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Buffering the savanna: fire regimes and disequilibrium ecology in West Africa

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Abstract According to contemporary ecological theory, the mechanisms governing tree cover in savannas vary by precipitation level. In tropical areas with mesic rainfall levels, savannas are unstable systems in which disturbances, such as fire, determine the ratio of trees to grasses. Precipitation in these so-called "disturbance-driven savannas" is sufficient to support forest but frequent disturbances prevent transition to a closed canopy state. Building on a savanna buffering model we argue that a consistent fire regime is required to maintain savannas in mesic areas. We hypothesize that the spatiotemporal pattern of fires is highly regular and stable in these areas. Furthermore, because tree growth rates in savannas are a function of precipitation, we hypothesize that savannas with the highest rainfall levels will have the most consistent fire pattern and the most intense fires—thus the strongest buffering mechanisms. We analyzed the spatiotemporal pattern of burning over 11 years for a large subset of the West African savanna using a moderate resolution imaging spectroradiometer active fire product to document the fire regime for three savanna belts with different precipitation levels. We used LISA analysis to quantify the spatiotemporal patterns of fires, coefficient of variance to quantify differences in peak fire dates, and center or gravity pathways to characterize the spatiotemporal patterns of the fires for each area. Our analysis confirms that spatiotemporal regularity of the fire regime is greater for mesic areas that for areas where precipitation is lower and that areas with more precipitation have more regular fire regimes.

Keywords Africa · Buffering model · Disequilibrium · Fire regime · Savanna

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Introduction

Savannas pose a conundrum for scientists—how do trees and grasses coexist on the landscape and what factors prevent one vegetation form from dominating the other (House et al. 2003; Bond 2008; Hanan et al. 2008; Laris and Dembele 2012)? Explaining the mechanisms that determine the ratio of savanna trees to grasses has long been of interest to ecologists and geographers who seek to understand the basic functioning and distribution of the Earth's ecosystem. Concern about the role of savannas in the carbon cycle has heightened the need for understanding the mechanisms that govern tree cover because savannas hold the potential to be major carbon sources or sinks depending upon the amount of tree cover they support (Bond and Keeley 2005; Staver et al. 2011a). Fire, which can prevent trees from establishing or maturing in savannas, differentiates high and low tree cover and

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produces emergent alternative states. These alternative states may cover vast areas, including parts of Amazonia, the Congo, and West Africa. As such, tree cover varies significantly depending on the fire regime in large areas of the Earth's surface with major consequences for carbon sequestration, biodiversity, as well as local livelihoods (Mistry 2000; Bond et al. 2005; Staver et al. 2011a).

Recent developments in savanna ecological theory, backed by empirical results, find that the mechanisms governing tree cover vary by precipitation level. In tropical areas with wet/dry climates and intermediate precipitation levels (between ~750 and 2000 mm), both forests and savannas persist (Jeltsch et al. 2000; Sankaran et al. 2005). In such mesic environments, research indicates that savannas represent unstable systems in which disturbances can shift the ratio of trees to grasses (Sankaran et al. 2005; Staver et al. 2011a). These "disturbance-driven savannas" are prevented from transitioning to a closed canopy state by frequent disturbances, especially fires. In more arid savannas where annual precipitation is below 750 mm, vegetation cover is determined by soil moisture more so than disturbance (Sankaran et al. 2005; Staver et al. 2011a).

It has further been argued that disturbance-driven savannas represent unstable systems that are inherently in disequilibrium and can potentially "flip" between more tree or more grass-dominated landscapes depending upon the disturbance regime because more frequent and intense fires favor grasses over trees (e.g., Scholes and Archer 1997; Sankaran et al. 2005; Hirota et al. 2011; Staver et al. 2011a, b). According to this model, a shift in the fire regime can radically alter the tree cover in a given savanna (Louppe et al. 1995; Mayer and Khalyani 2011). Savannas are conceptualized as highly dynamic systems in "constant disequilibrium" shaped by disturbance factors (Furley et al. 2008) with quick and frequent shifts in state between grasslands and woodlands (Ratajczak and Nippert 2012).[1]

