

Pulse-Driven Loss of Top-Down Control: The Critical-Rate Hypothesis

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ABSTRACT

In systems ranging from lakes and woodlands to coral reefs, the long-term ecosystem state may often be determined largely by rare extreme events such as wet ENSO years, droughts, or disease outbreaks. Such events can flip these systems into a contrasting state that represents either an alternative attractor or a transient that is slow enough to persist even if the frequency of events that push the system to this state is low. Here we show that escape from herbivores is a mechanism that can play a role in several state shifts of this kind. This can happen if plants become less susceptible to herbivory as they grow. Using a model we show that, surprisingly, this mechanism can lead to a situation where a brief resource pulse for plants may invoke a persistent shift to a high biomass state whereas gradual enrichment to the same resource level is insufficient

to allow such a change. This counterintuitive phenomenon occurs if the numerical response of herbivores is sufficiently slow to allow the plants to use the resource pulse to escape to a safe biomass at which herbivory is reduced. Our results imply that rates of environmental change can sometimes be more important than their magnitude. This has many ramifications. On the conceptual side, our findings suggest that key mechanisms that regulate long-term ecosystem dynamics are easily missed by the traditional focus of modelers on equilibria. A more practical corollary is that increased climatic variability may have more profound effects in some ecosystems than gradual change in conditions.

Key words: regime shift; resource pulse; trophic cascade; coral reefs; forest dynamics; stability.

INTRODUCTION

Extreme events such as very wet years, droughts, storms, or epidemics may profoundly affect ecosystems, but eventually most systems settle again to essentially the original state. An exception to this rule may occur if an ecosystem has more than one stable state (Scheffer and others 2001). In this case a

rare extreme event may tip the system into an alternative basin of attraction, leaving it in a persistent contrasting regime. Some of the most striking examples of this phenomenon are characterized by shifts between contrasting groups of primary producers. For instance, shallow lakes can shift between dominance by submerged macrophytes and phytoplankton (Scheffer and others 1993), or by floating plants (Scheffer and others 2003), or cyanobacteria (Scheffer and others 1997). In marine systems, coral reefs can shift to a state dominated by macro-algae (Hughes 1994), whereas kelp forests can be turned

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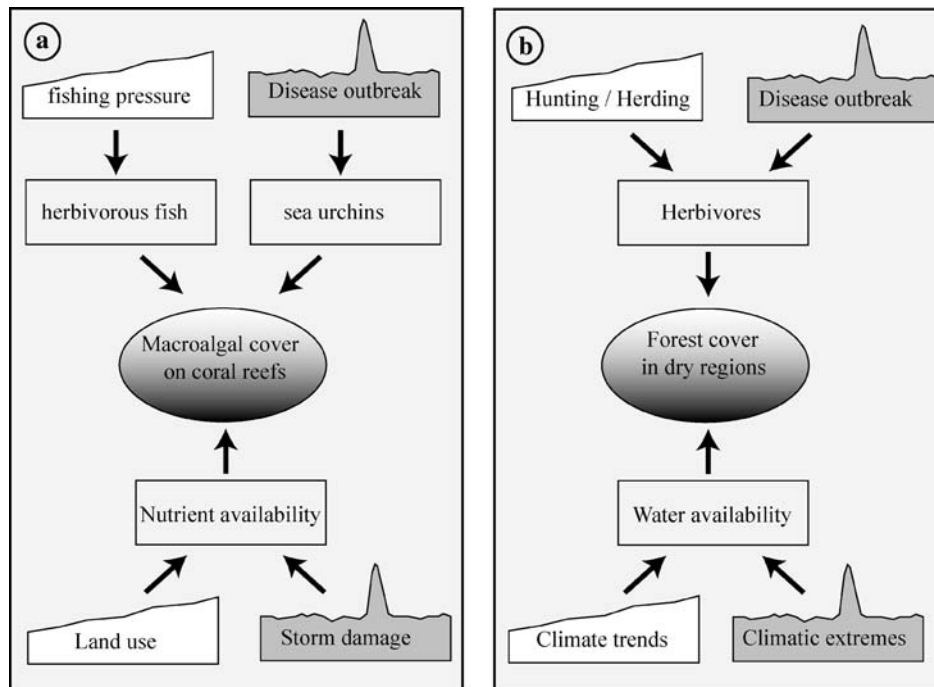


Figure 1. Two examples of systems where extreme events may trigger a shift to a plant-dominated state through the herbivore escape mechanism. Gradual trends in important conditioning factors (*light boxes*) are often insufficient to cause such a shift but may affect the likelihood that pulsed events (*shaded boxes*) do trigger a transition. Disease outbreaks in herbivores have been convincingly shown to lead to escape from top-down control of macro-algae as well as trees. Similar shifts in response to an environmentally driven productivity pulse seem to be less common but have been documented for some semi-arid systems.

into sea urchin barrens where only crustose coralline algae are prevalent (Steneck and others 2002). In terrestrial systems, shifts in dominant growth form include transformations between woodland and herbaceous vegetation (Dublin and others 1990), and between abundant perennial vegetation and desert (Van de Koppel and others 1997).

Here, we argue that specific attributes of rare events, often related to climatic extremes, may have profound effects on the long-term state of such ecosystems. We focus on a class of mechanisms that appears to be relatively widespread: escape from herbivore control. After reviewing two examples of ecosystem shifts in coral reefs and semi-arid forests (Figure 1), we discuss evidence for the mechanisms in more depth and use a model to explore its potential consequences.

TWO EXAMPLES OF TRIGGERED ECOSYSTEM SHIFTS

Macro-algal Cover of Coral Reefs

The widespread degradation of reefs by pollution and overfishing has focused attention on their growing susceptibility to regime shifts, from coral

dominance to macro-algae (Hughes and others 2003; Bellwood and others 2004). By definition, a resilient coral reef is characterized by its ability to absorb disturbances (such as recurrent hurricanes) and to rebuild coral assemblages and avoid regime shifts. Three factors are key to recovery from a local disturbance—the availability of a larval pool from a nearby source, water quality (sediment and nutrient loads), and herbivory.

