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Many shades of green: the dynamic tropical forest-savanna transition zones

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Summary

The forest-savanna transition is the most widespread ecotone in tropical areas, separating two of the most productive terrestrial ecosystems. Here we review current understanding of the factors that shape this transition, and how it may change under various drivers of local or global change. At broadest scales the location of the transition is shaped by water availability, mediated strongly at local scales by fire regimes, herbivory pressure and spatial variation in soil properties. The frequently dynamic nature of this transition suggests that forest and savanna can exist as alternative stable states, maintained and separated by fire-grass feedbacks and tree shade-fire suppression feedback. However, this theory is still contested and the relative contributions of the main biotic and abiotic drivers and their interactions are yet not fully understood. These drivers interplay with a wide range of ecological processes and attributes at the global, continental, regional and local scales. The evolutionary history of the biotic and abiotic drivers and processes plays an important role on the current distributions of these transitions as well as in their species composition and ecosystem functioning. This ecotone can be sensitive to shifts in climate and other driving factors, but is also potentially stabilised by negative feedback processes. There is abundant evidence that these transitions are shifting under contemporary global and local change, but the direction of shift varies according to region. However, it still remains uncertain how these transitions will respond to rapid and multi-faceted ongoing current changes, and how increasing human influence will interact with these shifts.

Introduction

One of the main foci of ecological science over the last decades has been of the understanding how global change will translate into shifts in species composition, vegetation structure and biogeochemical cycling over space and time. Although there has been much progress, it remains a major challenge to reliably predict how the various agents of global change are going to shift ecosystem functioning and distribution.

Most research efforts on studying the effects of global change have focused on comparing distinct ecosystems and communities, with areas of transition between them receiving much less attention. Vegetation transitions, or ecotones, are border regions of transition between communities, ecosystems or biomes, reflecting both local and regional changes in abiotic conditions (1–3). They are expected to be especially sensitive to global change, since relatively minor shifts in environmental drivers (e.g. climate, soils or herbivory) can translate into dramatic changes in their ecosystem structure and composition. With increasing human-caused disturbances and landscape fragmentation, ecotones will become even more common and important to the dynamics of the ecosystems on either side of the transition, redefining their boundaries and influencing their structure and function (4).

Probably the most emblematic vegetation transitions are those between closed canopy forests and savannas, the latter being more open and less wooded ecosystems and include a significant proportion of grass cover. The relative abundance of two very different plant life forms (tree *vs* .grass) strongly shapes ecosystem biogeochemistry, microclimate, fire regimes and fauna. Although forest-savanna transitions in the broadest sense occur in many climates, perhaps the most striking examples occur in the tropics, where C_4 grasses predominate. Tropical forests and savannas account for >60% of terrestrial productivity (5), and hence the transitions between these two biomes are of particular importance.

The transition zones are being acted on by multiple drivers of contemporary anthropogenic change, including changes in rainfall regimes, length of dry season, rising temperatures, rising atmospheric CO_2, changes in fire regime (increases in some areas, decreases in others), changes in herbivory (often a decline in wild herbivores, but an increase in domesticates), an influx of invasive species, extraction of fuelwood and direct land clearance. As a result, forest-savanna transitions may be key indicators of the net effects of anthropogenic change, but it is important to understand the many processes that drive these transitions if we are to interpret observed changes correctly.

In this review we examine some of the key literature and concepts in forest-savanna transitions, synthesize the major findings and identify the main challenges in obtaining an understanding of the dynamics of these transitions and how they will respond to global change. We address the following questions: (1) What defines forest-savanna transitions? (2) How are the characteristics of forest-savanna transitions affected by different evolutionary history, vegetation type and abiotic factors? (3) What are the patterns of temporal change in diverse forest-savanna transitions, and how do differences reflect in the ecological processes operating at different spatial or temporal scales? In particular, we highlight the role of the historical pathways and evolutionary processes in shaping these distributions, and the complex interactions among several abiotic and biotic drivers and ecological processes operating simultaneously across scales.

Concepts and definitions

In this review, we address tropical forest-savanna transitions as forest-grassy vegetation ecotones (Figure 1). Grassy vegetation ecosystems, or savannas, are ecosystems with a grass layer that includes true grasses (Poaceae), and sedges (Cyperaceae), and a woody vegetation that provides a crown cover that is insufficiently dense to form a closed canopy (Figure 1, (6)). Here we restrict the term savanna to tropical tree-grass systems with a predominantly C_4 grass layer. This approach is consistent with the definitions provided by Scholes and Archer (1997) (7) as well as with previous reviews in addressing both vegetation structure and community and species functional traits (8–11). The open canopy allows sufficient light to reach the ground to support a largely continuous herbaceous layer consisting primarily of C_4 grasses. Tree densities are not necessary low (*e.g.* woody savannas such as the Cerrado of Brazil can have tree densities approaching that of forests) but crown size and form and leaf density allow sufficient light to penetrate to support a grassy understorey. In the tropical lowlands, the grassy layer is generally dominated by species employing the C_4 photosynthetic pathway (8), which supports higher temperature and drought tolerance, although in some regions C_3 grasses are still important, as for example the common C_3 grass found in Brazilian savannas, *Equinolaena inflexa*. With their high growth rates, frequent flammability and tolerance of high temperatures and drought, C_4 grasses are a key feature determining the characteristics and distributions of tropical savannas.

It is important to recognise (especially in a climate mitigation agenda that intensively promotes trees as carbon sinks) that savannas are not “degraded” forests, but taxonomically rich and in many cases ancient ecosystems with high intrinsic value (10–12). In the case of long-established open grassy vegetation types, presence of forbs with large underground storage organs and geoxylix suffrutices (“underground trees” with massive belowground “branches” supporting short aboveground stems that resprout rapidly after fire) can be a unique and valuable indicator of ancient status (12,13).

Here, we use the term “vegetation transition” as a synonym of “ecotone”, in the *sensu lato* meaning as a “zone of tension” (ZOT) (14). The first formal definition of ecotone was made by Odum (1954) (15): “an ecotone is a transition between two or more communities; it is a junction zone or tension belt which may have considerable linear extent but it is narrower than the adjoining community areas themselves”. Myriad ecotones are found at different scales, from large environmental ecotones to regional and local ecotones driven with both environmental and biotic factors (3). Indeed, at the local scale, and to a lesser extent at the regional scale, local biotic factors like species interactions can override larger environmental factors determining the range and distributions of vegetation transitions, as we discuss in later sections.

