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Tree/grass ratios in East African savannas: a comparison of existing models

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Abstract. Tropical savannas are commonly described as biomes with continuous grass strata and discontinuous tree or shrub strata. A number of simple models have been developed that allow tropical savannas to be compared to one another. Older models were based on two or three variables such as rainfall, temperature, and soil texture, but newer ones either include a greater number of environmental variables or utilize biologically relevant factors such as the moisture and nutrients available to plants during their growing season. In this paper, the effectiveness of these models in describing the structure and function of the savannas of East Africa is examined.

Key words. Tropical savannas, East Africa, conceptual models, edaphic grasslands, woodlands.

INTRODUCTION

Plant communities or biomes can be compared by contrasting their biotic and abiotic environments or by examining their relative positions within simplified models. Although comparisons of environmental characteristics are instructive, differences in floristic, climatic and edaphic detail may obscure similarities in form and function. As a result, ecologists often use conceptual models to identify key similarities and differences among vegetation types.

An initial attempt to compare the savannas of East Africa to other tropical savannas using realistic existing models exposed a variety of conflicting models and hypotheses, each emphasizing different aspects of savanna ecology (cf. Huntley & Walker, 1982; Bourliere, 1983; Tothill & Mott, 1985; Cole, 1986; Frost *et al.*, 1986; Walker, 1987). All models agree with the core definition that tropical savannas are characterized by a continuous grass stratum and a discontinuous tree or shrub stratum. Beyond that, the models emphasize different aspects of the structure and function of tropical savannas and the different factors limiting their distributions. The goal of this paper is to examine the validity of these models in relation to East African savannas and to determine which models, if any, realistically describe this biome.

GLOBAL MODELS

Whittaker's model

Among the early models were those by Whittaker (1975) and Holdridge (1947), who described the environmental conditions defining and limiting all terrestrial ecosystems, including tropical savannas. In Whittaker's model, tropical savannas are characterized by low to moderate annual rainfall (500–1300 mm) and by high mean annual temperatures (18–30°C) (Fig. 1). They are bounded by woodlands and forests at higher rainfall regimes, by thorn-scrublands and deserts at lower rainfall regimes, and by temperate grasslands and steppes at lower temperatures. Although the savanna biome within this model is limited by rainfall and temperature, savanna physiognomy (i.e. the ratio of woody plant to grass cover) is dependent on edaphic characteristics and recurrent fire. Deshmukh (1986) recently expanded Whittaker's model to include herbivory as a factor altering tree/grass ratios in tropical savannas.

East African savannas fit Whittaker's model (Fig. 1) exceptionally well. Different locations within the Serengeti ecosystem in northern Tanzania, for example, have mean annual rainfalls of 400–1200 mm (Norton-Griffiths, Herlocker & Pennycuick, 1975) and mean annual temperatures of 15–21°C (Schmidt, 1975; Jager, 1982), placing them within, to slightly below, the rainfall and temperature ranges in Whittaker's model. The few other exceptions include savannas in the Kenyan highlands having mean annual temperatures of less than 18°C (Griffiths, 1969), parts of Tsavo and Amboseli National Parks in southern Kenya that receive an average of 300–500 m rainfall (Western, 1983; Wijngaarden, 1985), and savannas of Turkana District in northern Kenya that receive an average of 150–600 mm annual rainfall (Coughenour *et al.*, 1985).

The close fit between East African savannas and Whittaker's model can be attributed to his allowing tree/grass ratios to fluctuate temporally within the climatic borders of savannas. Many of the areas of East Africa that still support relatively natural biotic systems are characterized by non-equilibrium plant communities in which the vegetation