Short-lived algal blooms often occur on coral reefs following a hurricane, typically lasting a few weeks (Woodley and others 1981; Hughes 1994). Hurricanes release huge amounts of nutrients from rainfall and terrestrial runoff, by disturbing reef sediments, and from the rotting tissues of damaged coral, sponges, and other reef organisms. There is also a temporary reduction in herbivory caused by mortality, disorientation, and displacement of fishes and sea urchins. Opportunistic algae, such as *Liagora*, can become locally very abundant under these temporary conditions, but they soon disappear, leaving the substrate suitable for re-colonization by coral larvae.

Although such recovery following hurricane disturbance illustrates the resilience of reef systems to productivity pulses, a dramatic regime shift that

transformed Caribbean reefs in the 1980s revealed that the system had become vulnerable to another kind of perturbation. A species-specific pathogen caused mass mortality of the sea urchin *Diadema antillarum*, with far-reaching consequences throughout the Caribbean. Urchin densities crashed to 1% of the original level, and many reefs became overgrown by unprecedented blooms of algae. The new algal assemblages prevented coral recruitment, and smothered juvenile and low-lying adult corals. With the benefit of hindsight, it is now clear that the reefs had become vulnerable to a regime shift because overfishing had reduced the diversity of herbivores to a single hyper-abundant species of sea urchin (Hughes 1994).

One could argue that the disease outbreak was a rare, chance event and that the dramatic regime shift might never have occurred. However, slow changes had undermined the resilience of the reefs over time, making a regime-shift more and more likely. Firstly, changed land use and increasing human population densities resulted in gradually increased nutrient loading, especially in lagoonal areas close to coastal settlements. Secondly, fishing had decimated fish, leaving urchins as the only abundant macro-herbivores controlling algae. Also, fishing may have allowed the urchins to become very abundant in the absence of their major competitors and predators. On some shallow patch reefs, the average density of *Diadema* exceeded 50 per m² (Sammarco 1980). As the density of a species increases, the risk of an epidemic increases too. Thus, although there is always a large random component in the incidence of epidemics, they are more likely in simplified systems with reduced biodiversity, because such systems tend to have high-density populations of key species.

More than 20 years later, most Caribbean reefs continue to slowly degrade, and remnant corals face new threats from climate change and emergent diseases (Gardner and others 2003). Potential mechanisms that stabilize the alga-dominated state include the continuation of overfishing and local enhancement of nutrient loads, the relatively low palatability of large adult algae (as opposed to small intensely grazed forms), the sharply reduced brood stocks of adult corals, and the inhibition of coral recruitment by abundant algal cover.

In conclusion, although nutrient loading may increase the likelihood of coral reefs becoming covered by algae, neither elevated nutrient concentrations nor resource pulses following hurricanes are sufficient to trigger an escape by macro-algae from control by intense herbivory. Apparently, the response of herbivores is usually

sufficiently fast to control the algae, upon their initial increase. By contrast, mass mortality of the key herbivore in the Caribbean has been sufficient to cause a shift to the algal-dominated state because alternative herbivores have been repressed by fishing.

Woodland Dynamics

Recruitment dynamics of woodlands are also governed to a great extent by herbivory and resource levels. As in the case of macro-algae on coral reefs, a mortality event among herbivores may allow massive recruitment of plants. The reconstructed long-term history of African savanna dynamics provides a good example (Dublin and others 1990). A massive rinderpest epidemic that swept through the region in the 1890s greatly reduced numbers of ungulates allowing large-scale woodland expansions. These extensive woodlands were apparently stable for 30–50 years, before they were eliminated by human-induced fires followed by renewed top-down control by recovered populations of elephants and ungulates. Similarly, devastation of the rabbit population by myxomatosis has led to massive tree recruitment in many places. A well-documented example is the shift of the open landscape of Silwood Park, UK, to a dense oak woodland following the myxomatosis epidemic of 1955 (Dobson and Crawley 1994). Although the rabbit population has recovered, the tree stands persist because they have achieved an escape in size from herbivory by rabbits.

Interestingly, episodic rainfall may also trigger woodland expansion. This is especially obvious in semi-arid regions where ENSO events can lead to increased rainfall of an order of magnitude or more. Tree ring analyses in Peru have revealed that rare, wet El Niño periods have been key years for tree recruitment (Holmgren and others 2006), whereas aerial photographs and satellite images confirm that massive woodland expansion can occur following extreme rainy El Niño events (Bravo-Ferro and Rodríguez-Sánchez 2003). In contrast, rainfall pulses do not drive recruitment in an area of Chile that is superficially quite similar to Peru. Controlled field experiments suggest that the combination of herbivory and rain dynamics may explain the difference in tree recruitment (Holmgren and others 2006). Smaller herbivores (lizards as opposed to rabbits) as well as faster plant growth at the higher temperatures in Peru imply that plants may reach an escape in size from herbivory there more rapidly than in Chile.

The key roles of episodic climate and herbivory are also suggested by a long-term study of tree

recruitment in the Pilga woodlands of semi-arid Australia (Austin and Williams 1988). Severe droughts in 1876–1877 devastated sheep and cattle populations, allowing abundant regeneration of trees following heavy rainfall in 1878. The resulting dense forests made subsequent grazing impossible. Some years later rabbits were introduced and blocked further recruitment of trees, although due to the longevity of trees the forest remained dense for many decades. The critical role of rabbits was revealed in the 1950s when they were practically eliminated by myxomatosis. Since then natural tree recruitment has occurred every rainy year.

In conclusion, a shift from open area to forest may be driven by a temporary collapse of herbivore populations. However, unlike in the coral reef example, resource pulses (rainy episodes) may by themselves also trigger an escape from an herbivore-controlled open landscape to a forested state. Whether or not this happens appears to depend among other things upon the dominant kind of herbivore and plant growth rates.

THE HERBIVORE ESCAPE MECHANISM

In the discussed examples, dominance by the new type of primary producers (macro-algae or trees) is stabilized by a positive feedback that makes it difficult to return to the original state. We have stressed the role of herbivory. However, a range of mechanisms is often involved in such feedbacks. For instance, in the case of macro-algae on reefs, settlement of coral larvae becomes difficult once algae are dominant. Similarly, facilitation of seedling recruitment under a developing canopy may represent a positive feedback in the establishment of dry forests and shrublands in semi-arid regions.