It is important to note, however, that fire frequency alone is not sufficient to determine the vegetation response to fire in savannas. Fire intensity and severity are critical. In savannas, intensity and severity are functions of fire timing because grasses, which compose the majority of the fuel, are more thoroughly cured and burn with more intensity later in the dry season. Fires burning late in the dry season tend to be more damaging to trees (especially juveniles)—thus more severe—than fires burning early in the dry season (e.g., Aubréville 1953; Govender et al. 2006). Field experiments have found that periodic fires during the late dry season prevent the establishment of new trees. Indeed, intensity may be a more critical variable than frequency in some contexts; it has been well documented through experimental research that a change in fire intensity can have dramatic effects on tree cover (Louppe et al. 1995; Higgins et al. 2007; Ryan and Williams 2011).

Based on existing research then, the spatiotemporal pattern of fire in mesic regions would need to be sufficiently *frequent* and *intense* as well as *regular* from year to year to prevent woody species from overtaking grasses. Tree cover in mesic savannas is suppressed because many small trees remain trapped in a juvenile state due to fires—the so-called "fire trap." This unique feature imposes a significant demographic bottleneck on tree recruitment. According to the theory, saplings may be killed by fires or they may be repeatedly burned down to the rootstock and thus held in check (Bond and Van Wilgen 1996). This phenomenon has been appropriately dubbed the 'Gulliver syndrome' because if trees do manage to escape fire, they quickly grow tall (Van Wilgen et al. 1990; Laris 2008). As such, even a brief (2 or 3 years) gap in the fire return interval, or change in fire intensity, would have significant and long-lasting impacts on savanna woody vegetation because once savanna trees establish and grow to several meters (tall enough to escape the main impacts of fire), they become resistant to fire and are long lived. In this sense, even a temporary alternation of a disturbance regime could result in a shift to a new steady state, because once a closed canopy of trees is established, fire intensity declines due to a reduction of grasses.

As Jeltsch et al. (2000) note, however, if something is inherently 'unstable' how is persistence possible?[2]

[1] Long-term fire studies reveal that grassland to shrubland transitions are triggered when fire-free intervals increase from 1–3 to ≥ 3–8 years, and longer fire returns (10 years or more) result in transitions to woodlands (Ratajczak et al. 2014).

[2] Indeed, the mesic savanna of West Africa is "remarkably stable" according to Goetze et al. (2006) who conducted a study in northern Ivory Coast and found that 94.5 % of the forest patches within the savanna landscape were unchanged in size during the 40-year period.

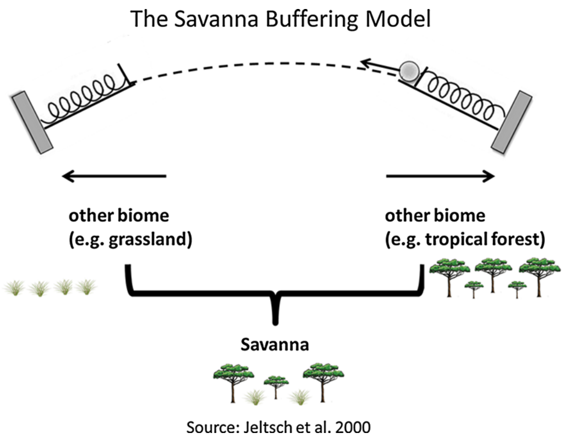

Fig. 1 The savanna buffering model modified from Jeltsch et al. (2000)

These authors suggest that rather than conceptualize the savanna as perpetually in disequilibrium, as others have done, a more appropriate and unifying concept of the savanna is one based on "ecological buffering mechanisms." Buffering refers to mechanisms which—like mechanical buffers—prevent the savanna system from crossing the boundaries to other types of systems, i.e., "pure grassland or tropical forest." In their model, buffering mechanisms provide stability and prevent the savanna from shifting to other ecosystems (Fig. 1). In a sense, Jeltsch and colleagues turn disequilibrium theory on its head—because some savannas are inherently unstable, their persistence requires continual buffering.

