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Tropical grassy biomes: linking ecology, human use and conservation

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Abstract

Tropical grassy biomes are changing rapidly the world over through a coalescence of high rates of land use change, global change and altered disturbance regimes that maintain the ecosystem structure and function of these biomes. Our theme issue brings together the latest research examining the characterisation, complex ecology, drivers of change, and human use and ecosystem services of tropical grassy biomes. Recent advances in ecology and evolution have facilitated a new perspective on these biomes. However, there continue to be controversies over their classification and state dynamics that demonstrate critical data and knowledge gaps in our quantitative understanding of these geographically dispersed regions. We highlight an urgent need to improve ecological understanding in order to effectively predict the senstivity and resilience of tropical grassy biomes under future scenarios of global change. With human reliance on tropical grassy biomes increasing and their propensity for change, ecological and evolutionary understanding of these biomes is central to the dual goals of sustaining their ecological integrity and the diverse services these landscapes provide to millions of people.

1. Introduction

Historically extensive across the global tropics, tropical grassy biomes (TGBs) are now changing rapidly through high rates of land clearance (1), increasing land use intensity (2, 3), woody encroachment (4) and disruption of the disturbance regimes (5, 6) that maintain ecosystem function. These biomes were the cradle of human evolution (7), and in our contemporary world, they support the livelihoods and wellbeing of over one billion people (8). With the population of Africa alone set to treble by 2050 (3), the continuing pace of climate change (9), increasing atmospheric CO_2 concentrations (9), and the increasing agricultural development of TGBs (3, and Estes et al., in this issue (10)), there is an urgent need to understand the unique ecology of these systems. TGBs, like tropical forests, are subject to a complex set of pressures as a result of human actions. However, unlike other biomes, the contrasting life forms and physiologies of the dominant C_3 woody plant species and grass species utilising the C_4 photosynthetic pathway sees the future of this biome linked, in a profound way, to the ever-rising atmospheric CO_2 concentration and the global political agenda to reduce these emissions. Further, TGBs have generally few policy and legislative mechanisms in place for their protection (11, see also the example provided by do Espirito Santo et al. (12)).

TGBs contribute 30% of global terrestrial net primary productivity and store 15% of the world's carbon (13). While TGBs are less carbon dense than forests (by an order of magnitude or more), their productivity is such that large proportions of the carbon gained in a single year, are rapidly released back to the environment via fire, herbivory and human use (14, 15 and see analysis of this in Archibald and Hempson (16)). Indeed, the disequilibrium nature of TGB vegetation dynamics means that these biomes are highly sensitive to annual and decadal changes in environmental controls (14). The degree to which this dynamism will influence trajectories of vegetation change in grassy biomes into the future is unresolved. However, it is apparent that many intact savannas are now on a trajectory of increasing woody biomass, although the degree of gain varies regionally, with Australian savannas most stable over time (4).

Tropical grassy biomes first arose approximately 10 million years ago and expanded such that by two million years ago, tropical savannas and grasslands were a dominant biome covering the tropics (17). Today, these biomes, cover in excess of 20% of the global land surface. At the last glacial maximum, TGBs extended more widely throughout Asia, Africa and the Americas than today (18-20). The extent of these vast biomes has shifted with glacial - inter-glacial cycles in response to changing atmospheric CO_2 concentrations, rainfall, rainfall seasonality, temperature and fire (19, 21). Given that all of these aspects of our environment are now changing at unprecedented rates, extensive alterations in the distribution and dynamics of TGBs over the coming century will be inevitable and are likely already being observed (1, 4, 22, see the analysis provided by Stevens et al. (23)).

The last decade has seen a revolution in our understanding of the evolution (17, 24, 25), antiquity (26-28), distribution (29, 30) and ecosystem dynamics of TGBs (14, 31), as well as their role in the global carbon cycle (32). Some of these advances have sparked controversies that are now active debates in the literature (e.g. ancient grasslands and afforestation policies (33-35); the existence or not of alternative vegetation states (29, 36, 37)). Indeed, insights and theory from savanna ecology have challenged long standing ecological assumptions of climate determinism in defining the limits of biomes (38).