Lowland forest-savanna transitions are the most widespread ecotone in the tropics, occurring in large areas of South America, Africa, Australia and Asia (16). These transitions are characterised by many shades of green: there exists a wide range of grassy vegetation types that vary in degrees of tree-grass coexistence depending on the geographical location, local abiotic and climatic conditions, and disturbance regime (Figure 1). However, there is not a universally accepted tropical vegetation classification scheme but rather numerous descriptions with different criteria, a feature that has led to frequent misclassification of tropical grassy biomes and can result in substantial conservation threat for many (11). For example, large areas in peninsular India with vegetation that meets the technical definition of savanna are misclassified as “tropical dry deciduous forests” for historical reasons (8). Recent work has extensively reviewed the different classifications and highlighted the problems associated with such classifications and terminology (11,16). Torello-Raventos et al (2013) provide the first global classification of forest-savanna transitions, based on height and canopy cover of the dominant upper tree stratum, and the extent of lower-strata woody shrub cover and grass cover. This represented a step forward with regards to previous classifications that were exclusively based on tree height and canopy cover and ignored the lower strata (11). The three most important structural variables defining these transitions are changes in vegetation height, tree crown cover and grass cover (Figure 1). Wherever canopies are able to close, grass cover decreases and there is less fuel for fire to spread. A more closed canopy induces cooler and more humid micro-climatic conditions, and different types of forest exist depending, once again, on the geographic location and local abiotic and climatic conditions. In addition to these structural differences, differences in tree species composition and functional traits are also important in differentiating forests from savannas (8).

Since the early 2000s, studies highlighting the degradation from closed-canopy forests to more open formations after human-induced disturbances have raised concern about the appearance of degraded “savanna-like” vegetation formations dominated by a few large remnant forest trees, short-lived pioneers and grasses (17–19). We confine our review to longer-term forest-savanna boundaries that have been in existence for many decades, centuries or longer, although we briefly discuss the recent human impacts on those boundaries. However, it is important to recognise that humans have probably been affecting these boundaries since hominids first started managing fire and hunting large herbivores in

Africa over 0.2-1.0 Mya (20,21). Since *Homo sapiens* spread from Africa across the world's tropical biomes, virtually no forest-savanna boundary can be regarded as devoid of human impact (20).

Why are these transitions the way they are?

Evolution

The emergence of tropical savanna ecosystems as a significant global biome at the expense of tropical forests is a striking and relatively recent feature of Earth history. It seems broadly associated with the decline atmospheric CO_2 and the resulting cooling and drying of the atmosphere (as a result of increasing amounts of water being locked up in ice caps) that has occurred since the Eocene (around 50 Mya) (22,23), but key transitions have not been synchronous, suggesting that multiple factors are involved (24). Decreasing atmospheric CO_2 and increasing daytime water stress favored the C_4 photosynthetic pathway, which is physiologically competitive but metabolically expensive so cannot be sustained in shady conditions (25). The opening up of forests into predominantly C_3 grasses occurred in the Early-Middle Miocene (11-24 Mya) (24,25). As C_3 grasses do not have an intrinsic photosynthetic advantage over C_3 trees, this transition is unlikely to have been triggered by atmospheric CO_2 falling below a critical threshold value. Rather, it seems likely that this transition was driven by an increasing fire regime in an increasingly arid tropical biosphere, and further reinforced by the co-evolution of ungulate grazers and mixed grazers/browsers (*e.g.* horses, rhinos, antelope and elephants) adapted to exploit the abundant and easily available ground vegetation and through browsing or trampling tree sapling survival and growth (24).

C_4 grasses were a feature of these early tropical grassland landscapes soon after their origination, especially in drier parts of floodplains, but did not rise to global dominance until much later (6-8 Mya), and notably only a few taxa (in particular the Andropogonae) were able to spread to global dominance (23). This suggests that, although low CO_2 may have created the opportunity for C_4 grasses to be competitive, it was other traits associated with selected C_4 grass species that led to their global spread and dominance, including high wet season growth rates and slow decay rates (both generating highly fuel load and greatly facilitating fire), protected buds, storage organs and an ability for rapid resprouting (9). These C_4 grasslands constructed and promoted a highly flammability niche, largely displaced the previous C_3 grasslands, and also spread further into forests, pushing back the forest-savanna transition (23).

Throughout the Quaternary (2.6 Mya-present), the forest-savanna transition has moved back-and-forth in broad synchrony with the ice sheets. During cold periods (globally drier and with $CO_2 \sim 200$ ppm), savannas have advanced into forests, and during warmer interstadials and interglacials including the Holocene (globally moister and with $CO_2 \sim 280$ ppm) forests and woodlands have encroached into savannas (26). Local differences in hydrology, soil fertility and herbivory modified the patterns of advance. In West and Central Africa there is evidence of extensive retreat of forests into wet refugia during glacial maxima (27); in Amazonia and SE Asia the retreats were widespread but more probably more muted in extent (28). Even in the relatively stable climate of the Holocene there have been substantive shifts tropical rainfall regimes associated with solar precession; in a peak dry period ~ 3000 ya savannas were extensive in the Congo basin (27), and both Africa and Amazonia have witnessed an advance of forest into savanna of the past few thousand years (28). Since the Late Pleistocene humans have been an increasingly important modifier of this system, primarily through changing fire regimes (sometimes intensifying fire regimes, but at other times modifying fire regimes through management) and through declines in megaherbivores, most notably in South America and Australia but to some extent in Asia and even Africa (21).

Hence the broad history of the forest-grassy vegetation transitions shows a highly dynamic interaction between trees and C_4 grasses, mediated at largest spatiotemporal scales by rainfall patterns and atmospheric CO_2 concentrations, but reinforced by feedbacks with fire and herbivory and plant adaptations to all these factors (29).

Current sharp boundaries

One remarkable feature of transitions between tropical forests and savannas is that they are frequently quite abrupt, as opposed to being a gradual gradation in tree cover. In mesic environments, some studies argue that forest and savanna stands may represent alternative stable states modulated by fire-mediated feedbacks (30–32). The alternative stable states theory postulates that two ecosystems states can occur under the same set of environmental conditions, and the presence of one or the other is determined by disturbance and historical pathway at the community and larger scale (33).

In an alternative-stable states interpretation of the forest-savanna boundary (Figure 2), the broad-scale vegetation cover is set by precipitation regime and seasonal water supply, with low rainfall unable to sustain a closed canopy of woody vegetation. However, at intermediate rainfall amounts, both open canopy and closed canopy stands can exist (31), but the shift in canopy cover is often abrupt. One proposed mechanism for this abrupt threshold is the presence of two positive feedback loops associated with fire and/or herbivory (Figure 2) (34,35). Within the savanna ecosystem, the relatively open canopy cover allows a dry microclimate with plentiful light that supports establishment of a light-demanding and stress-tolerant grass layer, which in turn favours consumers (recurrent fires and/or large herbivores) (36), that in turn prevent forest tree seedlings breaking through a fire-trap or herbivore-trap, favouring the continued presence of the grass layer. Within the forest ecosystem, the closed canopy inhibits the establishment of the light-demanding grasses in the understory and also maintains a humid microclimate, which in turn suppresses fire occurrence and intensity, allowing tree seedling establishment and the maintenance of a closed canopy. These two feedback loops tend to drive the spatial gradients in vegetation cover away from a smooth and gradual reduction in tree cover in favour of relatively sharp transitions to alternative states (Figure 2).

One of the main empirical pieces of evidence supporting the alternative stable states theory is that the frequency distribution of remotely sensed tree cover in the tropics is not a smooth unimodal function but has three distinct modes, which seem to correspond to forest, savanna and treeless states (31,37,38). A recent study based on field based-data on tree basal area for African and Neotropical forests and savannas also found evidence supporting the tri-modality (grasslands, savannas and forests) (37).

