



Functional differentiation of biomes in an African savanna/forest mosaic



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ABSTRACT

Tree densities in tropical and sub-tropical vegetation have, until recently, long been understood as increasing proportionally in response to precipitation. Current understanding is that trees are organised into alternative states with divergent properties that are linked, in the case of savannas, to frequent grass-fuelled fires or the absence of fire in non-savannas. In this paper we explored the hypothesis of functional divergence in three biomes, defined structurally by their dominant growth forms: savannas, 'thicket' and forest, within the vegetation of a South African park (Hluhluwe-iMfolozi). Thicket and forest both lack a continuous C4 grassy layer and are therefore non-savannas. 'Thicket', as defined here, has shorter trees than forests (4–6 m vs. >10 m) and, often a dense understorey of sub-shrubs. We analysed tree species composition in 253 sites across these three biomes. We then compared herbivore use and fire frequency among the three biomes. Finally we characterised functional traits for 58 tree species including several linked to fire and herbivore responses. In support of the emerging alternative states paradigm for both tree density and phylogenetic composition, we found that the three structurally defined biomes had separate tree species assemblages. Differences in growth form, especially the presence or absence of C4 grasses had key consequences for consumers with high fire frequency in savannas, low in thickets and none in forest and high grazing in savannas, high browsing in thickets and very low herbivory in forests. Trait analysis was consistent with these differences among biomes. Consumers appear to be important environmental filters by admitting some tree species to a biome and excluding others, depending on their functional traits. Positive feedbacks between vegetation and consumers may explain the coexistence of biomes in areas with similar climate and geology.

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1. Introduction

The biome concept was introduced more than a century ago to categorise ecologically similar ecosystem types, regardless of floristic compositional differences, at large spatial scales (e.g. tropical forest, Mediterranean-type shrubland, boreal forest, etc.; Schimper, 1902). At that time, there was little global data on climate, and biome distributions were assumed to be mainly the result of climate control (e.g. Whittaker, 1975). Climate classifications such as those of Köppen–Geiger were designed to align with major vegetation patterns (Keddy, 2007; Peel et al., 2007). This has resulted in a circular argument linking climate and biome distribution that has become an obstacle to understanding the true determinants of major vegetation patterns. Bond (2005) showed for example that Whittaker's ordination of world ecosystems based on temperature/precipitation fails to predict biome distribution in a large fraction of the world where wildfire is common.

An alternative to the climate-based definition of biomes defines them as having particular growth forms or mixtures of growth forms (Woodward et al., 2004), such as trees and grasses in savannas (Ratnam et al., 2011). Separating biomes on the basis of their vegetation structural components (i.e. growth forms) allows objective assessment of the relative influence of various environmental factors, including climate, soil type, herbivory or fire regimes, on biome distribution (Lehmann et al., 2011, 2014). In some vegetation types, the growth forms themselves create the critical environmental conditions that permit or exclude competing plant types. Growth forms that promote, or exclude, fire are widespread examples (Mutch, 1970). Considerable research over the last decade has led to the recognition of alternative biome states constructed from fire-promoting or fire-suppressing growth forms (e.g. Wilson and Agnew, 1992; Warman and Moles, 2009; Staver et al., 2011a,b; Hirota et al., 2011; Wood and Bowman, 2012). Savannas and forests are widely divergent vegetation types, with strikingly different growth forms, growing in the same climate and, often, on the same soils. Mesic savannas occur in climates suitable for forests but are maintained by frequent fires creating a positive feedback that promotes the shade-intolerant and highly flammable C4 grasses that characterise this biome (Bond et al., 2005; Staver et al., 2011b). Identifying the

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environmental filters that are created by the vegetation itself that are responsible for these alternative stable states and the functional responses of species is now a promising way of understanding biome distribution (Hoffmann et al., 2012a,b; Dantas et al., 2013).

The vegetation found in Hluhluwe-iMfolozi Park (HiP), South Africa, illustrates well how strikingly different vegetation types (forest and savanna) can coexist within the same landscape in the same climate and similar soil types (Coetsee et al., 2013). Past research has revealed that both herbivores and fire can play a role in maintaining the discontinuous woody cover that is characteristic of savanna (Staver et al., 2009; Staver and Bond, 2014). Since grazers and fire both consume limited grass biomass and can in extreme cases exclude each other, they can produce divergent species compositions and trait distributions (Bond et al., 2001; Staver et al., 2012). Forest trees, meanwhile, cast sufficient shade to exclude C4 grasses (Sage and McKown, 2006) removing fuel for fire (Hennenberg et al., 2006), and alter microclimates reducing wind speed and maintaining higher moisture conditions in the understorey. This inhibits the spread of fires into forest understoreys (Hoffmann et al., 2012b; Little et al., 2012; Ibanez et al., 2013).

