

## The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis

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**ABSTRACT.** Current hypotheses to explain dynamic transitions between savanna grasslands and woodlands in Africa focus on grazing by elephant or the influence of fire. Using a simple mathematical model, this paper argues that interactions between small herbivores such as impala or buffalo and large herbivores such as elephant or giraffe may provide a plausible alternative hypothesis. The interplay of competition and facilitation between these types of herbivores could explain transitions between grassland and woodland and vice versa. A review of the literature is presented in support of this hypothesis.

**KEY WORDS:** competition, facilitation, functional response, herbivory, plant-herbivore model, savanna ecosystems

### INTRODUCTION

African savannas have proven to be highly dynamic ecosystems, alternating between woodland and grassland states (e.g., Sinclair & Arcese 1995). In order to explain the apparent instability within savanna ecosystems, much emphasis has traditionally been placed on the role of elephant (*Loxodonta a. africana* (Blumenbach)) (Laws 1970, Myers 1973, Pellew 1983). Destructive behaviour by elephants increases tree mortality and may result in conversion of woodland to grassland. Caughley (1976) hypothesized a cyclic interaction between elephants and trees. Elephant populations increase under woodland conditions, leading to overexploitation of woodland and conversion of the vegetation to

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grassland. Elephants decrease in density under grassland conditions, allegedly due to lack of suitable food resources (Caughley 1976, Laws 1970). Low elephant browsing pressure in turn allows resurgence of woodland, completing the cycle. Dublin *et al.* (1990) hypothesized that fire rather than elephants acts as the prime agent of woodland turnover. They argued that two stable states occur in savannas, one characterized by woodland and one characterized by grassland. Intense fires may shift the vegetation from the woodland to the grassland state. Once grassland is formed, however, elephants are able to maintain the situation. According to this hypothesis, both elephant and fire are necessary for a permanent shift from one state to another.

Prins & Van der Jeugd (1993) suggested that grassland-woodland transitions are not solely determined by elephants or fire. Dramatic reduction of impala numbers (*Aepyceros melampus* (Lichtenstein)) following outbreaks of rinderpest and anthrax enhanced seedling recruitment of *Acacia tortilis* (Forsk.), evidenced by even-aged stands of *Acacia*. These authors suggested that when browsing pressure by impala is high, *Acacia* seedling establishment is rare. The impact of impala and other medium-sized herbivores is reduced with tree maturation as most foliage of a mature tree grows beyond reach of these herbivores. Although the impact of elephant on stands of mature trees is beyond question (Buss 1990), the influence of elephant on the stability of grassland may be much more limited. Smaller herbivores seem to play a greater role (Belsky 1984), as epidemic disturbances among ungulates create narrow windows for seedling establishment (Prins & Van der Jeugd 1993).

None of the papers devoted to explaining the dynamics of African savanna woodlands considers the consequences of interactions between herbivores. This paper presents a first step in this direction. Using an illustrative model, we show that transitions between grassland and woodland may result from the interplay of facilitation and competition between herbivores. We argue that interactions between herbivores are a plausible alternative explanation to current hypotheses about the dynamics of African savanna woodlands. A review of evidence is presented in support of this hypothesis.

#### A SIMPLE PLANT-HERBIVORE MODEL

In the following section, we analyze a simple model of a system consisting of two herbivores (i.e. two species of herbivore) and a single vegetation compartment. The model is used as an illustrative tool that provides insight into our arguments. Many different, and maybe even better models can be made to describe the dynamics of savanna woodlands. However, we choose to use a very simple model in order to keep the investigation as clear as possible.

Consider an assemblage of two herbivores, a small herbivore not capable of handling mature trees and a large herbivore capable of removing trees from the vegetation. Note that 'small' and 'large' are merely used here as comparative labels. The large herbivore could be a megaherbivore like elephant or giraffe (*Giraffa camelopardalis* L.), whereas the small herbivore could be impala,

wildebeest (*Connochaetes taurinus* (Burchell)), or even buffalo (*Syncerus caffer* (Sparrman)). The vegetation, consisting of both trees and grass, is considered as one compartment. In this analysis we assume that grasses dominate when the vegetation is at a low- to intermediate-biomass state, whereas trees dominate whenever the vegetation is at a high-biomass state. This is a reasonable assumption at least for areas with an annual precipitation above 750 mm (Keay 1959, White 1983). Consequently, herbivore feeding rate changes with plant standing crop. At low plant standing crop (typically a low density of grasses), the feeding rate by herbivores is low due to the small bite size. At intermediate plant standing crop, feeding rate is maximal. At high plant standing crop, when trees are abundant, the herbivore feeding rate is low again, because much of the forage is out of reach. The extent to which herbivore feeding is reduced at low or high plant standing crop is species-specific.