However, the remote-sensing based evidence is still controversial. Reported discontinuities on tree cover may be an artefact of the statistical- and classification method used (39,40). Furthermore, the satellite-derived tree cover product cannot detect variation in tree cover less than 10%, and is therefore of limited applicability below 30% tree cover (41). Other studies suggest that coexistence may be confined to a well-defined edaphic/climate envelope, with both soil and climate playing a role as the key determinants in the relative location of forest and savanna (37), and that other mechanisms related to strong climate control may also be operating (42).

There are still many question marks on the scale of operability of these factors (43–45) and on the hysteresis (historical pathway dependence) operating in these systems (44,46). Whether a forest or savanna dominates at any particular point depends on microsite factors (e.g. soils, drainage) but crucially may depend on historical pathway. For example, a long past temporary release of herbivory or fire pressure may have enabled tree saplings to grow to a size where they could survive fire or herbivory (34,36). Similarly, if the historical climate on a given place has become gradually drier over time, ecological inertia and feedbacks may maintain a forest even when current climate conditions favour a savanna (47). The scale of operability of hysteresis and current drivers and processes varies regionally. For example, Lehmann et al (2014) (48), in a global study that encompassed field and remote sensing data for Australia, Africa and South America, found that the magnitude of main drivers in determining savanna woody structure varied substantially across continents. They concluded that evolutionary history and environmental differences are likely to drive the regional variation in the functional relationships between woody vegetation, fire, and climate.

At local scales, the potential of co-existing alternative stable states would tend to increase with spatial heterogeneity. Small differences in contemporary abiotic factors (*e.g.* soils, drainage), biotic factors (*e.g.* herbivore behaviour) or in disturbance pathway can result in radically different canopy cover. When considering changes over time, the two stabilising feedback loops described above and in Figure 2 tend to inhibit continuous and gradual shifts back-and-forth in the boundary in response to climatic variability. However, this may increase the likelihood of abrupt changes in response to extreme events, such as successful fire penetration of the forest during an extreme dry spell. Indeed, the migration of these sharp boundaries over longer time scales time is another strand of evidence in favour of the alternative stable states hypothesis, suggesting that the location of a particular vegetation type is not fixed by local soil conditions.

Drivers and processes shaping forest-savanna transitions

As mentioned above, there are many factors that influence the existence and stability of tropical vegetation transitions. These factors consist of abiotic and biotic drivers, and ecological processes and attributes, that interplay at the global (> 10000 km), regional (10-10000 km), community (1-10 km) and local (< 1 km) scales (Figure 3). Indeed, the role of biotic interactions on shaping species distributions beyond local scales, as well the impact on abiotic drivers at small scales it is increasingly being recognised.

To understand the ways in which forest-savanna transitions respond to environmental drivers, one must take into account the enormous diversity of life history characteristics, functional types and ecological strategies among the huge biodiversity that characterizes these transitions. Even if species coexist in the same community, they may well have completely opposed strategies of growth and reproduction (49,50). For example, in most savannas and often along many seasonal forests too, a mixture of deciduous, semi-deciduous and evergreen tree species coexists. Similarly, in open grassy environments, one finds both grass species that start to grow shortly after the first rains or after fire, and quickly go to the reproductive phase, and grasses that grow more gradually and enter into reproductive phase in the middle or late rainy season (51). The main drivers and processes operating in shaping forest-savanna transitions and their scale of operability are illustrated in Figure 3. Each subsection below focuses on one of the main abiotic or biotic drivers, and the ecological strategies and attributes associated to these drivers, with a focus on how each driver shapes the forest-savanna transition.

Water availability and species hydraulic strategies

Despite precipitation being one of the primary drivers of the distribution of tropical forest and savannas (43,48), there are no simple threshold precipitation values that determine the transition. While closed canopy humid forests tend to predominate at annual rainfall values above 1800 mm (31,37), forests and savannas can both be found at intermediate rainfall regimes (800-2500 mm) (30) and even at lower precipitation regimes areas exist with dry forest patches mosaicking with dry savannas. Rather than total precipitation, rainfall seasonality (45) and the depth of the seasonal precipitation deficit can be a better predictor of biome boundaries at a coarse scale (52). These factors interact with local soil depth, texture, hydrology and topography to determine actual seasonal local water availability, leading to mosaic landscapes of forest and savanna.

How grasses, savanna and forest tree species deal with water availability is reflected through their hydraulic strategies. In the herbaceous layer, two different growth forms associated to drought adaptation are found in savannas (51): *(i)* the drought escaping ephemeral or deciduous perennial grasses, which are active only in the wet season, and survive the period of drought stress as seeds or by going dormant; *(ii)* the deep-rooted phreatophytes, that escape the drought by gaining access to the water table.

For shrub and savanna trees and forest tree species, hydraulic strategies are varied and complex. Savannas tree species tend to be drought-resisters, exhibiting isohydric behaviour, a conservative strategy limiting transpiration rates and stomatal conductance during periods of water stress to maintain water potential (53), and buffering water supply through tissue water storage (54,55). Studies on dry forest species suggest that most species are either droughtavoiders (deciduous species with sophisticated root morphology to maximize resource capture during a limited growth season (56) or evergreen drought-resisters that minimize transpiration rates and cavitation risk to persist under dry conditions (57,58). A third group consists of light-demanding pioneer species with anisohydric behaviour (i.e. they do not regulate stomatal conductance in order to maintain high productivity, but at the risk of hydraulic cavitation), but these species are usually precluded from very dry environments (58). Nevertheless, in mesic environments they may play a crucial role on colonizing savanna environments especially if the conditions during the dry season still allow them to operate below their safety margins (*e.g.* if they establish during periods without extreme drought events).

At the forest-savanna transition, congeneric forest and savanna trees tend to employ different suites of functional traits to deal with limited water availability (59,60). Brazilian savanna species tend to have greater leaf area specific hydraulic conductance and greater transport capacity on a leaf area basis than congeneric forest trees (59,60) and higher leaf water potential and stomatal conductance in the late dry season relative to forest trees (60), but there is little difference in wood density and minimum water potential (60). The proportion of stem stored water used appears to be larger in savanna tree species (16-31%) (55) than in tropical tree species (9-15%,) (61), but there appear to be no reported values on stem water use on from forest species that establish near savanna boundaries. Another important feature of species and the zone of transition is their water uptake strategy, which varies among species and vegetation types, and is mostly reflected in differences in root morphology and root water uptake. For example, in Brazilian cerrado, woody savanna vegetation has deep roots that can uptake up to 82% of water from below 1 m soil depth, while more grassy environments (*campo sujo)* take up about 67% of the water from below the same depth (62). When grasses and woody vegetation share the same space, grasses can take up topsoil water sufficiently rapidly to reduce drainage into the subsoil, as well as take up subsoil water directly, thus decreasing water supply to woody plants and limiting seedling and sapling establishment (9,63).