Over the coming decade, we anticipate important in-roads will be made in reconciling the complex ecology and biogeochemical cycling of these geographically dispersed biomes via integration of remote sensing, modelling, ecology and evolution. However, it will be critical to incorporate the role of people in shaping and responding to changing ecosystem dynamics and function across this global region, as in the Anthropocene people will be increasingly important agents of landscape change, directly and indirectly influencing the environmental controls and ecological processes that structure TGBs from global to local scales.

2. This Issue

Tropical Grassy Biomes are expansive and changing rapidly, yet our capacity to predict trajectories of change in these biomes is limited, despite their importance to human livelihoods, biodiversity and biogeochemical cycling. In this issue, we highlight the need for integration among research related to the ecology and dynamics of these biomes: characterization and definition of tropical grassy biomes; complex ecology;

patterns and drivers of change; and, human use and ecosystem services. For the first time, analyses are presented on the biogeography and potential distributions of Asian savannas (39). Other significant steps forward in our understanding include: methods for characterizing ancient versus derived grassy biomes (40, 41), comparative data on the species diversity of TGB regions across the globe (42), an improved understanding of the complex ecology of herbivory and fire (16, 43) and the context dependent response of vegetation to global change (44), and finally, tools to examine tradeoffs in biodiversity, carbon and agriculture to aid land use planning and policy (10).

3. Defining Tropical Grassy Biomes

Tropical grassy biomes include C_4 grass dominated savannas and grasslands (following the definitions of (30, 45)). Definitions of tropical grassy biomes have historically been varied and fraught with problems. Functionally, TGBs are characterized by a grassy ground layer (generally dominated by grasses using the C_4 photosynthetic pathway - with a noted exception in Brazil (46) and Indochina (39)) and an overstorey varying from 0% up to 60 - 80% woody cover (45). The biota, depending on its biogeographic and environmental settings, is tolerant of any, or all of, fire, grazing and browsing (31). However, universally, the flora is shade intolerant, at least at the establishment phase, due to the open canopy overstorey (45). While the biodiversity value of these systems to-date has been typically overshadowed by that of tropical forests (26), Murphy et al. (2016) in this issue (42), illustrate the biodiversity value of TGBs, particularly of vertebrates and range-restricted species, and emphasize variation in diversity among the TGB regions (the South American region generally being the richest).

The disequilibrium nature of tropical grassy biome vegetation dynamics, with varying levels of woody cover, has consistently posed problems for the categorization of these ecosystems (8). This problem has been compounded by a focus on trees, rather than ground layer composition and function; for example, the Millennium Ecosystem Assessment focuses on drylands and forests (47, 48), but does not explicitly consider tropical savannas. While tropical rainforests have been mapped globally, no accurate global map of the tropical grassy biomes exists. The most widely used general vegetation map and classification scheme is Olson et al.'s (2001) ecoregions (49), although this biome classification is problematic because it does not recognize some of the world's major savannas and grasslands, including those in Asia (e.g. India, Thailand, Burma) and Madagascar. Wide use of such maps for research, policy and conservation has the potential to have adverse impacts on landscape management and the perceived conservation value of these regions (e.g. conversion of TGBs, perceived as degraded land, for agriculture, see (50)). For the first time, Ratnam et al. (2016) focus on this issue in Asia (39) by reviewing the scattered literature on the distribution of Asian savannas and evidence for the antiquity and diversity of TGBs across this continent.

In many regions, including Madagascar, south east Asia and South America, grassy biomes have historically been considered either to be a degraded form of forest of anthropogenic origin created via tree clearing, burning and grazing, or a subclimax or secondary successional stage (28, 39). While true in some locations (see Veldman 2016, this issue (40)), in the majority of areas this perspective is misplaced (34). A wealth of new information including dated phylogenetic analyses demonstrates the antiquity of both tree and grass species (and lineages) specialised to these biomes (25, 27, 28). The presence of endemic plant lineages and species, as well as species with unique life histories and architectures, including forbs with large underground storage organs, are strong indicators of the antiquity of TGBs (35, 41).

