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Biodiversity and Savanna Ecosystem Processes

A Global Perspective

With 40 Figures

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10 Biodiversity As Regulator of Energy Flow, Water Use and Nutrient Cycling in Savannas

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10.1 Introduction

A central question of the Diversitas program, Brasilia (1993), was how the reduction of biodiversity, or more precisely species richness in a given ecosystem, will affect the processes characterizing its functioning in those aspects related to energy and matter flow, to reproduction and perpetuation in time, and to resistance and resilience in the face of disturbances of variable intensities.

In order to discuss the role of biodiversity on biogeochemical cycles in savanna ecosystems, it is necessary to define the systems we are dealing with. This definition includes aspects of "savanna structure" and "savanna function" and is broad enough to include the ecosystems that are heuristically referred to as savannas, while adding constraints that provide boundaries on our definition.

10.2 Savanna Structure

A savanna is a structurally simple but spatially patchy tropical ecosystem characterized by a herbaceous layer dominated by xeromorphic C_4 grasses and, in most cases, having a woody component consisting of deciduous or evergreen trees or shrubs. Savanna composition and

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structure vary both spatially and temporally as the height and density of the woody components change in response to fire, herbivory, nutrient availability, or climate.

10.3 Savanna Function

Savannas are ecosystems characterized by relatively low biomass compared to forests. This low biomass may result from a variety of naturally occurring factors: low amounts of plant-available moisture (PAM), low concentrations of plant-available nutrients (PAN), shallow soil depth, recurrent fire, or intensive herbivory. Plant biomass is further restricted by the strong seasonality of tropical climates, which reduces the activity and/or leaf area of many species during part of each year, and by the dramatic effects of fire and herbivory on above-ground biomass and below-ground mineralization processes. Of unique importance to savanna ecosystems are their below-ground systems, which serve as energy and nutrient reservoirs that protect individual plants and entire ecosystems from recurrent perturbations such as drought, fire, and herbivory.

10.4 Biogeochemical Cycles in Savannas

Biogeochemical cycles have been extensively documented for different ecosystems; however, information on savannas is far from exhaustive (Frost et al. 1986; Walker 1987). The mechanisms involved in the processes of organic matter production, water and nutrient cycling, and decomposition are well understood, even though their quantitative aspects have not been worked out satisfactorily (Menaut et al. 1985; Goldstein and Sarmiento 1987; Medina and Silva 1990; Medina and Bilbao 1991). A scheme of the complexity of processes that are defined as biogeochemical cycling in savanna ecosystems must incorporate primary production, water uptake and transpiration, nutrient uptake, and organic matter decomposition as primary variables, as well as biomass-allocation patterns, herbivory, and interactions among all these processes (Table 10.1, following in part the descriptions of Main 1992 and Hobbie et al. 1993).

Table 10.1 Schematic description of the processes involved in biogeochemical cycles in savanna ecosystems.

Biogeochemical cycle	Processes involved
Energy and carbon fixation	Photosynthesis Allocation of biomass for leaf area development
Water cycling	Water uptake and transpiration by primary producers Allocation for: leaf area development, root biomass and area
Nutrient cycling	Nutrient uptake by primary producers Roots Symbiosis and mutualisms Rhizosphere Mycorrhiza *Rhizobium* symbiosis *Frankia* symbiosis
	Nutrient transfer and redistribution Living plant matter consumption (herbivores) Dead plant matter consumption (detritivores) Secondary consumers
	Nutrient release Decomposition processes (soil microorganisms) Mineralization
	Soil formation Organic matter conditioning and humification
Interactions	Organic matter production requires nutrient and water uptake, while water cycle in the system introduces nutrients into, and leaches nutrients out of, the system

Savanna ecosystems are characterized by a number of structural and functional features that may have significant bearing on the efficiency and stability of biogeochemical cycles:

1. The coexistence of trees and grasses in a dynamic equilibrium that is regulated by water availability and fire regimes has strong implications for the dynamics of the system regarding light interception, water balance, and layering of soil-resource utilization (Walker and Noy-Meir 1982).
2. Within the herbaceous matrix, the cooccurrence of grasses and sedges, having in general a C_4 photosynthetic pathway, and forbs, having in general a C_3 photosynthetic pathway, results in patchiness of herbaceous

layer productivity and water- and nutrient-use efficiency (Medina 1982; Sarmiento 1984). In addition, the diversity of phenological types (early and late growers, annuals and perennials) provides a temporal dimension, which allows primary productivity to take place throughout the year (Sarmiento 1983).