Fire

At the global scale, fire regimes (the spatial and temporal distribution of fires, and their intensity) are closely associated to different biomes, with tropical forests usually being fire-sensitive ecosystems and grassy biomes usually fire-dependant or fire-adapted ecosystems

(64,65). However, fire is not unilaterally responsive to climate or to vegetation (66). Although the fire regimes characteristic of the modern world can be explained with reference to current vegetation and climate, there are complex interactions among fire, climate, vegetation and human activities. As such, a biome can contain different fire regimes, and contrasting biomes may effectively converge on a common fire regime (66).

fire at a given location will be determined by the availability and continuity of flammable dry biomass, which is largely determined by dry grass biomass (horizontal fuel continuity) but also by other variables such as canopy height and structure (vertical fuel continuity). Fire return intervals are a key aspect of these transitions, as they determine the operability of a two threshold phenomena in tree-grass interactions (34). At the community scale, the "fire-suppression threshold" exists. When tree canopy cover closes sufficiently (typically > 45-50% tree cover (71)) it reduces the community flammability by increasing air humidity and inhibiting light-demanding grasses and resulting fuel loads, thereby by reducing and disconnecting the distribution, intensity and propagation of fires. The level of this threshold depends on the fire return interval, as well as on several attributes of the adult tree species and herbaceous understorey species, such as tree crown size and density, and the shade tolerance of grasses or other herbaceous understory species (34). At the level of individual saplings, a second threshold exists, the "fire-resistance threshold". Saplings need to grow above the level of the grass to avoid topkill by fire – the destruction of above-ground biomass (34,72,73)- or complete mortality. The suppression of juveniles by repeated topkill results in a demographic bottleneck often referred to as a 'fire trap', which results in many individuals being trapped in the grass flame zone for many years (a phenomenon also known as the "Gulliver effect", (74). Recruitment into an adult size class is possible only if the sapling experiences a fire-free interval of sufficient duration to allow it to reach a critical size at which it is no longer susceptible to topkill (34). Other factors such as nutrient availability, water supply, browsing and grass competition can interact with this fire trap if they increase the growth rate of saplings and thereby enhance their chances of escaping the fire trap in a particular fire interval.

The ability of herbaceous and woody species to resist or to recover from fire depends on four main mechanisms, which are not mutually exclusive: fast growth rates, structural protection, flammability and regeneration. As explained above, those individuals with faster growth rates are more likely to escape the fire trap and avoid topkill (34,73). Many species have developed several structural adaptations to fire such as woody geoxylic suffrutices with enlarged underground xylopodia or lignotubers, thick corky barks, or thick shoots and leaves concentrated at shoot tips (12,75,76).

Flammability can be defined through three characteristics that define how well the fuel ignites (ignitibility), how well it burns (combustibility) and how long it burns (sustainability) (77,78). Studies on flammability along forest-savanna transitions are still scarce, but some evidence suggest that fires in the savanna are faster and more intense than in the nearby forests, primarily driven by the dominance of grassy fuels (79). However, grasses are not homogeneous fuels to fire. A recent study on the flammability of grasses from South African fire-prone environments showed different degrees of flammability driven by different functional traits and ultimately by evolutionary history (80). Finally, regeneration will depend on the ability of the already established vegetation to persist after fire by resprouting, or by favouring new individuals to germinate (*e.g.* serotinous species, that require heat to germinate) (81–83).

There are strong feedback mechanisms between dry atmospheric conditions and fire. A drier environment (defined as an extended period without rain with high temperatures and low air humidity) increases ignition probability by rapidly drying vegetation and making a larger portion of the vegetation available to be consumed by flames. The high amount of fuel increases the chance of fires that consume a larger fraction of the vegetation (*e.g.* tree canopies) than a fire occurring under less extreme dry conditions. Under exceptional dry conditions fires may exhibit extreme behaviour, and in exceptionally cases firestorms that create and sustain their own wind conditions though strong convective effects (84). In these conditions high intensity fires may penetrate into closed canopy environments, creating light gaps that favour grass invasion and tree mortality. For example, in an experimental treatment in southeast Amazonia, the combined effect of drought and fires has led to massive tree mortality, reducing original tree cover by half (85).

In these vegetation transitions, the interaction between water availability and fire has played a major role in the evolution of vegetation, such as the geoxyle life-forms in African savannas

(12,13). Water-fire-vegetation interactions are especially complex in forest-savanna transitions located in seasonally dry regions, and the frequency and intensity of both fire and dry periods often determine the current state of those transitions in terms of abruptness and species composition. For example, in regions where fire has been excluded, one usually finds a suit of relatively drought-tolerant forest species that are able to establish into the open savanna environments (86). Similarly, a fire event during an intense drought period may stimulate cavitation of woody species (87), thereby killing more individuals than a fire in less extreme dry conditions.

Soil

Over large regions, different soil types deriving from different substrate support different vegetation types. Soil in grasslands and savannas are often poor compared to forests (43,88). For example, South African savannas have lower cation exchange capacity than Central African rainforests, but also lower than South American savannas (89). Similarly, it is well known that the soil fertility of seasonally dry forests is higher than savannas under comparable climates in Brazil (90,91). Soil cation status appears to be a key determinant of vegetation formation type distributions across tropical South America (92).

At the community scale soils can also vary spatially along the forest-savanna transition in fertility (*e.g.* organic matter, cation exchange capacity, macronutrients), soil physical properties (*e.g.* percentage of sand), and soil depth, the latter two factors combining to determine soil water availability. This variation can limit tree seedling establishment (93) and determine different below-ground biomass allocation strategies (94). However, despite the fact that soil fertility has long been recognised to be lower in savanna soils, some studies suggest that savanna soils are indeed low in nutrients on the topsoil, but that deeper soil layers would have adequate nutrient stocks to sustain forest (93). This could perhaps explain the ability of some woody species to establish in savanna soil, but given the diverse species-specific nutrient-uptake strategies (95) this deserves further investigation.

The interaction of soil fertility with water availability and soil water holding capacity can strongly influence forest-savanna boundaries (43). A key feature of many seasonal wet-dry climates is the formation of impermeable hardpans at 1-2 m depth, which determine and limit soil depth. Forest patches are usually found located in areas with higher soil moisture than savanna patches, but in seasonally flooded parts of the landscape the waterlogging can create anoxic conditions for roots, favouring short lived grasses that grow in the non-flooded season. Conversely, a more regular water supply and shallower water table enables gallery forests to persist in savanna landscapes.

At the local scale, higher levels of soil-fertility are found beneath tree-crowns in savannas of Belize (96) and Brazil (97). This small-scale soil differentiation influences the nutritional status and productivity of grasses in these environments (98) and may play a pivotal role in tree seedling establishment. Fire recurrence also has effect over soil fertility. The effect of ashes deposited in the soil surface after fires tends to increase pH in places with high fire recurrences, and provide a higher availability of cations in the soil (99).

CO_2

CO_2 is a global driver that can potentially increasing productivity, tree growth rates and water use efficiency (100–102). Atmospheric CO_2 concentration has increased from around 280 ppm in the pre-industrial era to around 400 ppm by 2015, an almost 50% increase, and a number of lab and field studies suggest that this may be stimulating the photosynthesis and water use efficiency of C_3 plants (103).