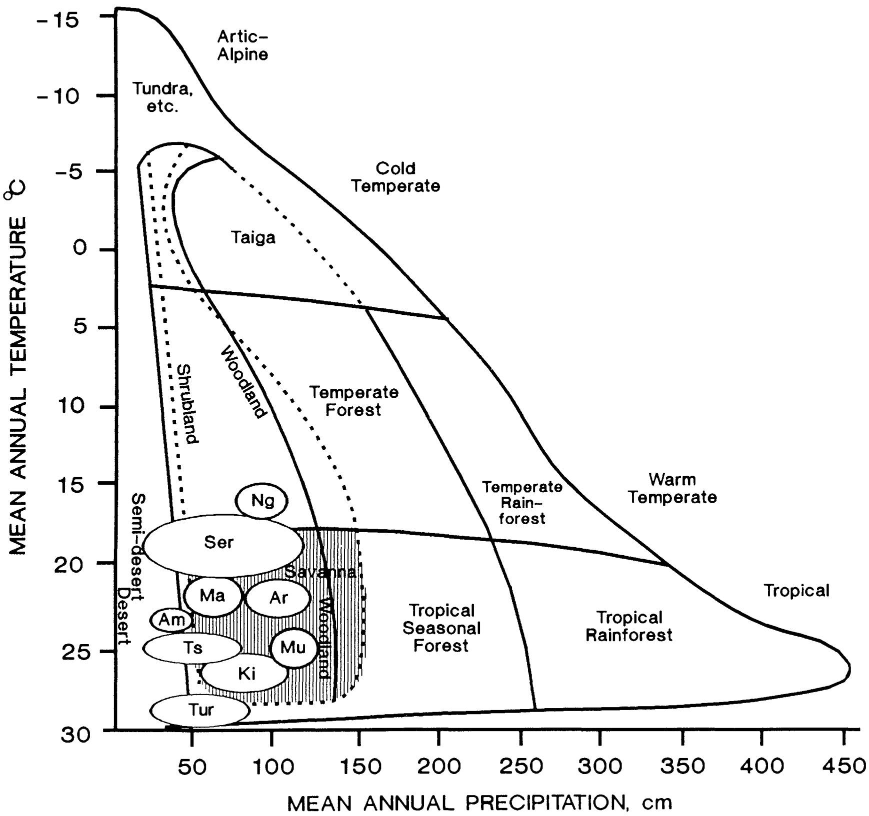

FIG. 1. Relationships of major terrestrial biomes to temperature and rainfall gradients (modified from Whittaker, 1975). The tree/grass ratios within tropical savannas (the shaded area) are determined by edaphic characteristics, fire and large herbivores, especially elephants. The ovals represent the relative positions of Amboseli (Am) and Tsavo (Ts) National Parks and Turkana (Tur) District in Kenya; Arusha (Ar), Manyara (Ma), Ngorongoro (Ng) and Serengeti (Ser) National Parks in Tanzania; and Murchison Falls (Mu) and Kidepo (Ki) National Parks in Uganda. (References are in text.)

cycles between open savanna and woodland (or thorn-scrubland). In areas of high annual rainfall (800–1200 mm) such as the northern, western and central parts of the Serengeti ecosystem in Tanzania, Murchison Falls and Kidepo Valley National Parks in Uganda, and Akagera National Park in Rwanda, woodlands are converted to open savannas during periods of high elephant density or high fire frequency, but they revert back to woodlands when fire frequencies and the densities of elephant and other browsers are reduced (Buechner & Dawkins, 1961; Laws, 1970; Spinage & Guinness, 1971; Harrington & Ross, 1974; Norton-Griffiths, 1979; Pellew, 1983; Smart, Hatton & Spence, 1985; Dublin, 1986). In the Serengeti, this cycling between woodlands and grasslands is accompanied by vegetational changes that have received considerable attention and for which many of the causes are known or can be inferred (Belsky, 1989). In areas of lower rainfall such as in Tsavo National Park, grass productivity and standing dead biomass is low, and fires less frequent. In these areas, natural bush and thorn scrublands are converted to open savannas predominantly by elephants (Thorbahn, 1984; Wijngaarden, 1985).

Holdridge's model

Holdridge devised a triangular model (1947) based on three climate-related parameters – rainfall, temperature and evapotranspiration. In this model, tropical savannas are bounded by dry forest at higher rainfall (>1000 mm), by thorn-forests at lower rainfall (<500 mm), and by thorn steppe and temperate savannas at lower temperatures (<18°C). Although Holdridge increased the number of environmental parameters from two to three, his model is less informative than Whittaker's since the possibility of temporal cycling between grassland and woodland is not included.