Nonetheless, a reduction in palatability as plant biomass increases may be one of the most widespread phenomena that can stabilize a new state. Most trees and shrubs, for instance, are grazed more intensively as seedlings than as adults, making the early stages of recruitment critical for forest expansion (Holmgren and Scheffer 2001). In general, as plants grow larger, less foliar biomass is reached by small ground-based herbivores, and also dense vegetation and bushes may be difficult for mammals to enter. Even for herbaceous vegetation, foraging efficiency of herbivores decreases at high standing crop (Parsons and others 1983; McNaughton 1984). Herbivores may avoid larger plants because they tend to have lower protein content and reduced palatability compared to smaller plants (Ludlow and others 1982; Fryxell 1991). Also, herbivores may devote less time to

foraging in dense vegetation if the potential presence of hidden predators causes them to be more vigilant (Underwood 1982; Loughry 1993). Just like terrestrial vegetation, freshwater phytoplankton communities can be herbivore-controlled at low biomass, but are less prone to exploitation at high densities. For instance, dense populations of large colonial cyanobacteria in lake plankton are usually only lightly grazed by herbivorous zooplankton, whereas these species are heavily consumed at earlier unicellular life stages (Gliwicz 1990; Gragnani and others 1999). On coral reefs, the relatively low palatability of large adult algae may help stabilize the algal-dominated state. Similarly, along rocky cold water coasts, sea urchins keep algal biomass very low in barren systems that are dominated by coralline algae, whereas fully grown kelp forests are less palatable and not easily grazed down. Furthermore, the presence of predators and the physical barriers afforded by dense kelp stands may also reduce herbivory (Steneck and others 2002; Konar and Estes 2003).

In summary, although different mechanisms may be involved in stabilizing alternative stable communities, reduced foraging efficiency of herbivores at high standing crops appears to be a widespread phenomenon across aquatic and terrestrial systems. In the following sections we use a model of this particular mechanism to explore under which conditions enrichment, resource pulses, diseases, and other mechanisms may be expected to cause shifts between alternative states.

Model

To explore how herbivore escape may be expected to work, we use a simple plant-herbivore model (Table 1) in which we assume foraging efficiency to be reduced at high standing crop:

$$\frac{dP}{dt} = rP - CP^2 - r_H c_{\max} H \frac{P^2}{P^2 + a^2} e^{-b_c P} \quad (1)$$

$$\frac{dH}{dt} = \left(E e^{-b_p P} c_{\max} H \frac{P^2}{P^2 + a^2} e^{-b_c P} - m H \right) r_H \quad (2)$$

Logistic growth of the plant population (P) is determined by the maximum growth rate (r) and the competition coefficient (C). In the absence of herbivores (H) growth stabilizes at a carrying capacity (r/C). In the analyses we vary r to mimic the effects of resource availability (for example, water or nutrients) on plants. Note that, unlike the familiar version of the logistic equation ($rP(1-P/K)$,

Table 1. Description of Parameters and Default Values

Symbol	Description	Unit	Default value
C	Competition factor of plants	$\text{g}^{-2} \text{m}^4 \text{s}^{-1}$	0.02
a	Half-saturation constant of functional response	g m^2	10
b	Exponent determining the reduced quality of food if food biomass is high	$\text{g}^{-1} \text{m}^2$	0.02
b_c	Exponent determining the predation efficiency of herbivores at high food biomass	$\text{g}^{-1} \text{m}^2$	0.02
c_{\max}	Maximum food intake of herbivores	d^{-1}	1
E	Assimilation efficiency of herbivores	–	0.4
m	Loss factor of herbivores (respiration, mortality)	d^{-1}	0.1
r_H	Factor to reduce the speed of herbivores	–	1
r	Maximum growth rate of plants	d^{-1}	1

variation in r in our model affects maximum growth rates as well as carrying capacity. Because factors that affect productivity (such as precipitation in dry regions) often appear to affect both the carrying capacity and growth rate of plants, mimicking the effect of productivity this way seems a reasonable approach. The formulation of grazing is based on a classical type-III functional response to plant biomass, with a maximum specific grazing rate (c_{\max}) and a half-saturation constant (a). The use of the sigmoid in this kind of model is classical and implies that foraging is less efficient at removing the last fraction of plants (such as near-ground biomass and rhizomes). The exponential term represents the decline in grazing at higher plant biomass (Van de Koppel and others 1996) and is tuned by the constant (b_c). Grazed plant biomass is transformed to herbivore biomass with efficiency (E), which is assumed to decline with increasing plant standing crop.

For simplicity, this palatability effect is assumed to follow the same exponential decline as grazing rate. Herbivores are also affected by the loss rate (m). Finally we added a parameter (r_H) that allows us to scale the rates of change in the herbivore population to explore the potential differences in non-equilibrium dynamics between systems with herbivores that have fast numerical responses (for example, invertebrates or rodents) and those with slower rates of change (for example, deer).

The essence of this model goes back to early theoretical work on bi-stability of vegetation (Noy-Meir 1978) and outbreak cycles (Ludwig and others 1978), but has not been analyzed from the pulse perturbation perspective that we will take. A similar model has also been analyzed in a different context by Van de Koppel and colleagues (1996). Note that an important simplifying assumption is that total standing crop is correlated with individ-

ual plant size. As discussed, it is often plant size rather than vegetation biomass that makes plants less vulnerable to herbivory. If one would want to capture that aspect explicitly, an individual based or size structured model is needed. The simplest approach would be to include an extra differential equation for the total biomass of individuals that have reached an invulnerable size class, as done some times for animal growth (Chase 1999). However, for the present purpose we stick with the minimal formulation of two differential equations.

The model was analyzed using Grind for MATLAB (<http://www.aew.wur.nl/uk/grind/>) which uses a Runge Kutta numerical procedure.

MODEL RESULTS

Basic Behavior

The herbivore equation (2) implies that assimilation rates first increase with plant biomass and then decline again as a result of the reduced foraging efficiency at high plant density (Figure 2A). If this decline of assimilation rates at high plant densities is strong enough, it can produce two plant densities at which herbivore loss rates are just balanced by the gains. The lower plant density at which this happens (P_1) represents the minimum plant biomass needed to sustain net growth of the herbivore population. By contrast, the right-hand intersection point in this graph (P_2) corresponds to the plant biomass beyond which foraging efficiency becomes too low to allow net growth of the herbivore population. Thus, only intermediate plant densities (shaded section) allow herbivore growth.