At the local scale, higher CO_2 concentrations favour the C_3 photosynthesis pathway over the metabolically more costly C_4 pathway. Water use efficiency is increased because the stomata need to open less to allow a certain amount of carbon uptake, reducing water loss from the leaves per unit of carbon uptake (102). The observed long-term increase in biomass observed in old-growth forest plots across the tropics may be caused by increasing atmospheric CO_2 (104), thus favouring trees over most abundant lowland savanna grasses (105). For example, there is evidence that elevated CO_2 levels stimulate resprouting cerrado species (81), and stimulate growth in South African Acacia species but do not stimulate growth on C_4 grasses (101,106). At the regional scale, therefore, increasing CO_2 can be expected to favour both woody thickening of savannas and forest encroachment into savannas, by altering the fine competitive balance at the transition between trees and C_4 grasses (see *Contemporary changes in forest-savanna transitions* section). The net impact may be greater in mesic than in arid savanna environments (107,108). Such a broad scale shift relative competitiveness would interact with other processes, for example increasing the likelihood of tree saplings to escape fire and herbivory traps.

Herbivory

Large herbivores (mass 45 kg – 1000 kg) and megaherbivores (> 1000 kg) can influence vegetation structure through destruction and opening-up of woody vegetation, through browsing and trampling of tree saplings, and through grazing of ground layers that can promote the success of grasses over tree saplings (21,109). On the other hand, they can favour woody vegetation by facilitating large-scale seed dispersal through their dung, and grazers interact with fire regimes by reducing grass biomass fuel loads and fire return frequency (110). Herbivory accelerates nutrient cycling by the break-up and consumption of tough vegetation and excretion of resulting products in more labile forms (21). Megafauna also strongly facilitate the lateral transfer of nutrients across landscapes, creating high fertility latrine hotspots in the short term, but on longer timescales facilitating the diffusion of nutrients along concentration gradients (21).

Proboscideans (elephants) seem particularly important as keystone species that shape the savanna-environment and the forest-savanna threshold. Exclosure studies in African savannas show that African elephants (*Loxodonta africana*) reduce tree cover by 15-95% and are the primary cause of tree death, far exceeding fire and drought in importance as agents of adult tree mortality (111). In Kruger National Park in South Africa, they uproot up to 1500 trees per elephant per year (112), However, a recent study in the Serengeti suggests that repeated, low-intensity damage from elephants was more important to mortality than acute but less frequent damage (111). The effect of bush elephants on the actual forest-savanna transition is less clear. Forest dwelling species can also influence the vegetation transition. For example, the African forest elephant *Loxodonta cyclotis* favours trails along the forest-savanna boundary, behaviour which may facilitate dispersion but suppress seedling recruitment, and also act as a moderate fire break limiting fire penetration of forests (*pers.com.*).

At near-equilibrium abundances, an abundance of large herbivores may stabilise the forest-savanna boundary, limiting forest seedling establishment in the savanna and decreasing risk of fire penetration of the forest by decreasing grassy fuel loads. It follows that a decline in large herbivores may increase the instability of the transition, facilitating woody encroachment of the savanna but also increasing fire intensity and frequency, with the net result dependent on local climate trends and fire regimes (122). A high abundance of megaherbivores, as seen in Kruger National Park, may also destabilise the transition and cause reductions and retreat in tree cover (112).

High densities of herbivores are today mainly associated with African savannas, but until 10-50,000 years ago similarly high animal biomass were likely found in all major tropical savannas (113). The decline and loss of these megafauna is generally coincident with the arrival of humans, with the most severe extinctions (Australia, Americas) occurring where human arrival was abrupt and without a long history of earlier *Homo* presence. Even in Africa, with a long history of gradual human evolution, early *Homo* may have been responsible for the decline in many megafauna over the Pleistocene, including the large grazing elephant *Elephas iolensis* that once dominated the grasslands, and perhaps confined the browsing bush elephant *Loxodonta africana* to woodlands. Globally the Late Pleistocene hosted 50 species of megaherbivore (> 1000 kg), compared with only nine remaining today (the African forest and bush elephants and Asian elephant, five rhinoceros and the hippopotamus, all of which are generally severely depleted in range and abundance (21). Proboscideans are particularly important shapers of vegetation and were a dominant feature of savannas in every continent except Australia. For example, South American savanna woodlands hosted *Stegomastodon platensis* (a browser, mass 5 tonnes) and *Stegomastodon waringi* (a grazer, mass 7.5 tonnes) (113). South Asian savanna woodlands hosted various species of *Stegodon* (mass up to 13 tonnes). By comparison, the African bush elephant, the largest extant land mammal, has a typical mass of 4 tonnes. Australia, Darwin's "separate creation", was distinct in being the only tropical continent lacking probiscideans but hosted large browsing diprotodons (mass 2.8 tonnes). Prehistoric biomass and abundance is challenging to estimate, but it seems likely that the abundances of these "lost elephants" were similar to as those of pre-19th century African bush elephants, with consequent impacts of vegetation structure, fire regimes and seed dispersal. The lack of megaherbivores that once were abundant may partially explain broad differences in the forest-savanna boundary (e.g. the greater extent of woody savannas in South America *vs.* open grassland woodlands in African and the different rainfall thresholds at which the boundary exists in different continents).

Biological invasions

Another key feature of contemporary global change is the rapid global mixing of species, either deliberately or by accident through global transport. Because they are sites of frequent fire disturbance, savannas are among the ecosystems most vulnerable to biotic invasions (114). Invasive species can significantly alter ecosystem functioning, fuel loads and fire regimes, and create new pressures of forest-savanna transitions (114). In fact, invasions seem to be facilitated in ecotonal environments (115), where invasive species can include both grasses and woody vegetation. Most invasive grass species are used in pastures as forage species, and their invasion to the forest-savanna areas is closely associated with fire (*e.g.* (116–119). A large body of literature exists on the grass invasion of savannas in the Neotropics and northern Australia, where African grasses in particular have had major impacts. For example, many African grasses have successfully invaded Neotropical regions and nowadays species such as *Melinis minutiflora* and several *Urochloa* species have altered many forest-savanna boundaries across across the Neotropics (120,121). These grass species are often being reported to be the main drivers of the "savannization" process (19). In Africa, most invasive plants are woody species, with *Lantana camara* and *Chromolaena odorata* being the most prominent species (122). *Andropogon gayanus,* which is a native African grass, is one of the most spread exotic grasses in Australian tropical savannas, but its presence is widespread also in Brazil and other Neotropical countries (122).

Other relevant ecological processes

Forest and savanna seedling and sapling dynamics

Seedling and sapling dynamics operate at the local scale, but play a major role on the probability of a vegetation shift at a given point in space and time. Seedling traits are different from adult tree traits but are critical in determining characteristics of the adult tree community in a given environment (123). For example, there is empirical evidence for the existence of a fire trap for many woody savanna species, and the Gulliver Effect is a recurrent characteristic of woody species living in grassy vegetation with high fire frequency (9,34,124).

