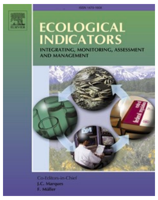
Ecological Indicators 150 (2023) 110220

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Do limits exist on potential woody cover of Brazilian savanna?

Xuebin Yang[a,b,*], Kelley A. Crews[c], Thoralf Meyer[c]

[a] *Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA*
[b] *Department of Geography and the Environment, Syracuse University, Syracuse, NY 13244, USA*
[c] *Department of Geography and the Environment, University of Texas at Austin, Austin, TX 78712, USA*

ARTICLE INFO

Keywords:
Potential woody cover
Cerrado
Precipitation
Soil moisture
MODIS tree cover
Quantile regression
GEE

ABSTRACT

With the increasing concern of woody plant encroachment worldwide in savanna ecosystems, many studies endeavor to examine the upper bound of woody plant cover, which is referred to as potential woody cover. Potential woody cover defines the maximum possible woody plant encroachment and bears strong implications on savanna dynamics. Both African and North American savannas have been reported to exhibit limits on potential woody cover below 650 and 660 mm of mean annual precipitation (MAP), respectively. At present it is less clear whether that limit exists and at what level in the Brazilian savanna (the Cerrado) of South America, throughout which MAP is above 790 mm. This study models the potential woody cover pattern of Brazilian savanna over the present precipitation gradient and in relation to surface and subsurface soil moisture (SM) separately. Remotely sensed products were processed in Google Earth Engine (GEE), and included MODIS tree cover (MOD44B), TRMM monthly precipitation (3B43), and NASA-USDA Enhanced SMAP Global soil moisture. Quantile regression results suggest that below respective thresholds of MAP, surface SM, and subsurface SM, potential woody cover in Brazilian savanna is constrained. Comparison to the savanna in central Texas of the United States reveals that water availability is not the only determinant of potential woody cover. Regional context such as precipitation seasonality and woody plant species are important factors. This study also underscores the discrepancy between potential woody cover modelled based on MAP and that based on soil moisture (surface and subsurface).

1. Introduction

Savanna ecosystems are characterized by the variable coexistence of woody plants (both tree and shrub morphologies) and herbaceous vegetation (e.g. grasses), as well as a distinct dry season (Sankaran et al., 2004; Woodward et al., 2004). They occur across a range of mean annual precipitation (MAP), generally from about 300 to 1800 mm (Accatino et al., 2010). Spanning one fifth of the Earth's terrestrial surface, savanna ecosystems are inhabited by a large population of human beings, livestock and wildlife (Staver et al., 2011), and are critical for food security globally (Warth et al., 2020). Additionally, these systems are important in regulating the global carbon cycle particularly through soil carbon sequestration (Bai and Cotrufo, 2022), and in maintaining biodiversity and fire regimes (Myers et al., 2000; Poulter et al., 2014; Schmidt and Eloy, 2020).

Woody plant encroachment, the directional increase of woody plants in cover and dominance at the cost of herbaceous vegetation, has long been observed worldwide in savanna ecosystems (Stevens et al., 2017), and noted to shift not only spatially but temporally as well (Huan et al., 2020). Ratajczak et al. (2012) reported 21 different encroaching woody species across North American savannas. In the Brazilian savanna (the Cerrado) of south America, 19% of the intact area has exhibited a strong woody plant encroachment trend over the last 15 years (Rosan et al., 2019). Sub-Saharan Africa increased 8% in woody plant cover in the past three decades (Venter et al., 2018). Lunt et al. (2010) documented an increase of 18,730 ha in woody plant cover from 1989 to 2005, for the grassy woodlands of Victoria, Australia. Yang and Crews (2020) observed juniper encroachment in the savanna of central Texas of the United States at 100 m scale, and found that the mean annual encroachment rate ranged from 0.16% to 3.46%, depending on precipitation level and initial woody cover.

The unfavorable shift in the proportion of woody plants severely impaired savanna ecosystems' structure and function. Anadón et al. (2014) quantified the impact of woody plant encroachment on livestock production in North and South America, and found that each 1% increase of woody cover led to 0.6 to 1.6 less reproductive cows per square

---

* Corresponding author at: Department of Geography and the Environment, Syracuse University, Syracuse, NY 13244, USA.
E-mail address: xyang110@syr.edu (X. Yang).

https://doi.org/10.1016/j.ecolind.2023.110220
Received 30 December 2021; Received in revised form 13 February 2023; Accepted 3 April 2023

kilometer. The encroachment also resulted in the decline of endemic plant species, as well as habitat loss and fragmentation in North American and Brazilian savannas (Ratajczak et al., 2012; Alofs et al., 2014; Pellegrini et al., 2016). Honda and Durigan (2016) revealed in Brazilian savanna that an increase of 1 m^2 tree basal area per hectare reduced rainfall reaching the ground by 0.9%, and concluded that woody plant encroachment could potentially lessen river and groundwater recharge. Moreover, Smit and Prins (2015) showed in African savannas that increased woody plant may have ripple effects throughout atmospheric cycles, tourism industry, and subsistence livelihoods.

These consequences aroused widespread concern on woody plant encroachment among conservationists, ranchers, and government agencies (Stevens et al., 2017). In particular, potential woody cover, the maximum realizable woody plant cover of a given site, increasingly garners attention (Sankaran et al., 2005; Scholtz et al., 2018; Ji et al., 2019). Potential woody cover marks the maximum possible woody plant encroachment: higher potential woody cover means higher possibility of transition into woodland or forest following the encroachment (Bucini and Hanan, 2007; Yang et al., 2016). As such, savanna areas with higher potential woody cover are in more urgent need for management efforts in face of woody plant encroachment (Strömberg and Staver, 2022). The magnitude of potential woody cover can also inform choices of state-and-transition models versus succession models when conceptualizing the dynamics of a specific savanna region (Fowler and Simmons, 2009; Bestelmeyer et al., 2017). While state-and-transition models highlight alternate stable states (e.g. savanna, grassland, woodland) and reversible transitions between them without human manipulation, succession models stress ordered and irreversible transitions between different states. High potential woody cover (e.g. canopy closure) could lead to the establishment of woodland or forest and therefore preclude cyclical transition between grassy and woody dominance in savanna landscapes, consequently undermining the applicability of state-and-transition models. Additionally, potential woody cover is indicative of existing woody cover level relative to the maximum possible, which signals savanna ecosystems' remaining carbon storage capacity (Huang et al., 2018; Scholtz et al., 2018).

Woody plant cover in savannas is under the control of soil moisture (SM), soil nutrients, fire regime(s), and herbivory (House et al., 2003; Sankaran et al., 2004). For instance, Kulmatiski and Beard (2013) found in savannas of South Africa that higher precipitation intensity leads to deeper penetration of water into soil, and therefore increases water availability for woody plants and facilitates their growth. Fire suppression has been identified as the major reason of woody plant encroachment in Brazilian savanna in recent years (Durigan and Ratter, 2016). Increasing grazing herbivores and decreasing browsing herbivores were suggested to favor woody plant growth in North American and African savannas (Van Auken, 2009; O'connor et al., 2014). In addition, the rising CO_2 concentration has been postulated to enhance woody plant proliferation by promoting water-use efficiency in dry savannas, and by increasing carbon allocation to woody plant root, thus improving recovery from disturbance in wet savannas (Devine et al., 2017).