3. The occurrence of nitrogen-fixing organisms, both free-living microorganisms (Cyanophyceae and bacteria) and symbiotic higher plants (rhizobial symbionts), creates further spatial heterogeneity in nutrient distribution, particularly that of nitrogen and calcium (Medina and Bilbao 1991). In addition, the role of widespread mycorrhizal symbiosis for water balance and phosphorus uptake in savanna plants has not been properly documented yet.
4. Root/shoot ratios in savanna ecosystems, particularly within the herbaceous layer, are considerably greater than 1, a feature providing resistance to stress and disturbance from drought, fire, and herbivory (Sarmiento 1984; MacNaughton 1985; Frost et al. 1986).
5. Interactions of fire, herbivory by large animals, and the activity of ants and termites in nutrient conservation and cycling constitute a unique feature of savannas that requires precise documentation and modeling.

According to Table 10.1, there are a number of points in which changes in biodiversity could modify both quantitatively and qualitatively the pattern of biogeochemical cycle in a given ecosystem. Biogeochemistry is essentially determined by the development of biological surfaces, i.e., photosynthetic surfaces chemically fixing incoming sunlight and absorbing CO_2 (primary production of organic matter) and water- and nutrient absorbing surfaces. Primary production is proportional to the amount of light energy intercepted, which is a function of shoot development and architecture, and the intrinsic capacity of the biochemistry of the photosynthetic apparatus to incorporate CO_2 into organic compounds, which is greatly dependent on nutrient availability. Moreover, because of the stomatal control of both water loss (transpiration) and CO_2 uptake, these processes are intimately related. The ratio of water consumed in transpiration per unit of organic matter produced is a valuable index of water-use efficiency at the ecosystem level. Development and spatial distribution of photosynthetic surfaces depend on the morphology of the species. In savannas, predominance of grasses and forbs is associated with dense packing of photosynthetic surfaces that are located near the soil surface, while predominance of trees results in a vertical distribution of light-intercepting surfaces leading to a more efficient process of energy capture. Efficiency of water- and nutrient use for primary production is also species-dependent.

Nutrient and water absorption depend on development of root biomass and the effective surface of interaction with the soil matrix. Patterns of biomass allocation, root depth, and efficiency of symbiotic associations also vary with the species composition of the primary producers. Primary producers with different habits tend to differ substantially in the quality of organic matter they produce (i.e., carbon:nitrogen and lignin:nitrogen ratios; proportion of protein, lipids, and carbohydrates). Therefore, changes in species composition in a given ecosystem may result in changes of patterns of herbivory and in nutrient sequestering by the organic-matter decomposers within the soil matrix.

There are several examples in the literature documenting the potential and actual effects of certain species on the rates of processes determining biogeochemical cycling in natural and disturbed ecosystems. Some species might be particularly efficient in recycling nutrients that are critical for ecosystem functioning (Muller and Bormann 1976), while the introduction of some species can open different pathways for ecosystem succession. That has been the case with the introduction of nitrogen-fixing species (Vitousek et al. 1987) or the invasion of fire-resistant grasses in Hawaii (Hughes et al. 1991). The former improved nutritional conditions in the soil, allowing the survival of more nitrogen-demanding species, while the latter increased the fire risk in non-fire-resistant systems.

