ECOLOGICAL SOUNDING

When is a 'forest' a savanna, and why does it matter?

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ABSTRACT

Savannas are defined based on vegetation structure, the central concept being a discontinuous tree cover in a continuous grass understorey. However, at the high-rainfall end of the tropical savanna biome, where heavily wooded mesic savannas begin to structurally resemble forests, or where tropical forests are degraded such that they open out to structurally resemble savannas, vegetation structure alone may be inadequate to distinguish mesic savanna from forest. Additional knowledge of the functional differences between these ecosystems which contrast sharply in their evolutionary and ecological history is required. Specifically, we suggest that tropical mesic savannas are predominantly mixed tree–C_4 grass systems defined by fire tolerance and shade intolerance of their species, while forests, from which C_4 grasses are largely absent, have species that are mostly fire intolerant and shade tolerant. Using this framework, we identify a suite of morphological, physiological and life-history traits that are likely to differ between tropical mesic savanna and forest species. We suggest that these traits can be used to distinguish between these ecosystems and thereby aid their appropriate management and conservation. We also suggest that many areas in South Asia classified as tropical dry forests, but characterized by fire-resistant tree species in a C_4 grass-dominated understorey, would be better classified as mesic savannas requiring fire and light to maintain the unique mix of species that characterize them.

Keywords
Degraded forests, fire tolerance, functional traits, mesic savannas, shade intolerance, South Asia, tropical dry forests, tropical savannas.

Savannas are mixed tree–grass systems characterized by a discontinuous tree canopy in a continuous grass layer (Scholes & Archer, 1997; House *et al.*, 2003, and references therein). Within the bounds of this definition, actual tree cover in the world's savannas is highly variable, such that they range from sparsely 'treed' grasslands to heavily 'treed' woodlands, often along a gradient of increasing precipitation, but also modified by edaphic factors (Scholes & Archer, 1997; Sankaran *et al.*, 2005; Lloyd *et al.*, 2008). This classical definition of savannas accurately captures the salient structural features of savanna vegetation, but contains little information about the functional ecology or evolution of these ecosystems. This distinction can be a critical one in a few important instances, as we illustrate below.

Across the globe, there is much concern over what is referred to as the 'savannization' of tropical forests but this is primarily a structural reference to loss of trees from tropical forest areas to clear felling or logging, often followed by fires (see Barlow & Peres, 2008, for more on the 'savannization' issue). While such degraded forest areas, which are extensive in the tropics, may 'look' like savannas due to low tree cover, their functional ecology in terms of which species predominate and how these communities respond to perturbation is entirely different from that of true savannas (Barlow & Peres, 2008; Malhi *et al.*, 2009). Likewise, at the mesic end of the tropical savanna biome where densely wooded savannas occur alongside forests, transitions between the savanna and forest may either be abrupt or may occur gradually through a savanna–forest

ecotone. In the latter case, distinguishing a 'treed' savanna from a degraded forest based only on vegetation structure may be problematic, whereas there would be large functional and compositional differences between the two ecosystems. Clearly, in these contexts, the structural definition of savannas alone is inadequate to distinguish mesic savanna from forest; what is additionally needed is knowledge of differences in the functional ecology of these ecosystems. In this contribution, we outline critical differences between tropical mesic savanna and forest environments, and identify a suite of contrasting physiological, morphological and life-history traits that differ between them from the individual to the community level. We suggest that these functional traits, which reflect both ecological function and evolutionary history, should be used to dis-

tinguish between mesic savannas and degraded forests (Key 1, Table 1) and thereby aid in appropriate management and conservation of these systems.