Among the above factors, water availability has proven to be the primary determinant of savanna woody cover (Sankaran et al., 2005; Lehmann et al., 2013; Axelsson and Hanan, 2018; Ji et al., 2019). It imposes a limit on potential woody cover (represented by 99th quantile of observed fractional woody cover of sample plots), for example in part of African savannas (Sankaran et al., 2005; Devine et al., 2017). Specifically, potential woody cover in African savannas increases linearly with mean annual precipitation (MAP) untill the threshold of ~ 650 mm, then stabilizes at higher levels of MAP. Following this water availability-limited scheme, various studies have modeled the potential woody cover of other savanna ecosystems. Scholtz et al. (2018) reported a similar two-segment potential woody cover pattern over North American Great Plains. There, potential woody cover was constrained by MAP below the thresholds of 690 mm and 710 mm in areas of high and low fire frequency respectively. Whereas MAP above the respective thresholds is sufficient for woody plant growth. Yang et al. (2020) found in Texas savanna of the United States that potential woody cover is limited by MAP to different degrees below 660 mm. More importantly, they revealed that the spatial scale of observation (sample plots) matters in potential woody cover modelling. That is, the upper bound fractional woody cover (by 99th quantile) under given precipitation level decreases with observation scale, but stabilizes by the 250 m scale. A spatial scale between 250 m and 500 m was thus recommended for potential woody cover modelling.

The Brazilian savanna, throughout which MAP is typically above 790 mm (Fig. 1), has been less frequently assessed in terms of potential woody cover. Meanwhile, many sites in this region have transformed into forest, mainly due to fire suppression (Pinheiro et al., 2010; Stevens et al., 2017). It raises the question on the proportion of Brazilian savanna that can persist in the absence of fire (Durigan and Ratter, 2016). By considering climate alone, Bond et al. (2005) predicted that the whole Brazilian savanna would become forest without fire, which would indicate that there is no limit on potential woody cover throughout Brazilian savanna. However, this prediction has not been rigorously investigated yet. As such, the primary objective of this study is to test whether limits exist on potential woody cover of Brazilian savanna despite its high precipitation level, by modeling potential woody cover over the precipitation gradient.

It is worth noting that long-term MAP has been applied as the proxy of plant water availability in previous studies to model potential woody cover, due to the scarcity of large spatial and temporal scale soil moisture data at the time (Good and Caylor, 2011). Although MAP plays an important role in determining soil moisture, other factors such as topography, soil property and solar radiation can also make a difference to soil moisture (Korres et al., 2015; Huang et al., 2016). Therefore, modelling potential woody cover with soil moisture data could lead to more accurate results. Now the increasing availability of large scale soil moisture data (e.g. NASA-USDA Enhanced SMAP Global soil moisture) provides us the opportunity to improve on past efforts. Thus the second objective of this study is to relate potential woody cover to surface and subsurface soil moisture in the Brazilian savanna. Overall, this study will advance our understanding of the limitation mechanism(s) of savanna potential woody cover.

2. Materials and method

2.1. Study area

The Brazilian savanna (the Cerrado), located in central Brazil (Fig. 1a), occupies over one fifth (204 million ha) of the country's territory (Olson et al., 2001; Sano et al., 2010). It encompasses a broad rainfall gradient, with MAP ranging from ~ 790 mm to ~ 2000 mm (Fig. 1b). The distinct dry season in this region occurs between May and September (Oliveira and Marquis, 2002). Elevation varies widely between 49 m and 1621 m (Fig. 1c). The Cerrado area is a high priority for conservation, particularly in consideration of its highest biodiversity level among global savanna ecosystems (Myers et al., 2000; Ratter et al., 2006).

The Brazilian savanna is characterized by high heterogeneity. For instance, woody plant abundance varies greatly from grassland with sparse shrub to closed woodland/forest (Silva et al., 2006; Franke et al., 2018). Sano et al. (2019) divided the Brazilian savanna into 19 ecoregions according to their biophysical attributes of topography, vegetation, precipitation, and soil type. These ecoregions differ in the degree of endangerment for conservation and restoration.

Historically, fire played a most important role in maintaining the structure, function, and biodiversity of Brazilian savanna (Staver et al., 2011; Durigan and Ratter, 2016). However, in response to the widely misused fires related to deforestation and ranch management, Brazilian government enforced fire suppression policy over the past several decades (Brannstrom et al., 2008; Eloy et al., 2019). Along with other

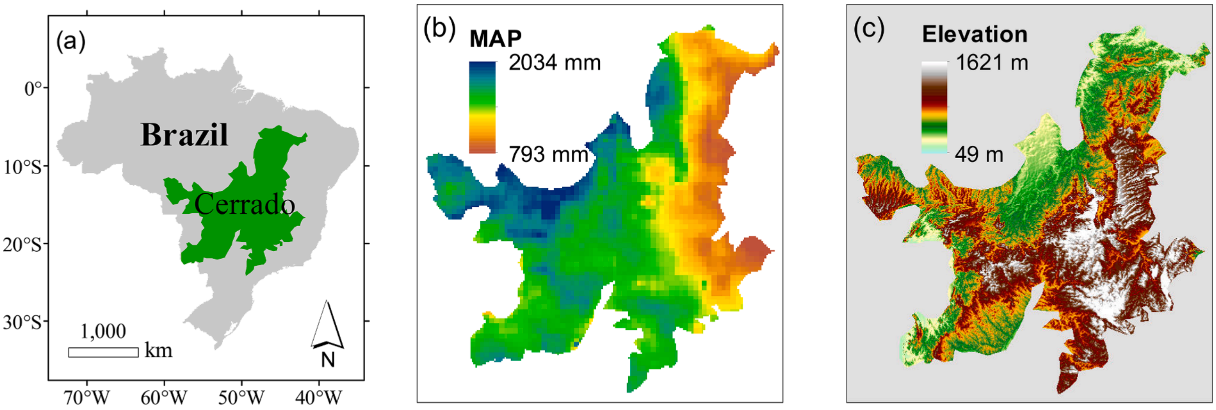


Fig. 1. (a) The distribution of Brazilian savanna (the Cerrado) in Brazil, (b) mean annual precipitation of 2008–2017 (data source: TRMM 3B43), (c) elevation of Brazilian savanna (data source: GMTED2010).

human intervention such as landscape fragmentation and transformation, the fire suppression policy has led to remarkable decreases in fire frequency and extent (Schmidt and Eloy, 2020). Since then, substantial woody plant encroachment has been documented across this region (Durigan and Ratter, 2006; Rosan et al., 2019). For instance, Abreu et al. (2017) reported an annual carbon stock increase rate of 1.2 Mg per hectare since 1986, accompanied by acute plant and animal species loss. In the wake of the encroachment, many sites across the Brazilian savanna may have already realized their potential woody cover, which would facilitate accurate potential woody cover modelling.

2.2. Data and preprocessing

2.2.1. MODIS tree cover product

The tree cover layer of MODIS Vegetation Continuous Fields (VCF) product (MOD44B) depicts the proportion of canopy cover of trees above 5 m in height at 250 m resolution (Hansen et al., 2002; DiMiceli et al., 2017). It covers the global terrestrial surface on an annual basis since 2000. This tree cover layer provides research communities improved opportunity to examine the gradation of tree cover over broad environmental gradients. Particularly, it has served as the best proxy of woody plant cover in savanna ecosystems (Bucini and Hanan, 2007; Good and Caylor, 2011; Yang et al., 2016).

Yang and Crews (2019a) found that short woody plants are proportionally captured by the MODIS tree cover product due to their similar spectral reflectance as tall trees. In particular, the MODIS tree cover product is capable of revealing the general pattern of potential woody cover over precipitation gradient. Additionally, the 250 m scale was proven suitable for potential woody cover modeling (Yang et al., 2020). Given so, the 2018 MODIS VCF tree cover layer (collection 6) was used in this study to model potential woody cover pattern of the Brazilian savanna. As displayed in Fig. 2a, the fractional tree cover at 250 m scale is as high as 85%. This tree cover layer, along with the following soil moisture and precipitation products, were accessed from and processed in Google Earth Engine.