10.5 Functional Groups

Species occurring in any given ecosystem are differentiated according to their morphological and physiological characteristics. Differentiation between species may be substantial among species growing in high-stress (resource poor or severely and/or frequently disturbed) ecosystems and subtle in resource-rich, low-stress ecosystems. In semiarid ecosystems the rate of species differentiation and extinction is higher than in mesic ecosystems (Stebbins 1952). Therefore, at a given time, semiarid systems sustain lower species diversity than mesic ones, although that is not necessarily true in a historic perspective. In highly stressed ecosystems, resource availability limits the number of cooccurring species with similar ecological requirements. Only those species highly adapted to the stressing factor survive. Higher availability of resources in low-stressed ecosystems allows the packaging of more species with similar ecological requirements within a certain space and time. These considerations have to take into account species richness and diversity, which are a function of the area, age, and evolutionary history of the habitat, as well as the size and environmental requirements of cooccurring species. Another aspect necessary for understanding the relationship between stress and biodiversity is that the nature of stress is multiple in ecological settings (Chapin 1991). For example, drought stress frequently leads to disturbances in nutrient acquisition, and occurs under conditions of high irradiation and possibly high temperature.

Different combinations of stresses may lead to widely different responses at the ecosystem level, resulting in variable numbers of species.

In principle, species can be ordered according to their role and relative importance in ecosystem processes. Groups of species that are classified on the basis of their morphophysiological and phenological properties and have possibly "similar" impacts on ecosystem processes are called functional groups (Hobbie et al. 1993; Vitousek and Hooper 1993; for a more extensive and recent discussion see Huston 1994). There is a standing controversy on the similarity of functions of species classified within a certain functional group. For instance, primary producers in a savanna represent a complex functional group consisting of species of different habit, size, and physiological requirements. The subdivision of the primary producers into morphological types such as herbs and trees also results in complex groups, when physiological traits and other morphological characteristics are taken into account. The herbs can be further separated into grasses and forbs, C3 and C4 photosynthetic types, nitrogen-fixing and nonfixing, deep- and shallow-rooted, early and late growers, and so on. However, in many savanna types the number of species that can be attached to a certain functional group (i.e., primary producers, consumers, decomposers, etc.) is large, therefore the question of species equivalence (or redundancy) within a given functional group has scientific significance (Walker 1992). The probability of finding equivalent species within functional groups that are important for biogeochemical cycling in a savanna ecosystem is high, but it does not mean that those species are also redundant regarding other aspects of ecosystem function, for example in regard to stability and resilience (Lawton and Brown 1993).

Definition of functional groups depends on which process is being analyzed. Clearly, a given species may belong to several functional groups; and to a certain extent, species belonging to more than one functional group may be more critical for ecosystem function than are species restricted to a single group. In addition, functional groups with a large number of species are characterized by a larger number of species interactions, which might be of significance in strongly fluctuating environments or in environments having a high frequency of disturbances. Both characteristics apply to savanna ecosystems and should be remembered when analyzing the importance of a certain species in biogeochemical cycling (Frost et al. 1986).

Here only a few examples of functional groups in savannas will be given, including those of primary producers, megafaunal herbivores, and soil invertebrates. A high priority should be given to defining functional groups within the decomposer community, because very little is known about their population properties and physiological requirements. Prediction of the response of savanna ecosystems to changes in macroorganism diversity will depend on the understanding of the impact of physicochemical stress and changes in substrate quality on the proportion, abundance, and activity of soil microorganisms.

10.6 Primary Producers

Plant functional groups can be defined according to habit and size. In savanna ecosystems, it is important to distinguish between herbaceous and ligneous plants, because these plants are related to different rates of organic matter production and accumulation and to patterns of organic matter allocation to above- and below-ground organs. It has been shown that there is a strong correlation between degree of woodiness (and plant size) and the availability of resources (water and nutrients). As the availability of nutrients and water increases, the number of woody species, particularly trees, increases. Under conditions of light limitation, trees are more competitive because of the vertical displacement of their photosynthetic area. In addition to this general tendency, tree/grass ratios are influenced by intensity of herbivory and fire regimes (Belsky 1990; Medina and Silva 1990). In both cases, above-ground biomass is particularly affected. However, while fire impact is generally restricted to the dry season, and is neutral in destroying above-ground dead grass biomass and canopies of evergreen trees, herbivory occurs primarily during the rainy season, is selective, and is accompanied by the effect of trampling. The effect of herbivores is not necessarily unidirectional; they may either increase or reduce the tree/grass ratio of a given savanna, depending on the degree of environmental stress and their selectivity. Another important difference between fire and herbivory is that fire causes a relative homogeneous volatilization of organic matter and certain nutrients (N, S, K), while herbivory leads to nutrient relocalization and patchiness. The comparatively large root/shoot ratios in savannas minimize the loss of nutrients due to burning during the dry season.

