Understanding plant community assemblage, functional diversity and soil attributes of Indian savannas through a continuum approach

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Abstract: Globally, tropical dry forests and savannas have decreased considerably during the past few decades, which may have climatic repercussions. Forests and savannas are considered important sources of food and fuel for the local inhabitants, along with their rich biological and functional diversity. Anthropogenic pressure and climate change are becoming a growing global concern due to their adverse effects on vegetation structure and diversity. In general, savannas occur within forests and grasslands as a mosaic of patches. These adjacent systems (forests and grasslands) may represent a gradient of various geological and ecological attributes (e.g. climatic, edaphic and functional diversity) which can be better understood by studying these in a continuum approach (forest-savanna-grassland continuum) and through the identification of variations at grassroots level. Moreover, this enhanced understanding would be important in a global climate change perspective, since a change in the forest-savanna-grassland continuum, or its community dynamics, may have consequences on soil C sequestration and CO₂ efflux, which may exacerbate changes in future climate due to its significant impact on the global C cycle. Mosaic of patches in the forest-savanna-grassland continuum show rapid species loss and ultimately reduced regulatory and cultural services. A lack of reliable data on ecological attributes of the herbaceous and woody vegetation jeopardizes desired policy making for conservation and management of savanna. Since plant community assemblage, functional diversity and soil attributes in the forest-savanna-grassland mosaics of India remain understudied, therefore, comprehensive and long-term studies on the community structure and dynamics in such ecosystems are necessary.

Key words: Biodiversity, C sequestration, community assembly, forest-savanna-grassland continuum, savanna.

Introduction

Savannas occupy approximately 10–25% of the global land surface (Dintwe et al. 2015), and accounts for ~30% of global net primary production (Grace et al. 2006). Savannas range from ecosystems with dense woody layers, or woodlands, to ecosystems where the tree layer is sparse, usually along a gradient of growing rainfall, the characteristics of which are that the canopy of the tree is not closed and the ground is grassy (Lehmann et al. 2014; Sankaran et al. 2005). The climate of savannas is characterized by distinct wet and dry seasons, inducing correspondingly strong patterns in physiological and eco-physiological processes (Eamus & Prior 2001).
These landscapes contain substantial species diversity, much of which has evolved as a direct response to the environmental conditions associated with savannas (Crisp et al. 2011).

It is recognized globally that savannas are majorly regulated by, soil nutrient status, atmospheric deposition (CO₂, N, P, S) and disturbances such as fire and herbivory. These drivers may further lead to the destruction of biodiversity and the functional diversity of savanna vegetation (Ratnam et al. 2016). Based on existing vegetation types across India, Ratnam et al. (2016) described mainly three distinct savanna groups, i.e. deciduous broadleaf savannas in southern India and Vindhyan Highlands; fine-leaved and spiny savannas in arid and semi-arid regions of India; and pine savannas in the Himalayan foothills of Dehradun in northern India. In savannas, low rainfall limits the tree density, and hence, canopy covers (Sankaran et al. 2005). However, at higher rainfall, the use of prescribed disturbances such as fire or vertebrate herbivory can be used as a management tool for maintaining heterogeneity of savannas, biodiversity and functional diversity of the tree-grass system, which is well established practice elsewhere in the world (Ratnam et al. 2016).

Indian savannas sustain dense and tall woodlands, whose physiognomies mimic forests rather than open grassy landscapes (Sankaran et al. 2005). However, savanna ecosystems are anticipated to be among the ecosystems that are most sensitive to future changes in land use and climate (Stevens et al. 2016). Savannas in India often occur within forests and grasslands as a mosaic of patches (Ratnam et al. 2011; 2016). These adjacent systems (forests and grassland) may represent a gradient of various geological and ecological attributes (e.g. climatic, edaphic and functional diversity) which can be better understood by studying these in a continuum approach and through the identification of variations at the grassroots level (Singh et al. 2017). Mosaic of patches in forest-savanna-grassland continuum shows rapid species loss and ultimately reduced regulatory services such as bioregulation and cultural services (Maass et al. 2005). Considering the scenario of Indian savannas, lack of data on ecological attributes of the herbaceous and woody vegetation in addition to C stock and C-sequestration potential of individual species compromises the policy making for conservation and management. Thus, detailed studies on the community structure and dynamics in such ecosystems employing continuum approach are necessary.