2.2.2. Surface and subsurface soil moisture data

The NASA-USDA Enhanced Soil Moisture Active Passive (SMAP) global soil moisture dataset was utilized in this study (Entekhabi et al., 2010). It provides surface and subsurface soil moisture information of the earth’s surface at 10 km resolution. This product is available dating back to 04/01/2015. It has been utilized to model soil water balance and monitor agricultural drought globally (Mladenova et al., 2019; Mladenova et al., 2020). In this study, the mean surface soil moisture and mean subsurface soil moisture data of the time period 04/01/2015 to 04/01/2018 were used. As shown in Fig. 2b and c, the surface SM varies between 6.8 mm and 17.9 mm, while the subsurface SM ranges from 23 mm to 153 mm.

2.2.3. Precipitation data

The monthly precipitation product 3B43 (version 7) from NASA Tropical Rainfall Measuring Mission (TRMM) was utilized in this study. This product is developed from several independent precipitation estimates that involve microwave data of multiple satellites (Bowman et al., 2007). For each calendar month since the year 1998, the product 3B43 has a single estimate of precipitation rate (mm/hour) for each 0.25° by 0.25° grid cell (27,830 m), between 50°N and 50°S of the earth. This product has been widely applied in research and application (Jaber and Abu-Allaban, 2020; Yu et al., 2020). In this study, the monthly precipitation data of 2008 to 2017 was converted to mean annual precipitation

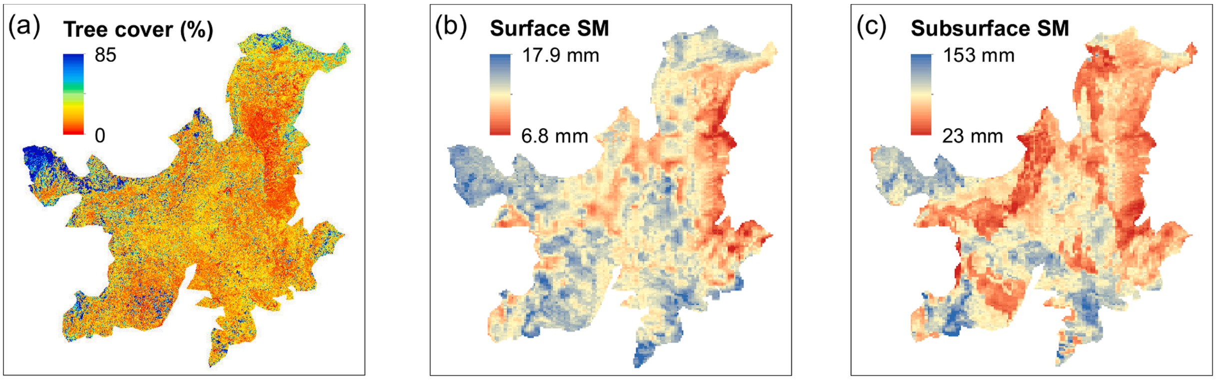


Fig. 2. (a) 2018 MODIS fractional tree cover (250 m) in Brazilian savanna, (b) 3-year (04/01/2015 to 04/01/2018) mean surface soil moisture, (c) 3-year (04/01/2015 to 04/01/2018) mean subsurface soil moisture.

(mm) of this 10-year period. As shown in Fig. 1b, the resulting MAP falls within the range of 793 mm to 2034 mm.

2.3. Method

2.3.1. Data sampling

To model the potential woody cover pattern in relation to precipitation, surface SM, and subsurface SM, a total of 20,000 MODIS tree cover pixels (2018) were randomly sampled across Brazilian savanna. These sample pixels cover 0.064% of the study area. Then the corresponding MAP, surface SM, and subsurface SM of each MODIS tree cover pixel were extracted from respective layers. As displayed in Figs. 3 to 5, this sizable sample spans different levels of tree cover, MAP, surface SM, and subsurface SM, and is used as representative of the study area.

2.3.2. Quantile regression

Traditionally, regression analysis focuses on the mean of response distribution and its relationship with independent variables (Chatterjee and Hadi, 2015). Koenker and Bassett (1978) proposed to relate different parts of response distribution to independent variables, known as quantile regression. Since different parts of response distribution may respond differently to independent variables, quantile regression can provide a more complete assessment of the relationship between response and independent variables (Hao et al., 2007). It enables better investigation of possible causal relationships among variables involved in ecological processes (Cade and Noon, 2003).

Quantile regression is particularly useful in estimating the upper bound of response variable(s) (Axelsson and Hanan, 2018). This is because there can be many factors associated with the response variable, but not all of them can be measured or included in the analysis. However, the upper bound set by the measured factors cannot be exceeded even if other unmeasured factors were included in the analysis (Fornaroli et al., 2015). In this study, while potential woody cover is primarily limited by annual total precipitation (or soil moisture), it could also be affected by other factors such as precipitation intensity and evapotranspiration (Good and Caylor, 2011; Kulmatiski and Beard, 2013). However, data on these other factors are not always available. The upper bound of woody plant cover modelled with annual total precipitation will not be exceeded even when other factors are incorporated. Consequently, quantile regression has been very popular in potential woody cover modeling (Scholtz et al., 2018; Ji et al., 2019; Yang et al., 2020).

A predefined function linking the response and independent variables is required for quantile regression (Hao et al., 2007). In addition, a set of initial values (estimates) for the parameters of the predefined function is necessary to run the quantile regression. In this study, all the quantile regression was conducted using the *R* package *quantreg* (Koenker, 2004).

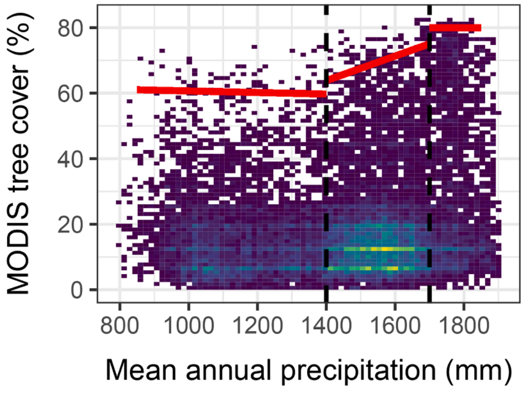


Fig. 3. Density plot of MODIS tree cover versus MAP and 99th linear quantile regressions over three MAP segments of Brazilian savanna.

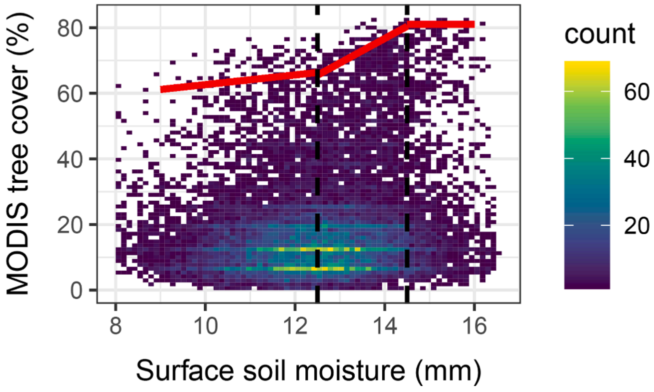


Fig. 4. Density plot of MODIS tree cover versus surface SM and 99th linear quantile regressions over three surface SM segments of Brazilian savanna.

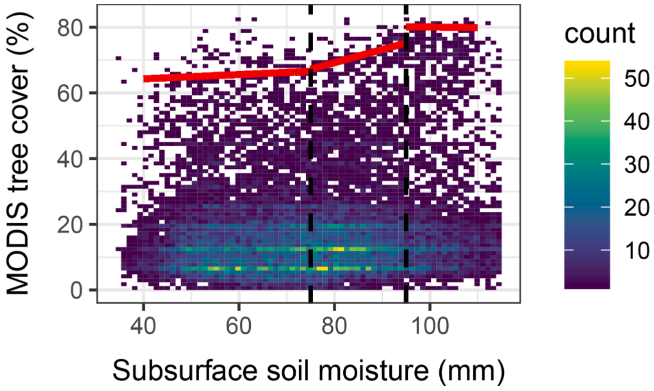


Fig. 5. Density plot of MODIS tree cover versus subsurface SM and 99th linear quantile regressions over three subsurface SM segments of Brazilian savanna.