A scheme of the distribution of functional groups of primary consumers has been devised following suggestions of Hobbie et al. (1993; Fig. 10.1). The scheme hypothesizes that the dominant type of functional group among primary producers will be related to the availability of resources (water and nutrients) (Tilman 1990) and will be modulated by the impact of fire and herbivory (Medina and Silva 1990). As the availability of resources increases, numbers of trees increase, resulting in greater competition for light (Schulze and Chapin 1987; Hobbie et al. 1993). As stated before, establishment of the equivalence of the species within each functional group is of paramount importance in order to determine if they can be replaced under certain circumstances. Substitutability may be measured as the compensation by density increase of some species, after elimination of one or more species within a given functional group (Walker 1992). The establishment of interspecific equivalence requires both spatial and temporal dimensions, therefore the analysis should take into account morphology, nutritional requirements, intrinsic relative growth rate (RGR), productivity, and phenology.

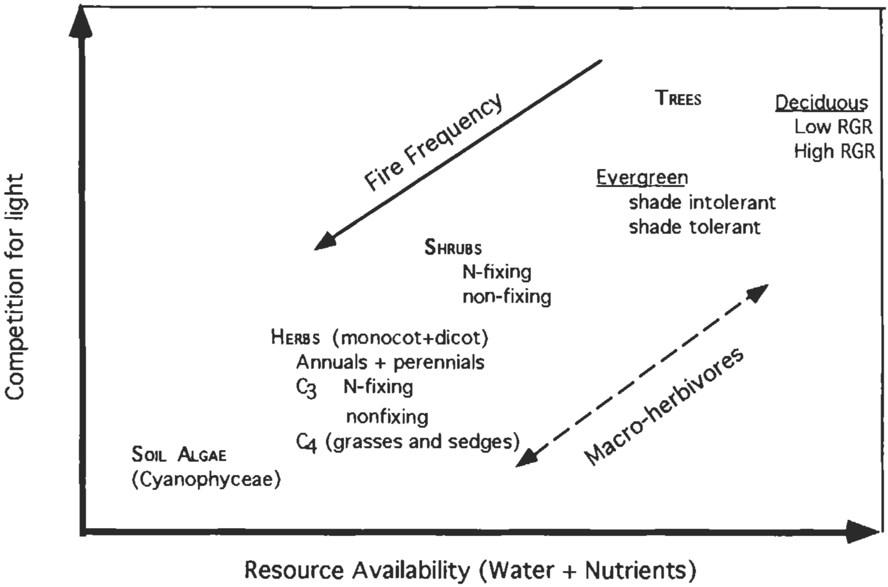

Fig. 10.1. Variation in the predominance of functional groups of primary producers (≈ lifeforms arranged according to size and ecophysiological properties) (in analogy to Hobbie et al. 1993)

10.7 Faunal Functional Groups

Examples of functional groups of savanna macroherbivores are defined according to their diet:

Grazers: feed mostly on the herbaceous layer.
Browsers: feed mostly on the shrub and tree layers.
Granivores: feed mostly on plant seeds.
Nectivores: feed mostly on nectar produced in floral and extrafloral nectaries.
Frugivores: feed mostly on fruits.

10.8 Soil Fauna

The soil fauna plays a critical role in processing plant residues, which are subsequently incorporated into soil organic matter (SOM) or rendered more accessible to decomposition (mineralization) through soil microorganisms. Lavelle (1987) distinguishes three major groups of soil macroinvertebrates:

1. Epigeics live in and feed on litter. As a result of their feeding activities, they produce fecal pellets in which accelerated release of nutrients may be observed at short scales of time; in the longer term, mineralization of soil organic matter may be slowed down because the initial flush of mineralization rapidly comes to an end as a result of reduced oxygen supply and porosity.
2. Anecics export organic matter from the litter system to other decomposition systems, i.e., to the subsoil itself (anecic earthworms) or to nests of social insects. There, organic matter is eventually digested and the residues are mixed with mineral elements taken from different soil horizons. Structures created by these organisms include galleries, mounds, macropores and aggregates (micro- and macroaggregates).
3. Endogeics include different subgroups living in the soil and feeding on soil organic matter. Their activities result in the formation of casts, which are stable macroaggregates at the scale of years, and macropores. These structures affect SOM and water dynamics at different scales of time and space. In earthworm casts, for example, mineralization of SOM is strongly enhanced at the scale of hours to days, but at the scale of months to years SOM, is protected. After the initial flush of mineralization following deposition of the fresh cast, the compact structure of the cast soon decreases mineralization rates (Lavelle and Martin 1993).

Examples of the types of organisms classified within each group are listed in Table 10.2.

Table 10.2. Examples of functional groups of soil macroinvertebrates according to Lavelle (1987)

Invertebrate Group	Examples
Epigeics	Xylophages (termites and nonsocial arthropods) Leaf litter feeders (nonsocial arthropods, epigeic earthworms, epigeic termites)
Anecics	Burrowing earthworms Fungus growing + foraging termites Leaf cutting ants Diplopoda
Polyhumics endogeics	Humivorous termites Polyhumic earthworms
Mesohumic endogeics	Mesohumic earthworms
Oligohumic endogeics	Oligohumic earthworms

10.9 Relationship Between Biodiversity and Biogeochemical Cycling

10.9.1 Hypothesis Formulation

Developing hypotheses and experimental tests to measure the impact of biodiversity on the function of savanna ecosystems is inherently difficult. First, it demands an alteration in the way in which biodiversity is normally viewed. Whereas ecologists have traditionally asked how different ecosystem variables affect biodiversity, in this chapter we ask whether biodiversity has an impact on ecosystem function. In other words, we attempt to develop a hypothesis on how ecosystem processes, such as energy, water, or nutrient fluxes, respond to increases or decreases in species richness.

The goal of our discussion is to develop a set of nontrivial hypotheses that can be tested to determine whether biodiversity has an effect on the fluxes of energy, carbon, water, or nutrients through savanna ecosystems. In our considerations several basic guidelines are taken into account, although it is not always possible to follow them consistently:

- Biodiversity is a measure both of species richness (total number of species) and of structural diversity (i.e., leaf-area distribution, canopy structure, soil heterogeneity, etc.). For simplicity, our discussions deal mainly with the α-diversity of limited areas rather than the β-diversity over larger areas, although it is recognized that biodiversity needs to be examined at different spatial scales.
- Hypotheses on productivity should be divided into primary productivity and secondary productivity. These two levels may have differing relationships to biodiversity.
- Species richness and species equitability (evenness) should be kept separate in all discussions; ideally, hypotheses should be developed as parallel sets for both components of biodiversity.

We discuss three approaches for testing hypotheses: comparative, experimental, and use of natural experiments. Each approach offers a range of advantages and disadvantages.

Comparative Approach.
Biodiversity and ecosystem variables such as PAM, PAN, productivity, horizontal structure, fire, maximum and minimum temperatures, rainfall could be measured in a large number of savannas and the relative importance of biodiversity on productivity, nutrient use, water-use efficiency, etc. could be determined by multiple regression, factor analysis, or path analysis. The advantage of this approach is that it would facilitate

the study and comparison of savannas around the world. Therefore, it may allow the collection of data on little-known processes while avoiding the problems associated with disturbing plots (see below). The disadvantage of this technique is that the comparative approach requires the collection of large amounts of data, without the results being strongly predictive.

Experimental Approach.
Biodiversity could be manipulated by removing or adding individual species or functional groups of species from savanna plots and then measuring ecosystem responses such as changes in nutrient or water movement through the soil, rainfall interception, quantity of runoff, rainfall-use efficiency, etc. This approach has the advantage of holding most important variables constant while testing one factor at a time. It also allows straightforward modeling of ecosystem responses and strong inferences can be made while testing meaningful hypotheses.