The fauna of these regions also contains numerous endemic species specialized to open and grassy environments providing additional evidence for the origin and age of the tropical grassy systems. Fauna include species of granivorous birds (e.g. the Madagascan mannikin, *Lonchura nana*), a suite of grazing ungulates (e.g. the critically endangered Kouprey, *Bos sauveli*, from Cambodia, and the chital deer, *Axis axis*, from India) and a high diversity of small marsupials in Australia (42). Many of these species are endangered and threated with imminent extinction (51). Fire is a frequent disturbance in the TGBs and has been part of these systems for millions of years (17, 21); consequently the plants and animals they contain are generally adapted to its occurrence (25).

To date it has been difficult to distinguish ancient, old-growth grasslands and savannas from secondary systems given superficial similarities in structure. Here, Veldman (2016) and Zaloumis & Bond (2016), examining the Neotropics and South

Africa respectively, differentiate ancient and secondary systems, noting differences in species composition with the former particularly rich in forbs, many with well-developed underground storage organs that facilitate survival in seasonally dry climates with frequent fire. The challenge is to test the generality of these compositional characteristics across TGB regions.

4. Ecology

The ecology of TGBs is complex by virtue of the numerous environmental controls, acting across different scales of influence, both directly and indirectly to structure these ecosystems (Figure 1). The last decade has seen a shift from a long-standing view of deterministic relationships among vegetation, climate and soils, focused on niche separation between trees and grasses for water use, to one that integrates niche separation (e.g., phenological, water use) with the controls of fire and mammal herbivory structuring vegetation via the restriction of woody plant growth (31). Archibald and Hempson (16) explore trade-offs in fire and mammalian herbivory across the African continent where realms of influence can change through space and time. Complementing this research is that of Anderson et al. (43) who examine spatial associations of African mammalian herbivores relative to body size and influences on ecosystem function relative to species composition. Both of these studies raise important questions about the function or dysfunction of TGBs in the context of changing disturbance regimes.

Integration of bottom up (e.g., climate and soils) and top down (e.g., fire and mammalian herbivory) controls in structuring TGB vegetation has significantly improved our process understanding of the dynamics and limits of these systems (14, 52). But, it has also highlighted the degree to which contemporary dynamics of TGBs, from local to continental scales, are a function of historical contingencies (44, 53). In assessment of regional patterns and dynamics of vegetation, emergent patterns of woody cover can appear almost stochastic, due to the array of structural states possible for a given set of environmental conditions (29). At the heart of the current disagreement around alternate vegetation states prevalent in the tropical savanna and forest literature (all of state shifts between savanna and forest, grassland and savanna, and variation in tree cover within savannas) may be a lack of recognition of both the role of contingency in influencing contemporary dynamics of TGBs, and that the relative role of environmental controls in structuring vegetation varies across savanna systems: i.e., some savannas likely exist due to soil barriers to woody plant growth, while others exist because of controls, such as prevalent fire, that also act to limit woody plant recruitment and growth. That is, the similarities in structure among TGBs (open canopied vegetation with a predominantly C_4 grassy ground layer) have led to an unfounded assumption in the literature that the processes regulating vegetation structure across these varied and geographically dispersed ecosystems are directly equivalent. Finally, the presence of numerous, well-documented, feedbacks structuring TGBs where the species composition can influence the strength and direction of effects (Figure 1; tree cover - fire; fire - grazing; grazing - browsing), combined with the importance of historical contingencies means that multiple states influencing both the limits and structure of TGBs are highly likely. In this issue, Oliveras and Malhi (54) examine the shades of green in our understanding of the processes structuring the limits of TGBs highlighting how biotic and abiotic processes operate at different scales and that nature of vegetation dynamics is context dependent.

Savanna vegetation dynamics have been shown to vary as a function of plant traits that aggregate from the individual to ecosystem level (14, 55). However, current model simulations generally represent TGBs as functionally identical, in contrast to ecological knowledge (although see Moncrieff et al. in this issue (44)). TGBs constitute a geographically dispersed set of regions, where the flora and fauna representing unique evolutionary and environmental histories (14). The relative importance of environmental controls in structuring these systems varies across these geographic regions, and relative to the environmental niche of each region (14). For example, the high rainfall Australian savannas dominated by tall, fast growing, narrow canopied evergreen *Eucalyptus* species are less sensitive to fire than the wide canopied deciduous *Brachystegia* and *Julbernardia* species that dominate a savanna region equivalent in area across southern Africa (56, 57). Thus, for a given set of environmental conditions, similar fire frequencies and intensities could produce different vegetation structures, and the difference in sensitivity to fire of these floras is highly likely underpinned by the functional traits of the plant species themselves (55). It is increasingly appreciated that the functional biogeography of TGBs has critical implications for our capacity to determine the sensitivity and resilience of TGB regions to global change (e.g., Moncrieff et al., this issue (44)), and yet, our quantitative understanding of functional biogeography of TGBs remains limited. This information is needed as our capacity to predict future change will rely on a quantitative representation of the aggregation the traits that characterize these floras in influencing ecosystem dynamics and responding to environmental variation.