To explore how herbivore dynamics may interact with plant dynamics we plot the lines of zero growth (the ‘nullclines’) of herbivores and plants in the phase plane (Figure 2B). The two densities of

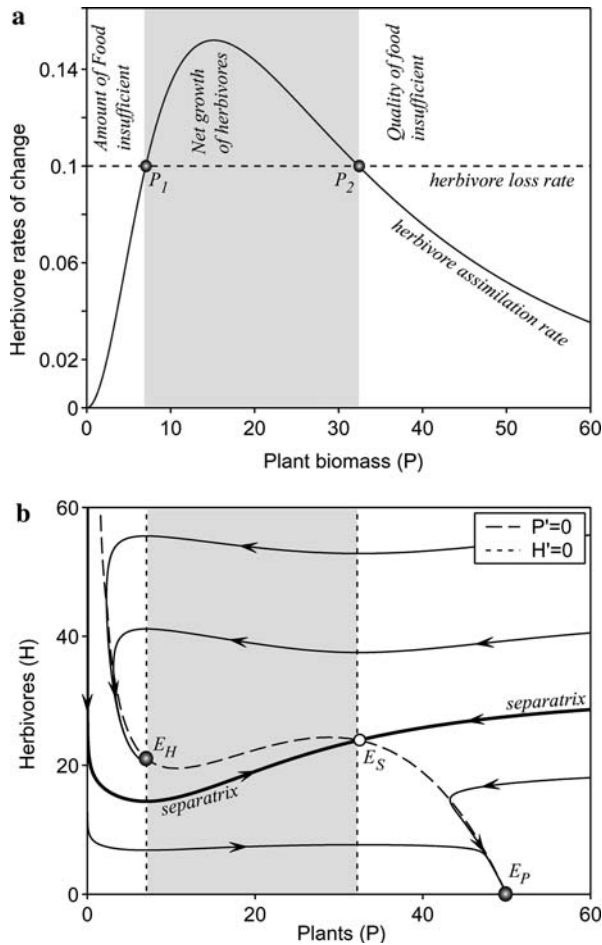


Figure 2. (A) The rate of change in the herbivore population depends on the difference between assimilated gains and losses. At intermediate plant biomass the net growth is positive (shaded section). At lower plant biomass food quantity is too low for herbivore growth, whereas at higher plant biomass foraging efficiency becomes too low. (B) The nullclines (where net growth is zero) for herbivores and plants. The heavy dots are stable equilibria, the light dot is an unstable point (see text for explanation). Parameter setting here and in other figures (unless indicated otherwise) $C = 0.02$; $a = 10$; $b = 0.02$; $b_c = 0.02$; $c_{max} = 1$; $E = 0.4$; $m = 0.1$; $r = 1$; $r_H = 1$.

plants at which herbivore losses just balance assimilation correspond to two vertical herbivore nullclines ($H' = 0$), separating the region of herbivore net growth (shaded section in the figure) from regions of net herbivore decline. The nullcline of plants ($P' = 0$) separates the region of net plant growth (below the curve) from that of net decline in plant biomass (above the curve).

In the default parameter setting, the model has three equilibria. There is a herbivore-controlled equilibrium (E_H) at low plant density and a plant-dominated stable state (E_P) at which herbivores are

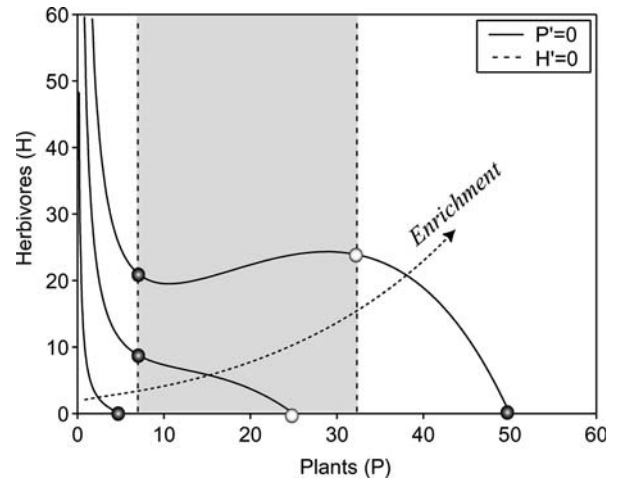


Figure 3. Enrichment (increasing r) affects the nullcline of plants, causing the equilibria to shift. In the shaded region, herbivore growth is positive, implying that the plant-dominated equilibrium (open dot) is unstable. The other equilibria shown are stable. Parameter setting as in Figure 2 but with $r = 0.1$ (lower plant nullcline), 0.5 (middle), and 1.0 (highest).

absent. Between these alternative stable states, there is an unstable equilibrium (saddle point) (E_S) where the right-hand herbivore nullcline intersects the plant nullcline. This saddle point is on the separatrix which marks the border between the basins of attraction of the herbivore-controlled equilibrium and the plant-dominated state.

If one changes the parameter values the positions of the nullclines and equilibria shift. For instance, if the herbivore loss rate (horizontal line in Figure 2A) is lowered, the herbivore escape biomass (P_2 in Figure 2A) may exceed the plant carrying capacity (E_P) and there is no stable plant-dominated state anymore. On the other hand, if herbivore loss rates increase, P_1 and P_2 collide, implying the end of the herbivore-dominated equilibrium (E_H). (In fact, slightly before that bifurcation E_H becomes unstable through a Hopf bifurcation, and soon thereafter the resulting stable limit cycle disappears through a 'basin boundary collision' as it hits the saddle point, a phenomenon highlighted by others (Van de Koppel and others 1996)).

