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Biodiversity and Savanna Ecosystem Processes

A Global Perspective

With 40 Figures

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12 Savanna Biodiversity and Ecosystem Properties

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12.1 Introduction

The overall question addressed here is the effect of different degrees of biodiversity on the function of savanna ecosystems. Function can be interpreted in two different ways. It can refer to the flow of energy and nutrients through an ecosystem or to the flow of species populations through time, i.e., the persistence of species populations and their properties, which we call the structure of the system. Here we discuss the effect of biodiversity on ecosystem function in this second sense. The role of biodiversity in the flow of energy and nutrients is addressed in Chapter 10.

When an ecosystem persists in time we say that it is stable. Stability may be the result of an environment that is invariant, or it may be due to the ability of species populations to persist (either by internal genetic adjustments, or by having broad tolerances) even when external conditions change. Stability has three components: resistance, resilience, and persistence. Each of these terms has a different meaning with respect to its interpretation of system dynamics following a perturbation.

Stability can be exhibited by different ecosystem properties. One measure of stability is floristic composition, including not only species combinations, but also diversity, i.e., species richness and evenness (for example as measured by the Shannon index or some other index, see Chap. 6). Demographic behavior, total biomass, cover, and similar system properties can also be used as measures of stability.

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While definitions of stability have previously carried implicit assumptions of an equilibrium or steady state as a reference point, more current definitions of stability recognize that a range or cloud of system states may be used for reference (Nicolis 1991, 1992). This range may contain regular cycles at different temporal scales, threshold responses, and apparently chaotic behaviors with underlying order (e.g., "strange attractors"). When cycling among system states is a characteristic system dynamic, it becomes essential to differentiate measures of short- and long-term stability, because while a short-term measure may indicate instability, a longer-term measure may indicate stability. While savannas may oscillate or fluctuate among a range of states, they still can be stable systems.

Interpretations of system stability responses depend upon the scale and level of organization of the stability measurements, as well as the expected system behavior at that scale or level of organization. Unfortunately, expected behaviors or states often erroneously assume that tree-dominated systems are the norm where mixtures of trees and other life-forms have persisted for millennia. Because interpretations of response measures are relative to some expected system behavior, they may be dependent upon the objectives of a study or upon the human uses of a system. It is important to recognize that the lack of a disturbance may constitute a perturbation if the system is normally subjected to disturbance. Therefore, the reference point or range of expected system dynamics needs to be explicitly stated and justified.

Measures of stability that are based upon floristic composition may provide results different from measures based upon functional group compositions due to functional redundancies among species within the functional groups. When species are more redundant in their functions, then it is less critical to maintain the same species, as long as all functions are preserved. Thus, the level of redundancy within groups must be known to interpret the significance of changes in floristic composition.

There are several important modifiers of disturbance responses. These modifiers must be taken into consideration to interpret responses to disturbances accurately. These are:

1. Time since disturbance.
2. Direct and indirect interactions among species.
3. Abiotic variables like soil depth, soil fertility, rainfall (PAM and PAN).
4. Other disturbances such as fire.

In particular, time-dependent variables like rainfall may confound responses to disturbance. When rainfall has changed over time since a disturbance, the effects of the change in rainfall must be disentangled from the effects of the disturbance in order to interpret the response.

It is important to recognize that the disturbance response depends upon the initial system state. In other words, system dynamics are sensitive to initial conditions. In the terms of sensitivity analysis, local sensitivity is likely to be different from global sensitivity. The shape of the global sensitivity response must be known in order to interpret system responses to disturbance. It is most likely that when there are a high number of species, there will be an increased probability that some of them might be adapted to the disturbance. If the system experiences a wide range of disturbances, then it may be more important that the system harbors even larger species pools. Density-dominance graphs can be used to determine if systems are under stress at the outset of the disturbance.

The history of disturbance has an important impact, through selective forces, upon the presence of species that are adapted to subsequent disturbances of the same kind. Indeed, savannas may be intrinsically stable relative to other systems, but only because they have evolved under disturbances like fire, herbivory and drought. Thus, continued persistence of savannas may necessitate continued disturbance to preserve stabilizing components and properties.

Modifiers of disturbance responses may be hierarchically ordered, with abiotic factors such as soils and climate constraining the effects of biotically mediated disturbances like herbivory or fire (Solbrig 1991). Other constraints on disturbance responses arise from evolutionary and biogeographic processes, inasmuch as these affect the pool of available species and their functional capabilities.