REGIONAL MODELS

Simple abiotic models – the Walter/Walker model

Walter (1971) identified rainfall as the major factor governing savanna physiognomy in African savannas. According to his interpretation, in low rainfall areas (<250 mm annually) only grass species, which are shallow rooted, received sufficient moisture to grow, and grasslands dominate. Where rainfall is higher (250–500 mm annually), trees and grasses coexist since rainfall is sufficient for water to percolate to lower soil horizons, allowing the more deeply rooted trees to survive periods of drought. In areas of high rainfall (>500 mm), woodlands dominate since soil moisture is sufficient to support a closed canopy, which shades out the grasses.

Walter's description of savanna function was developed

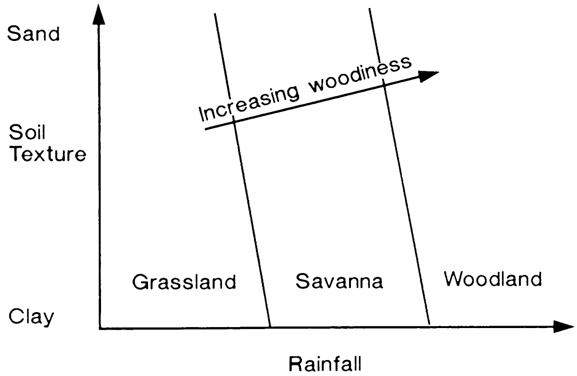

FIG. 2. The Walter/Walker model of tropical savannas (reproduced from Walker & Noy-Meir, 1982). (Permission to reproduce this figure was granted by B. H. Walker.)

and expanded into a series of models by Walker *et al.* (1981) and Walker & Noy-Meir (1982). Their simplest model (Walker & Noy-Meir, 1982) is based on two environmental gradients, rainfall and soil texture (Fig. 2). It predicts an increase in tree density along a gradient of increasing rainfall (but see Walker (1985) for a modified version of this model).

Walter's original model, which was developed for savannas in S.W. Africa, and subsequent models by Walker and his colleagues (1981, 1982) are not valid for East African savannas where communities at the low end of the rainfall gradient are dominated by thorn-scrublands, not by grasslands. In addition, tree/grass ratios in East Africa are determined by fire, soil and herbivory, not by rainfall. Most regions of East Africa that have the proper climatic and edaphic characteristics can, and often do, support a temporal succession of different communities – from grassland to woodland and back again (Belsky, 1989). This capability of supporting a range of tree densities has been demonstrated by vegetational trends monitored within fire- and mammal-proof enclosures. When grassland plots in the central and northern sections of the Serengeti ecosystem were protected from herbivores and fire for more than 2 years, they developed dense thickets of tree seedlings and sprouts, with more than 1000 stems per hectare (Belsky, 1984). Similarly, when open savannas in Tsavo National Park were protected from elephants and fire by deep trenches, they developed into dense thorn-scrublands (Oweyegha-Afunaduula, 1984; Wijngaarden, 1985).

If tree and bush thickets in low rainfall areas are left undisturbed long enough for natural thinning of the trees and bushes to occur, they may eventually develop into open savannas or grasslands. Walter (1971) described the reversion of an *Acacia mellifera* (Vahl.) Benth. subsp. *detinens* (Burch.) Brenan thicket in S.W. Africa to an open savanna after 50 years of protection from grazing. It is also possible that in the absence of fire and elephants the number and density of trees in mature communities would increase along a gradient of increasing rainfall. However, existing pristine vegetation suggests that thorn-scrublands and thickets, not grasslands, would still dominate the lower end of the rainfall gradient. Large sections of Tsavo National Park, for example, are currently covered by *Acacia–Commiphora* scrub, even though rainfall (250–350 mm; Wijngaarden, 1985) and elephant numbers (Ottichilo, 1986) are low.

Natural grasslands do occur in East Africa, but only in areas of unusual edaphic conditions. The Serengeti Plains in the southeastern Serengeti ecosystem consists of treeless grasslands, even when protected from herbivory and fire (Belsky, 1986a, b). This absence of trees has been attributed both to low rainfall (Belsky, 1983, 1987) and to herbivory by large mammals (Bell, 1982; McNaughton, 1983). Low rainfall has been implicated since these grasslands are at the low end of the strong rainfall gradient (400–1200 mm; Norton-Griffiths *et al.*, 1975) that appears to dominate the Serengeti ecosystem. However, 400–700 mm annual rainfall is adequate for tree growth elsewhere in East Africa. In fact, trees grow within the Serengeti Plains on granitic outcrops, called kopjes or inselbergs, where soils are deeper and less alkaline than in the surrounding plains (Anderson & Talbot, 1965; de Wit, 1978). The absence of trees in the plains, therefore, is probably not due to low rainfall.