2.3.3. Preliminary analyses of potential woody cover pattern

Before rigorously modeling the potential woody cover of Brazilian savanna, preliminary analyses were performed to explore its general pattern over the gradients of MAP, surface SM, and subsurface SM, respectively. Following Sankaran et al. (2005), potential woody cover was represented by 99th quantile of the fractional tree cover of sample pixels. Specifically, linear quantile regression ($y = a + bx$) was performed separately over different segments of each environmental gradient.

Firstly, the potential woody cover pattern was examined in relation to MAP. The density scatterplot of fractional tree cover versus MAP is displayed in Fig. 3. After iterative testing, it was found that the relationship between potential woody cover and MAP varies, roughly across the three segments of 850–1400 mm, 1400–1700 mm, and 1700–1850 mm. Fitted potential woody cover is represented by the three red lines overlaid on the scatterplot (Fig. 3). According to the p-values (Table 1), there is no significant relationship between potential woody cover and MAP over the first and third segments. In contrast, the potential woody cover exhibits a significant positive linear relationship with MAP over

Table 1
Details of 99th quantile regression ($y = a + bx$) over three MAP segments of Brazilian savanna.

MAP segment	*a*	*b*
850–1400 mm	63.1	−0.0024 (0.7)
1400–1700 mm	11.5	0.037 (<0.01)
1700–1850 mm	80.0	0 (1.0)

The values in the parentheses are p-values.
All the estimates for *a* are statistically significant at $p < 0.01$ level.

the middle segment of 1400–1660 mm. As such, potential woody cover in the Brazilian savanna exhibits a three-segment pattern over the precipitation gradient. That is, it stays at a low level at the low end of MAP and stays at a high level at the high end of MAP, with a linear transitional level in between.

Secondly, the potential woody cover pattern was examined in relation to surface SM. The density scatterplot of fractional tree cover versus surface SM is displayed in Fig. 4. It was revealed that the relationship between potential woody cover and surface SM varies, roughly across the three segments of 9–12.5 mm, 12.5–14.5 mm, and 14.5–16 mm. The fitted potential woody cover is represented by the three red lines (Fig. 4). According to the p-values (Table 2), potential woody cover shows no significant relationship with surface SM over the first and third segments. It exhibits a significant positive linear relationship with surface SM over the middle segment of 12.5–14.5 mm. Therefore, the potential woody cover follows a similar three-segment pattern over the surface SM gradient as that over precipitation gradient.

Thirdly, the potential woody cover pattern was examined in relation to subsurface SM. The density scatterplot of fractional tree cover versus subsurface SM is displayed in Fig. 5. It was shown that the relationship between potential woody cover and subsurface SM varies, roughly across the three segments of 40–75 mm, 75–95 mm, and 95–110 mm. The fitted potential woody cover is represented by the three red lines (Fig. 5). According to the p-values (Table 3), the potential woody cover has no significant relationship with subsurface SM over the first and third segments. It shows a significant positive linear relationship with subsurface SM over the middle segment of 75–95 mm. Therefore, potential woody cover in Brazilian savanna exhibits a three-segment pattern over the subsurface SM gradient, similar as that over precipitation and surface SM gradients.

2.3.4. *Potential woody cover modeling*

According to the above preliminary analyses, potential woody cover in Brazilian savanna exhibits a three-segment pattern over each of the three environmental gradients. That is, it has a lower asymptote at the low end of each environmental gradient, an upper asymptote at the high end, and a growing section in between. As such, the potential woody cover pattern could be best represented by a Gompertz function. This function is characteristic of minimal change at the low and high ends of independent variable, but growth in the middle. The curve also allows asymmetry between the low and high ends.

Specifically, the following Gompertz equation was applied to model the overall potential woody cover pattern. This function has four parameters where a represents the lower asymptote, sum of a and c corresponds to the upper asymptote, b refers to the maximum growth rate, and m is the displacement point along the x-axis (Tjørve and Tjørve, 2017). This function has been previously successfully applied in potential woody cover modeling of Texas savanna (Yang et al., 2016, 2020). In this study, the regression was performed over the overall range of each environmental gradient that applied in the preliminary analyses.

$$Y = a + ce^{-e^{-b(x-m)}} \tag{1}$$

Table 2

Details of 99th quantile regression ($y = a + bx$) over three surface SM segments of Brazilian savanna.

MAP segment	a	b
9–12.5 mm	47.8	1.48 (0.20)
12.5–14.5 mm	–27.7	7.46 (<0.01)
14.5–16 mm	81.0	0 (1.0)

The values in the parentheses are p-values.
All the estimates for a are statistically significant at $p < 0.01$ level.

Table 3

Details of 99th quantile regression ($y = a + bx$) over three subsurface SM segments of Brazilian savanna.

MAP segment	a	b
40–75 mm	61.7	0.065 (0.38)
75–95 mm	37.2	0.4 (<0.01)
95–110 mm	81.7	−0.016 (0.88)

The values in the parentheses are p-values.
All the estimates for a are statistically significant at $p < 0.01$ level.

2.3.5. *Compare Brazilian savanna to Texas savanna*

To better understand the limitation mechanism of potential woody cover in savanna ecosystems, a comparison was made between Brazilian savanna and Texa savanna. Firstly, potential woody cover patterns of the two savannas over precipitation gradient were assembled in one graph. To match the observation scale of tree cover (250 m) in this study, the potential woody cover pattern of Texas savanna at 250 m scale was used for comparison (Yang et al., 2020). Secondly, the probability distribution of MAP, surface SM, and subsurface SM were compared between the two savannas. For Brazilian savanna, the data of MAP, surface SM, and subsurface SM from Figs. 3-5 were used. For Texas savanna, all the 1145 pixels of surface SM and subsurface SM (10 km, from NASA-USDA SMAP) within it were used, along with MAP data (1981–2010) of 1500 random pixels (250 m, from Yang and Crews, 2019b).

2.3.6. *Explore the relationship among MAP, surface SM, and subsurface SM*

To clarify the rationality of using MAP as the proxy of plant water availability, we examined the relationship among MAP, surface SM, and subsurface SM, with the data of Figs. 3-5. Specifically, a simple linear regression was performed between every two of the three variables. Both p-value and R-squared value were recorded for each regression.

3. Results

3.1. *Potential woody cover pattern of Brazilian savanna*

Details of the quantile regressions with Gompertz function over each environmental gradient are summarized in Table 4. The resulting regression lines are overlaid on respective scatterplots in black in Fig. 6. As shown by Table 4, all the coefficients are highly statistically significant. The regressions do not cover the very low end and very high end of each environmental variable, mainly due to the very sparse observations (samples) at the two ends (Fig. 6).

Potential woody cover varies across the Brazilian savanna (Fig. 6). Overall, it exhibits a three-segment pattern over each of the three environmental gradients. It starts from a low stable level of 60 ~ 66% (parameter a) and ends at a high stable level of 80 ~ 81.2% (sum of a and c). The low stable level and high stable level were connected by an approximately linear transition in between. The magnitude of potential woody cover modeled based on surface SM is very close to that modeled in relation to subsurface SM (65% vs. 66% for low stable level, 81.2% vs.

Table 4

Details of the 99th non-linear quantile regression over each environmental gradient of Brazilian savanna..

	a	b	c	m
MAP (850–1850 mm)	60.0 (0.6)	0.01 (0.002)	20.0 (1.3)	1500.0 (14.0)
Surface SM (9–16 mm)	65.0 (0.8)	1.7 (0.37)	16.2 (1.3)	13.2 (0.1)
Subsurface SM (40–110 mm)	66.0 (0.6)	0.18 (0.04)	14.8 (1.0)	86.2 (1.0)

The values in the parentheses are standard errors of the estimates.
All estimates are statistically significant at $p < 0.001$ level.