The invasion by alien species, particularly into South American savannas, is of great significance (see Chap. 5), as there are invasive challenges virtually everywhere that humans are present. Importantly, biotic diversity often decreases in systems that have been invaded, thus the implications for global biodiversity are great.

A number of important functional differences were pointed out between African invaders and South American native grasses (see Chap. 5). Thus, there are many possible secondary effects that may arise at the ecosystem level, via effects on herbivory, hydrology, decomposition, and nutrient cycling. Invaders may also initiate new successional processes due to their effects on abiotic and biotic processes. It is important, however, to demonstrate whether invasions are the result of differences in competitive abilities or if they are due to the primary disturbances of soil disruption and clearing of native species. Indeed, most invasions in South America have followed such primary disturbance of the soil and vegetation, and there is evidence that the invaders may not persist unless these anthropogenic disturbances continue. Furthermore, results from long-term fire exclosures in Venezuela demonstrate that African invaders are not as tolerant of fires as South American species, possibly due to the greater fuel accumulations they produce over long fire-free intervals. There is evidence from the

Serengetti in East Africa that native species are highly resistant to invasion on natural disturbances such as termite mounds, excavation patches of digging mammals, etc. While this may suggest that there may be differences among savannas in invasive resistance, there were invasions along roadcuts in the Serengetti.

12.2 Relationships Between Biodiversity and Stability: Some Hypotheses

Developing hypotheses and experimental tests to measure the impact of biodiversity on ecosystem stability is extremely difficult. In the first place, it requires a clear definition of biodiversity and an accurate way to measure it. As discussed by Luis Bulla in Chapter 6, there is no simple way of measuring diversity, all indices being fraught with methodological and conceptual problems. Furthermore, stability implies time, and as discussed above, long periods of time. We have no way of ascertaining the diversity of savannas in the immediate past, much less in the remote past. The time factor also makes any experimental approach to the testing of system stability extremely difficult.

The goal of the discussion group was to develop a set of hypotheses that would circumscribe the problem, and that would identify those properties of the system that should give instability. Experiments, observations, and computer simulations can then be designed to test the effects of these properties on the behavior of the system.

After discussing the comparative, experimental, and natural experiments approaches presented above (see Chap. 10), we add a fourth approach, computer simulation.

Computer simulation is no substitute for natural experiments and observations; but computer simulations can help to define parameters and test whether certain propositions are feasible. They are particularly useful when testing propositions that include random components and long time series.

12.3 Specific Hypotheses on Species Diversity and Ecosystem Stability

Global Hypothesis 1 Savannas are relatively stable systems, in terms of resistance and resilience. Savannas persist as savannas even though they experience an ongoing regime of disturbances from fire, drought, and herbivory.

Global Hypothesis 2 Savannas may, nevertheless, be pushed beyond the limits of their resilience and resistance domains into new configurations, by disturbances that are intense and uncharacteristic for the system.

Rationale These two general hypotheses state the perception based on the fossil record and their present broad distribution that savannas have persisted over a long time, at least since mid-Pliocene and probably before (van der Hammen 1983; Cole 1986). Yet, we know that some savannas can be transformed through human intervention into forests when fire is excluded (Chap. 2), or into grasslands through intensification of fire and other anthropogenic disturbances. These two hypotheses should then be seen as null hypotheses.

The term "stability " will be used to refer to both resistance and resilience components in the following hypotheses.

Hypothesis 1 Savannas are stable because a large fraction of nutrients, biomass, organisms, and meristems are located below ground, where they are protected from disturbance.

Rationale Savannas are exposed to frequent disturbances, especially fire. Since fire tends to be fast-moving and of short duration, it has a minimum effect on underground structures, and the large proportion of these may explain their stability.

Hypothesis 2 Savannas are stable because they are composed of a diverse array of species that have different functional properties. It would therefore be expected that there is a significant relationship between patterns of species richness and patterns of stability across sites within a savanna site as well as across savannas.