**Savannas in India**

Savannas are incredible ecosystems with a mixture of woody trees, shrubs and grass, often seen as transitional communities between forests and grasslands (Ratnam 2011). In India, savannas have historically misclassified as dry deciduous forests (Ratnam et al. 2016; Whittaker 1975). Fires and seasonal drought in dry deciduous forests in India are also observed by several researchers (Mondal & Sukumar 2016; Ratnam 2016), which are also the characteristic of savannas. These findings add to an increasing array of evidence that these systems are actually savannas.

Starting from the colonial era, South Asia including India's official policy on the management of protected areas was primarily to resist fire and livestock grazing (Ratnam et al. 2016). Contrary to the scientific belief that fire and herbivory are quintessential to maintain the ecological health and diversity in savannas, Indian Forest Act of 1927 officially considered the unauthorized setting of fire in protected areas a punishable offense. For example, in the mixed deciduous savannas of Central and Northern India, it was observed in the early 1900s that teak (Tectona grandis) and Sal (Shorea robusta) seedlings were not recruited in areas of continuous fire suppression (Wanthongchai & Goldammer 2011). Moreover, Saha and Howe (2003) found that annual low-intensity fires in a deciduous savanna in central India allowed a very limited range of tree species being regenerated and predicted major declines in tree diversity for these communities in the coming century. Official policies excluded large-bodied grazing cattle from Southern India's broadleaf savannas, leading to the understory dominance of tall grass species with low nutrient quality that eventually eliminate populations of small-bodied wild herbivores to whom these grasses are unpalatable (Sankaran 2005).

In India, a great challenge is to differentiate derived savannas from ancient savannas, which need conservation owing to their unique biodiversity, particularly in their herbaceous strata and the herbivorous communities they harbor (Ratnam et al. 2011; Veldman et al. 2015). Further, this differentiation could be made on the basis of the identification of indicator tree, grass
and herbaceous species (Veldman et al. 2015). Moreover, savannas in India are also facing widespread invasion, which may shift the fundamental state of these ecosystems (Rawat & Adhikari 2015). Studies including the balance of woody and herbaceous components, the fire and herbivorous responses, carbon and water dynamics, and how these could interact to predict climate change in the future using continuum approach are urgently needed to understand the impact of invasions on the altered functional ecology of these ecosystems. Studies investigating recruitment and growth response of savanna species under changing temperature, precipitation and nutrient regimes will provide critical insights into possible patterns for the conservation of savannas over the next century.

**Challenges to Indian savannas**

Savannas in India are facing several challenges, some of which are listed below:

**Lack of recognition**

Savannas are poorly defined in India and remain unrecognized as a distinctive biome locally and continued to be regarded as degraded forests or seasonal tropical dry forests (Jha & Singh 1990; Singh et al. 2017). If descriptions on savanna diversity and adjacent systems in India continue to be neglected, we run the risk of not implementing conservation planning properly, and several savanna communities could be lost. Moreover, a major challenge to their existence is the inappropriate management of fire and herbivores resulting from a lack of understanding of the functional roles of these disturbances in such ecosystems. Furthermore, factors like unsustainable extraction of resources, land-use conversion to tree plantations and agriculture, invasions by exotic woody species (woody encroachment) are also becoming severe threats to Indian savannas. Studies incorporating satellite data revealed increased leaf area of vegetation due to land use management and various indirect factors such as climate change and atmospheric deposition (Zhao et al. 2018; Zhu et al. 2013, 2016), however, most of the increased leaf area was observed from crop land (Ambika et al. 2016; Chakraborty et al. 2018) and there is no evidence of savanna vegetation.

Importantly, there seems to be little research into the savannas of India whereas there appears to have been detailed research into woody plant physiology and phenology across Indian savannas (Ratnam et al. 2016). Additionally, satellite imagery with very high spatial and temporal resolution, available from the Google earth platform shows closed and open canopy forest, but they could not identify savanna structure perfectly (Bastin et al. 2017). In future, it may also put them at risk of inappropriate conversion to plantations for carbon trading schemes, as is occurring in other parts of the world (Veldman et al. 2015).