Bell (1982) assumed that the lack of trees in the Serengeti Plains was due to intense herbivory and McNaughton (1983) concluded that the dominant environmental gradient controlling species composition and community physiognomy in the Serengeti ecosystem was grazing intensity. Attributing the lack of trees in the Serengeti Plains to herbivory, however, is refuted by the fact that trees do not grow in these plains, even when protected from herbivores (Belsky, 1986a, b).

The absence of trees in the Serengeti Plains is due primarily to its unique soils, which are shallow (30–100 cm deep) and highly alkaline (pH 8.0–10.0). The soils are derived from sodic, carbonitic ash originating from nearby volcanoes and are underlain by shallow calcium carbonate (calcrete) layers (de Wit, 1978). It is not clear which factor is more important in limiting tree growth. In the driest part of the Serengeti Plains near Olduvai George (≈400 mm annual rainfall), seedlings of *Acacia tortilis* (Forsk.) Hayne occasionally occur in the grasslands, but they do not grow taller than 50 cm except where soils are deeper (on dunes) or have been modified by high concentrations of cattle dung inside abandoned stock enclosures (Belsky & Amundson, 1986).

The dominant gradient influencing the vegetation of the Serengeti, from short grasslands in the south to dense woodlands in the north, is most properly labelled a 'complex' gradient (Whittaker, 1975) since it consists of a combination of: increasing rainfall, decreasing grazing, and decreasing soil salinity (soil pH declines from 10.0 to 6.0). These three factors are not independent since salts are more strongly leached out of soil by the higher rainfall occurring in the north (Anderson & Talbot, 1965; de Wit, 1978), and grazing patterns are directly related to grass productivity, which increases with increasing rainfall. All three factors affect vegetational composition and distribution independently (McNaughton, 1983; Belsky, 1983, 1986b), but in the Serengeti Plains it is the high salinity and shallow soils that exclude trees, not herbivores or rainfall.

The importance of saline, sodic conditions in creating

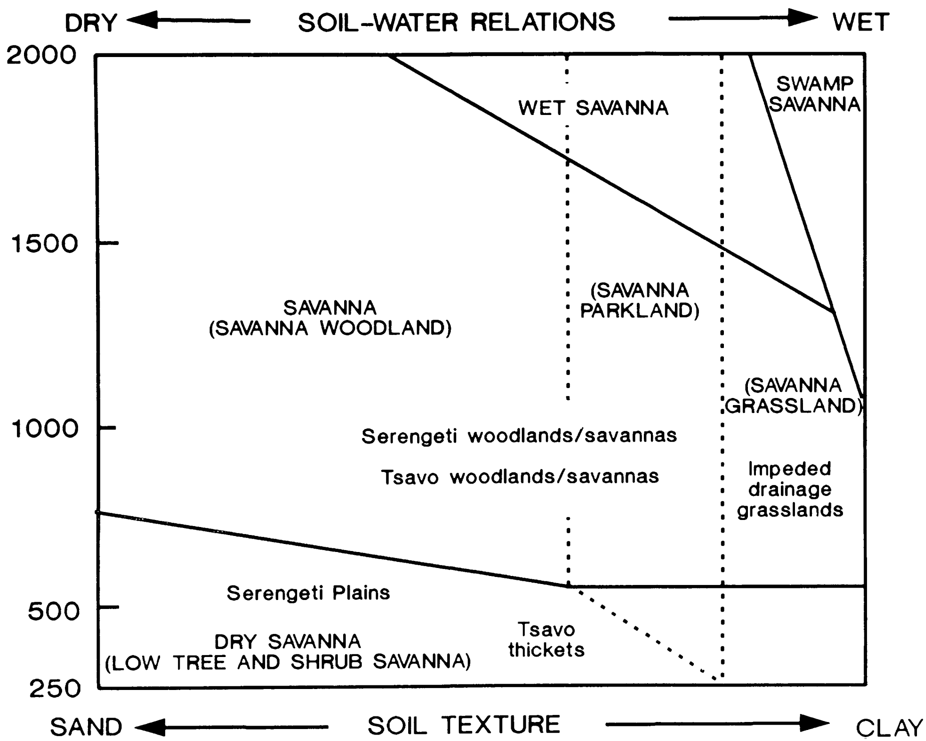

FIG. 3. The Johnson/Tothill model of tropical savannas (modified from Johnson & Tothill, 1985), including the relative locations of East African savannas within the model.