Across tropical grassy biomes, vegetation composition, woody cover and grass biomass are considered key determinants of ecosystem function. However, quantitative links between structure and function, ultimately, remain poor and there is no consensus of these relationships among TGB regions (8). Despite, the antagonistic dynamics between tree and grass dominance being central to savanna ecology, we retain a limited predictive capacity of vegetation structure. It could be argued that our current lack of knowledge about the physio-ecological responses of TGBs to global change is hindered by both the functional differences among the TGB regions and our weak quantitative understanding of the processes that structure vegetation due to the complexity of interactions and scales of feedbacks in operation (Figure 1). To aid the management of global change impacts for both people and biodiversity, we need to determine the relative sensitivities of savanna vegetation types to key environmental controls – CO_2, water availability, and disturbance dynamics – and identify structural thresholds where critical ecosystem functions change.

5. Drivers of Change

Tropical vegetation is changing at broad spatial scales but there is a limited understanding of current trends. On one hand, rates of land use change are increasing (3, 11), and on the other, woody encroachment is widespread across savannas especially in Brazil and South Africa (in this issue, see Honda & Durigan, 2016 and Stevens et al. 2016). The extent to which drivers that enhance tree growth (e.g., increasing atmospheric CO_2 concentrations $[CO_2]_a$), reduced disturbance, improved plant water use efficiencies), prevail over drivers of enhanced tree mortality (e.g., reduced rainfall, increasing intensity of El Niño, increased temperature, increased harvesting) is unknown, but this is the key to the future management and integrity of the biome.

Rising $[CO_2]_a$ has long been hypothesised to be a key driver in the re-organisation of tropical vegetation, specifically in savannas where the contrasting life forms and physiologies of the dominant C_3 trees and C_4 grasses are expected to respond differently (58). While modelling of the proposed mechanisms underpinning shifts in the competitive interactions between C_3 trees and C_4 grasses is improving (i.e. increased plant water use efficiencies of C_3 plant species, specifically woody plant species; carbon allocation and storage patterns that vary between life forms; reduced photorespiration in C_3 grasses), demonstrating the potential for regional shifts in biome extent and woody biomass (59), there is a major gap in the experimental evidence of the responses of tropical plant species to altered CO_2 concentrations, especially with regards to interactions with other environmental controls (8). In particular, dominant woody taxa in each savanna region have different life histories, allocation strategies, and architectures (14, 55, 60). Increasingly, functional traits are recognised as phylogenetically conserved (61), and differential responses to CO_2 would likely be expected relative to both ecological and environmental settings. Looking across a rainfall gradient and landuse types in South Africa, Stevens et al. (2016) report large increases in woody cover in just a few decades providing support for a global driver (23), while also noting the interaction with megaherbivores (elephants). Woody encroachment may provide carbon benefits, but will undoubtedly come at a biodiversity cost (62).

Tropical grassy biomes are characterised by seasonally dry and hot climates (30). While climates across this swath of the world are changing, particularly in terms of the frequency and intensity of El Niño drought events, disagreement among model predictions contributes to the lack of certainty for climate change predictions across tropical regions (63). Novel climates, in combination with rising CO_2 will generate novel interactions among organisms, where small shifts in the season and timing of rainfall may have large consequences for the phenological cycles of plants and animals, and stark consequences for crop production (3). In contrast, small changes in total rainfall may be of limited consequence, where increasing $[CO_2]_a$ will drive improvements in plant water use efficencies (64). Temperature is assumed important in determining plant distributions and function primarily based on assumptions from the Northern Hemisphere. Yet the importance of temperature in the dynamics of TGBs is poorly understood. The small body of research suggests if there is sufficient water, a warming climate may enhance plant success through improved germination (65, 66) and sapling growth rates (67), and an extended growing season (68).