**Poor understanding of functional drivers and diversity along forest-savanna-grassland continuum**

Plant functional traits are morphological, chemical and physiological features of plants that determine how they respond to environmental factors (i.e. their ecological strategies) and also how they affect trophic interactions and ecosystem properties (Pérez-Harguindeguy et al. 2013). They are widely used as a predictive method for explaining both the present distribution of plant communities and ecosystems and how these will respond to climate change and human-driven processes in the future (Adler et al. 2014; Pérez-Harguindeguy et al. 2013).

In India, the functional drivers and diversity of savannas along with adjacent forests and grasslands are poorly understood (Ratnam et al. 2016; Singh et al. 2017). Insufficient information on this limits the formulation of appropriate management strategies. Savanna ecologists have a strong grasp on many of the functional traits that describe differences between savanna types around the world (Staver et al. 2012; Tomlinson et al. 2013), therefore, a proper assessment of the functional diversity of these communities can inform us about their management needs.

Savannas are often unstable environments and dependent on disturbance for their persistence and maintenance. Since these disturbances are intrinsic parts of the savanna ecosystem, their removal may have negative ramifications. For example, they will slowly convert to other vegetation types, probably closed forests and shrublands or open grasslands and the unique flora and fauna they contain will be lost. In Africa, this change, known as bush encroachment, has been observed across a large range of the continent (Bond 2008). The functional diversity of recognized and unrecognized savanna communities in India needs evaluation to guide appropriate management relevant to savannas and
adjacent ecosystems. This will help in the assessment of the functional diversity and physiology of savannas in India and related to environmental drivers (resources and disturbance). Further, this diversity could be compared with other savanna communities around the world to understand how savannas in India relate to global savannas.

Poor understanding of biomass dynamics and C-stock of savannas

Biomass dynamics and C-stock of savannas are also the matter of interest for the researchers as it plays a major role in global C-cycle and contributes around 30% of global terrestrial net primary productivity (Grace et al. 2006), which is poorly quantified in the Indian scenario. Thus, there is a need to explore these dynamics for enumerating the potential of savannas for the climate change mitigation.

Drivers of different vegetation types (Forests, savannas, grasslands)

Major environmental drivers (Fig. 1) responsible for the change in vegetation types (such as forest, savanna and grassland) and their management needs are poorly understood in the Indian context. Tropical dry forests and savannas in India are under immense threat due to increased human population density, increased land-use change (e.g. conversion to cropland), increased resource demand and habitat fragmentation (Chaturvedi et al. 2017; Sagar et al. 2003). Habitat fragmentation in these forests creates patches of different sizes which generally exist as forest, savanna, and grasslands, which are spatially and temporally diverse (Raghubanshi & Tripathi 2009). Further, several factors thought to maintain open canopy structure of savannas and tree–grass coexistence namely, rainfall variability, fire, vertebrate herbivory, heterogeneity in soil nutrient status and atmospheric depositions (Bond 2008; Sankaran et al. 2004). Moreover, these factors play an important role in adjacent vegetation types (forest and grassland). Further degradation of savanna owing to grazing and anthropogenic pressures leads to the formation of relatively tree-less grassland. Some of the key drivers, responsible for the formation of different vegetation types are listed below:

Anthropogenic factors

Savannas and adjacent systems are under serious threat from human activities such as land-use change, fire suppression, atmospheric N and CO$_2$ increase, causing declines in plant diversity and supporting wildlife population (Sankaran et al. 2005). Fire is a global phenomenon in savannas and grasslands, and has long been used as a tool in ecosystem management (Sankaran et al. 2004, 2005). The implication is that fire is most likely a natural part of these systems and it is probable that the savanna species are favored over nonsavanna species through their ability to tolerate fire. Therefore, the suppression of fires in savannas is selecting against these species in the long-term and favours forest species, which could lead to a substantial loss of biodiversity in savannas of India. It is, therefore, necessary to evaluate whether the suppression of fire has changed the structure of these systems.