pure or natural grasslands (called edaphic grasslands by Vesey-Fitzgerald, 1973) is confirmed in other parts of East Africa. Trees are absent from saline-sodic soils in Ngorongoro and Manyara National Parks in Tanzania (Anderson & Herlocker, 1973; Prins, 1987) and Amboseli National Park in Kenya (Western, 1983). In Amboseli, neither trees nor shrubs grow inside grazer-proof exclosures erected on sodic soils, but they do occur inside nearby exclosures constructed on more neutral soils (personal observations).

The natural grasslands of East Africa are also strongly associated with poorly drained soils. Trees and shrubs are often excluded from clay-rich black-cotton soils at the bottoms of soil cantenas due to poor water penetration, and from river flood-plains due to seasonally anaerobic conditions (Anderson & Talbot, 1985; Anderson & Herlocker, 1973; Vesey-Fitzgerald, 1973, 1974; Pratt & Gwynne, 1979; de Wit, 1978; Prins, 1987; Jager, 1982).

Simple abiotic models – the Johnson/Tothill model

Johnson & Tothill (1985) published a model of savannas (Fig. 3) that is similar to the Walker/Noy-Meir (1982) model in that it is also based on rainfall and soil texture. However, in their model, grasslands occur under the wettest conditions (600–2000 mm annual rainfall and high soil clay concentrations), not under the driest conditions. At the dry end of their rainfall/soil texture gradient (≈375 mm rainfall and sandy soil), savanna-woodlands and parklands are replaced by low tree and shrub savannas, not by grasslands. East African savannas fit comfortably within this model since natural grasslands often occur on the wettest soils. In Fig. 3 the placement of the grasslands of the Serengeti Plains on the dry end of the gradient is due to their unique soil characteristics (see above).

Walker's multi-factor model

Taking a less reductionistic approach to the description of tropical savannas, Walker (1987) developed a model that incorporated all important environmental factors influencing the vegetation structure of tropical savannas. This model shows the complexity of ways that environmental factors interact. A modified example of this model (Fig. 4) illustrates that the vegetation of East African savannas is most strongly influenced (the large arrows) by rainfall, which influences species composition through its effects on soil moisture and chemistry, by soil chemistry, which effects tree and grass species composition (Anderson & Talbot, 1965; Herlocker, 1976; de Wit, 1978; Jager, 1982; Wijngaarden, 1985), by fire and elephants, which reduce tree cover and prevent its regeneration (Laws, 1970; Buechner & Dawkins, 1961; Norton-Griffiths, 1979; Pellew, 1983; Dublin, 1986), and by grazing ungulates, which affect grassland species composition (Lock, 1972; Edroma, 1981; McNaughton, 1983; Belsky, 1984, 1986a, b, 1987).

Functional classification model

Savanna ecologists have recently developed a new functional model of tropical savannas (Frost *et al.*, 1986; Medina, 1987; Goldstein *et al.*, 1988). This model is based