Yet, across TGBs, rates of land use and cover change appear to exceed the effects of climate change (1, 11). With increasing global scarcity of lands for agriculture and increasing food demands (69), land use intensity is only likely to increase. There are a multitude of land use types across TGBs, many of which are context dependent, from shifting cultivation and grazing lands to commercial agriculture (see Ryan et al., in this issue). However, all affect the continuity of ecosystems and, some land use types more so than others (see Estes et al., in this issue). Increasing land use intensity and fragmentation disrupts disturbance regimes and vegetation dynamics (70), potentially amplifying encroachment by further reducing tree mortality. To date, 50% of the Brazilian cerrado has been transformed for agriculture, a rate of land use change roughly double that of the Amazon forest (71, 72). Land has historically been perceived as being of marginal agricultural value across TGBs (see Estes et al. and Ryan et al. in this issue). However, technical innovations in managing highly weathered tropical red soils and the breeding of suitable crop varieties have transformed agriculture in Brazil (3). This tropical agricultural revolution has been proposed as a viable development model for wetter African savannas (Estes et al. 2016 and (3)). do Espírito Santo et al. (this issue) document land abandonment and encroachment in secondary savannas of the cerrado (12), where this development policy has been to the detriment of the integrity of the system and where, globally, rates of encroachment are highest (4).

Finally, people also directly influence disturbance regimes at broad scales (6, 70). Active suppression of fire in the savanna regions of Asia and Brazil in particular has facilitated woody or weed encroachment (see Honda & Durigan, 2016 and (73)). The increasing extent of roads and fences act as fire breaks and also prohibit large scale animal movements (6). These changes to the major savanna processes of fire and herbivory, combined the effects of the poaching crisis of Africa and Asia, are likely to have profound consequences for ecosystem function (Archibald and Hempson; Anderson et al. in this issue).

6. Human use and value

Quantifying and understanding the value of TGBs to humans is challenging because in many regions, particularly in Asia, data on the value of TGBs to human livelihoods are limited. TGBs are sometimes described as "unused" or "degraded", although these systems provide fundamental resources and ecosystem services supporting the livelihoods of the millions of people living in these regions. Further, the people of these regions are among the worlds poorest and most vulnerable (74), and global change will inevitably affect ecosystem services and resource availability. Perhaps more so than any other TGB region, direct use by local communities is greatest in Afrca and Asia (see Ryan et al. 2016, this issue), given the urbanization of Latin America and the sparse population densities of Australia. Ryan et al. (2016, this issue) highlight the diversity and number of ecosystem services (supporting, regulating and cultural services) provided by TGBs (specifically in relation to southern Africa) that, to-date, have typically been either overlooked or considered at small spatial scales. Critical resources provided include food (wild fruits, tubers, nuts, edible insects, bushmeat), NTFPs for sale (e.g. honey, beeswax, insects), fuel (fire wood and charcoal), construction materials (e.g. thatching grass, timber), water, nutrient cycling and medicinal plants (Ryan et al. this issue).

Across Africa, Asia and even South America, fuel wood harvesting is a significant activity (see Woollen et al. and do Espirito-Santo et al. in this issue). Although the fuel wood crisis predicted in the 1970s has not materialized, projections surrounding levels of fuel wood sustainability are varied (75). In some regions (e.g. South Africa) fuel wood harvesting is considered sustainable due to regeneration after coppicing (76), possibly facilitated by CO_2 fertilization (e.g. (77)). Elsewhere, wood demand is anticipated to increase due to increasing populations and a switch to charcoal, which has an increasing international market (75). The implications of changing wood demands are raised by Woollen et al. (2016, in this issue (78)): wood for construction material is now traded off against wood for charcoal. How changes in wood resources in the context of global change will influence the integrity and functioning of TGBs needs urgent attention.