Effects of Enrichment

We analyze the effects of gradual resource enrichment in our model by varying the plant maximum growth rate (r), which affects the plant nullcline (Figure 3). At very low growth rates the entire plant nullcline remains in the section at which

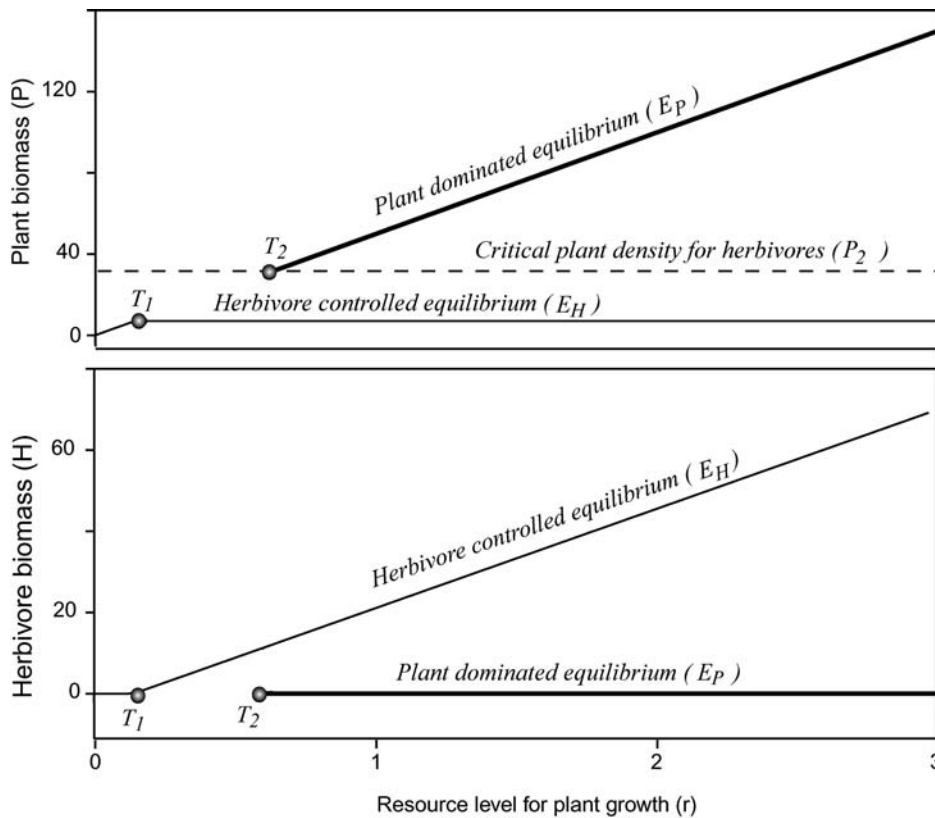


Figure 4. Effect of resource level for plant growth (varying r) on the equilibria of the model.

plant biomass is too low to sustain herbivore growth. Increasing the plant growth rate, first there is a so-called transcritical bifurcation point (T_1 in Figure 4) when the plant nullcline touches the left-hand herbivore nullcline, and the herbivore-dominated equilibrium (E_H) comes into existence. From that point onward, further increase in plant productivity results in an increased herbivore biomass, whereas plant biomass remains constant (E_H keeps moving upward along the herbivore nullcline). This result is well known from the classical paper on the “paradox of enrichment” (Rosenzweig 1971) and follow-up work on systems with more trophic levels (Oksanen and others 1981). However, the behavior of our model differs in two crucial aspects.

Firstly, if we increase productivity (r) sufficiently for the plant nullcline to touch the right-hand vertical herbivore nullcline, there is another transcritical bifurcation (T_2 in Figure 4) at which an unstable equilibrium (saddle point E_S) is born. The intersection of the plant nullcline with the x -axis (E_P) becomes stable again, as herbivores become unable to develop a population where foraging efficiency has dropped below a critical level. Perhaps the most surprising aspect here is that this equilibrium cannot be reached simply by increasing

productivity. Once the system is in a herbivore-dominated state (E_H), gradual enrichment can never shift it to the plant-dominated state (E_P). E_H remains stable and any increase in productivity is simply ‘transferred’ to an increase in herbivores that subsequently keep plants at the same fixed level (Figure 4). Note that this outcome depends on the verticality of the herbivore nullclines, which results from the assumption that herbivore density is regulated only by food availability.

The second difference from the classical “paradox of enrichment” model is that for most parameter ranges we do not observe herbivore-plant cycles as productivity is increased. This result is due to the sigmoidal functional response in the current model. If one uses a simple saturating functional response instead (Holling type-II) the plant nullcline does not bend upward at the left-hand side, and the herbivore-dominated state (E_H) becomes the unstable focus of a cyclic attractor whenever the plant nullcline has a positive slope at E_H . The resulting cycles provide an escape route from the herbivore-dominated state (Van de Koppel and others 1996).

In summary, the model demonstrates that gradual enrichment alone may be insufficient to allow plants to escape from herbivore control, provided