The manipulation of biodiversity in natural savannas involves the development of whole-ecosystem experiments, and therefore the planning has to be based on long-term observations and measurements. Disturbances resulting from species removal, additions, or changes in environmental stresses (i.e., fire regime, water or nutrient availability, composition of the herbivore community), possibly leading to changes in species composition, dominance, and density, have to be documented on both a short- and a long-term basis. Species deletion can be performed either directly (disturbing the community in the short term) or indirectly through changes in the ecosystem regulating factors associated with the occurrence of a given species. The general type of experiment that could be conducted may be related to individual species or to groups of species that presumably play significant roles in the ecosystem. This knowledge would be obtained initially from a detailed analysis of ecosystem species composition and abundance, and could be tested using the following examples:

1. Species deletion using specific biocides for:
   - dominant primary producer,
   - most abundant herbivore,
   - soil invertebrates,
   - soil microflora and microfauna.
2. Species addition through:
   - dispersal of propagules of exotic species of various habits,
   - introduction of herbivore species,
   - inoculation of new soil microorganisms (for example, *Rhizobium* varieties or spores of mycorrhizal fungi).
3. Manipulation of environmental constraints:
   - modifications of water availability,
   - increases in nutrient availability,
   - modification of the fire regime.

Some disadvantages of this approach are:

1. The removal of rare species would most probably produce changes below the level detectable in natural systems having a normal degree of temporal and spatial variability. Therefore, studies consisting of the removal of rare species can be considered futile.
2. The removal of common or dominant species would definitely produce changes in ecosystem function, but changes related to the loss of these species may be confounded with the disturbance required to remove the species. For instance, the direct elimination of a certain species of primary producers involves either the removal of roots, which would disturb the soil, or the roots would be left in place after killing the organisms, enriching the soil column as they decompose. In addition, the time necessary for the system to equilibrate following species removal would be unknown. It is also important for investigators to distinguish between the effects of the disturbance and the effects of a reduction in biodiversity. In addition, it is not clear whether the removal of one common species would provide a measure of a change in biodiversity or simply a measure of the importance of that one species to the community. For example, would changes resulting from the removal of elephants from African savannas tell us about the importance of consumer biodiversity or simply about the function of elephants in savannas?
3. Removal of whole functional groups would, without doubt, alter ecosystem function; but once again, these results might inform us more about the importance of each functional group than the importance of high species diversity.

Natural Experiments.
Analyses of natural experiments (for example, the relatively recent invasion of African grasses into South American savannas) offer the advantage of a long period of equilibration so that communities will have adjusted to the perturbation. In addition, these natural experiments often occupy large and diverse areas, which would provide adequate replication and facilitate the measurement of response. Although this type of experiment has few pitfalls, the answers to several questions are already known; the invasion of African grasses, for example, has lowered biodiversity in South American savannas while increasing productivity. However, the impact of exotic grasses on the rate of biogeochemical cycling, or on the mechanisms that prevent reinvasion of native grasses remain as fruitful lines of inquiry in understanding the relationship between biodiversity and ecosystem function (Baruch and Fernández 1993).

10.9.2 Hypothesis Testing

Testing of any hypothesis regarding the regulatory effect of biodiversity on biogeochemical cycling will have to measure the fluxes of energy and matter through natural or disturbed ecosystems. For savanna ecosystems the methodology is comparatively well known and it involves the measurement of all relevant environmental parameters (light, rainfall, temperature, soil percolation, nutrient concentrations) as well as a description of ecosystem compartments (producers, consumers, decomposers, soil).

Standard measurements should provide a quantitative assessment of:

- Energy balance of the ecosystem (radiation input, output, and retention).
- Water balance: rainfall, evapotranspiration, run-off and percolation.
- Nutrient concentration in water fluxes and estimation of inputs, losses, and recirculation.
- Compartmentalization of biomass and nutrients and seasonal variations in primary and secondary production.
- Soil organic matter quality.
- Microbe community composition.
- Processes of nutrient transfer and release due to:
  - herbivory,
  - decomposition (comminution and mineralization rates, soil respiration).