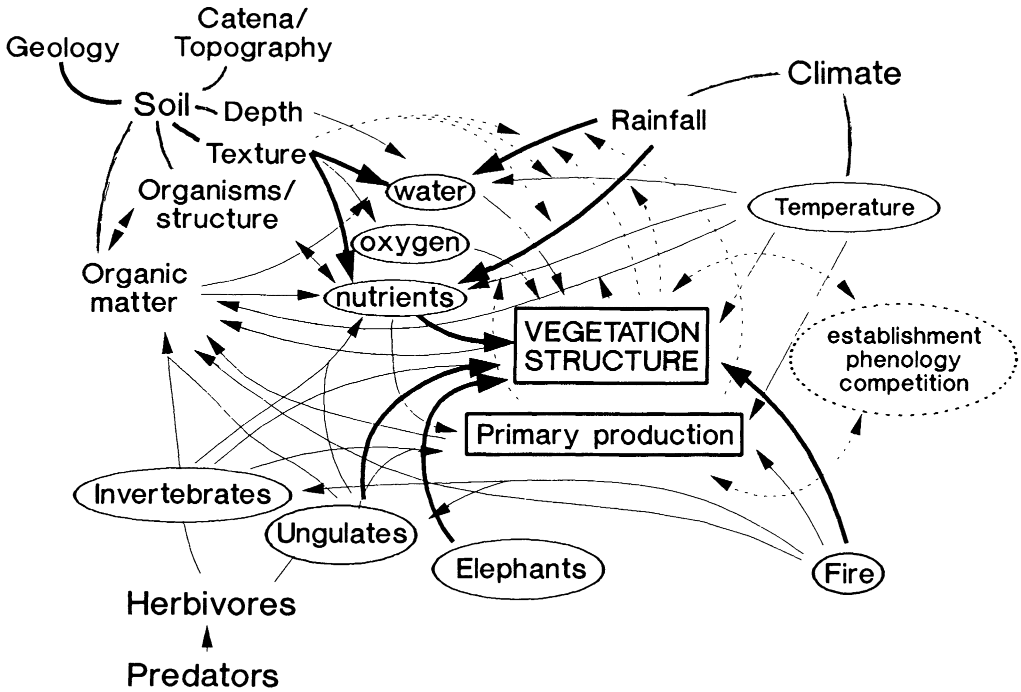

FIG. 4. Walker's multi-factor model of the determinants of vegetation structure in East African savannas (modified from Walker, 1987). The large arrows indicate the major environmental determinants of vegetation structure.

on two variables – plant available moisture (PAM), which integrates rainfall, water infiltration, evapotranspiration, soil texture, and hydrologic regime into a single measure of the soil moisture available to plants, and available nutrients (AN), which is a measure of the nutrients available to plants during their period of growth (Fig. 5). This model is novel since it substitutes biologically meaningful measures (PAM and AN) for purely physical variables.

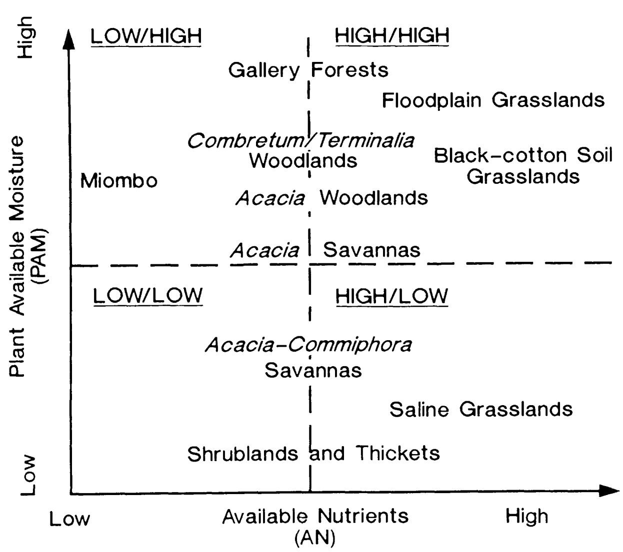

FIG. 5. Functional classification model of tropical savannas along gradients of available moisture and nutrients, and the relative positions of East African savannas within the model (modified from Frost *et al.*, 1986).

Since the axes of the functional model have not yet been well defined, the placement of savannas or community types within the model can only be approximate. East African grasslands were placed high on the AN axis, supporting Bell's (1982) observation that plant biomass in savanna communities decreases with increasing soil nutrients. It does not confirm his theory that the decrease is due to increased herbivory (Bell, 1982). Instead, it is probable that the low plant biomass (i.e. a low density of trees) in East African savannas is due to edaphic characteristics such as high soil salinity and anaerobic conditions that are often positively correlated with high soil-nutrient content.

CONCLUSION

Of the several models available for the comparison of tropical savannas around the world, those by Whittaker (1975) (Fig. 1) and Johnson & Tothill (1985) (Fig. 3) have the most immediate utility. Mean annual rainfall and temperature and descriptions of soil texture are already available in the literature or are easily collected. And they are heuristically acceptable. The functional classification model (Frost *et al.*, 1986; Medina, 1987) allows for the most accurate comparison of savanna function, but until the axes of this model are associated with quantifiable variables, the model provides little improvement over earlier models.

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