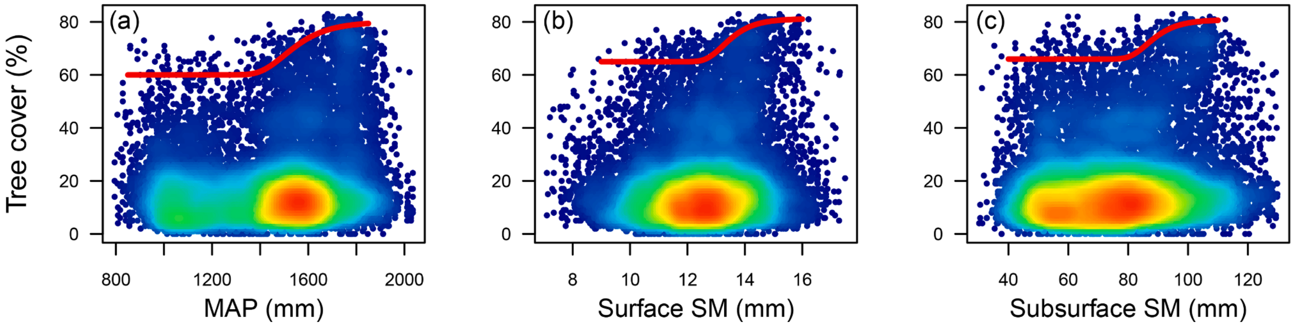


Fig. 6. Modelled potential woody cover pattern (red curve) of Brazilian savanna, over the gradient of (a) mean annual precipitation, (b) mean surface soil moisture, and (c) mean subsurface soil moisture.

80.8% for high stable level) (Fig. 6b, 6c). However, they are higher than that modeled in relation to MAP (60% for low stable level, 80% for high stable level) (Fig. 6a).

It is clear that above certain thresholds of MAP, surface SM, and subsurface SM, water availability is sufficient for woody plant growth, and potential woody cover (~80%) reaches canopy closure. Below the respective thresholds, water availability is insufficient, imposing a limit on potential woody cover to different degrees. The connection points of the three segments over each environmental gradient were not calculated. This is because although the MODIS tree cover product is capable of revealing the general potential woody cover pattern, it falls short of quantifying the thresholds of alternate stable states (Hanan et al., 2014; Yang and Crews, 2019a).

3.2. Comparison between Brazilian savanna and Texas savanna

As shown in Fig. 7, Brazilian and Texas savannas exhibit a similar three-segment potential woody cover pattern, despite their different MAP range. While Brazilian savanna occupies the high end of x-axis (MAP), Texas savanna occupies the low end. It is evident that there is an overlap of MAP level (850–955 mm) between the two savannas. Under the overlapped MAP level, potential woody cover in Texas savanna reaches canopy closure (~86%) but is much limited in Brazilian savanna.

According to Fig. 8, the high ends of surface SM and subsurface SM in Texas savanna also overlapp with the respective low ends of Brazilian savanna. Surface SM and subsurface SM in the overlapped range is sufficient for woody plant growth in Texas savanna (Yang et al., 2020), but not for Brazilian savanna. This finding further corroborates that water availability is not the only determinant of potential woody cover across savanna ecosystems.

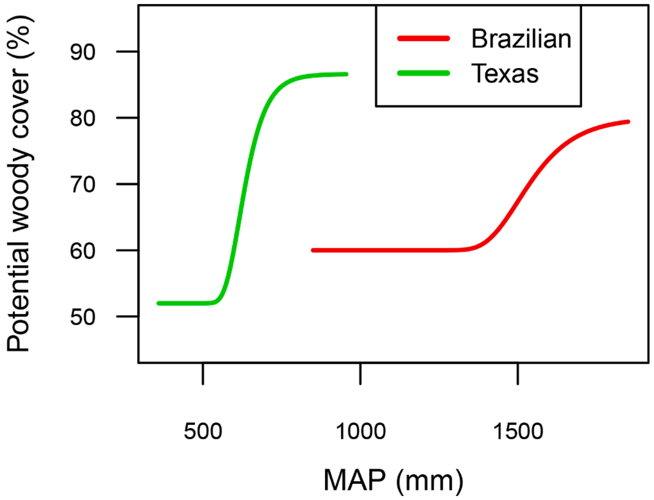


Fig. 7. Potential woody cover pattern of Brazilian savanna over precipitation gradient and that of Texas savanna at the same observation scale of 250 m (Yang et al., 2020).

3.3. Relationship among MAP, surface and subsurface SM

As displayed in Fig. 9, MAP has a significant positive linear relationship with both surface SM and subsurface SM. It indicates the rationality of applying MAP as the proxy of plant water availability in previous potential woody cover studies (Sankaran et al., 2005; Scholtz et al., 2018). On the other side, both R-squared values (0.25 and 0.08) were relatively low, as reported in African savannas (Campo-Bescós et al., 2013). The weak relationship between MAP and SM is likely responsible for the discrepancy between the magnitude of low stable potential woody cover based on MAP (60%) and that based on SM (65–66%).

4. Discussion

This study modelled the potential woody cover pattern of the Brazilian savanna, over the gradients of MAP, surface SM, and subsurface SM separately. The unanimous three-segment potential woody cover patterns confirmed limit on potential woody cover in parts of this savanna system, despite its high precipitation/soil moisture level. Under the overlapped MAP (SM) level, the high stable level versus low stable level of potential woody cover in Texas and Brazilian savannas (Figs. 7 and 8) demonstrates that, in addition to water availability, there should be other factors responsible for potential woody cover of savanna ecosystems.

Firstly, regional climate should be considered. The Brazilian savanna has an extremely seasonal climate, with a dry season of up to six consecutive months (Rodrigues et al., 2016). Only about 10% of annual precipitation occurs in the long dry season (Vourlitis and da Rocha, 2011). The very low precipitation in the dry season, combined with remarkably high evaporative demand driven by climate (referred to as potential evapotranspiration), induces huge drought stress for woody plants in Brazilian savanna (Rodrigues et al., 2014; Júnior et al., 2020). In addition, the potential evapotranspiration is not fully reached due to limited water availability, which becomes a constraining factor for woody plant growth (Campo-Bescós et al., 2013). The extreme precipitation seasonality was also found to exhibit a direct negative impact on woody plant cover, probably through its effect on tree physiology (Good and Caylor, 2011; Lehmann et al., 2011).

Secondly, functional traits of woody plants can make a difference. According to Stevens et al. (2017), only 10% of encroachment sites in Brazilian savanna are occupied by woody species with nitrogen-fixing ability. In contrast, 94% of encroachment sites in Africa are dominated by nitrogen-fixing woody plants. Texas savanna have also been noted as having nitrogen-fixing species such as honey mesquite (Fowler and Simmons, 2009). Increased nitrogen fixation could match the higher

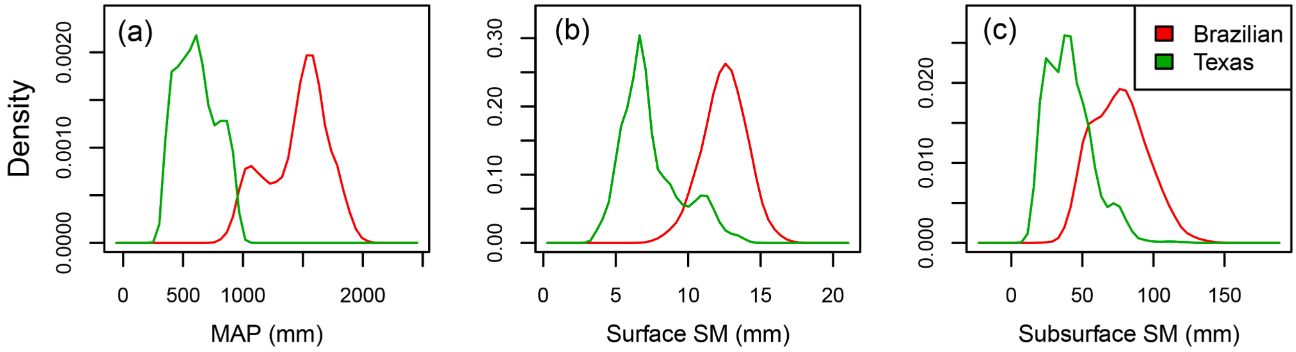


Fig. 8. Probability distribution of MAP, surface SM, subsurface SM in Brazilian and Texas savannas.