Water availability will change with growing populations, altered landscapes and global change, and in the seasonally dry climates of these regions water availability is critical to both ecosystem dynamics and human use of landscapes, yet understanding of the nature of this change and the implications is restricted to a few regions (75). Honda and Durigan (2016, this issue (79)) provide, for the first time, estimates of rainfall partitioning in the cerrado and demonstrate how fire suppression, indirectly via woody encroachment, can reduce rain interception. Given many TGB regions are experiencing woody encroachment, this is a reminder of the functional role of disturbance in the provision of water resources. Across TGBs, afforestation (often of exotic species) is common (8), in part, to meet fuel wood needs; improved examination of the trade-offs between fuel wood and woody encroachment with water are desperately required. Further, much needed are examinations of the biophysical and biogeochemical consequences of woody encroachment and land cover change, such as albedo and nutrient cycling.

People and institutional structures can strongly influence and affect TGBs - their biodiversity, functioning and services (8). For example, in many areas declines in mammal species have been reported due to bushmeat hunting and poaching, savannas have become degraded through overgrazing, land abandonment, and afforested monocultures (80-82). The economic importance of the wildlife across TGBs, particularly in African and some Asian regions (and to a lesser extent Australia), is a unique economic advantage that contributes to the tourism industries of these regions. Major ecological changes driven by the global changes set out above, combined with human pressures could threaten these economic benefits. Human usage needs to be reconciled with ecological values in these areas, including biodiversity; human activity has already reduced the richest botanical savanna region, the Brazilian cerrado, to a series of, arguably, dysfunctional fragments. Finally, the climate change mitigation agenda could represents a threat to TGBs, as there is increasing talk of the need for “negative emissions” to meet the emissions targets set out at the Paris climate conference (COP21) in 2015 where inappropriate application of these targets could lead to afforestation of TGBs (34).

7. Conclusions

The pace and scale of change in TGBs is astonishing and will affect human livelihoods, biodiversity, carbon and biogeochemical cycling. Yet, our capacity to predict the direction and extent of change, as well as the consequences, is currently limited. Research will improve our ecological understanding of TGBs, and it is clear that our capacity to effectively predict the sensitivity and resilience of each TGB region is dependent upon understanding the cascading and interacting effects of ecological, socioeconomic and global drivers across contrasting contexts. This is no easy task even from a purely ecological perspective as these systems are complex, ecosystem dynamics are context dependent and uncertainty surrounds the influence of global change drivers.

In order to better conserve and manage TGBs for the future, we must look beyond a simplified view considering only the tree layer, to a perspective that embraces the grassy ground layer and the unique functions associated with this. Only with this broader perspective will we be in a position to consider the range of trajectories and possible states that are likely across the different regions and how the influence of key drivers may vary. To apply the most appropriate conservation and management efforts in the right place, field studies are needed to characterize and determine the antiquity and value of TGBs more broadly. Additionally, field studies will help us understand how the multiple pathways for structural (and compositional) change links to the functioning of these biomes.

Experiments manipulating global change drivers (e.g. water availability, temperature, and CO_2) will help unravel the complexities of savanna process and dynamics so we are in a stronger position to understand how different TGB regions may respond to future change. We need to work with land managers and politicians to ensure that processes critical to the healthy functioning of TGBs (i.e. fire, herbivory) are maintained. This will mean revisiting carbon mitigation initiatives, taking a more nuanced approach to applying REDD+ in TGBs, and ultimately recognizing TGBs are wholly different to forests in terms of ecosystem function. Many of the world's poorest live in the TGBs; it is therefore essential that the dual goals of sustaining the ecological integrity of this biome and supporting the people who live in these landscapes must not be viewed as competing demands.

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Figure 1: *The complex ecology of tropical grassy biomes*. The network of interactions governing the structure of tropical grass biomes, adapted and expanded from (83) and of particular relevance is the extent of consumer centred feedbacks in structuring these ecosystems. Direction of effects are indicated as positive (+) or negative (-) based on literature (summarised in 14 and throughout this issue), and where the literature is sparse or poorly reconciled, uncertainty of effects are indicated with (?). With respect to interactions between CO_2 and plants, estimated effects are positive, but there is uncertainty associated with the strength of interactions due to a lack of experimental evidence and the potentially hysteretic effects of consumer centred feedbacks. It must be noted that in some instances, species and their traits can modify the direction and strength of effects, as is the case with interactions between fire and grazing as outlined in (16) and relative to the ecological and environmental setting. Hence, not all interactions are present across all TGBs and not all interactions are of equal relative influence across ecological and environmental settings.