Building on the buffering model, we argue that a consistent, frequent, and intense fire regime is required to maintain savannas in mesic areas. We thus expect the fire regime to be more regular, with frequent and intense fires, in areas of higher rainfall because tree growth rates in savannas are a function of precipitation (Mayer and Khalyani 2011). Our working hypothesis is that in mesic savannas, the spatiotemporal pattern of fires is sufficiently regular and intensive from year to year to maintain a mixture of trees and grasses. We hypothesize, therefore, that the savannas with higher rainfall levels will have a more consistent spatiotemporal pattern and more frequent and intense fires—thus, the strongest buffering mechanisms—when compared to less humid savannas. The latter will have less frequent and intense fires and more variation in the spatiotemporal pattern of fire.

To address these hypotheses, we examine the spatiotemporal pattern of burning for a large subset ($362{,}000\ km^2$) of the savannas of West Africa—the region thought to burn most frequently and widely (Giglio et al. 2010). We use active fire data generated from moderate resolution imaging spectroradiometer (MODIS) imagery to document and analyze the fire regime for three areas corresponding to three different savanna belts in West Africa. MODIS fire data is used to plot and analyze the spatiotemporal patterns of fires. We represent the spatiotemporal patterns using two geovisualization techniques—Local Indicator of Spatial Association (LISA) and center of gravity maps following Caillault et al. (2015). We then interpret and discuss the causes of the documented fire regimes based on results from previous work that used an analysis of medium-resolution Landsat data to develop linkages between vegetation cover and fire regime (Laris et al. 2015).

Methods

We divided our study into three regions: (1) a northern (semi-arid) belt where precipitation is generally below 750 mm, (2) a central (mesic) belt where it is from 750 to 1000 mm, and (3) a southern (mesic) belt where it is between 1000 and 1250 mm (Fig. 2). These belts roughly correspond to different savanna types for the region, the Northern Sudanian, Southern Sudanian, and Guinean savanna. We further divided each of these savanna belts into study areas corresponding to the area covered by the corresponding Landsat scenes giving us a total of 12 sub-areas (about four areas for each rainfall regime). The division into sub-areas allows for a more local-scale analysis of spatiotemporal pattern as well as for comparison with our previous work using Landsat data (see below). We mapped the spatiotemporal patterns of fires based on MODIS active fire data for an 11-year period for each sub-area and for the belts as a whole. We used the active fire product because we are specifically interested in the spatiotemporal pattern of fires and not the burned area per se; and because of the latter's low-resolution bias. We created a database allowing pixel-based analysis of average burn date and fire frequency (return interval). We next used spatial statistics including LISA (Anselin 1995) and center of gravity (point density) pathway, to characterize and visualize the spatiotemporal patterns of the fires for each sub-area (Caillault et al. 2015). Using these results, we