Recent literature on savannas explicitly recognizes that tropical savannas are predominantly mixed tree–C_4 grass systems (Bond *et al.*, 2003; Bond, 2008; Lehmann *et al.*, 2009; Bond & Parr, 2010; Edwards *et al.*, 2010). More importantly, regardless of the extent of tree cover, which can be highly variable, and with rare exceptions such as some regions of Neotropical cerrado where C_3 grasses co-dominate (Lloyd *et al.*, 2008; Edwards *et al.*, 2010), the presence of a C_4 grass-dominated understorey is the key feature that distinguishes tropical savanna from forest. C_4 grasses have two key traits which in turn feed back to define the functional ecology of mesic savanna

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Key 1

A guide to distinguish between true forests, degraded forests and mesic savannas using a combination of community and species level traits.
1. Closed canopy (Forest)
1. Not closed canopy (2)
2. C_4 grass species absent (Not savanna)
2. C_4 species present (3)
3. Dominant tree species able to regenerate in closed canopy forest (Degraded forest)
3. Dominant tree species do not occur in forest (Savanna)
3. Tree habitat uncertain (refer to Table 1)

Table 1 Comparison of physical environments, species composition and traits of dominant tree species in savannas versus forests.

Habitat type	Mesic savanna	Forest
Environmental descriptors	High-light understorey	Low-light understorey
	Frequently burnt	Fires rare, catastrophic
Vegetation composition	Trees	Trees
	Herbs	C_3 grasses
	C_4 grasses	Herbs
Adult trees		
Architecture	Relatively shorter	Relatively taller
	Narrower canopy diameter for a given basal area	Wider canopy diameter for a given basal area
Bark	Thick bark	Thin bark
Canopy	Lower specific leaf area	Higher specific leaf area
	Open crowns and higher light penetration through canopy	Dense crowns and lower light penetration through canopy
	Post-fire recovery of canopy either epicormic, or from protected apical buds	Limited post-fire recovery of canopy
Saplings	Many have vertical pole-like architecture	Varied, branched and unbranched architecture
	High root: shoot ratio	Low root: shoot ratio
	Large underground storage	Low underground storage
	Post-fire resprouting common under frequent, intense fires	Post-fire resprouting rare under frequent, intense fires
Seedlings	Rapid acquisition of resprouting ability through early allocation to root	No obvious acquisition of resprouting ability
	Persist through competition with C_4 grasses and repeated fire to sapling stage	Cannot persist through competition with grasses and repeated fires
Reproductive strategy of tree community	No or few species are obligate seeders, reproduction through root-suckering common	Reproduction through root-suckering uncommon

communities in high-rainfall regions: they are highly fire tolerant and highly shade intolerant. Given sufficient biomass (as occurs when rainfall is high), C_4 grasses are highly flammable when the grasses cure during the dry season. Consequently fire becomes a fundamental feature of the more humid savanna systems (Sage, 2004; Bond et al., 2005; Beerling & Osborne, 2006; Bond, 2008; Cardoso et al., 2008; Chuvieco et al., 2008; Bowman et al., 2009; Bond & Parr, 2010). We emphasize here that the source of the fire, whether natural or anthropogenic, is not useful in distinguishing between natural savannas and degraded forest systems, because anthropogenic fire has long replaced natural fire in almost all ecosystems. What is important is that C_4 grasses have high productivity, low decomposition rates, high C:N ratios, a fuel structure that readily carries fire and dry out rapidly in the dry season; they are thus inevitably flammable and promote fires where they produce sufficient biomass (d'Antonio & Vitousek, 1992; Mouillot & Field, 2005; Bond, 2008; Cardoso et al., 2008). Because of this association with fire, both C_4 grasses and the savanna trees that grow with them are typically highly fire tolerant. In contrast, most C_3 grasses are shade loving (Klink & Joly, 1989) and do not tolerate fire as readily as C_4 grasses. They remain green much longer into the dry season, have smaller below-ground reserves and do not recover biomass as rapidly after fires (Ripley et al., 2010), and thus do not drive the fire ecology of systems where they occur as do C_4 grasses.