Let  $V$  be vegetation biomass,  $H_1$  the density of large herbivores, and  $H_2$  the density of small herbivores. In general, the dynamics of the system can be described mathematically by the following differential equations:

$$\frac{dV}{dt} = f(V) - \sum c_i(V)H_i, \quad (1a)$$

$$\frac{dH_i}{dt} = g_i(V)H_i, \quad (1b)$$

where  $i$  is 1 or 2 for the large or small herbivore respectively,  $f(V)$  describes vegetation growth as a function of its density,  $c_i(V)$  describes the consumption rate of herbivore  $i$  as a function of vegetation density, and  $g_i(V)$  describes the per capita net population growth of herbivore  $i$  as a function of vegetation density. In our model, vegetation growth  $f(V)$  is modelled by the logistic equation:  $f(V) = rV(1 - V/K)$  where  $r$  is the intrinsic rate of plant growth and  $K$  is the maximum standing crop of vegetation in the absence of herbivores. Both herbivore feeding rate and herbivore population growth have a maximum at intermediate plant standing crop.

The two herbivore species differ from each other in one critical aspect. The large-herbivore population has a positive growth rate as long as plant standing crop exceeds a minimal value  $V_1^*$ . Its growth rate may decrease at high plant standing crop due to foraging limitations imposed by plant height. It remains positive, nevertheless, even if the vegetation reaches  $K$  (Figure 1). Foraging limitations imposed upon the small herbivore at high plant standing crop are more severe. The small-herbivore population is unable to grow when the vegetation is at maximum standing crop. In this case, herbivore population growth is zero at two levels of plant standing crop, denoted  $V_2^*$  and  $V_T$  (Figure 1). Herbivore population growth is positive when  $V_2^* < V < V_T$  whereas it is negative if  $V < V_2^*$  or  $V > V_T$ . One might say that below  $V_2^*$ , the scarcity of forage limits the small-herbivore population, whereas above  $V_T$  access to forage

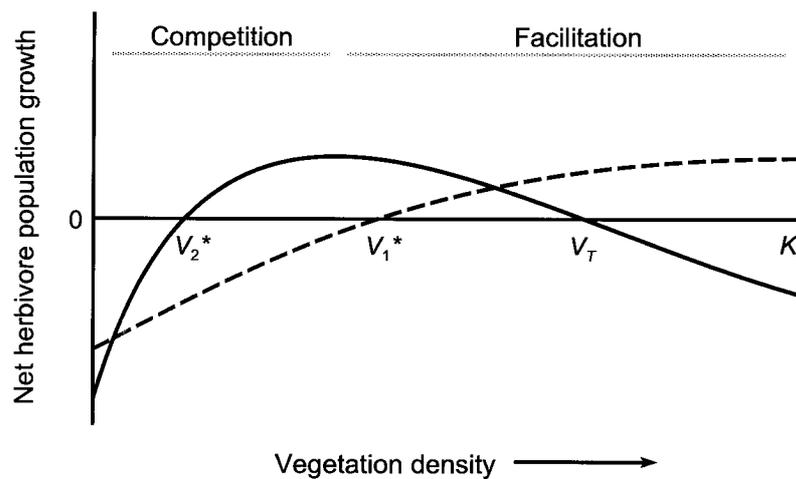


Figure 1. Per capita net growth rate of the small-herbivore population (solid line) and the large-herbivore population (dashed line) as a function of vegetation density. The growth rate of the large herbivore is zero at  $V_1^*$ , the growth rate of the small herbivore is zero at  $V_2^*$  and  $V_T$ .

limits the small-herbivore population, even though plant tissue is superabundant.