Techniques for measurement of relevant ecosystem processes such as primary productivity, energy interception, and nutrient cycling have been adequately documented and described (see Bormann and Likens 1979; Walker and Menaut 1988; Pearcy et al. 1989; Hall et al. 1993). Methodology for the measurement of soil processes has been described in detail in the *Manual of Methods of the Tropical Soil Biology and Fertility Group* (Anderson and Ingram 1993). Therefore the hypotheses formulated include only a proposition considered to be true and a brief rationale to explain the extent and implications of the proposition. Specific predictions are indicated in those cases where testing procedures are not obvious from the rationale.

10.10 Specific Hypotheses on Species Diversity and Ecosystem Function

10.10.1 General

Hypothesis 1 Savanna ecosystems having high biodiversity will be better able to acquire and sequester limiting environmental resources than those of lower biodiversity.

Rationale Diverse ecosystems should be more efficient at acquiring and retaining limiting resources (rather than nonlimiting resources) because most of the species will be adapted for taking up and sequestering those resources. Reduction in species richness might cause the loss from the system of a fraction of those resources, since fewer species would be available to take up and hold the resources during all parts of the year. Ecologically similar (or redundant) species should protect the ecosystem from a loss of resources in case of species extinction, disturbance, normal environmental fluctuations, or extreme climatic conditions.

Hypothesis 2 The loss of species from ecosystems will affect the availability of resource for the remaining species (even if the resources are not lost), which may further alter species composition in the community.

Rationale The replacement of native species by African species in South America resulted in a reduction in biodiversity in these communities and may have altered the availability of nutrients, water, or energy, and initiated a new and progressive loss of species from the community. Another example is in the Great Basin of the United States, where *Bromus tectorum* has replaced many native herbaceous species, primarily by reducing the amount of water available to these species. As a result, the frequency of fires has increased, leading to further loss of native species. Species turnover and fire are most likely accompanied by losses in soil fauna and microorganisms, preventing recolonization by native species. Therefore, the high dominance of one introduced species, *B. tectorum*, has altered the ability of the ecosystem to recover its original species.

Hypothesis 3 Loss of biodiversity will have greater consequences at the landscape level than at the community level.

Rationale Species that may be rare or redundant in one habitat may be critical in another. Therefore, loss of certain species may have no effect on their local community but may result in a loss of resources in neighboring communities. For example, the grass *Cynodon plectostachys* occurs at low density and is probably redundant in open grassland-savannas in southern Kenya; however, it forms a monoculture under the crown of most tree species in the drier parts of the ecosystem. Loss of this species would probably result in the loss of nitrogen from subcrown habitats, which might affect tree growth.

Hypothesis 4 The removal of dominant species will have greater impact on ecosystem function in less diverse than in more diverse communities.

Rationale In highly diverse communities, the removal of a single dominant species should not result in a significant loss of important resources because there is some probability that other species in the community will increase in size or frequency and thereby capture the resources that have been released. In less diverse communities, there will be fewer similar species and perhaps none that are able to control the resources the same way.

10.10.2 The Role of Functional Groups in Maintaining Ecosystem Function

Hypothesis 5 Functional diversity in a savanna ecosystem minimizes loss of resources (energy, water and nutrients). Any change in functional diversity will decrease the amount of resources used, leaving some unutilized resources that eventually could be lost from the system.

Rationale If a functional group is totally eliminated from the system, some resources will not be captured and then their flux within the system will decrease. Thus, if trees are eliminated from a savanna, (a) total leaf area will decrease, resulting in less energy entering the system, (b) total root length will decrease, reducing both the amount of water transpired and the amount of mineral elements absorbed.

10.10.3 Relations Between Biodiversity and the Structure of the Primary Producers Functional Group

Hypothesis 6 Changes in biodiversity of primary producers that result in variations of system structure (biomass allocation, leaf area amount and distribution, etc.) affect water, nutrient, and energy flow.

Rationale Rates of water, nutrient, and energy cycling through ecosystems depend on the horizontal and vertical structural features of their primary producers, as represented by leaf area development, extension and area of the root system, and vertical stratification of the above-ground biomass.