Natural factors regulating savanna vegetation

Fire

It is evident that fire has influenced savannas for millions of years (Bond 2008; Bond & Keeley 2005; Staver et al. 2012). A warm dry season with ample amount of fuel loads leads to frequent fires, which is a well-established practice for the maintenance of heterogeneity and biodiversity in savannas (Smit et al. 2010; van Langevelde et al. 2003). Therefore, fire suppression can alter tree–grass ratios (Higgins et al. 2007). Functional traits characteristic of tree species in fire-prone systems include thick, fire resistant bark (Stott 1986), subcutaneous meristems and tuberous roots (Ratnam 2011). For instance, studies show that tropical savannas are almost always trees interspersed with grasses that follow the C$_4$ photosynthetic pathway. C$_4$ photosynthetic plants lose as little water as possible and are adapted to live in hot and dry environments. Therefore, C$_4$ grasses in Indian savannas are subsequently highly tolerant to fire, but shade intolerant. They also prove to be highly flammable in the dry season and readily promote fires. Such fires create open environments with little shade and both grasses and savanna trees that are intolerant to shade depending on this fire to grow.

Savanna trees have a number of adaptations to live in a fire-driven ecosystem. Their large underground storage organs and roots contain much of their resources and are prevented from fire. Woody species quickly resprout after fire from subterranean stems (Charles-Dominique et al. 2015; Tomlinson et al. 2012). Therefore, various fire
Fig. 1. Factors regulating the vegetation composition and soil attributes in a forest savanna grassland continuum.

Regimes can result in the assembly of distinct populations and communities functionally clustered for diverse characteristics (Forrestel et al. 2014; Simpson et al. 2016). For instance, resprouting species are favoured in frequent, low-intensity fire regimes, and obligate seeders that persist via seedling recruitment are favoured in infrequent, high-intensity fire regimes (Pausas & Keeley 2014). Adult trees have less dense canopies than forest species, allowing more sunlight to permeate to the ground level. Mature trees also have thick bark. The researchers compared traits of trees from areas classified as dry deciduous forests and evergreen forests, in order to see how savanna species differed from forest species.

Water availability

Water is the main limiting resource for plant growth in savannas and tropical dry forests (Bhadouria et al. 2016, 2017). Savannas are characterized by periods of ample rainfall and soil moisture (wet seasons) followed by extended periods of high evaporative demand, lack of rainfall and declining soil moisture (dry seasons).
Deciduous broad-leaved savannas occur in central and southern India (Sagar & Singh 2005; Bunyavejchewin et al. 2011), where rainfall is 700 mm < MAP < 2100 mm (Suresh et al. 2011). Fine-leaved and spiny savannas found in arid and semi-arid regions of India having rainfall 400 mm < MAP < 1000 mm (Ratnam et al. 2016). Pine savannas are found at higher altitudes than fine-leaved and broad-leaved savannas (Ratnam et al. 2016). These are able to tolerate colder conditions and are often associated with low-nutrient soils (for example—fothills of Dehradun, India). The species of pine are present in a wide rainfall range of MAP 900 mm to 3200 mm (Hijmans et al. 2005). The deciduousness in savanna trees is a mechanism adopted to tolerate water stress during dry seasons. Extensive root systems have commonly been observed in drought-resistant species (Comas et al. 2013; Tomlinson et al. 2012), since deep roots can take up water from moister soil layers.

Herbivory

Herbivores also affect woody vegetation cover and play an important role in maintaining savanna vegetation (Asner et al. 2009; Shannon et al. 2011). For example, smaller herbivores browse on lower seedlings and saplings, preventing them from growing into larger ones. While larger bodied herbivores, like elephants, knock down trees, stop them from growing as much and prevent them from dominating (Sankaran et al. 2004, 2005). Therefore, the impact of large mammal herbivory may be strongest on savannas and hence apparent in the plant functional traits pertaining to defenses. Herbivory is an ecological and evolutionary agent exerting a strong selective pressure on plant communities by increasing plant mortality, removing biomass that might be allocated to growth or reproduction (Coley et al. 1985), reducing plant competitive ability (Coley & Barone 1996) and consequently, it may lead to a decrease in the abundances of certain plant species (Craine 2009). As a result, plants have evolved different chemical, mechanical, phenological, or physiological anti-herbivore defenses (Coley & Barone 1996), and the possession of such defenses may determine whether a plant species will occur or not in a given location (Fine et al. 2006). Hence, species dominance and rarity in some plant communities are strongly influenced by the top-down effects of herbivory (Brown & Gange 1989; Carson & Root 1999).

