BIODIVERSITY: IMPLICATIONS FOR GRASSLANDS

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ABSTRACT
Biodiversity refers to the variety of life on Earth. In its simplest definition, it is the number of species per unit area. However, conceptually, biodiversity ranges from the genetic variation (e.g. heterozygosity) within individuals, to all the species, an unknown number, present in the biosphere. Grasslands are not major centers of biodiversity, with two major taxonomic exceptions: the grasses, naturally, and ungulates; that is, the plant family, Poaceae, and the animal orders, Artiodactyla and Perrisodactyla. Because of their human dietary importance, these groups represent biodiversity of overriding social and economic consequence. From a spatial standpoint, biodiversity ranges through a hierarchy of increasing scale: point diversity of a completely censused sample, α-diversity of local, homogeneous habitats, β-diversity across habitats, γ-diversity of a landscape region, δ-diversity of community-types in similar habitats, and the regional diversity of a defined geographic locale. A fundamental element of spatial diversity is pattern diversity, the difference in species composition from place to place.

KEYWORDS
Biodiversity, species diversity, heterogeneity, hierarchy, spatial pattern

INTRODUCTION
Ecologists and systematicists have always had terms for referring to variety in their collections, the most common being species diversity. The most widely used current term, biodiversity, was coined by Walter Rosen, a U.S. National Research Council staff member, when organizing a forum for that organization on the theme of biological diversity (Takacs, 1996). Biodiversity has come to be an all-inclusive term referring in a general manner to all biological levels of variety, from the gene to the biosphere. Therefore, this general term has a blanket application that directs us to focus on the idea of biological variety as embedded in a hierarchy of biological organization, spatial scale, and temporal dynamics. It can be profitably applied to phenomena from the number of species present in a pasture to the adaptive radiation of phyletic groups.

Among biomes, grasslands are not noted for their overall level of biodiversity (McNaughton et al., 1993). They are, however, repositories of very high diversity for taxa of extreme economic and conservation importance, the Poaceae, Artiodactyla, and Perrisodactyla. Much human food is derived both directly and indirectly from these three taxonomic groups. Moreover, it is reasonable to recognize that conservation of the genetic variation encompassed in both natural and cultural grasslands is of utmost importance to human well-being.

SPECIFIC EXAMPLES FROM THE SERENGETI ECOSYSTEM
The Serengeti ecosystem occupies about 25,000 km^2 in northcentral Tanzania and southwestern Kenya, with about half that area within Tanzania's Serengeti National Park (McNaughton, 1983). It is defined by the movements of large herds of migratory ungulates, the most abundant being 1.5 million blue wildebeest, or white-bearded gnu (*Connochaetes taurinus*), as well as more than a score of other large mammals. There is an annual rainfall gradient from an average of 40 cm in the SE to over 110 cm in the NW. The associated growing season for the vegetation herbaceous layer is from 90 days to near continuous, with the rainy season nominally from November to May. The migratory herds spend the peak of the wet season, March to May usually, in the SE and the peak of the dry season in the NW, calving in the SE on the open Serengeti Plains.

The vegetation ranges from open, treeless grasslands, which predominate at the dry end of the rainfall gradient, to open woodlands at the wet end of that gradient. My studies of grassland biodiversity (McNaughton, 1983) were explicitly placed in a hierarchical spatial context (Table 1). Utilizing that framework, we can consider grassland biodiversity from two viewpoints (McNaughton, 1994): (1) an explicit context of what we observe in nature within and across locations, and (2) a synthetic context of how various attributes of the grassland are related to biodiversity.

At the level of a homogeneous, local habitat, supporting a community with a certain α-diversity, one of the major contributors to community biodiversity was pattern diversity (Fig. 1). That is, patchiness of the vegetation (Collins and Gibson, 1990), or differences in species composition from local plot to local plot, was a principal element of community biodiversity. This has implications for foraging by large grazing herbivores. An animal with a preferred food source need not search every square meter of the vegetation to find a preferred food, but can walk from patch to patch to feed (McNaughton, 1983).

Within any ecosystem, we can consider explicit biodiversity as influenced by an interaction between a landscape region and topographic gradients. In the Serengeti, highest biodiversity is generally in the tall grasslands of the high rainfall regions of the NE, declining somewhat as we move down the rainfall gradient. Within any landscape region, there is a consistent tendency for biodiversity to be greatest on upper catenas and, particularly, rocky hills which create microgradients of soil depth and moisture availability, declining as we move down the hill to flatlands (Fig. 2).

Approaching grassland biodiversity from the synthetic standpoint, combining Fig. 1 with a functional property of vegetation related to biodiversity, biomass (Al-Mufti et al., 1977), revealed a dome-shaped relationship (Fig. 3). Biodiversity increased, as expected, with spatial patchiness but was influenced in an interactive fashion by biomass, peaking at intermediate levels of that variable, particularly as pattern diversity increased.

Grassland biodiversity is not a variable independent of the ungulate fauna (McNaughton, 1983; McNaughton and Banyikwa, 1995). Use of fences to exclude grazers results in a dramatic decline of biodiversity, with reduction in the evenness of species abundances evident within two years because taller species with a large investment in stem tissue overtop shorter species and begin the process of competitive exclusion. Within a decade, the vegetation is commonly reduced to a near monoculture of the tallest-growing grass.