However, the species contributing to forest encroachment in forest-grassy vegetation transitions are forest species, for which the fire trap may be more critical than for savanna species and the Gulliver Effect may not apply because forest species may lack adaptation to high fire frequency (for example, they may not be able to repeated resprout after fire, or to build taproots or large belowground storage organs). Savannas are harsh environments for seeds to germinate and seedling to establish. The seed rain is correlated with canopy cover, with open environments receiving lower seed amounts than closed canopy vegetation types (83). Seeds in open environments tend to have lower longevity and higher predation rates (more than 60% of seeds predated or removed within 30-45 days) than in closed canopy environments (83). The main bottlenecks for seedling establishment in grassy environments are water availability (125), competitive exclusion by existing grasses, soil fertility (112), and fire vulnerability (126,127). Fast growth rates seem to be the key for success for some forest species establishing into savanna environments, with only a subset of forest species having the appropriate traits to be successful colonisers (86,126). For example, Geiger *et al.* (2011) (86) showed that in a Brazilian savanna-gallery forest transition not burned for 35 years, only five forest species were successfully expanding into the adjacent grassy vegetation environment. Cardoso et al (2016) (125) showed that only a few forest species are sufficiently drought- and fire-resistant to be able to survive the establishment phase in an African savanna environment.

A variety of functional traits can determine seedling and sapling success rates. Pioneer forest species from West Africa survive better through fire and drought in open savanna environments than on closed-canopy vegetation types (125). This was likely a result of the open-canopied savanna providing greater access to light, thereby releasing seedlings from light limitation and enabling them to make and store more starch. Tomlinson et al (2012) (128), in a cross-continental experiment with seedlings from humid and semi-arid savanna environments, reported that the key functional traits differed across continents, suggesting different responses to the selection pressures imposed by the local environment. Savanna species from humid environments allocated more biomass to roots, especially in the topsoil. By contrast, species from semi-arid environments had less biomass but greater root length and taproot length, changing root morphologies to maximize water uptake at the expense to root longevity to maximize nutrient and water capture. Growth rates did not depend on water availability but on seed species, and suggested that selective pressures were more related to fire than to drought.

Leaf habit is emerging as a characteristic that differentiates species strategies at the seedling stage in forest-grassy vegetation transitions. Deciduous tree seedlings appear to have higher photosynthetic water use efficiency than evergreen species, but no difference in assimilation rates (94). They also have rapid root extension to search for water, while evergreens use fine root structures (129), suggesting that they capture water from a different environmental space.

Coexistence, competition and facilitation

In a closed canopy forest, plants compete for light, water and nutrients. In grassy environments, competition is primarily for water and nutrients. At the forest-savanna transition, small shifts in the competitive ability of forest *vs.* savanna vegetation can dramatically affect ecosystem structure and the position of the transition. Complex competitive and facilitative interactions between individuals can operate, with winners and losers at the transition depending on the interaction of the environmental variables and biotic conditions at different scales (Figure 3).

Along an increasing rainfall gradient, the impact of trees on grass productivity shifts from facilitative to competitive, and this shift coincides with the transition from arid to mesic savannas (130). At forest-savanna transitions, species coexistence is largely unstable due to the intrinsic dynamics of these boundaries. Tree-grass coexistence is thought to be mostly determined by either demographic or competition-based mechanisms. Demographic mechanisms refer to bottlenecks on juvenile growth and escape (131), such as the fire trap, herbivory trap and the Gulliver Effect (9,34,73); therefore, tree species with traits that enable them to grow above grass height rapidly enough to escape light limitation, root competition and the fire trap will have a competitive advantage in forest-savanna boundaries.

Competition-based mechanisms refer to a niche separation with respect to limiting resources like water or nutrients (132). One of the most addressed mechanisms is the “two-layer hypothesis” (133) based on the root-niche separation model (134), that postulates that trees and grasses differ in rooting depth, with grasses exploiting soil moisture in shallow layers while trees have exclusive access to deep water. Another possible mechanism is phenological niche separation (7): while most savanna tree species achieve full leaf expansion just prior or at the onset of rains, grasses only achieve it much later. Similarly, grass senescence usually occurs earlier than leaf shedding of deciduous tree species (7). Another competition-based mechanisms is the competition-colonization model (135), that postulates a trade-off between competitive ability and colonization potential of trees and grasses; for example, while some species may have successful seed dispersion mechanisms, other species may be more competitive by being light demanding species or having fast growth rates (135). All these models emphasize different subsets of the potential interactions between trees and grasses, and have been proved for different site-specific studies, and can be incorporated into a single framework that accounts for competition at each plant development stage (seed, seedling, sapling, adult) and for competition with grasses (135).

Tree-sapling facilitation processes can also also operate at the local scale. Tree canopy cover facilitates seedling establishment of woody species in grassy environments by reducing the impact of environmental stressors (light, soil nutrient and water availability) (83), by reducing grass growth and fire probability through crown shade, by possibly increasing local soil surface water supply through hydraulic redistribution, by increasing nutrient supply and remineralisation through litter fall, and by possibly providing some protection for seedlings from mammal herbivory.

Contemporary changes in forest-savanna transitions

By being the zone of tension between two very different biomes close to their climatic margins, forest-savanna transitions can be expected to be particularly sensitive to change, whether through global drivers such as rainfall and atmospheric CO_2, or through local drivers such as fire and herbivory regime. On the other hand, feedback processes may act as a stabilizing influence that resists gradual change from one biome to the other. Ecotones are characterised by different mechanisms playing simultaneously in opposite directions, therefore creating an inherent ecological tension in these areas. There is plenty of evidence that forest-savanna transitions are changing rapidly, with woody plants increasingly invading grasslands in many places (7), and *vice versa* in others (136). However, quantification and understanding of the mechanisms behind these changes is still very limited, which calls for bigger efforts for in-field study of these changes in these transitions at decadal time-scales.

The details of climate change predictions for the tropics are notoriously inconsistent across climate models, but some broad conclusions can be drawn. There is virtual certainty that temperatures and atmospheric CO_2 concentrations will continue to rise for some time, and there is high likelihood of general intensification of rainfall variability on seasonal and interannual timescales, and more extreme wet or dry events (137,138). There is also a general tendency for expansion of the tropical arid zones and contraction and strengthening of the humid zones as global atmospheric circulation intensifies, but with substantial regional variation in exact patterns. Hence at tropical forest-savanna transitions we can expect at broad scales an interplay between increased water stress favouring savanna expansion, and high CO_2 favouring forest expansion and alleviation of water stress. The consequences of this interplay at any specific site will be mediated by local factors, including soil fertility, invasive species and changes in fire management, wild animal and domesticate herbivory pressure and land use. Studies from forest-savanna transitions across the tropics show evidence of both forest encroachment and retreat.

A number of studies report evidence of forest encroachment (106,139–141). For example, some areas of central Cameroon have had an increase of canopy cover of more than 12% for the period 1986 - 2000 (142), and widespread forest encroachment into savanna have been reported for the Congolean-West African forest zone (143,144). In South Africa, forest expansion over the grassy vegetation been consistently been reported to be occurring since the late 1930s (106,145,146). In some areas of central Brazil, borders of gallery forests had been expanding into savanna for over 4000 y (139), and some cerradão sites are undergoing a rapid shift in species composition from savanna species towards forest species (147). In this region, however, forest expansion is not consistent across the landscape and there are many other areas whether the transition has remained stable or even shown forest retreat (148). Similarly, there is also evidence of widespread bush encroachment in Australian savannas (149), and scenarios predict an increase in encroachment over the next decades (150).