A system with only the large herbivore has one internal equilibrium at  $V = V_1^*$ , provided that plant productivity is sufficiently large to support the herbivore population. The stability of this equilibrium depends on the efficiency of exploitation by the herbivore. When exploitation is severe, the herbivore may overutilize the vegetation, leading to collapse of the herbivore population and cyclic behaviour (Caughley 1976, DeAngelis 1992, Rosenzweig 1971).

A system with only the small herbivore has been studied in detail by Van de Koppel *et al.* (1996). Their analysis shows that two internal equilibria may exist in this system, depending on the magnitude of primary production. In systems of low primary productivity, a single stable plant-herbivore equilibrium occurs, whenever primary productivity is sufficient to support a herbivore population. In systems of intermediate primary productivity, two stable equilibria exist: one with both vegetation and herbivores, and another with only vegetation at maximum standing crop  $K$ . In systems of high primary productivity, the herbivore is unable to keep plant growth in check, and a dense vegetation without herbivores is the only stable state.

In a system that contains two populations of herbivores, both will affect each others food availability by reducing plant standing crop. A large body of literature exists that deals with two consumers competing for one resource (Armstrong & McGehee 1980, DeAngelis 1992, Tilman 1982). In these studies, consumption reduces plant standing crop and thereby the growth rate of the consumers. In the present model, herbivore growth may be enhanced by consumption at high plant standing crop, because low quality vegetation is removed (Figure 1). Hence, a herbivore may facilitate the growth of another

herbivore by removing plant standing crop. Whereas facilitation may occur at intermediate to high plant standing crop, competition prevails at low plant standing crop. A reduction of plant density at low standing crop due to foraging reduces the growth rate of both herbivore populations. If both populations are regulated by a single plant resource, as is the case in the model above, this may lead to competitive exclusion (Armstrong & McGehee 1980).

When the vegetation is at high biomass (if  $V > V_T$ ), only the large herbivore population is able to grow. Consequently, the population density of the large-herbivore increases, whereas the population density of the small herbivore decreases. Grazing pressure is increased, however, as the large-herbivore population becomes dense, and as a result, plant standing crop decreases. This, in turn, increases the growth rate of the small herbivore. Competition becomes more important as soon as the vegetation reaches the low-biomass grassland state, and competitive exclusion may occur.

Simulations show that whenever the large herbivore is the superior competitor (if  $V_1^* < V_2^*$ ), it obviously will exclude the small herbivore (Figure 2a, c, e). In such a system a single equilibrium occurs. An efficient large herbivore, however, may cause the system to oscillate as was found in the models of Rosenzweig (1971) and Caughley (1976). McGehee & Armstrong (1977) showed analytically that two species with non-decreasing numerical responses may coexist on one biotic resource during cyclic interactions. These cycles result from overutilization of the resource by the superior competitor, allowing the other species to maintain a positive population density.

Whenever the small herbivore is the superior competitor (if  $V_1^* > V_2^*$ ), it will exclude the large herbivore at low plant standing crop (Figure 2b, d, f). As the population of the large herbivore decreases, the system changes to a system with two attractors: a plant-herbivore equilibrium at  $V = V_2^*$ , and an equilibrium without herbivores at maximum standing crop (Van de Koppel *et al.* 1996). If the plant-herbivore equilibrium is unstable, limit cycles of small amplitude may occur, but more likely the system will shift to the dense-vegetation state. While the small herbivore cannot sustain its population, the large-herbivore population becomes viable in dense-vegetation conditions. In the simulation presented in Figure 2d, f, the large-herbivore population has not disappeared entirely when the vegetation shifts to the high biomass state, and consequently the large-herbivore population recovers. This, in turn, leads to oscillations between a high biomass woodland and a low biomass grassland. Contrary to the former scenario, the cycles do not result from the interaction of the superior herbivore and the vegetation. Rather, they result from the interplay of facilitation and competition between large and small herbivores. These interactions keep the system in a continuous state of disequilibrium. Contrary to the models analyzed by Armstrong & McGehee (1980), the system described in Figures 2d and f does not exhibit cycles if it only contains one of either species. The system remains at the herbivore-dominated state if the