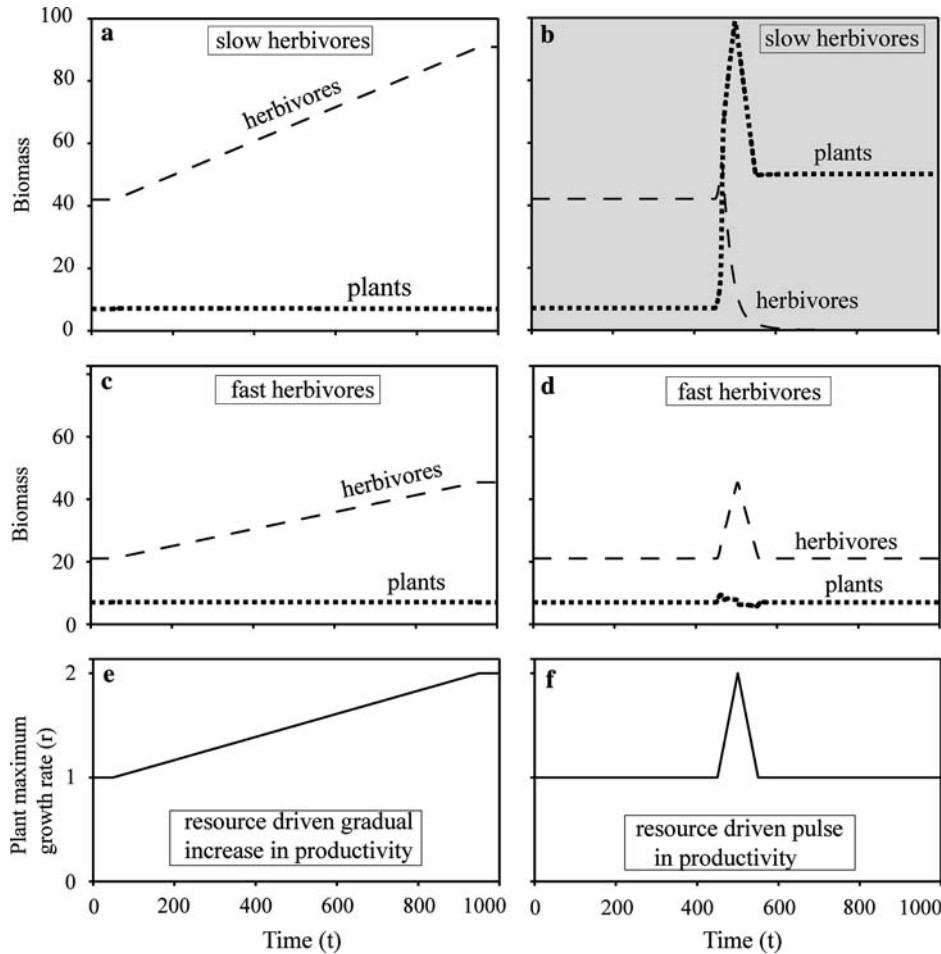


Figure 5. Simulated effects of a resource-driven doubling in productivity (r) on herbivore plant dynamics. If the productivity increase is gradual (*left-hand panels*) plant biomass remains top-down controlled and only herbivore biomass increases. If the productivity doubling takes the form of a rapid pulse (*right-hand panels*) the effect depends on the potential growth rates of the herbivores (scaled by r_H). If herbivore growth is slow (*panel B*; $r_H = 0.5$) plants may escape top-down control and settle to the alternative stable state of high biomass where herbivory is inefficient. By contrast, if the herbivore population can increase sufficiently fast (*panel D*; $r_H = 1.0$) the initial increase in plant biomass is rapidly suppressed by herbivores that show a burst in abundance in response to the environmentally driven productivity pulse.

that herbivore density is food regulated and no internal cycles occur with enrichment.

Effects of Resource Pulses

In the previous section we have assumed that with gradual enrichment, the system will track the changes in equilibrium resulting from an increase in plant growth rate (r). Indeed, numerical experiments show that a gradual increase in r from below T_2 lets the system track the herbivore-dominated equilibrium (Figure 5 left-hand panels). However, if environmental conditions change rapidly enough, the system will no longer track the change in equilibria. To explore the potential effects of gradual change versus a brief episode of enhanced growing conditions (such as a rare rainy episode in an otherwise dry region or a nutrient pulse from a cyclone), we exposed the model to a brief pulse in the value of the parameter r , the maximum plant growth rate (Figure 5 right-hand panels). The effect of such a simulated resource pulse depends on the potential rates of increase of plants and herbivores.

Obviously, nothing will happen if maximum plant growth is too slow relative to the length of the resource pulse (for example, 1 day of wet conditions for a slow-growing plant). More interestingly, if the resource pulse is long enough in principle to allow plants to grow to a high biomass, things become critically dependent on the potential rate of increase of the herbivores.

If the response of herbivores is fast, plant biomass increases upon the resource pulse, but herbivore biomass increases soon after (Figure 5D). As a result of this slightly delayed top-down control plant biomass drops again. There is a small overshoot effect causing plant biomass to drop briefly below the normal herbivore-controlled equilibrium values. By contrast, if herbivores are sufficiently slow, the same pulse may allow plants to escape herbivore control 'far enough' to generate the plant-dominated state (Figure 5B). The reduced foraging efficiency then prohibits herbivores from restoring the herbivore-dominated equilibrium (even after the resource pulse is over and the plant growth rates return to normal). Note that in all cases we

simulated a doubling in plant maximum growth rate. It is perhaps surprising that a slow doubling in growth rate (left hand panels) does not allow plants to shift to the high biomass equilibrium, whereas a fast but transient doubling in growth can allow a permanent shift to a high biomass state.

To explore the critical role of the rates of change further, we systematically analyzed the conditions for escape from top-down control through an increase in productivity (compare left-hand panels in Figure 5). It appears that much depends on the potential rate of increase of herbivores (scaled by R_H) relative to the environmentally driven rate of increase in plant productivity (Figure 6A). Put simply, if the rate of change in plant productivity doubles, then herbivory also needs to be twice as fast to maintain top-down control. An important factor is the critical plant biomass needed to escape (which will depend among other things on the kind of herbivore). The critical biomass at which plants become sufficiently unpalatable for herbivore populations to start declining (P_2 in Figure 2) can be tuned in the model by means of the parameter b . Not surprisingly, escape from top-down control becomes increasingly more difficult if this critical biomass is high. A more rapid jump in plant productivity can help reach a higher critical biomass in time to escape top-down control, but only up to a certain level (Figure 6B).

In summary, the model predicts that a resource pulse may induce an escape from a herbivore-controlled state even if a gradual increase in resources to the same level does not have this effect. Whether such an escape takes place or not depends on whether the boost in plant growth is fast enough relative to the response of the herbivores to reach the safe critical biomass. It follows that escape will be particularly difficult from herbivores that can either increase rapidly in numbers or consume plants back from a relatively high biomass.