It can be hard to disentangle ultimate causes of forest encroachment, which can at the local scale be a combination of atmospheric change, stochasticity in fire events, and land use history. The widespread forest encroachment observed in some regions through remote sensing studies (e.g. across northern central Africa by Mitchard and Flintrop 2013 (141)), suggests that climate and increased CO_2 may be important large-scale drivers. The strongest evidence for a CO_2 effect at the landscape scale comes from two studies that found a consistent direction of change towards woody encroachment across different fire regimes (106) and land use changes in South Africa (145). The effect of increased CO_2 over an increase on tree woody cover in savannas appears more consistent in mesic savannas than in arid savannas (107,108).

In other areas of the tropics, a number of studies report forest retreat (151) and the conversion of closed canopy forest to degraded open formations with a different species composition than natural savannas (19). For example, Veldman and Putz (2011) (19) reported over 8% of forest replaced by savannas (formed by a mixture of native pioneers and light demanding species, and exotic grasses) over an area of 1420 km^2 in Bolivia. Southern Africa appears to show large areas of decline of tree cover in miombo and mopane woodlands (141).

Many studies report forest retreat in the same areas where forest expansion has also been observed (143,148), probably associated to degradation and deforestation processes (19,143). For example, there is evidence of forest retreat in the Congolean – West Africa region (143,144), even through there is also widespread woody encroachment of savannas. However, the forest converted areas are being replaced by derived savannas with a very different floristic and structural features than natural savannas: these derived savannas are species-poor and dominated by light-demanding fast-growing invasive or native grasses, palms and pioneer forest species (19).

Although forest-savanna transitions have always tended to be dynamic, the speed of contemporary changes in drivers may override the speed at which ecological processes may adapt to these new and continuously changing conditions. This may lead to profound changes that will result not only on the expansion of forest into grassy vegetation types, but also on the degradation of forest and expansion of degraded, biodiversity-poor grassy environments.

Conclusions

We have shown that tropical forest-savanna transitions are represented by many shades of green. These reflect, on one hand, the evolutionary history of changes in abiotic drivers and the co-evolution of a wide range of ecological processes and attributes that allow the coexistence of thousands of woody and non-woody species. On the other hand, the interaction of a range of drivers and processes shapes the current vegetation at a given scale in time and space. The stability of that vegetation formation depends on the stability of the current biotic and abiotic interactions occurring in that particular point as well as at larger scales. Under contemporary global change, large changes in abiotic and biotic drivers are occurring in a short time-frame, and a question remains on how these transitions will shift as a consequence of these change changes, and how direct human influence will interact with these shifts.

This review has highlighted the importance of different processes operating at different scales in shaping the location and trajectories of these transitions. At larger spatial and temporal scales, present day location of forest-savanna transitions reflects a combination of abiotic factors (soil, climate, CO_2 concentration), interacting with biogeographical and evolutionary history, and historical and contemporary disturbance regimes. At the fine scale, local variation in soils and hydrology interact with species-specific plant traits (in particular hydraulic and fire adaption traits) and demography to shape the transition and its sensitivity to change.

We identify a series of research priorities to further understand how these drivers and processes interact and operate at different scales, and how global change in the next decades is going to affect the extent, diversity and ecosystem functioning of these fascinating areas. We identify four main axes for further research: (1) In what contexts is the alternative stable states framework useful to explain and predict the spatial pattern and dynamics of these transitions? (2) How specifically do differences in biogeographical and environmental history across the tropics result in differences in functioning, environmental thresholds and future change in these transitions at different spatial and temporal scales? (3) How do different ecological strategies at the species level determine the permeability of forest-savanna transitions? (4) Can we predict and manage future shifts in the position of forest-savanna transitions based on understanding of the combined effects of rising CO_2, climate change and shifting fire, herbivory and land use regimes?

Despite the increase in scientific efforts to understand these transitions and describe and quantify their rates of change, more empirical studies with standardised methodologies are needed to provide large scale evidence of the dynamics of these transitions and compare across different places and temporal scales. A useful step forward would be the development of a network of forest-savanna transition studies adopting standardised methodologies (similar to the networks already existing ones for tropical forests, such as ForestGeo (http://www.forestgeo.si.edu/), RAINFOR (http://www.rainfor.org) or GEM (http://gem.tropicalforests.ox.ac.uk). Such standardised protocols and scientific collaboration networks (like the TROpical Biomes in Transition, TROBIT, programme, (16)) foster cross-sites comparisons and help identify research priority areas, knowledge gaps and, more importantly, result in high quality collaborative science able to provide answers these pressing issues.

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Author contributions

Both authors made equal contributions

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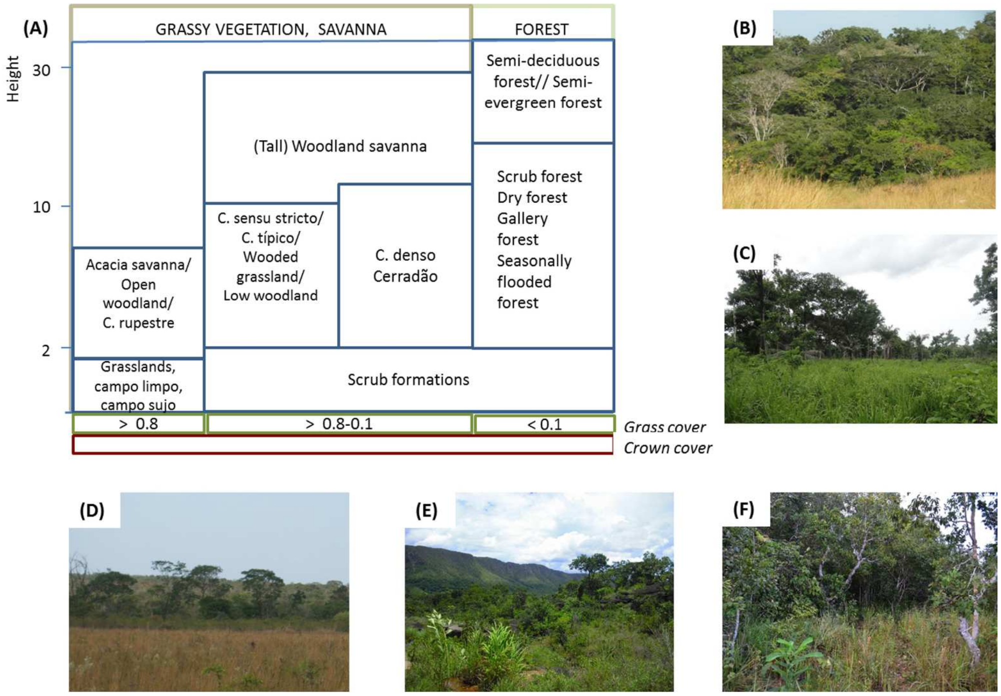
Figure 1. (A) Schematic representation of the main vegetation types between grassy vegetation and forests [modified from (5)] and examples of forest-savanna transitions (B-F). (A) Crown cover and grass cover are inversely related. The most herbaceous formations are characterised by the absence or marginal presence of woody vegetation, such as grasslands (B), open woodlands in West Africa (C), *campo sujo* (D) and *cerrado rupestre* (E) in Brazil. In the mid-range of grass and crown cover one finds a wide variety of vegetation formations ranging from more open (for example a *cerrado típico* in Brazil [E- F]) to more closed formations like *cerradão* (F). Forests are characterised by tall vegetation and high crown cover, and absence or marginal presence of grasses, *e.g.* the tropical forests of Central Africa (B), gallery forests in Brazil (D-F). (B) grassland-forest transition in Lope National Park, Gabon; (C) typical open-tall woodland transition in Ghana; (D) *campo sujo*-gallery forest transition near Brasilia (Brazil); (E) transition from *a cerrado rupestre* to *cerrado denso*, with patches of gallery forests scattered on the landscape (Chapada dos Veadeiros, Brazil) and (F) transition from *cerrado típico* to *cerradão* (Serra das Araras, Mato Grosso, Brazil). *Photo credits: (B) Sam Moore; (C-F) Imma Oliveras.*