Structurally defined 'biomes' also differ functionally. Ratnam et al. (2011) noted the importance of a functional definition to separate savanna woodlands versus closed forests in Indian savannas. When 'forests' are defined simply by the presence of some minimum cover, density, or biomass of trees, profound ecological differences between forest and savannas with similar tree cover are obscured. The consequence of such definitional confusion is to group together vegetation types with completely divergent responses to management interventions. For example the role of a frequently burning C4 grassy understorey could be overlooked potentially leading to fire suppression and cascading consequences for the fire-adapted biota of a savanna misclassified as a forest (Stott, 1988; Bond and Parr, 2010; Parr et al., 2012; Veldman et al., 2013; Parr et al., 2014). Ratnam et al. (2011) suggest a range of functional traits of woody species that differ between pyrophytic savannas and pyrophobic forests. These include, for savannas, thick bark, insulated buds facilitating epicormic sprouting, and root suckering all enabling post-burn resprouting. Several studies have supported these, and other, functional trait differences between forest and savannas in South America (Hoffmann et al., 2003, 2005, 2012a; Simon and Pennington, 2012) and Australia (Lawes et al., 2013). However there seem to have been no formal studies in Africa exploring functional differences across biomes.

Hluhluwe-iMfolozi Park hosts a diverse mega-fauna and has spatially variable fire regimes, making it an ideal place to test the following hypotheses: (i) that biomes, as defined by their dominant growth-form, have divergent woody communities; (ii) that the vegetation structure of biomes affects herbivore use and fire frequency; and (iii) that functional traits related to herbivory, fire or competition for light are distinct across biomes. In this paper, we analysed the species composition of the woody communities in three hypothesised biomes (savanna, forest, and thicket), defined by their vegetation structure at 253 sites in HiP. We then compared the herbivore use and fire regimes in the three biomes. Lastly we analysed functional traits of the most abundant tree species in each biome related to life in the shade, survival of mammalian herbivory and of fire.

2. Materials and methods

2.1. Vegetation description

This study was conducted in Hluhluwe-iMfolozi Park (28°00'S to 28°43'S, 31°70'E to 32°14'E) in KwaZulu-Natal, South Africa. The vegetation in the park ranges from acacia-dominated savannas to treeless grasslands at the highest elevations and includes broad-leaved thickets and tall forests (Whateley and Porter, 1983). Rainfall in the park varies with elevation and the study sites received rainfall of ~600 to ~1000 mm per year (Balfour and Howison, 2002).

We identified three 'biomes' based on differences in vegetation structure associated with different dominant growth forms (Woodward et al., 2004; Ratnam et al., 2011):

- Savanna: discontinuous tree cover with a continuous layer of C4 grasses.
- Thicket: dense shrub and treelet vegetation. The canopy is generally 4 to 6 m tall and open. The understorey is variable with, usually, a dense layer of herbaceous sub-shrubs and shrubs but also occasional patches of shade-tolerant grasses.
- Forest: woody tall (>10 m) vegetation with no C4 grass layer; forests have an intermediate shade-tolerant tree layer. The forest floor is usually a litter layer with occasional patches of herbaceous plants, including C3 grasses.

We evaluated the proportion of each of these biomes from Whateley and Porter's (1983) vegetation map by re-defining plant communities according to biome type (Appendix). A total of 253 sites (Fig. 1) was selected in the park in a stratified manner designed to sample the three biomes in proportion to their relative extent in the park. We sampled 202 sites in savanna, 37 in thicket and 14 in forest. We sampled mature thicket patches that were more than 200 hectares wide in 1983 (except one patch that was 54 hectares).

Each site was sampled using a 40 m × 10 m transect where every woody plant taller than 50 cm was counted and attributed to one of the four different size classes: 0.5–2, 2–5, 5–10 and >10 m. Cumulative height was used to describe species abundance (Fei et al., 2005). Species nomenclature is based on Palgrave (2002).

2.2. Fire frequency and herbivore use

Spatially explicit fire records were available and the frequency of fires at each site for the period 2002–2012 at each site was extracted from Hluhluwe iMfolozi Park records. The number of fires for this decade ranges from 0 to 7. Herbivore use was estimated using dung counts as no spatially explicit record of herbivore density is available

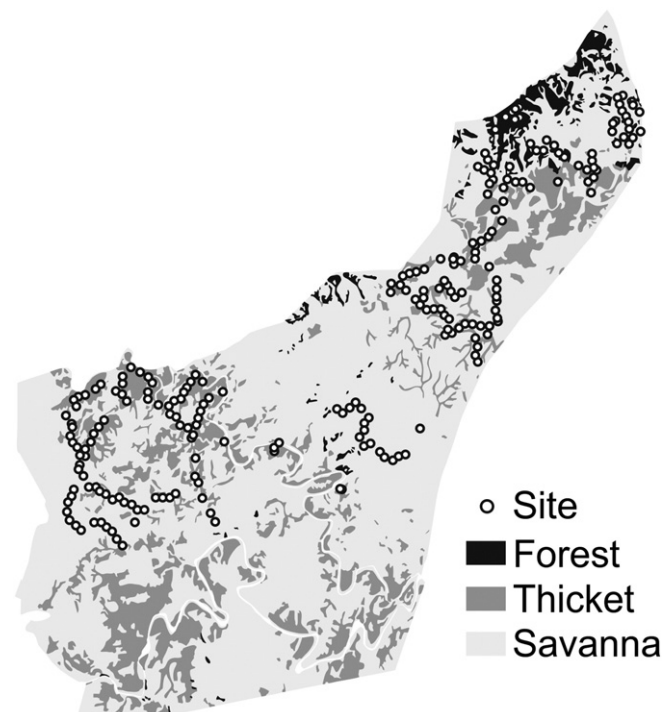


Fig. 1. Biome distribution in Hluhluwe-iMfolozi Park.

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