Other Mechanisms for Shifting

Another, less surprising way to escape from herbivore control is through an episode of herbivore mortality or recruitment failure due to a disease outbreak or similar adverse conditions. We showed in the section on basic model behavior how the herbivore loss rate affects the equilibria of the system. To explore non-equilibrium dynamics we simulated brief pulses of higher herbivore loss rate (results not shown). Indeed, it proved easy to invoke an irreversible shift to the plant-dominated state by such an event, as noted in practice for instance in the coral and woodland cases. However,

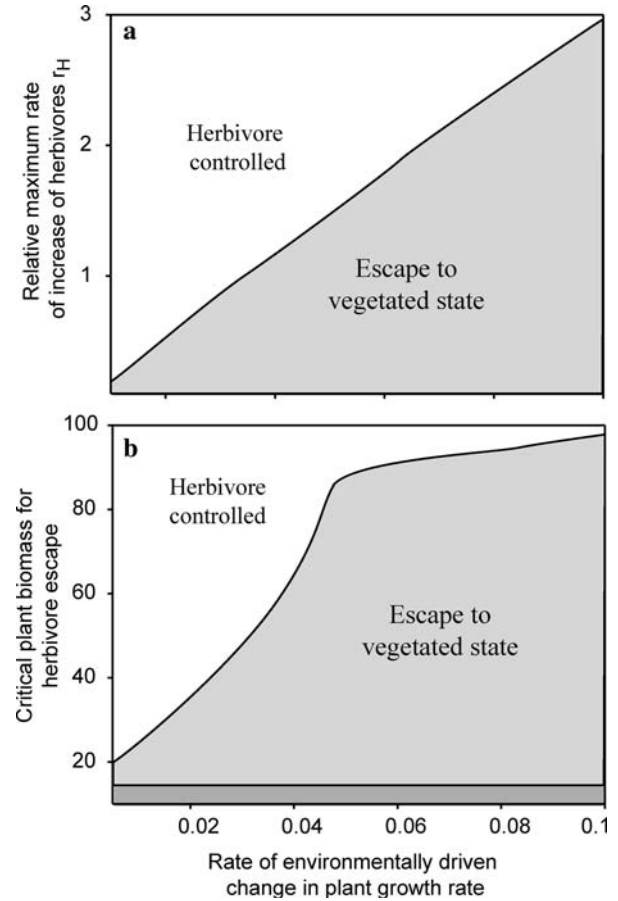


Figure 6. Conditions for which a two-fold rise in plant productivity (r) leads to an escape of plants from top-down control (see text). To find the critical conditions we simulated an increase of r from 1 to 2 as illustrated in the right-hand panels of Figure 5. The rate (t^{-1}) at which we let r increase over the simulations is given on the horizontal axis. The critical growth rate of the herbivores (scaled by r_H) needed to prevent plant escape increases linearly with the rate of simulated environmentally driven increase in plant growth rate (panel A). Another key factor (panel B) is the critical plant biomass for herbivore escape (defined as the critical plant biomass for herbivores to grow, P_2 in Figure 2). This critical plant biomass is not a parameter in the model, but was varied by adjusting the parameters that regulate the decline in plant vulnerability and palatability with biomass (b_c and b , maintaining $b_c = b$) solving the resulting critical plant biomass by

iterating
$$P = \frac{\ln\left(\frac{E_{\max}}{m} \frac{p^2}{p^2 + q^2}\right)}{b + b_c}$$
. Below a critical plant biomass of 16 the herbivore-dominated state becomes unstable (dark gray area). If the critical plant biomass exceeds 100 the plant-dominated state is never stable.

the effect of herbivore loss differs from that of an increase in plant productivity when it comes to the critical role of rates. In all our simulations the occurrence of a shift required that during the pulse

the bifurcation point (where the herbivore-dominated state ceases to exist) was exceeded for some time. This implies that rapidity of the rise in herbivore mortality does not promote the probability of an escape from herbivore control as a slow increase to the same maximum level of herbivore loss would also invoke a shift.

Finally, mass mortality of plants (for example, due to a forest fire, storm, or disease) may obviously take the system out of the plant-dominated state and allow it to become trapped once again in the herbivore-controlled state. In the model, this regime shift happens if plant biomass is reduced for a sufficiently long time below the critical level at which foraging efficiency of herbivores prevents a net growth of their population (not shown).

Robustness to Model Assumptions

As argued earlier, a decrease in foraging efficiency at a high plant standing crop appears to be a widely observed phenomenon in terrestrial and aquatic ecosystems. Although our model formulation is only one particular way of representing this, we explored some alternative models and found the same qualitative results. For instance, the same behavior can be maintained using the more classical formulation of logistic growth, with a carrying capacity (K) instead of a competition coefficient (C). Also, the same behavioral repertoire is produced by the model if the negative effect of plant biomass depresses only the grazing rate or only the herbivore assimilation efficiency. The implication of choosing a different herbivore functional response for stability of the herbivore-dominated state was discussed in the section on enrichment effects. Also, the prediction that gradual enrichment by itself will not cause an escape from herbivore control depends on the assumption that herbivore density is regulated by productivity of the system rather than by other factors (such as density-dependent predation, interference competition, or other density-dependent factors). We note that several mechanisms that reduce foraging efficiencies at a high standing crop depend on individual plant size rather than total biomass. More elaborate models that capture this and other aspects such as spatial dynamics would be worthwhile exploring for specific examples of herbivore-plant systems.

CONCLUSION

Although plant biomass often rises as productivity increases, our model analysis underlines the well-

known finding that this is not necessarily so. In line with classic theoretical results (Hairston and others 1960), our model predicts that herbivores may control plants up till arbitrarily large productivity. In this scenario, herbivores keep increasing with increased productivity, maintaining plant biomass constantly at a level where herbivore net population increase is zero. Although this may appear unrealistic, some of the case studies we reviewed do support this scenario. For instance, macro-algal biomass on heavily grazed coral reefs tends to remain low even if nutrient loading increases substantially. Also, grazers may prevent forest development over a wide range of productivity levels. In line with the model predictions, such ecosystems seem to need a pulse in resource (Holmgren and others 2006) and/or herbivore mortality (Hughes 1994) to escape from the grazer-controlled state.

A main prediction from the model is that the productivity pulses may invoke a shift away from top-down control only if the response of herbivores is sufficiently slow, and if a safe size can be reached easily. Indeed, one may wonder whether the remarkably devastating effect of rabbits around the world is in part related to their capacity to reproduce rapidly in response to enhanced resource availability, whereas they are also able to damage trees to a relatively large size (by removing the bark of saplings). Clearly, the mechanism of herbivore escape we studied can be thought of as related to masting as a strategy of trees to swamp seed predators. Because fruit production is low in normal years, populations of rodents and other seed predators remain sparse enough to be swamped in an erratically occurring masting year when trees synchronize massive fruit production over large areas (Herrera and others 1998).