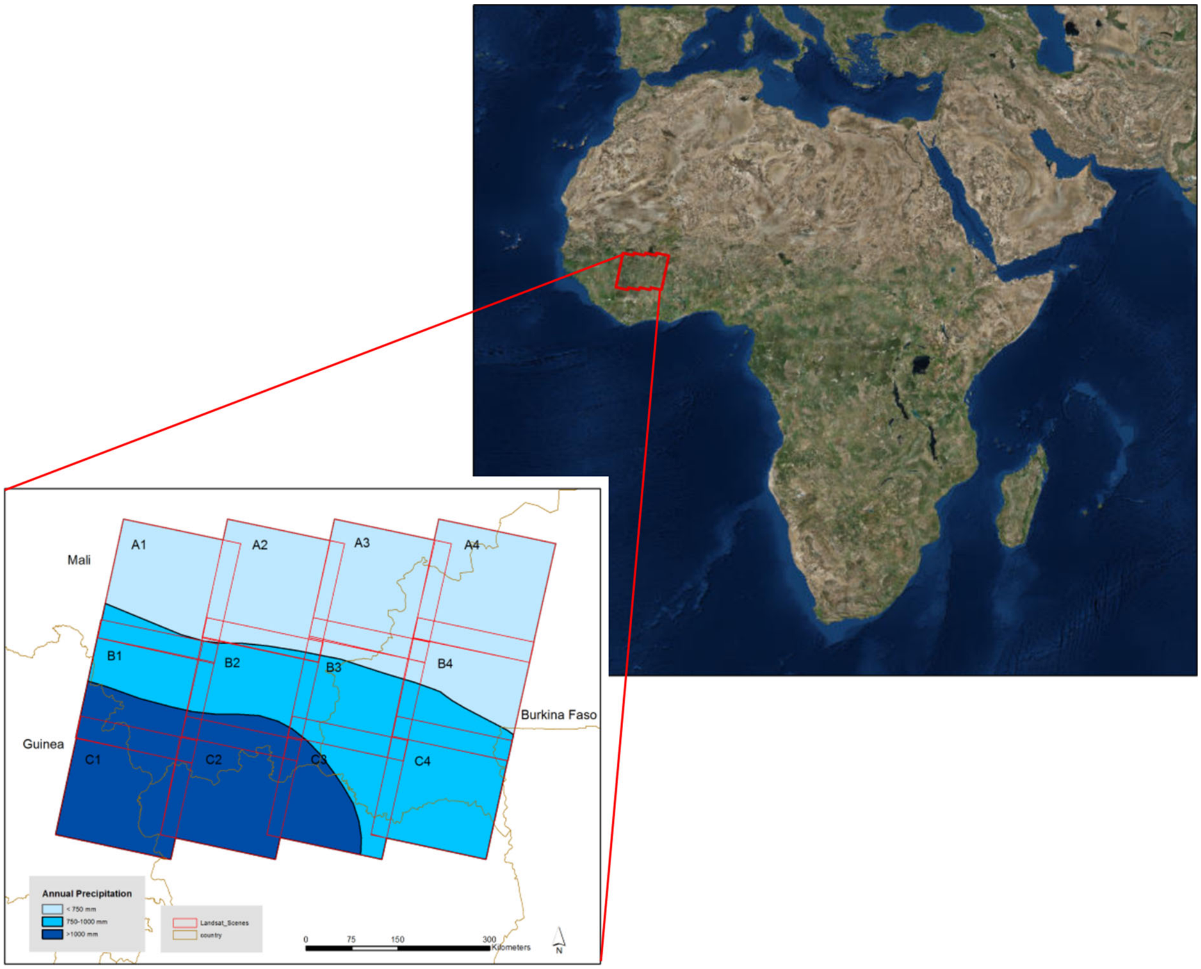

Fig. 2 Study areas in West Africa based on rainfall regime and Landsat footprints

examined the study areas according to the regularity of the spatiotemporal pattern of burning to test our hypotheses. Finally, we compared the results of the MODIS-based analysis with previous work for a sub-area for which high quality and fine resolution (Landsat) burned area and vegetation cover maps were available to explain the linkages between the fire regime and vegetation patterns.

Study area

Precipitation in the study area varies from approximately 600 mm in the north to 1200 mm in the south where the Sudan Savanna transitions to Guinean Savanna (White 1983; de Bie et al. 1998). The climate in the zone can generally be divided into three seasons: a hot and dry period from February to late May, a warm and rainy season from June to October, and a relatively cooler dry season from October to February. Rainfall patterns in the region generally follow the shifting ITCZ which moves north in June and retreats south in September. As such, the onset and end of the rainy season varies by approximately a week or more between the southern and northern study areas. The fire season begins shortly after the rains ends and typically runs from November through March, with the bulk of the burning occurring in late December and early January.

Vegetation in the Sudan and Guinean savanna is predominantly composed of a mixture of grasses, trees, and shrubs arranged in a complex mosaic. Ferricrete outcrops often referred to as Bowé, cover considerable areas. Bowé cover up to 25 % of the savanna in the region, but their distribution is highly uneven (Nasi and Sabatier 1988: 90). Soil on Bowé generally has high gravel content and is shallow, creating xeric conditions. Unproductive soils such as on Bowé support sparse vegetation compared with the deeper, loamy soils in the valleys or depressions. Bowé are dominated by short, annual grasses (principally *Loudetia tongoensis*, but also *Andropogon pseudapricus*) with only widely scattered trees. Except for the intensively cultivated areas, a near-continuous layer of tall perennial grasses (often up to 2 m in height) (*Andropogon gayanus, Hyparrhenia dissolute, Cymbopogon giganteus,* and *Schizachyrium pulchellum*) covers the more fertile soils although there are pockets where tree canopy is closed.