Figure 2. Conceptual illustration of the alternative stable states theory in forest-savanna transitions. At low rainfall levels, grasslands with limited woody cover dominate, grasses produce high fuel that enhances the probability of consumption by fires and/or herbivores, that create a 'trap' for juvenile woody vegetation. At high rainfall levels, woody cover closes the canopy, moistening the microclimate, shading out light-demanding grasses and therefore suppressing fire. At intermediate levels of rainfall, if fire/herbivore disturbances are suppressed the tree canopy will eventually be closed enough as to supress the herbaceous layer and therefore fire. On the other hand, if fire/herbivore pressure is heavy, an open environment is maintained by continuously preventing tree saplings from escaping escape the fire/herbivore 'trap'. The presence of these two positive feedbacks acting in different directions results in a tendency for relatively abrupt changes in tree and grass cover. See main text for more details.

Figure 3. Different drivers and processes operate at different spatial and temporal scales in determining tropical forest-grassy vegetation transitions. At the global scale, and at large time scales, climate (mean annual radiation, temperature, precipitation, seasonality and dry season length), fire regimes (frequency and intensity of fires) and soil types determine distribution between the forest (dark green), grassy vegetation (dark purple as natural, light purple has human-modified) and grassland biomes (redrawn from GlobCover 2009, http://due.esrin.esa.int/page_globcover.php). At the community scale fire regimes, soil properties and herbivory are the main drivers, and ecological processes are mostly reflected in tree-grass coexistence. At the local scale, many drivers and ecological processes affect the given vegetation existing at that precise point in space and time.



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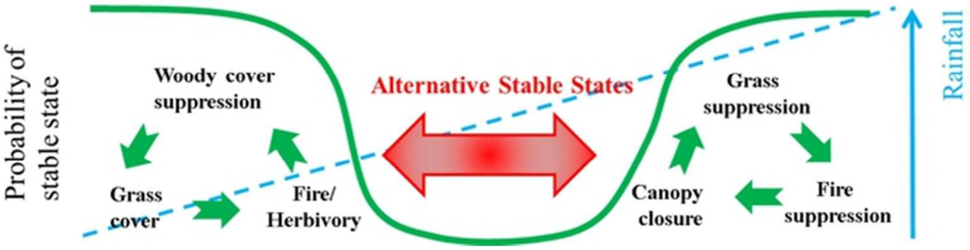

Conceptual illustration of the alternative stable states theory in forest-savanna transitions. At low rainfall levels, grasslands with limited woody cover dominate, grasses produce high fuel that enhances the probability of consumption by fires and/or herbivores, that create a 'trap' for juvenile woody vegetation. At high rainfall levels, woody cover closes the canopy, moistening the microclimate, shading out light-demanding grasses and therefore suppressing fire. At intermediate levels of rainfall, if fire/herbivore disturbances are suppressed the tree canopy will eventually be closed enough as to supress the herbaceous layer and therefore fire. On the other hand, if fire/herbivore pressure is heavy, an open environment is maintained by continuously preventing tree saplings from escaping escape the fire/herbivore 'trap'. The presence of these two positive feedbacks acting in different directions results in a tendency for relatively abrupt changes in tree and grass cover. Refer to text for more details.
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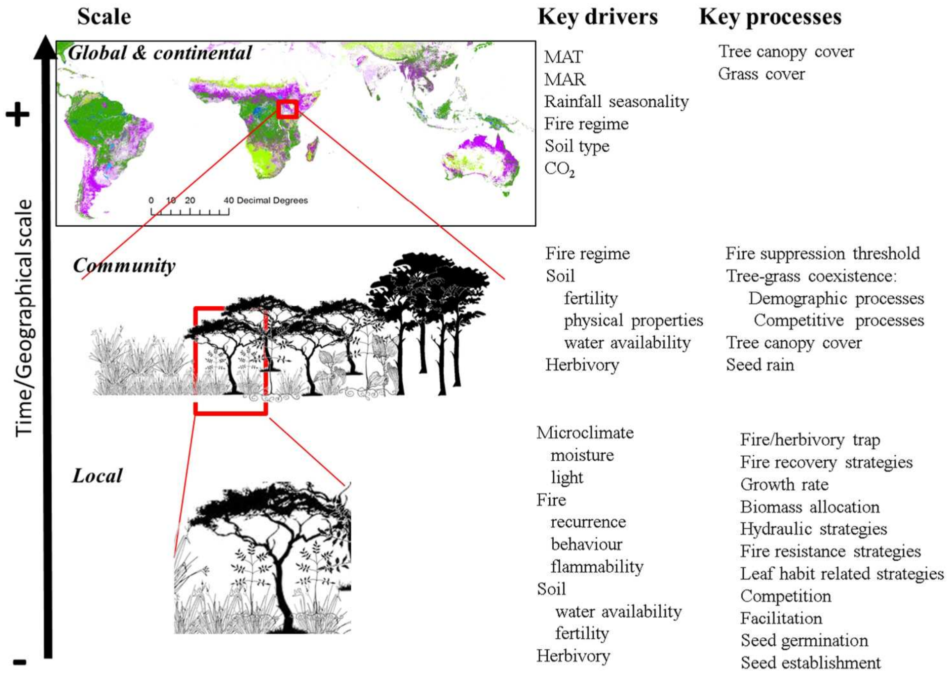

Different drivers and processes operate at different spatial and temporal scales in determining tropical forest-grassy vegetation transitions. At the global scale, and at large time scales, climate (mean annual radiation, temperature, precipitation, seasonality and dry season length), fire regimes (frequency and intensity of fires) and soil types determine distribution between the forest (dark green), grassy vegetation (dark purple as natural, light purple has human-modified) and grassland biomes (redrawn from GlobCover 2009, http://due.esrin.esa.int/page_globcover.php). At the community scale fire regimes, soil properties and herbivory are the main drivers, and ecological processes are mostly reflected in tree-grass coexistence. At the local scale, many drivers and ecological processes affect the given vegetation at that precise point in space and time.
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