Fires result in open, sunlit environments which lead to the other important characteristic of savanna communities: savanna species, both trees and C_4 grasses, do not readily tolerate shade. Indeed, C_4 grasses have high light requirements and are shade intolerant (Sage & McKown, 2006). In mesic areas, they indirectly depend on fires to maintain their preferred light levels, such that under regimes of fire exclusion these grasses can die from self-shading (Everson et al., 1988; Uys et al., 2004). Likewise, savanna trees appear to be largely shade intolerant as suggested by their inability to recruit in shaded conditions and their absence from shady, forest areas (Smith & Shackleton, 1988; Hoffmann et al., 2004). Shade intolerance thus becomes the other defining feature of savanna systems, inseparably linked to prevalence of fires. Mesic savannas are thus relatively open, sunlit environments where C_4 grasses dominate the understorey and fires are a frequent occurrence. In contrast, forests are characterized by closed, shaded environments where C_4 grasses are absent from the understorey, which is dominated by herbaceous life forms and may contain some C_3 grasses. Forest species, both trees and understorey herbs and grasses, are largely shade tolerant but markedly fire intolerant (Uhl & Kauffman, 1990; Cochrane et al., 1999; Barlow et al., 2003; Barlow & Peres, 2008; Gignoux et al., 2009). Although some forest species are shade intolerant, these are fast-growing pioneer species with a suite of life-history traits unlike those of savanna trees (Hoffmann & Franco, 2003).

A suite of morphological and physiological features of savanna trees (Table 1) are best interpreted as adaptations to fire.

1. Seedlings rapidly allocate resources to roots and large underground storage organs, both of which are important for establishment and resprouting in a fire-prone environment (Wilson & Witkowski, 1998; Hoffmann & Franco, 2003; Hoffmann et al., 2003; Fensham & Fairfax, 2006; Overbeck & Pfadenhauer, 2007; Schutz et al., 2009; Simon et al., 2009; Wigley et al., 2009; Bond & Parr, 2010).

2. Once established, saplings are often characterized by rapid upward growth as the sapling bolts to escape the flame zone (Higgins et al., 2000; Wigley et al., 2009). Since most fires in savannas tend to be surface fires, they generally only consume grass biomass and young trees, but not adult trees (Williams et al., 1999; Hoffmann & Solbrig, 2003; Bond, 2008; Hanan et al., 2008). As a consequence, savanna tree saplings are highly fire tolerant and generally recover by rapidly resprouting from large underground storage organs, often persisting through repeated fires that 'topkill' or remove all aboveground biomass (Hoffmann, 2000; Bond & Midgley, 2001; Hoffmann et al., 2004; Schutz et al., 2009).

3. As adult trees, many savanna species have thick bark which protects the inner cambium and minimizes damage from fire (Champion & Seth, 1968; Gignoux et al., 1997; Hoffmann et al., 2003, 2009). This feature, in combination with the surface fire regimes that are typical in savannas, results in very low fire-related mortality in adult savanna trees.

4. Finally, many savanna trees have the capacity to recover their canopy by epicormic sprouting and/or from protected apical buds following leaf scorch from fire (Burrows, 2002, 2008; Williams, 2009).

The frequent fires and high-light conditions that characterize savannas and the infrequent fires and shaded conditions that characterize forests are also reflected in the architecture of adult trees. Forest trees growing in shade are under selective pressure both to rapidly grow tall to access light and to grow wide to shade out neighbours. Forest trees may thus have tall trunks and branch into relatively wide and dense canopies. In contrast, mesic savanna trees, primarily under selection to escape from the flame zone, are shorter and, for a given girth, branch into crowns with relatively narrower diameters (Archibald & Bond, 2003; Rossatto et al., 2009; Wigley et al., 2009). Interestingly, adult savanna trees also have lower specific leaf areas (SLA; leaf area per unit leaf mass) than forest trees (Prior et al., 2003; Hoffmann et al., 2005; Rossatto et al., 2009), and canopies that are less dense and more light permeable than forest trees (Hoffmann et al., 2005). These features allow C_4 grasses and shade-intolerant savanna seedlings to persist in the understorey.

