unravelling the interplay of effects of fisheries and effects of changes in the physical climate or ocean system.

The coupled ocean–climate system may also go through shifts between alternative stable states that are much more drastic than the regime shifts mentioned above[15,48]. For example, simulation studies indicate that gradual climate warming may cause an increase in freshwater inflow into the North Atlantic that prevents the formation of dense deep water, which is needed to power the 'global conveyor belt' oceanic current that transports warm water to eastern North America and western Europe[15]. Such a change causes the climate in these regions to become dramatically colder. Reconstructions of palaeoclimate show that similar large shifts have happened in the past and can be very swift indeed, occurring in less than a decade[48].

Emerging patterns

All of these case studies suggest shifts between alternative stable states. Nonetheless, proof of multiplicity of stable states is usually far from trivial. Observation of a large shift *per se* is not sufficient, as systems may also respond in a nonlinear way to gradual change if they have no alternative stable states (for example, as in Fig. 1b)[49]. Also, the power of statistical methods to infer the underlying system properties from noisy time series is poor[7,50,51]. However, mere demonstration of a positive-feedback mechanism is also insufficient as proof of alternative stable states, because it leaves a range of possibilities between pronounced hysteresis and smooth response, depending on the strength of the feedback and other factors[49]. Indeed, the strongest cases for the existence of alternative stable states are based on combinations of approaches, such as observations of repeated shifts, studies of feedback mechanisms that tend to maintain the different states, and models showing that these mechanisms can plausibly explain field data.

Although the specific details of the reviewed state shifts differ widely, an overview (Table 1) shows some consistent patterns. First, the contrast among states in ecosystems is usually due to a shift in dominance among organisms with different life forms. Second, state shifts are usually triggered by obvious stochastic events such as pathogen outbreaks, fires or climatic extremes. Third, feedbacks that stabilize different states involve both biological and physical and chemical mechanisms.

Perhaps most importantly, all models of ecosystems with alternative stable states indicate that gradual change in environmental conditions, such as human-induced eutrophication and global warming, may have little apparent effect on the state of these systems, but still alter the 'stability domain' or resilience of the current state and hence the likelihood that a shift to an alternative state will occur in response to natural or human-induced fluctuations.

Implications for management

Ecosystem state shifts can cause large losses of ecological and economic resources, and restoring a desired state may require drastic and expensive intervention[52]. Thus, neglect of the possibility of shifts to alternative stable states in ecosystems may have heavy costs to society. Because of hysteresis in their

Table 1 Characteristics of some major ecosystem state shifts and their causes

Ecosystem	State I	State II	Events inducing shift from I to II	Events inducing shift from II to I	Suggested main causes of hysteresis	Factors affecting resilience
Lakes	Clear with submerged vegetation	Turbid with phytoplankton	Killing of plants by herbicide Killing of *Daphnia* by pesticide High water level	Killing of fish Low water level	Positive feedback of plant growth Trophic feedbacks	Nutrient accumulation
Coral reefs	Corals	Fleshy brown macroalgae	Killing of coral by hurricane Killing of sea urchins by pathogen	Unknown	Prevention of coral recolonization by unpalatable adult algae	Nutrient accumulation Climate change Fishing
Woodlands	Herbaceous vegetation	Woodlands	Fires Tree cutting	Killing of grazers by pathogen Hunting of grazers	Positive feedback of plant growth Inedibility of adult trees	Overgrazing Climate change
Deserts	Perennial vegetation	Bare soil with ephemeral plants	Climatic events Overgrazing by cattle	Climatic events	Positive feedback of plant growth	Climate change
Oceans	Various	Various	Climatic events	Climatic events	Physical	Fishing Climate change

response and the invisibility of resilience itself, these systems typically lack early-warning signals of massive change. Therefore attention tends to focus on precipitating events rather than on the underlying loss of resilience. For example, gradual changes in the agricultural watershed increased the vulnerability of Lake Apopka (Florida, USA) to eutrophication, but a hurricane wiped out aquatic plants in 1947 and probably triggered the collapse of water quality[53,54]; gradual increase in nutrient inputs and fishing pressure created the potential for algae to overgrow Caribbean corals, but overgrowth was triggered by a conspicuous disease outbreak among sea urchins that released algae from grazer control[8]; and gradual increase in grazing decreases the capacity of Australian rangelands to carry the fires that normally control shrubs, but extreme wet years trigger the actual shift to shrub dominance[27,55].

Prevention of perturbations is often a major goal of ecosystem management, not surprisingly. This is unfortunate, not only because disturbance is a natural component of ecosystems that promotes diversity and renewal processes[56,57], but also because it distracts attention from the underlying structural problem of resilience. The main implication of the insights presented here is that efforts to reduce the risk of unwanted state shifts should address the gradual changes that affect resilience rather than merely control disturbance. The challenge is to sustain a large stability domain rather than to control fluctuations. Stability domains typically depend on slowly changing variables such as land use, nutrient stocks, soil properties and biomass of long-lived organisms. These factors may be predicted, monitored and modified. In contrast, stochastic events that trigger state shifts (such as hurricanes, droughts or disease outbreaks) are usually difficult to predict or control. Therefore, building and maintaining resilience of desired ecosystem states is likely be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change. □

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