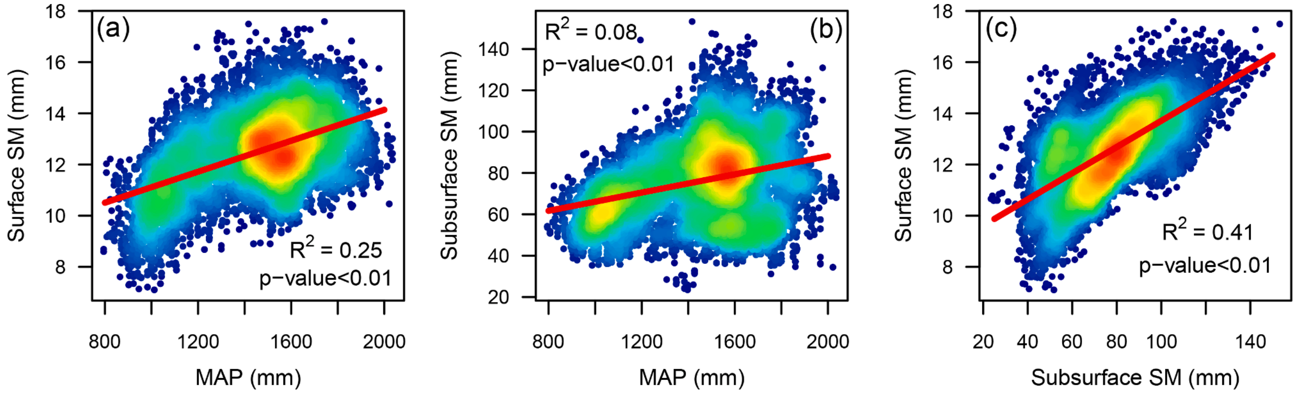


Fig. 9. Density plots of (a) mean surface soil moisture vs. MAP, (b) mean subsurface soil moisture vs. MAP, and (c) mean surface soil moisture vs. mean subsurface soil moisture.

rate of photosynthesis due to elevated CO_2 level, and consequently facilitate woody plant growth (Leakey et al., 2009; Rogers et al., 2009). Additionally, nitrogen-fixing woody plants have been reported as more resistant to drought (Rogers et al., 2009). As such, the different proportion of nitrogen-fixing woody species may partly explain why the overlapped MAP (SM) level is sufficient for woody plant growth in Texas savanna, but not in Brazilian savanna, and justify why MAP above 650 mm in Africa can support woody canopy closure.

Thirdly, the role of other environmental factors in savanna vegetation pattern should not be overlooked under wet conditions. Campo-Bescós et al. (2013) found in high precipitation areas (MAP $>$ 900 mm) of southern African savannas that fire and mean temperature are the most important drivers of NDVI, followed by evapotranspiration. Precipitation and soil moisture exhibited minimal effect on NDVI in the area, partly because trees and grasses respond differently to temperature variation. Trees were noted as not as adapted to high temperature as grasses and thus being more susceptible to temperature (Campo-Bescós et al., 2013).

With regard to the magnitude of potential woody cover, plant structure could be an important factor. The ratio of canopy diameter to stem diameter was observed to vary among different savanna ecosystems (Dantas and Pausas, 2013; Moncrieff et al., 2014). For instance, canopy width of trees with a given stem diameter in African savannas is about twice that in Australian savanna (Moncrieff et al., 2014). Tonello et al. (2021) examined the canopy height-to-width ratio of 36 tree species in Brazilian savanna, and found it ranging from below 1 to above 2, with an average ratio of 1.62. These structural differences could contribute to the variation in the magnitude of potential woody cover among savanna ecosystems (Fig. 7).

The estimated high stable level of potential woody cover (80%-81.2%) for the Brazilian savanna in this study is discrepant to the highest level of almost 100% canopy coverage observed in the field (Hoffmann et al., 2005). This discrepancy could be largely attributed to the underestimation trend of MODIS tree cover product for short woody plants, as well as its saturation at high canopy cover (Dantas and Pausas, 2013; Tang et al., 2019; Yang and Crews, 2019a). This tree cover product falls short of quantifying the starting and ending points of the alternate stable states of savannas (Hanan et al., 2014). It could explain why the potential woody cover pattern of the Brazilian savanna did not show a distinct high stable level as Texas savanna (Fig. 7), which was modelled with woody cover data of higher accuracy (Yang and Crews, 2019a). It is also the major reason why this study does not provide an estimation of the proportion of Brazilian savanna that could never shift to forest without fire occurrence, a question proposed by Durigan and Ratter (2016). Nevertheless, this study offers an operational way to answer this question, as long as more accurate woody cover data becomes available for Brazilian savanna.

The results of this study support existing work stressing the critical role of precipitation (soil moisture) in savanna structure and woody cover (Staver et al., 2011; Axelsson and Hanan, 2018). The varying relationship between potential woody cover and precipitation (soil moisture) over the precipitation (soil moisture) gradient is consistent with the finding in African savannas that the actual woody cover is positively correlated with MAP below 700 mm, but shows no significant relationship with MAP above 700 mm (Sankaran et al., 2008). It also stands with the varying role of precipitation in juniper encroachment rate across the semiarid and mesic regions of Texas savanna (Yang and Crews, 2020). The different levels of potential woody cover over the precipitation gradient agree well with the revelation of changing woody plant structure across three rainfall zones of African savannas in terms of woody cover, crown size, and density (Axelsson and Hanan, 2017).

Limitations of this study should be noted. Firstly, this study was not able to determine the exact magnitude of potential woody cover in Brazilian savanna and the transition points of the alternate stable states, mainly due to the shortfall of the MODIS tree cover product. Secondly, with regard to the discrepancy between potential woody cover modelled based on MAP and that modelled based on SM (surface and subsurface), further testing is needed to identify which one is more accurate. Thirdly, more spatial variation of precipitation and soil moisture may have been revealed if higher spatial resolution products were available.

5. Conclusion

In conclusion, this study proves the limit of potential woody cover in part of Brazilian savanna, despite its high precipitation and soil moisture level. This study also highlights the discrepancy between potential woody cover modelled based on MAP and that modelled based on SM (surface and subsurface). It finds that potential woody cover pattern cannot necessarily be generalized across different savanna ecosystems simply based on precipitation or soil moisture levels, due to different regional context such as precipitation seasonality and woody plant species. Lastly, this study embodies the utility of remote sensing products and the cloud computing platform Google Earth Engine in large scale savanna ecology study.

CRediT authorship contribution statement

Xuebin Yang: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Kelley A. Crews:** Funding acquisition, Writing – review & editing. **Thoralf Meyer:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

References

Abreu, R.C., Hoffmann, W.A., Vasconcelos, H.L., Pilon, N.A., Rossatto, D.R., Durigan, G., 2017. The biodiversity cost of carbon sequestration in tropical savanna. Sci. Adv. 3, e1701284.

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D., Scholes, R.J., 2010. Tree–grass co-existence in savanna: interactions of rain and fire. J. Theor. Biol. 267, 235–242.

Alofs, K.M., González, A.V., Fowler, N.L., 2014. Local native plant diversity responds to habitat loss and fragmentation over different time spans and spatial scales. Plant Ecol. 215, 1139–1151.

Anadón, J.D., Sala, O.E., Turner, B.L., Bennett, E.M., 2014. Effect of woody-plant encroachment on livestock production in North and South America. Proc. Natl. Acad. Sci. 111, 12948–12953.