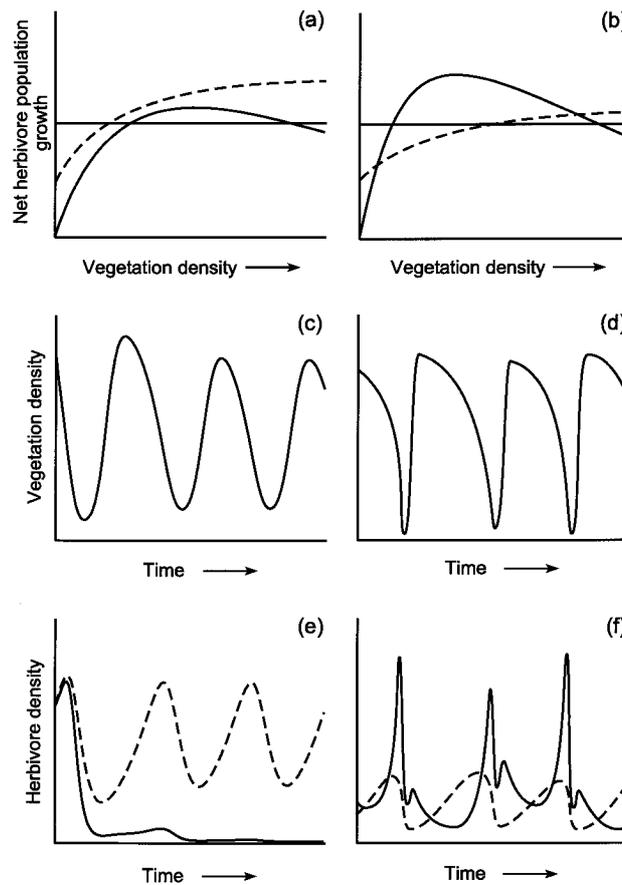


Figure 2. Simulation of a scenario where the large herbivore is the superior competitor (a, c, e), and a scenario where the small herbivore is the superior competitor (b, d, f). (a,b): Per capita growth rate of the small herbivore population (solid line) and the large herbivore population (dashed line). The dynamics of the vegetation (c, d) and of both populations of herbivores (e, f) with time are shown for each scenario, respectively. In (e) and (f) the solid lines again depict the change in the small herbivore, and dashed lines that of the large herbivore. The consumption and growth functions follow the reduced consumption model used by Van de Koppel *et al.* 1996. (Parameters:  $r=0.25$ ,  $K=30$ ,  $e_{max,1}=0.6$ ,  $e_{max,2}=1.5$ ,  $d_1=0.1$ ,  $d_2=0.05$ ; Scenario 1:  $a_1=33$ ,  $a_2=8$ ,  $b_1=0.037$ ,  $b_2=0.005$ ,  $e_{max,1}=0.6$ ,  $e_{max,2}=0.095$ , Scenario 2:  $a_1=10$ ,  $a_2=13$ ,  $b_1=0.045$ ,  $b_2=0.005$ ,  $e_{max,1}=0.41$ ,  $e_{max,2}=0.1$ ).

small herbivore does not overutilize the vegetation. This equilibrium, however, is not globally stable (Van de Koppel *et al.* 1996). Disturbances such as disease outbreaks among herbivores (Prins & Van der Jeugd 1993) or temporarily increased rainfall (Dunham 1994) could trigger transitions between low-biomass grassland and high-biomass woodland.

The scenario in which the small herbivore is the superior competitor at low plant standing crop seems to be most plausible on allometric grounds. A relatively small herbivore species is likely to have a higher foraging efficiency at low plant standing crop relative to that of a larger herbivore, due to for

instance their smaller mouths (Illius & Gordon 1987, Prins & Olf 1998). Elephant, a hind-gut fermenter, may have a competitive disadvantage relative to ruminant grazers (small herbivores in this context) at low plant standing crop, since ruminants are more specialized to digesting low quantities of relatively high quality food (Duncan *et al.* 1990, Janis 1976). Giraffe has an obvious disadvantage compared to smaller herbivores when grazing in grasslands, due to their specialized morphology.