The specific vegetation type in these savanna often varies on the scale of a number of hectares due to a combination of natural topographical factors and human disturbance regimes (Devineau et al. 2010; Duvall 2011). For example, vegetation cover can vary from edaphic grasslands composed of short annual grasses (about 1-m tall) with small scattered shrubs and trees, to tall grass savanna composed of perennial grasses (over 2-m) with a widely varying mixture of trees and shrubs, to a near closed canopy savanna woodland. In addition, closed canopy gallery forests often exists along the edges of streams.

The land cover in settled areas has been significantly modified. Perennial grasses are less common (except on long-fallow plots of over 15 years), and large portions of the occupied landscape are covered by annual grasses, particularly *Andropogon pseudapricus* and *Pennisetum pedicellatum* with scattered trees. The farming system and cycle—whether long-term rotational agriculture or a form of more intensive cropping—has important landscape effects. Long-fallow cycles can increase landscape heterogeneity by creating a patchwork of fallow plots in different phases of succession which are dominated by different types of grasses as well as tree and shrub cover. A shorter fallow cycle (less than 5 years for example) tends to produce a more homogeneous pattern composed of predominantly annual grasses mixed with frequently farmed fields.

Fire mapping

There are two common techniques for using satellite imagery to detect and map fires and their effects—active fire and burned area techniques. Active fire mapping involves detecting the thermal signature or high temperature of the flaming front of a fire. Even a small fire can cause a detection threshold to be reached. Active fire algorithms are most often used on satellite imagery that has a relatively high temporal frequency (such as MODIS) because once the flaming front has passed, the fire may no longer be detected. Active fire maps are best used for determining the broad spatiotemporal patterns of fire as opposed to quantifying specific areas burned. Burned area methods rely on detecting a drop in the reflectance due to the burn scar left behind by the fire. Satellite sensors used to map the burned area can generally be divided into two types based on their spatial and temporal resolutions. Sensors such as MODIS have a coarse spatial resolution (0.5–1 km) and high temporal resolution (daily). The advantage of MODIS is its high temporal resolution which assures that the drop in reflectance due to a burn will be detected before the ash and char are blown away and vegetation begins to recover. The downside of using MODIS is that the coarse spatial resolution introduces a bias that leads to the underestimation of small and/or fragmented burn scars. Landsat's higher spatial resolution enables the identification of areas that have burned, but the lower temporal frequency makes it difficult to detect all fires except in years when frequent dates are available with good quality.

Here, we used MODIS active fire data to map the long-term (11 years) annual spatiotemporal pattern of savanna fires. The MODIS active fire product is produced daily with a resolution of 1 km (Giglio et al. 2006). The resulting spatial database contains a daily census of reliable active fires recorded from September 2003 to May 2013 geo-referenced and classified by season. We complement the active fire analysis by comparing the results with previous studies using the burned area maps generated from Landsat data for a representative sub-area for which there exists sufficient imagery to map the fire regime for multiple years at high resolution (Laris et al. 2015).

Spatial statistics and visualization

The active fire data were used to produce graphs of the temporal frequency of fire over the 11-year period as well as peaks in the fire cycle and spatial density maps of fire occurrence. The variation in the mean peak for each area was also determined using a coefficient of variation (CV). The CV is the ratio of the standard deviation to the mean of a distribution and provides a normalized measure of dispersion probability distribution.

The annual monthly pattern of burning for each year was mapped using a center of gravity measure for each sub-area. The center of gravity (CG), or centroid, is defined as the geometric center (or the center of concentration) for a set of features in a given area. It is determined using the mean center spatial statistic tool in ArcGIS (ESRI 2015). We used the CG to determine the change in position of geographic center of fire activity over time. The CG map illustrates a "signature" of the spatiotemporal pattern of fires for each sub-area. It allowed us to compare the annual trajectory of fires across the landscape for multiple fire seasons for the study areas and provides a graphic assessment of the regularity of this pattern. We complemented this analysis by further quantifying the spatiotemporal pattern using the spatial statistic LISA to document the consistency of the burning patterns over 11 years. LISA was used to perform a space–time analysis to investigate the existence of annual seasonal pattern of fires. This allowed a visualization of areas affected by early fires (spatial and temporal proximity of fires burning at the start of the season—cluster early–early or 'EE') and the late fires (proximity of those fires burning at the end of the season—cluster late–late or 'LL') (Caillault et al. 2015). In this analysis, each fire point is classified as clusters of either late fires (LL), early fires (EE), or fires that have no statistically significant pattern between years. The contribution of points was determined within a specific threshold distance that represents the average distance between fire points (for each year) in each sub-area.