Axelsson, C.R., Hanan, N.P., 2017. Patterns in woody vegetation structure across African savannas. Biogeosciences 14, 3239–3252.

Axelsson, C.R., Hanan, N.P., 2018. Rates of woody encroachment in African savannas reflect water constraints and fire disturbance. J. Biogeogr. 45, 1209–1218.

Bai, Y., Cotrufo, M.F., 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. Science 377, 603–608.

Bestelmeyer, B.T., Ash, A., Brown, J.R., Densambuu, B., Fernández-Giménez, M., Johanson, J., Levi, M., Lopez, D., Peinetti, R., Rumpff, L., 2017. State and transition models: theory, applications, and challenges. Rangeland Syst. 303–345.

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165, 525–538.

Bowman, K.P., Hong, Y., Stocker, E.F., Wol, D.B., 2007. The TRMM multi-satellite precipitation analysis: Quasi-global, multi-year, combined-sensor precipitation estimates at finescale. J. Hydrometeorol. 8, 3855.

Brannstrom, C., Jepson, W., Filippi, A.M., Redo, D., Xu, Z., Ganesh, S., 2008. Land change in the Brazilian Savanna (Cerrado), 1986–2002: Comparative analysis and implications for land-use policy. Land Use Policy 25, 579–595.

Bucini, G., Hanan, N.P., 2007. A continental-scale analysis of tree cover in African savannas. Glob. Ecol. Biogeogr. 16, 593–605.

Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. Front. Ecol. Environ. 1, 412–420.

Campo-Bescós, M.A., Muñoz-Carpena, R., Kaplan, D.A., Southworth, J., Zhu, L., Waylen, P.R., 2013. Beyond precipitation: Physiographic gradients dictate the relative importance of environmental drivers on savanna vegetation. PLoS One 8, e72348.

Chatterjee, S., Hadi, A.S., 2015. Regression analysis by example. John Wiley & Sons.

Dantas, V. de L., Pausas, J.G., 2013. The lanky and the corky: fire-escape strategies in savanna woody species. J. Ecol. 101, 1265–1272.

Devine, A.P., McDonald, R.A., Quaife, T., Maclean, I.M., 2017. Determinants of woody encroachment and cover in African savannas. Oecologia 183, 939–951.

DiMiceli, C.M., Carroll, M.L., Sohlberg, R.A., Huang, C., Hansen, M.C., Townshend, J.R. G., 2017. Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000-2010.

Durigan, G., Ratter, J.A., 2006. Successional changes in cerrado and cerrado/forest ecotonal vegetation in western São Paulo State, Brazil, 1962–2000. Edinb. J. Bot. 63, 119–130.

Durigan, G., Ratter, J.A., 2016. The need for a consistent fire policy for Cerrado conservation. J. Appl. Ecol. 53, 11–15.

Eloy, L., A. Bilbao, B., Mistry, J., Schmidt, I.B., 2019. From fire suppression to fire management: Advances and resistances to changes in fire policy in the savannas of Brazil and Venezuela. Geograph. J. 185, 10–22.

Entekhabi, D., Njoku, E.G., O'Neill, P.E., Kellogg, K.H., Crow, W.T., Edelstein, W.N., Entin, J.K., Goodman, S.D., Jackson, T.J., Johnson, J., 2010. The soil moisture active passive (SMAP) mission. Proc. IEEE 98, 704–716.

Fornaroli, R., Cabrini, R., Sartori, L., Marazzi, F., Vracevic, D., Mezzanotte, V., Annala, M., Canobbio, S., 2015. Predicting the constraint effect of environmental characteristics on macroinvertebrate density and diversity using quantile regression mixed model. Hydrobiologia 742, 153–167.

Fowler, N.L., Simmons, M.T., 2009. Savanna dynamics in central Texas: just succession? Appl. Veg. Sci. 12, 23–31.

Franke, J., Barradas, A.C.S., Borges, M.A., Costa, M.M., Dias, P.A., Hoffmann, A.A., Orozco Filho, J.C., Melchiori, A.E., Siegert, F., 2018. Fuel load mapping in the Brazilian Cerrado in support of integrated fire management. Remote Sens. Environ. 217, 221–232.

Good, S.P., Caylor, K.K., 2011. Climatological determinants of woody cover in Africa. Proc. Natl. Acad. Sci. 108, 4902–4907.

Hanan, N.P., Tredennick, A.T., Prihodko, L., Bucini, G., Dohn, J., 2014. Analysis of stable states in global savannas: is the CART pulling the horse? Glob. Ecol. Biogeogr. 23, 259–263.

Hansen, M.C., DeFries, R.S., Townshend, J.R.G., Sohlberg, R., Dimiceli, C., Carroll, M., 2002. Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. Remote Sens. Environ. 83, 303–319.

Hao, L., Naiman, D.Q., Naiman, D.Q., 2007. Quantile regression. Sage.

Hoffmann, W.A., da Silva, E.R., Machado, G.C., Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., 2005. Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. Oecologia 145, 306–315.

Honda, E.A., Durigan, G., 2016. Woody encroachment and its consequences on hydrological processes in the savannah. Philos. Trans. R. Soc., B 371, 20150313.

House, J.I., Archer, S., Breshears, D.D., Scholes, R.J., Participants, N.-T.-G.-I., 2003. Conundrums in mixed woody–herbaceous plant systems. J. Biogeogr. 30, 1763–1777.

Huang, C., Archer, S.R., McClaran, M.P., Marsh, S.E., 2018. Shrub encroachment into grasslands: end of an era? PeerJ 6, e5474.

Huang, X., Shi, Z.H., Zhu, H.D., Zhang, H.Y., Ai, L., Yin, W., 2016. Soil moisture dynamics within soil profiles and associated environmental controls. Catena 136, 189–196.

Jaber, S.M., Abu-Allaban, M.M., 2020. TRMM 3B43 Product-Based Spatial and Temporal Anatomy of Precipitation Trends: Global Perspective. Environ. Monit. Assess. 192, 1–13.

Ji, W., Hanan, N.P., Browning, D.M., Monger, H.C., Peters, D.P., Bestelmeyer, B.T., Archer, S.R., Ross, C.W., Lind, B.M., Anchang, J., 2019. Constraints on shrub cover and shrub–shrub competition in a US southwest desert. Ecosphere 10, e02590.

Júnior, L.C.V., Ventura, T.M., Gomes, R.S., Nogueira, J. de S., Lobo, F. de A., Vourlitis, G. L., Rodrigues, T.R., 2020. Comparative assessment of modelled and empirical reference evapotranspiration methods for a brazilian savanna. Agricul. Water Manage. 232, 106040.

Koenker, R., Bassett Jr, G., 1978. Regression quantiles. Econometrica: journal of the Econometric Society 33–50.

Koenker, R., 2004. Quantreg: An R package for quantile regression and related methods. The Comprehensive R Archive Network website.

Korres, W., Reichenau, T.G., Fiener, P., Koyama, C.N., Bogena, H.R., Cornelissen, T., Baatz, R., Herbst, M., Diekkrüger, B., Vereecken, H., 2015. Spatio-temporal soil moisture patterns–A meta-analysis using plot to catchment scale data. J. Hydrol. 520, 326–341.

Kulmatiski, A., Beard, K.H., 2013. Woody plant encroachment facilitated by increased precipitation intensity. Nat. Clim. Chang. 3, 833–837.

Leakey, A.D., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., Ort, D.R., 2009. Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. J. Exp. Bot. 60, 2859–2876.

Lehmann, C.E., Archibald, S.A., Hoffmann, W.A., Bond, W.J., 2011. Deciphering the distribution of the savanna biome. New Phytol. 191, 197–209.

Lehmann, E.A., Wallace, J.F., Caccetta, P.A., Furby, S.L., Zdunic, K., 2013. Forest cover trends from time series Landsat data for the Australian continent. Int. J. Appl. Earth Obs. Geoinf. 21, 453–462.