Rationale This hypothesis extends and generalizes hypothesis 5 of Chapter 10. We content that if a functional group is totally eliminated from the system, then the system will be more vulnerable to disturbance. So, for example, if trees are totally eliminated from a dry tree savanna, seedling establishment (that is concentrated under trees, Belsky 1990) will be reduced and the savanna will take longer to recover from the fire, or will not recover at all, changing into a grassland. Two additional hypotheses connected to Hypothesis 2 are:

Hypothesis 2a Savanna species are composed of disturbance-adapted species, along with less disturbance-adapted species, due to evolutionary histories of exposure to disturbance, and either cycles of disturbance/disturbance-free periods, or patchiness of disturbance and disturbance cycles in space. Thus, savannas will be less stable if disturbance-resistant (e.g., fire-resistant) or disturbance-sensitive species (e.g., shade-adapted species in a fire-prone system) are removed.

Hypothesis 2b Woody elements of savannas are more sensitive to disturbance than herbaceous components.

Hypothesis 3 The relationship between species or functional diversity in savannas is curvilinear, due to the bell-shaped curvilinear relationship between species numbers and PAM. Thus, savannas that experience intermediate levels of PAM may be expected to be most stable.

Rationale The text of the hypothesis is self-explanatory. It is difficult to test, however. It is amenable to computer simulation and we recommend that this avenue be explored.

Hypothesis 4 Relationships between stability and diversity are sensitive to spatial scale. Specifically, stability will be more likely as the scale (extent) of a system is enlarged . Conversely, systems that are highly fragmented will be less stable than connected systems. Stability is promoted by functional complementarity among different spatial components in the system, and interchanges of functionalities among different spatial components.

Rationale Savannas are very heterogeneous systems. They consist of areas of pure grassland, patches of trees and grasses, and small groves of trees. Furthermore, the density and importance of the tree and herbaceous component changes over the landscape in response to topographic, climatic, and disturbance features, and the history of the system. The smaller the time and/or spatial dimension of a savanna, the more likely it is that it will be modified as a result of a disturbance. For this reason, fragmentation should lead to loss of stability. Three corollaries of this hypothesis are:

Hypothesis 4a At larger spatial scales, there is a greater diversity of species and interactions among species, which increases the functional diversity of system as a whole (i.e., functions are integrated at larger scales to yield emergent, stabilizing properties at a higher level of system organization). Thus, gamma diversity will increase with scale, and this increase should be positively correlated with stability.

Hypothesis 4b Increases in topoedaphic diversity at patch, catena, landscape, and regional scales promote functional diversity among species, which then contributes to system level stability. Because topoedaphic diversity increases with scale, stability will likewise increase with scale.

Hypothesis 4c As the sample of savannas used to construct the relationship includes a larger number of sites, the relationship between diversity and stability will strengthen, due to stochasticity and weak relationships at smaller scales.

Hypothesis 5 Savannas may be pushed into new and stable configurations due to subsequent modifications of the environment by the biota, analogous to succession. The new system may have a similar diversity, but be composed of different species. The components of the new system may have different levels of resilience compared to the original components. The path of recovery back to the original composition may be different than the path subsequent to disturbance in terms of floristic succession (i.e., it is hysteric).

Rationale With time, savannas may change in species composition. This can result in environmental modifications that create new stable configurations, for example as a result of an increase/decrease in woody species that change the physicochemical composition of the soil (Chap. 3). Although the overall diversity may not change, other components of the system, such as resilience, may be different.

Hypothesis 6 The path of recovery back to the original composition of a savanna following a disturbance or a move to a new stable or quasi-stable state may be different than the path subsequent to a disturbance in terms of floristic succession (i.e., it is hysteric).

Rationale What this hypothesis states is that initial conditions determine the trajectory of the system.

Hypothesis 7 Savannas are stable because they are composed of species that are plastic in form and functionality.

Rationale We define plastic behavior as the ability of a species to modify its form/and or function in response to a disturbance, thereby reducing mortality. Plastic behavior in response to common disturbances, such as fire and drought, two common occurrences in savannas, is a major contributor to stability. A corollary is:

Hypothesis 7a Savanna species are more likely to exhibit plastic responses to disturbance or stress than in most other biomes.

Hypothesis 8 Savannas are stable because there are many functional groups, that when arranged along a continuum show a high degree of overlap among groups, and few spaces along the continuum that are devoid of function.

Rationale The more species overlap in their functional characteristics, the greater the probability that there will be a set of them capable of withstanding extreme disturbances, such as changes in climate, fire regime, or outside invasion. This hypothesis expresses in more general terms some of the statements made in Chapter 10.

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