Results

The frequency of active fires over the 11-year period derived from the MODIS data was used to generate point density maps for each sub-region (Fig. 3). The maximum number of times a location was recorded as having burned was eight times over the 11-year period. The spatial regularity in terms of the frequency of the fire regime in each sub-area is evident. Here, one can see "hotspots" where fires are more frequent (burned 6–8 times) and cool spots (burned 1–3 times).

Graphs of the fire frequency and timing for each year by study belt and sub-area temporal pattern of fires are shown in Fig. 4 and the corresponding CV for

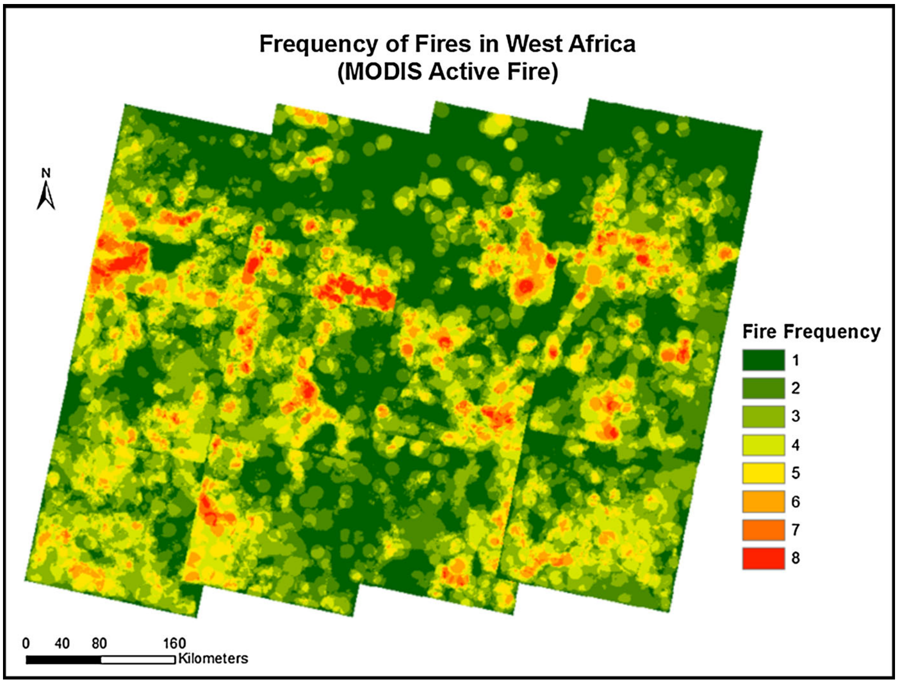

Fig. 3 Point density maps for the study region generated form Modis fire data points