In savanna tree communities that are regularly burnt, species that are obligate seeders are virtually absent, while reproduction from root suckering is a common feature (Champion & Seth, 1968; Lacey and Johnston, 1990; Hoffmann, 1998; Wakeling & Bond, 2007). Critically, savanna trees are able to recruit and persist through *repeated* fires (Bond & Midgley, 2001; Gignoux et al., 2009; Schutz et al., 2009). In forest communities, both obligate seeders and resprouters occur, but evidence from more humid forests suggests that while some resprouters do survive individual fires, they are unable to tolerate repeated burning (Uhl et al., 1981; Fensham et al., 2003; Bowman, 2005; Barlow & Peres, 2008; Gignoux et al., 2009). Studies from Neotropical dry

forests (Pinard *et al.*, 1999; Otterstrom *et al.*, 2006) and transitional evergreen forests (Balch *et al.*, 2008; Hoffmann *et al.*, 2009) suggest lower levels of fire-driven mortality in these tree communities following a single fire when compared with more humid forests, but little is known about the responses of these systems to repeated burning (but see Balch *et al.*, 2008). This potential differentiation between dry forests where fires occur at low frequency and humid forests where fire is a rare, catastrophic event clearly merits further study.

With fire protection, forest tree species can colonize a savanna (Bowman & Fensham, 1991; Fensham & Butler, 2004; Russell-Smith *et al.*, 2004; Hoffmann *et al.*, 2005; Rossatto *et al.*, 2009). Forest tree seedlings that colonize a savanna appear to have a wider range of shade tolerance and tend to present higher radial growth rates, and larger and denser crowns, despite the limited resources in savanna environments (Rossatto *et al.*, 2009). On the other hand, savanna seedlings appear to be far less shade tolerant than forest species (Lynch & Neldner, 2000; Hoffmann *et al.*, 2005), although this distinction requires more detailed investigation. In addition, it appears that there are other inherent barriers to the colonization of forest by savanna trees. Experimental evidence suggests that forest soils, despite being enriched in organic matter, may be hostile to savanna trees, potentially because of an antagonistic microbial environment (Bowman & Panton, 1993; Bowman & Fensham, 1995). These differences in seedling traits suggest that, all else being equal, tree species from forests are more likely to expand into savannas than vice versa. Indeed, several studies of the dynamics of forest–savanna boundaries in Asia, South America and Australia suggest a trend of forests expanding into adjacent savannas in recent historical time (Puyravaud *et al.*, 2003; Prior *et al.*, 2004; Russell-Smith *et al.*, 2004; Silva *et al.*, 2008; Rossatto *et al.*, 2009).

Regular fire regimes that are characteristic of mesic savannas sharpen the boundaries between savanna and forest. Fires extinguish at the savanna–forest edge where dry C_4 grasses are replaced by relatively moister leaf litter in the forest understorey (Biddulph & Kellman, 1998; Hennenberg *et al.*, 2006; Gignoux *et al.*, 2009). Fires also kill forest seedlings that have invaded savannas (Hoffmann, 2000; Fensham *et al.*, 2003; Fensham & Fairfax, 2006). The filtering of savanna and forest tree floras by fire and shade ensures that there are few species in common across regularly burnt boundaries, and this sharp turnover in species is diagnostic of two distinct biomes (Felfili & Silva Junior, 1992; Fensham *et al.*, 2003; Hoffmann *et al.*, 2009; Rossatto *et al.*, 2009; Bond & Parr, 2010). However, in extended forest–savanna ecotone regions where fire has been suppressed or where forests have been opened up by logging and disturbances, this distinction becomes blurred and may result in misidentification of a savanna as a forest and vice versa. However, a careful examination of functional traits of trees in these regions (Key 1, Table 1) should enable correct identification.