Lunt, I.D., Winsemius, L.M., McDonald, S.P., Morgan, J.W., Dehaan, R.L., 2010. How widespread is woody plant encroachment in temperate Australia? Changes in woody vegetation cover in lowland woodland and coastal ecosystems in Victoria from 1989 to 2005. J. Biogeogr. 37, 722–732.

Mladenova, I.E., Bolten, J.D., Crow, W.T., Sazib, N., Cosh, M.H., Tucker, C.J., Reynolds, C., 2019. Evaluating the operational application of SMAP for global agricultural drought monitoring. IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens. 12, 3387–3397.

Mladenova, I.E., Bolten, J.D., Crow, W., Sazib, N., Reynolds, C., 2020. Agricultural drought monitoring via the assimilation of SMAP soil moisture retrievals into a global soil water balance model. Front. Big Data 3, 10.

Moncrieff, G.R., Lehmann, C.E., Schnitzler, J., Gambiza, J., Hiernaux, P., Ryan, C.M., Shackleton, C.M., Williams, R.J., Higgins, S.I., 2014. Contrasting architecture of key A frican and A ustralian savanna tree taxa drives intercontinental structural divergence. Glob. Ecol. Biogeogr. 23, 1235–1244.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

O'connor, T.G., Puttick, J.R., Hoffman, M.T., 2014. Bush encroachment in southern Africa: changes and causes. Afr. J. Range Forage Sci. 31, 67–88.

Oliveira, P.S., Marquis, R.J., 2002. The cerrados of Brazil. Columbia University Press, New York.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., 2001. Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51, 933–938.

Pellegrini, A.F., Socolar, J.B., Elsen, P.R., Giam, X., 2016. Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. Glob. Chang. Biol. 22, 3373–3382.

Pinheiro, M.H., de Azevedo, T.S., Monteiro, R., 2010. Spatial-temporal distribution of fire-protected savanna physiognomies in Southeastern Brazil. Anais da Academia Brasileira de Ciências 82, 379–395.

Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier, F., Liu, Y.Y., 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature 509, 600–603.

Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93, 697–703.

Ratter, J.A., Bridgewater, S., Ribeiro, J.F., 2006. Biodiversity patterns of the woody vegetation of the Brazilian Cerrado. In: Neotropical Savannas and Seasonally Dry Forests. CRC Press, pp. 31–66.

Rodrigues, T.R., Vourlitis, G.L., Lobo, F. de A., de Oliveira, R.G., Nogueira, J. de S., 2014. Seasonal variation in energy balance and canopy conductance for a tropical savanna ecosystem of south central Mato Grosso, Brazil. J. Geophys. Res.: Biogeosci. 119, 1–13.

Rodrigues, T.R., Vourlitis, G.L., Lobo, F. de A., Santanna, F.B., de Arruda, P.H., Nogueira, J. de S., 2016. Modeling canopy conductance under contrasting seasonal conditions for a tropical savanna ecosystem of south central Mato Grosso, Brazil. Agricult. Forest Meteorol. 218, 218–229.

Rogers, A., Ainsworth, E.A., Leakey, A.D., 2009. Will elevated carbon dioxide concentration amplify the benefits of nitrogen fixation in legumes? Plant Physiol. 151, 1009–1016.

Rosan, T.M., Aragão, L.E., Oliveras, I., Phillips, O.L., Malhi, Y., Gloor, E., Wagner, F.H., 2019. Extensive 21st-century woody encroachment in South America's savanna. Geophys. Res. Lett. 46, 6594–6603.

Sankaran, M., Ratnam, J., Hanan, N.P., 2004. Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. Ecol. Lett. 7, 480–490.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.

Sankaran, M., Ratnam, J., Hanan, N., 2008. Woody cover in African savannas: the role of resources, fire and herbivory. Glob. Ecol. Biogeogr. 17, 236–245.

Sano, E.E., Rosa, R., Brito, J.L., Ferreira, L.G., 2010. Land cover mapping of the tropical savanna region in Brazil. Environ. Monit. Assess. 166, 113–124.

Sano, E.E., Rodrigues, A.A., Martins, E.S., Bettiol, G.M., Bustamante, M.M., Bezerra, A.S., Couto Jr, A.F., Vasconcelos, V., Schüler, J., Bolfe, E.L., 2019. Cerrado ecoregions: A spatial framework to assess and prioritize Brazilian savanna environmental diversity for conservation. J. Environ. Manage. 232, 818–828.

Schmidt, I.B., Eloy, L., 2020. Fire regime in the Brazilian Savanna: Recent changes, policy and management. Flora 268, 151613.

Scholtz, R., Fuhlendorf, S.D., Archer, S.R., 2018. Climate–fire interactions constrain potential woody plant cover and stature in North American Great Plains grasslands. Glob. Ecol. Biogeogr. 27, 936–945.

Silva, J.F., Fariñas, M.R., Felfili, J.M., Klink, C.A., 2006. Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. J. Biogeogr. 33, 536–548.

Smit, I.P., Prins, H.H., 2015. Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. PLoS One 10, e0137857.

Staver, A.C., Archibald, S., Levin, S.A., 2011. The global extent and determinants of savanna and forest as alternative biome states. Science 334, 230–232.

Stevens, N., Lehmann, C.E., Murphy, B.P., Durigan, G., 2017. Savanna woody encroachment is widespread across three continents. Glob. Chang. Biol. 23, 235–244.

Strömberg, C.A., Staver, A.C., 2022. The history and challenge of grassy biomes. Science 377, 592–593.

Tang, H., Armston, J., Hancock, S., Marselis, S., Goetz, S., Dubayah, R., 2019. Characterizing global forest canopy cover distribution using spaceborne lidar. Remote Sens. Environ. 231, 111262.

Tjørve, K.M., Tjørve, E., 2017. The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the Unified-Richards family. PLoS One 12, e0178691.

Tonello, K.C., Van Stan II, J.T., Rosa, A.G., Balbinot, L., Pereira, L.C., Bramorski, J., 2021. Stemflow variability across tree stem and canopy traits in the Brazilian Cerrado. Agricult. Forest Meteorol. 308, 108551.

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. J. Environ. Manage. 90, 2931–2942.

Venter, Z.S., Cramer, M.D., Hawkins, H.-J., 2018. Drivers of woody plant encroachment over Africa. Nat. Commun. 9, 1–7.

Vourlitis, G.L., da Rocha, H.R., 2011. Flux dynamics in the cerrado and cerrado-forest transition of Brazil. Ecosystem function in global savannas: measurement and modeling at landscape to global scales 97–116.

Warth, B., Marohn, C., Asch, F., 2020. Modelling land use change effects on ecosystem functions in African Savannas–A review. Glob. Food Sec. 26, 100421.

Woodward, F.I., Lomas, M.R., Kelly, C.K., 2004. Global climate and the distribution of plant biomes. Philos. Trans. R. Soc. London Ser. B: Biol. Sci. 359, 1465–1476.

Yang, X., Crews, K., 2019a. Applicability analysis of MODIS tree cover product in Texas savanna. Int. J. Appl. Earth Obs. Geoinf. 81, 186–194.

Yang, X., Crews, K.A., 2019b. Fractional woody cover mapping of Texas savanna at Landsat scale. Land 8, 9.

Yang, X., Crews, K., Frazier, A.E., Kedron, P., 2020. Appropriate spatial scale for potential woody cover observation in Texas savanna. Landsc. Ecol. 35, 101–112.

Yang, X., Crews, K.A., 2020. The role of precipitation and woody cover deficit in juniper encroachment in Texas savanna. J. Arid Environ. 180, 104196.

Yang, X., Crews, K.A., Yan, B., 2016. Analysis of the pattern of potential woody cover in Texas savanna. Int. J. Appl. Earth Obs. Geoinf. 52, 527–531.

Yu, Y., Wang, J., Cheng, F., Deng, H., Chen, S., 2020. Drought monitoring in Yunnan Province based on a TRMM precipitation product. Nat. Hazards 104, 2369–2387.