These changes in structure most likely result from variations in the proportions of functional groups within primary producers. Examples of such changes are the modifications in the proportion of species with extensive *versus* those with intensive root systems (trees and grasses respectively), or of species with symbiotic associations (rhizobial symbionts and mycorrhizal associations). These structural changes may affect ecosystem function more than changes in species richness alone. The concept of species substitutability is builtin, primary producers with similar structure and physiology can substitute for one another.

Corollary 1.
Provided that the structure of the system as well as the proportion of the different structural elements are maintained, species can be removed without affecting the water, nutrient, and energy fluxes.

Corollary 2.
Patches of savannas that are vertically complex affect neighboring resources by creating suitable habitats for species with a wide range of resource requirements (light, water, and nutrients). Therefore, changes in vertical complexity will affect energy and material fluxes through the system.

Test 1. In a situation of equal proportions of trees and grasses, removal of the same proportion of leaf area in both groups will have a lesser effect on ecosystem function than the removal of the same leaf area from the grasses or the trees alone.

Test 2. Sites with different numbers of species in the tree and grass layers, but similar standing biomass of each group, should have similar fluxes of energy, nutrients, and water.

Test 3. Similar proportional changes in structural properties in systems with different proportions of tree-grass covers, should give a similar magnitude of changes in the fluxes, irrespective of species composition.

Hypothesis 7 Introduction of alien species of a certain functional group (grasses, trees, shrubs) will lead to changes in biogeochemical cycling according to the physiological characteristic of the species.

Rationale
a) Introduction of highly productive grasses affects productivity, temporal distribution of biomass production and reproduction (phenology), flammability of the above-ground biomass, and quality of biomass for herbivores

b) Introduction of nitrogen-fixing organisms increases patchiness of nutrient availability in the savanna, increases pasture quality for herbivores, and accelerates decomposition chains.
c) Evapotranspiration and water interception are higher while water percolation and runoff are slower in savannas dominated by native, slow-growing grasses compared to introduced fast-growing grasses, because of less cover and lower steady-state leaf conductance of native grasses.

10.10.4 Diversity of Underground Communities and Biogeochemical Cycles

Hypothesis 8 The diversity of soil macroinvertebrates determines plant production through the creation of structures that improve the efficiency of water and nutrient use at different scales of time and space.

Rationale Soil macroinvertebrates have developed different strategies to move and feed in the soil system. Each of these strategies results in the formation of complex structures in which the patterns and rates of nutrient cycling may be highly diverse (Lavelle 1987).

Test:

Comparative Approach.

Soil macrofauna communities show significant variations along rainfall gradients as well as biogeographical patterns. The experiment will consist of comparing the soil physical structure in soils with similar textures, but colonized by different groups of soil macroinvertebrates:

1. Surface features ("états de surface" following methodology of Valentin and Casenave 1992) and physical parameters like, e.g., water infiltration rate;
2. Soil aggregation as measured by Blanchart et al. (1990), if soil texture allows it;
3. Bulk density and the structure of porosity, including description of burrow systems and nests (e.g., Braudeau 1988).

Experimental Approach.

Experiments will include (1) the selective removal of functional groups that would suffer no other disturbance, and (2) the progressive addition of species in an artificial system (mesocosm in which plants would be cultivated in a previously sieved soil in which different soil fauna groups could be introduced; see, e.g., Blanchart et al. 1990; Spain et al. 1992).

In these experiments relevant parameters of the soil structure will be assessed as in the comparative approach, as well as plant production and the efficiency of nutrient use based on the use of ^{15}N-labeled plant material deposited at the soil surface, or as fertilizers inside the soil.

10.10.5 Diversity of Insects and Ecosystem Function

Hypothesis 9 The structural and chemical diversity of plants affects the richness and functional diversity of insects.

Rationale Herbivore insects are completely dependent on the quality and quantity of plant material. Evolution has led to a high degree of specialization in the use of particular resources by different group of insects.

Test 1. Correlative approach: the diversity of insects and plants might be recorded in a series of otherwise similar savannas (same climate and production), and the relationship may be established through statistical methods.

Test 2. Experimental approach: manipulation experiments with the removal of functional groups (insect populations are not altered by the disturbance itself).

Test 3. Natural experiments: analysis of insect populations in areas of savannas invaded by African grasses, compared to natural, nearby communities.

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