Recognizing whether a given area is a mesic savanna or a degraded forest is not merely a semantic problem; it can have important functional consequences for how such areas are conserved and managed. Well-developed closed forest stands retard

fire. When closed forests do burn, often after logging and under extreme weather conditions, the results are catastrophic (Nepstad *et al.*, 1999; Cochrane & Laurance, 2002; Laurance, 2003). Even slow-moving fires with low flame heights can be disastrous in causing the canopy to open up, generating more fuel and making the forest vulnerable to more fires (Cochrane *et al.*, 1999; Cochrane & Laurance, 2002; Barlow & Peres, 2004). Forests opened up by fire are often colonized by exotic weeds including shrubs such as *Lantana* and perennial grasses (d'Antonio & Vitousek, 1992; Panton, 1993; Fensham *et al.*, 1994; Hiremath & Sundaram, 2005) which may inhibit the recruitment of native tree seedlings (Hoffmann & Haridasan, 2008). Forest restoration in such degraded areas is difficult, requiring fire suppression in combination with weed removal and/or planting of native forest tree seedlings to restore communities.

In striking contrast, mesic savanna systems require frequent burning to maintain the compositional mix of trees and grasses. Across large areas in South and Southeast Asia, the status of grassy forests is uncertain. We suggest that many of these areas that are categorized as tropical dry forests should in fact be considered tropical mesic savannas according to the criteria we have listed. Fire suppression in such systems may be just as disastrous for ecosystem structure and composition as deforestation fires in closed forests (Durigan & Ratter, 2006). Stott (1988) evocatively compares the deciduous *Dipterocarp* and *Shorea* 'savanna forests' in Thailand to a 'phoenix', outlining a range of species traits that promote regeneration following fire. The suite of traits he describes include thick bark, rapid regrowth and resprouting from dormant root buds following fire – traits that we recognize as characteristic of mesic savanna tree species. Likewise, large tracts of peninsular India classified as 'tropical dry deciduous forests' (*sensu* Champion & Seth, 1968) are characterized by varied associations of fire-resistant *Anogeissus*, *Lagerstroemia*, *Terminalia* and *Tectona* species dominating the tree community, and tellingly, an understorey rich in tall C_4 grasses (W.J.B., J.J.R. and M.S., personal observations). Yet, across South and Southeast Asia, management of these 'forest' systems is often characterized by an official policy of fire suppression (Stott, 1990), with potentially deleterious impacts in the form of excessive fuel loads building up in the understorey and reduced recruitment of shade-intolerant seedlings. At the other extreme, in some community-managed 'tropical dry forest' systems in western India, annual burns are set for the collection of forest produce such that composition of the tree community has shifted towards a less diverse subset of the most fire-resistant, root-sprouting species (Saha & Howe, 2003). Reinstating the correct burning and/or grazing regimes in these areas may be an important component of their restoration to their original state.

The distinction between mesic savannas and forests is also important from the perspective of biodiversity conservation. Apart from the fact that these communities contain broadly different and distinct floras, diversity in the two communities is differently structured. Specifically, mesic savannas may harbour much of their biodiversity in the form of a diverse forb

community within the grass layer. They may also harbour a distinct and diverse community of light-demanding shrubs (Bond & Parr, 2010). For example, Stott (1990) reports a high diversity of understorey species, including many geophytes in mesic *Dipterocarp* savanna-forests from Thailand, while Uys *et al.* (2004) report high forb diversity in mesic savannas of South Africa. In a study of 40 savanna-grassland communities in southern India, Sankaran (2009) reports 278 species of herbs and grasses in the understorey, with most species highly restricted in their distribution, and many used in traditional medicine in the region. Where mesic savannas are inappropriately managed as forest systems with a primary focus on tree species, or where they are viewed as transitional communities on a successional trajectory to forests, this enormous diversity in the understorey and the mechanisms that maintain it may be overlooked.

ACKNOWLEDGEMENTS

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BIOSKETCH

Working Group WG-49 'Savanna Structure and Variation' http://www.vegfunction.net/wg/49/49_Savanna_Structure.htm is a group of savanna ecologists from across the globe working together to better understand savanna structure and function. Using comparative data on savanna vegetation, climate, fire, edaphic factors and other drivers from multiple continents, the group is working towards a better understanding of the global distribution of savannas, similarities and differences between savannas on different continents and the potential drivers of these patterns.

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