#### EVIDENCE FROM SAVANNA ECOSYSTEMS

The model analysis presented above provides some clear predictions with respect to interactions between large and small herbivores. The model predicts that facilitation dominates herbivore interactions at high plant standing crop, whereas competition prevails at low plant standing crop. Although direct evidence is lacking, several authors have suggested that elephant and to a minor extent giraffe may facilitate small herbivores by opening up dense thickets (Dublin 1995, Jachman & Croes 1991, Pellew 1983, Prins 1996, Prins & Olf 1998). Enhanced light availability within gaps created by elephants promotes grass production (Norton-Griffiths 1979). Browsing by giraffe restricts lateral canopy growth (Pellew 1983). This should encourage other herbivores, for instance buffalo, to penetrate. A number of studies have suggested that facilitation may occur between migratory herbivores in savanna systems (Bell 1971, McNaughton 1976, Vesey-FitzGerald 1960), although on a smaller timescale. Grazing of coarse grasses by zebra (*Equus burchelli* Gray) and wildebeest stimulates the growth of new, high quality grasses and dicotyledonous material. This, in turn, may promote grazing by Thomson's gazelle (*Gazella thomsonii* Gunther). To what extent the foraging of small herbivores is limited in dense vegetation, and whether browsing of larger herbivores facilitates smaller herbivores in more productive woodland savanna, still needs further investigation.

In previous models, the population density of large herbivores decreased because of overexploitation of their resources. Hence, elephants decrease in density because the grassland that remains after the removal of the woodland is unsuitable for them (Caughley 1976, Laws 1970). The analysis presented above shows that an alternative explanation exists. The large herbivore, elephant or giraffe, may decrease in density because of competitive exclusion by smaller herbivores (see Figure 2b, d, f). There is evidence for competition between elephant and buffalo. De Boer & Prins (1990) report on a clear negative influence of the grazing of buffalo on that of elephant. On a time scale of several days, high grazing pressure by elephants in a specific patch on a given day takes place only in the absence of high grazing pressure by buffalo on preceding days, suggesting that elephants react to the grazing by buffalo. There is also evidence at the population level of competition between elephants and other herbivores: there were strong negative correlations between grass

consumption by elephants and that by all other grazers, and between elephants and buffalo (Prins 1996, Prins & Douglas-Hamilton 1990). With the high density of buffalo in Manyara, buffalo appear to have the selective edge in short-term competition with elephant.

Evidence also exists of competition between elephant and wildebeest. Dublin (1995) states that the general tendency for elephants to overutilize woodlands in the dry season may be a direct consequence of competition with migratory wildebeest. Wildebeest can sometimes remove as much as 90% of the herbaceous standing crop during its transient occupancy (McNaughton 1985, Onye-anusi 1989, Sinclair 1975). Immediately following cessation of the rains and prior to the arrival of the wildebeest, elephants show an obvious preference for grasses (Beekman & Prins 1989, Dublin 1995). However, upon the arrival of the wildebeest, a distinct change in diet occurs. Elephants immediately decrease feeding on grasses and, in the later stages of wildebeest occupancy, stop feeding on grasses altogether, despite the production of new grass following intermittent local thunderstorms (Dublin 1995). Wildebeest graze the grasses down to lawn height (McNaughton 1984), a height at which grasses may become difficult for elephants to eat, even though they can use their feet to kick up small plants (Beekman & Prins 1989).

The question whether lack of high quality food or competition causes the decrease in elephant density in grasslands has not yet been answered. Elephants are generally thought to be unable to meet their protein requirements on a diet consisting of only grasses, especially during the dry season, when the protein levels of grasses are minimal (Dublin 1995, Laws 1970, Pellew 1983, Prins 1996). Hindgut fermenters, such as the elephant, are generally thought to increase their daily food intake by increasing grazing time, in order to compensate for decreasing food quality (Janis 1976). Beekman & Prins (1989) found that elephant, instead of increasing their food intake, switch from feeding on grasses to feeding on browse and *Acacia* seedpods. Apparently, the low intake of the small seedpods is a better option than to increase grazing time on the short grasses. Since other herbivores determine to a large extent the availability of grasses, they are likely to influence the decision of elephants to feed on browse. More research is needed to determine whether competition or decreasing food quality, or a combination of both, forces elephants to focus on browse during the dry season.

#### DISCUSSION

Caughley (1976) hypothesized that the African savanna is subject to cyclic transitions between a low-biomass grassland state and a high-biomass woodland state, as a result of direct elephant-plant interactions. The model analyzed in this paper reveals that an alternative explanation is possible. Elephants may suffer from competition for grasses with herbivores like buffalo or impala, which are superior competitors. This results in elephants overexploiting woody

species, conversion of woodland to grassland, and competitive dominance by grazers. Lack of alternative food resources when the vegetation is at the grassland state will result in starvation or migration of elephant.