CONCLUSIONS
Biodiversity is a pervasive feature of natural ecosystems, including grasslands. Cultural grasslands, pastures, on the other hand, are designed as low diversity systems, usually a monoculture of a single grass or legume species, or a biculture of one of each, supporting, similarly, a single or a couple of grazing species. In pastures, spatial heterogeneity, a pervasive feature of natural grasslands, is culturally suppressed insofar as possible. Natural grasslands, however, maintain a reservoir of species and genotypes that may someday be important

sources of genetic variation for introduction into commercial grasslands, either the new species introductions presently widespread with the utilization of African-origin forages throughout the tropics and subtropics, or through genetic engineering to incorporate traits from genotypes adapted to such extreme grassland environments as those characterized by saline soils or very heavy grazing pressure.

REFERENCES

Al-Mufti, M.M., C.L. Sydes, S.B. Burness, J.P. Grime and S.R. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. J. Ecol. **65**:759-792.

Collins, S.L. and D.J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In Collins, S.C. and Wallace, L.L. (eds.). Fire in North American tallgrass prairie. U. Oklahoma Press, Norman. pp. 81-98.

McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol. Monogr. **53**:291-320.

McNaughton, S.J. 1994. Conservation goals and the configuration of biodiversity. In Forey, P.L., Humphries, C.J. and Vane-Wright, R.I. (eds.). Systematics and conservation evaluation. The Sytematics Association Special Volume No. 50. Oxford U. Press, Oxford. pp. 41-62.

McNaughton, S.J. and F.F. Banyikwa. 1995. Plant communities and herbivory. In Sinclair, A.R.E. and Arcese, P. (eds.). Serengeti II. Dynamics, management, and conservation of an ecosystem. U. Chicago Press, Chicago. pp. 49-70.

McNaughton, S.J., O.E. Sala and M. Oesterheld. 1993. Comparative ecology of African and South American arid to subhumid ecosystems. In Goldblatt, P. (ed.). Biological relationships between Africa and South America. Yale U. Press, New Haven. pp. 548-567.

Takacs, D. 1996. The idea of biodiversity. Philosophies of Paradise. Johns Hopkins U. Press, Baltimore. 393 pp.

Table 1
Levels of biodiversity organized in a spatial hierarchy from smallest to largest scale.

1. POINT DIVERSITY: local patch, completely censused

2. PATTERN DIVERSITY: across patches=differences from point to point; this can apply to all higher levels

3. α-DIVERSITY: within a stand, or community, including both POINT and PATTERN

3. β-DIVERSITY: between stands, across habitats

4. γ-DIVERSITY: within a landscape encompassing diverse habitats

5. δ-DIVERSITY: within a community-type encompassing similar stands occurring in similar habitats

6. REGIONAL DIVERSITY: within a region encompassing multiple landscapes

Figure 1
Relationship between α-diversity and pattern diversity, assessed as the difference between patches, within Serengeti grasslands. H'=Σ(pi*ln pi), where pi is the proportional abundance of the ith species.

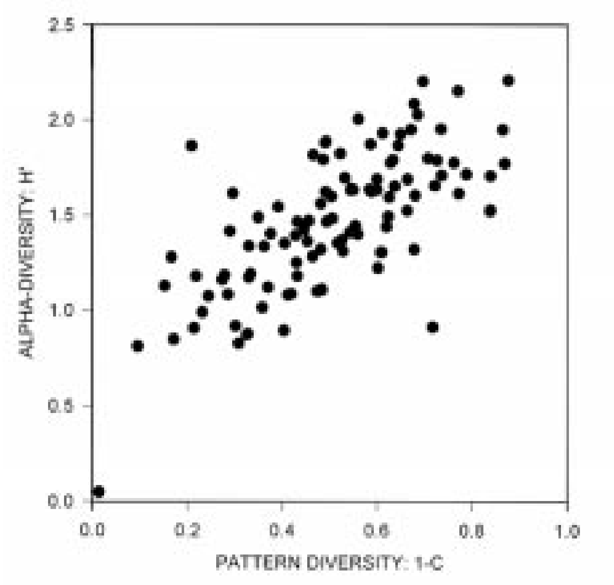

Figure 2
Relationship between α-diversity, topographic position from hilltop to flatland, and landscape region from NW to SE in the Serengeti grasslands. Variation across topographic position within a landscape region is related to β-diversity and is encompassed in γ-diversity, while variation across landscapes is regional diversity.

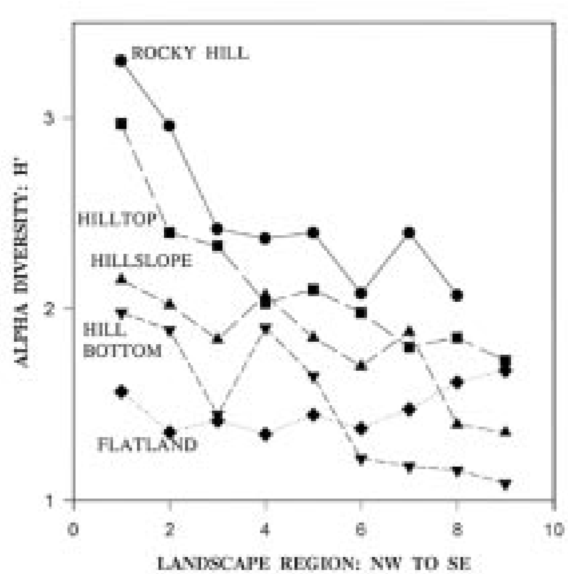

Figure 3
Relationship between α-diversity, pattern diversity, and peak aboveground biomass in Serengeti grasslands. Note that _-diversity varies little with biomass when pattern diversity is low, but peaks sharply at intermediate biomass when pattern diversity is high.