Savanna tree species have strategies to tolerate or avoid herbivory, such as spines or chemical compounds (Ratnam et al. 2016; Rohner & Ward 1997). Other important leaf defense traits include carbon to nitrogen ratio, specific leaf area, leaf water content, latex content, number of trichomes, toughness, and presence of alkaloids, terpenoids and tannins (Agrawal & Fishbein 2006; Dantas & Batalha 2012).

Nutrient deposition

Nutrient deposition can modify plant growth rates and potentially alter the susceptibility of plants to disturbance events, while also influencing properties of disturbance regimes. Studies show that increased availability of soil nutrients to plants can differentially affect plant growth amongst members of a community, bringing about compositional changes in vegetation (Powers et al. 2015; Stevens et al. 2016). In addition, increased nutrient availability can also indirectly modify plant communities by affecting properties of local disturbance regimes – which play a ubiquitous role in identifying the specific functional and/or phenological traits affected by atmospheric nutrients. This could be a key piece of information to help understand which species and plant communities may be most sensitive to chronic enhanced N deposition. The effects of atmospheric nutrient deposition on the dynamics and functional composition of mixed tree-grass ecosystems are relatively poorly investigated (Powers et al. 2015).

Edaphic conditions

Edaphic conditions are considered as the major regulatory factors since it provides a platform for other environmental variables favoring the growth and development of herbaceous as well as woody species (Chaturvedi et al. 2011; Li et al. 2004; Singh et al. 2017). In the dry deciduous forest light intensity, water and nutrients along with canopy cover are reported as the major determinants of the herbaceous (Sagar et al. 2012) as well as tree seedling growth (Bhadouria et al. 2016, 2017). The tropical dry soils are characterized by the patchy distribution of nutrients (Roy & Singh 1994) and seasonal variability in nutrient release (Powers et al. 2015; Singh et al. 2009). Further, studies indicate that conversion of tropical dry forests to savanna, primarily due to anthropogenic perturbations leads to crown cover opening, declined soil organic content and reduced nutrient cycling.
efficiency (Singh 1989; Tripathi et al. 2008). Further, these changes lead to change in soil physico-chemical characteristics such as soil organic matter content, soil-N and -P. Elaboration of edaphic factors which regulate the vegetation could lead to tools for the management of the vegetation. Such systems and transitions between them are expected to face major changes under future climate change scenarios (Baudena et al. 2014).

The holistic approach of investigation and research outlook

The community structure, as well as the related stature and spatial composition of tree species, are important determinants of various ecosystem processes and linked abiotic patterns. Such ecosystems and transitions between them will face major changes under future climate change scenario, hence warranting an immediate investigation in the forest-savanna-grassland continuum. Overall understanding of ecological attributes along the forest-savanna-grassland continuum has been restricted by the narrow scope of most field studies, which usually have been focused on a single ecosystem/site. Considering the above research gaps, a holistic approach of investigation encompassing the soil water and nutrient availability, species diversity (herbs and trees), biomass and C-stock assessment at multiple sites along the forest-savanna-grassland continuum in India would be of vital importance. The baseline data generated by such studies would help in government initiatives such as the ‘Green India’ project aimed at ‘increasing and enhancing tree coverage on 10 million hectares of forest and non-forest land’ within the subcontinent. Estimation of biomass and C-stock of the savanna-forest-grassland continuum will contribute to the national forest carbon inventory database, along with new forest management working plans. Additionally, quantification of plant functional traits will be further used as input variables for the development and validation of models to predict the response of savanna vegetation under climate change scenario.

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References


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