The long-dominant view on East African savannas can be described as a multiple stable state (or multiple climax) model (Belsky 1995). Dublin *et al.* (1990) proposed a multiple stable states model where fire caused the transitions between the states, whereas elephant browsing maintained the grassland state. Such a state, however, only persists in the long run if elephants are capable of maintaining high population densities, despite competition with other herbivores. The data available on interactions between elephant and other grazers suggest that elephant do suffer from competition with other herbivores (Dublin 1995, Prins 1996). Several studies stress the importance of other herbivores in maintaining the stability of grasslands (Belsky 1984, Prins & Van der Jeugd 1993). Belsky (1984) found that small browsers like Grant's gazelle (*Gazella granti* Brooke), Thomson's gazelle, Kirk's dikdik (*Rhynchotragus kirki* (Gunther)) and impala, instead of fire or elephants, were responsible for retarding woodland regeneration.

It would be unrealistic to claim that the dynamics of woodlands can be fully described by any model that considers only a single aspect or interaction. The influence of fire, a major factor determining the behaviour of the savanna woodlands of Serengeti-Mara (Dublin 1995, Dublin *et al.* 1990), is not considered in the model. In many aspects, fire can be regarded as a 'super-herbivore'. Fire facilitates the grazing of 'other' herbivores, in grasslands by releasing nutrients that were locked in dead or living plant standing crop, and in woodlands by opening up thickets. The interactions between fire and herbivores, however, are much more complex. While the damage that elephants impose upon trees is most severe when grasses are severely depleted (e.g., at high herbivore densities), damage by fire is most extensive when grasses are abundant and provide a large fuel supply during the dry season (Norton-Griffiths 1979). It is not unlikely that both fire and elephants are essential in explaining woodland-grassland transitions in the past years.

Migration of herbivores and spatial heterogeneity of the vegetation, which are obviously present in savannas, might prevent herbivore populations from collapsing. Moreover, spatial separation or restrictions in habitat use of herbivores may prevent competitive exclusion, at least on a small timescale. Predictive model studies may benefit from incorporating spatial heterogeneity in the vegetation and in herbivore grazing (Wu & Locks 1995). Human exploitation, however, which is becoming increasingly severe in most savannas, would limit the predictive value of models that do not incorporate factors such as human-induced fires, poaching and grazing by domestic livestock. Such detail is beyond the scope of this paper.

In more arid savanna regions, competition between woody species and grasses is to a large extent determined by the availability of water (Walker *et*

*al.* 1981). Therefore, our model is only valid for systems that would develop into woodland in the absence of herbivores, fire or other factors. Such systems are most likely to be found in areas with a high annual precipitation, although some semi-arid regions may also be included. A likely candidate for such a system may be the Lopé savanna in central Gabon, where for thousands of years a savanna was maintained by fire and herbivores in a high rainfall area (*c.* 1500 mm y<sup>-1</sup>). This savanna is surrounded by rainforest (Tutin & White 1998).

Although the predictive power of the model for savanna ecosystems presented here obviously has its limits, application of the insights obtained from it may extend beyond these ecosystems. Olf *et al.* (1997) reported that cattle introduced on a highly productive salt marsh along the Dutch Wadden Sea coast facilitated grazing by barnacle and brent geese. Geese are normally restricted to the low-productive areas, because they are unable to handle the low quality grass *Elymus athericus* that dominates the vegetation on the productive parts of the salt marsh. After cattle had removed the dense stands of *Elymus*, more palatable grass species began to dominate the vegetation, leading to the reappearance of geese.

Our study indicates that large herbivores may play an essential role in maintaining natural grazing systems (see also Owen-Smith 1989), because their physiology allows them to deal with forage which is unpalatable or out of reach for many small herbivores. By removing dense vegetation of low quality, large herbivores can facilitate growth of small herbivores, and allow them to gain control on the vegetation. Although removal of larger herbivores from the ecosystem need not immediately result in collapse, it may change the grazer-dominated community from a globally stable equilibrium to a locally stable one, vulnerable to perturbation. As a consequence, disturbances may result in a permanent shift from a grazer-dominated community to a community dominated by primary producers.

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