Taking an even wider perspective, it is interesting to note that the qualitatively different effect of pulses compared to average conditions that we describe here is not limited to ecosystems. For example, models of the thermohaline circulation of the North Atlantic suggest that it might shift to an alternative 'switched off' state causing a sharp and substantial drop of temperature in parts of Europe, Canada, and the US. Freshwater input into the North Atlantic is one of the major factors determining the resilience of the alternative states of the circulation systems. Most models indicate that expected overall increases in freshwater input with climatic change would not push the circulation across the tipping point (Rahmstorf 2000). However, the models also indicate that the circulation is much more sensitive to a sudden pulse than to a

gradual increase in freshwater input. Indeed, the most recent occasion at which the circulation appears to have slowed (the Younger Dryas event) seems to have been triggered by a sudden flush of freshwater from a huge meltwater lake upon breaking of an ice dam (Clark and others 2002).

The emerging scenario is that sometimes a pulse may cause a shift to an alternative state, which is not brought about as easily by equally strong but more gradual changes in conditions. Basically, this happens when processes that may counteract the effect of the pulse respond too slowly to keep the system in check. Even if the new state of the system is not stable in the long run, the return to the unperturbed state can still take a very long time, implying that even infrequent perturbations can cause the system to remain in the alternative transient state. For instance, the algal-dominated state of the Caribbean reefs following the sea urchin die-off, and African forest expansions after herbivore epidemics may be long transients that have set the state of the systems for decades or longer.

In conclusion, our analysis shows that episodes of rapid change can have fundamentally different effects than gradual (but equally large) change of conditions. This has profound implications for the way we may predict effects of climate change on ecosystems. It is thought that climate variability might increase markedly over the coming century. Our analysis suggests that such variability per se may have a strong and sometimes quite predictable effect. For instance, it might enhance the probability of forest expansion in situations where herbivores are much slower than plants to respond to productivity pulses.

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REFERENCES

Austin MP, Williams OB. 1988. Influence of climate and community composition on the population demography of pasture species in Semi-Arid Australia. *Vegetatio* 77:43–9.

Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. *Nature* 429:827–33.

Bravo-Ferro MA, Rodríguez-Sánchez M. 2003. Detección de cambios en los bosques secos del norte del Perú: un análisis temporal entre los años 1991 y 2000 en “Malinguitas”. *Zonas Áridas* 7:206–7.

Chase JM. 1999. Food web effects of prey size refugia: variable interactions and alternative stable equilibria. *Am Nat* 154:559–70.

Clark PU, Pisias NG, Stocker TF, Weaver AJ. 2002. The role of the thermohaline circulation in abrupt climate change. *Nature* 415:863–9.

Dobson A, Crawley W. 1994. Pathogens and the structure of plant-communities. *Trends Ecol Evol* 9:393–8.

Dublin HT, Sinclair AR, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara Tanzania woodlands. *J Anim Ecol* 59:1147–64.

Fryxell JM. 1991. Forage quality and aggregation by large herbivores. *Am Nat* 138:478–98.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–60.

Gliwicz ZM. 1990. Why do cladocerans fail to control algal blooms?. *Hydrobiologia* 200/201:83–98.

Gagnani A, Scheffer M, Rinaldi S. 1999. Top-down control of cyanobacteria: a theoretical analysis. *Am Nat* 153:59–72.

Hairston N, Smith FE, Slobodkin D. 1960. Community structure, population control, and competition. *Am Nat* 94:421–5.

Herrera CM, Jordano P, Guitián J, Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am Nat* 152:576–94.

Holmgren M, Lopez BC, Gutierrez JR, Squeo FA. 2006. Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biol* 12:2263–71.

Holmgren M, Scheffer M. 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems* 4:151–9.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–51.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–33.

Konar B, Estes JA. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84:174–85.

Loughry WJ. 1993. Determinants of time allocation by adult and yearling black-tailed prairie dogs. *Behaviour* 124:23–43.

Ludlow MM, Stobbs TH, Davis R, Charlesedwards DA. 1982. Effect of sward structure of two tropical grasses with contrasting canopies on light-distribution, net photosynthesis and size of bite harvested by grazing cattle. *Aust J Agric Res* 33:187–201.

Ludwig D, Jones DD, Holling CS. 1978. Qualitative analysis of insect outbreak systems the spruce budworm and forest. *J Anim Ecol* 47:315–32.

McNaughton SJ. 1984. Grazing lawns animals in herds plant form and coevolution. *Am Nat* 124:863–86.

Noy-Meir I. 1978. Stability in simple grazing models effects of explicit functions. *J Theor Biol* 71:347–80.

Oksanen L, Fretwell SD, Arruda J, Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–61.

Parsons AJ, Leafe EL, Collett B, Stiles W. 1983. The physiology of grass production under grazing .1. Characteristics of leaf and

- canopy photosynthesis of continuously-grazed swards. *J Appl Ecol* 20:117–26.
- Rahmstorf S. 2000. The thermohaline ocean circulation: a system with dangerous thresholds? An editorial comment. *Climatic Change* 46:247–56.
- Rosenzweig ML. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171:385–7.
- Sammarco PW. 1980. Diadema and its relationship to coral spat mortality—Grazing, competition, and biological disturbance. *J Exp Mar Biol Ecol* 45:245–72.
- Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–6.
- Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8:275–9.
- Scheffer M, Rinaldi S, Gagnani A, Mur LR, Van Nes EH. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* 78:272–82.
- Scheffer M, Szabo S, Gagnani A, van Nes EH, Rinaldi S, Kautsky N, Norberg J, Roijackers RMM, Franken RJM. 2003. Floating plant dominance as a stable state. *Proc Nat Acad Sci USA* 100:4040–5.
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–59.
- Underwood R. 1982. Vigilance behavior in grazing African antelopes. *Behaviour* 79:81–107.
- Van de Koppel J, Huisman J, Van der Wal R, Olf H. 1996. Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77:736–45.
- Van de Koppel J, Rietkerk M, Weissing FJ. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol Evol* 12:352–6.
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM. 1981. Hurricane allens impact on Jamaican coral reefs. *Science* 214:749–55.