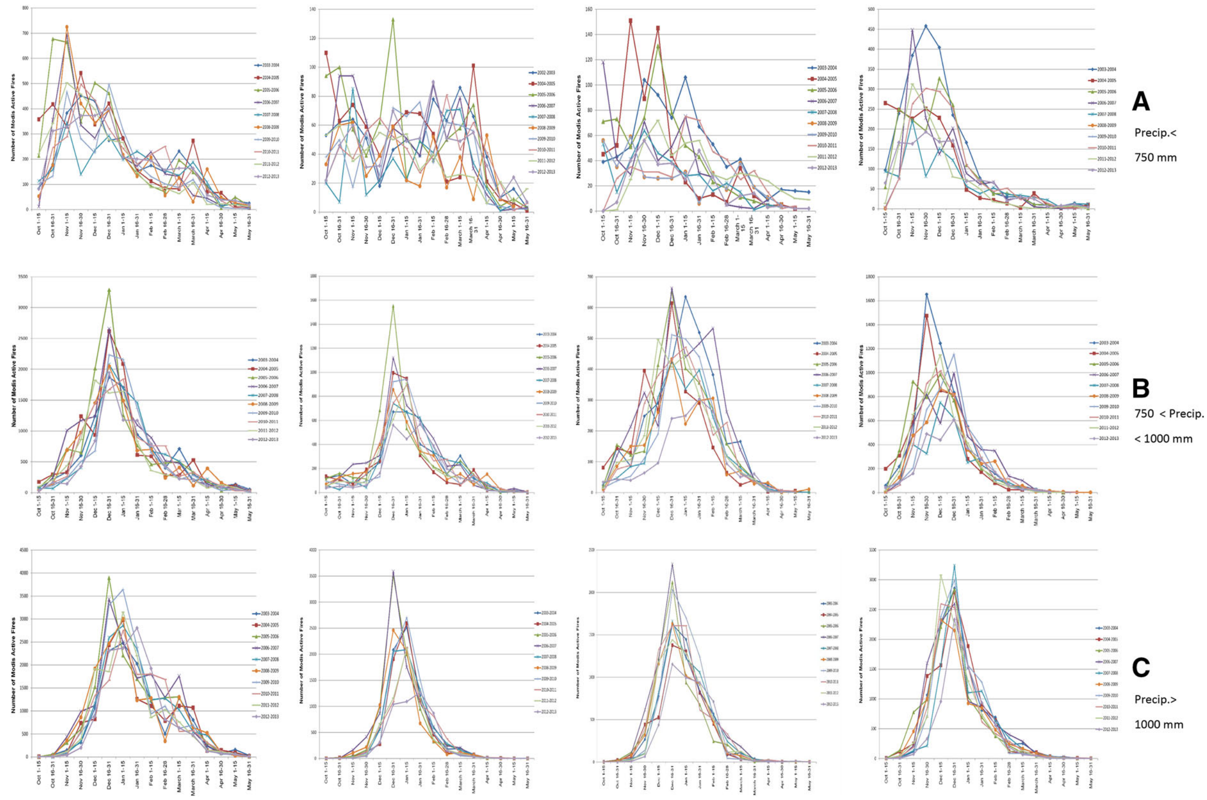

Fig. 4 Fire frequency and timing for each of the 11 years by study belt and sub-area. **A1–A4** cover the sub-areas in the northern belt (west–east); **B1–B4** are for the central belt and **C1–C4** are for the southern belt (refer to Fig. 2)

Table 1 Coefficient of variation for mean peak of fires detected by study zone and sub-area (A1–C4)

	Coefficient of variation				Mean
North (zone A)	0.23	0.61	0.37	0.36	0.39
Central (zone B)	0.08	0.11	0.13	0.15	0.12
South (zone C)	0.06	0.09	0.00	0.08	0.06

each sub-area are shown in Table 1. As can be seen in the figures, there is less variation in the graphs as one moves from north to south. Indeed, the southern two belts have far more regular annual temporal patterns of burning than the northern belt. The variation in the mean peak for each sub-area was determined using the CV. The lower the CV value, the lower the variation. Here, as well, there is less variation and more consistent peaks as shown in the CV values for the southern belts.

When plotted at the scale of the savanna (rainfall) belts, it is apparent that the fire regime in the northern-most zone (precipitation < 750 mm) has significantly fewer fires, an earlier peak, and a far less regular regime when compared to the two belts further south where precipitation is greater than 750 mm (Fig. 5). The northern peak in fires is at the end of November, the central peak is at the end of December, and the southern peak is in Mid-January.

The regularity of the spatiotemporal pattern was examined through measures of spatial autocorrelation using the LISA statistic. LISA analysis enables the disaggregation of MODIS points into those that consistently burn late in the dry season (LL), those that consistently burn early (EE), and those with no statistically significant relationship in spatiotemporal pattern of fire. The LISA analyses indicate a clear spatial pattern—*early* fires tend to regularly burn specific areas of the landscape while *late* fires burn others. This pattern is especially clear for the southern two belts (Fig. 6). This analysis also finds that average distance between fires is progressively smaller moving from the northern belt to southern one indicating a

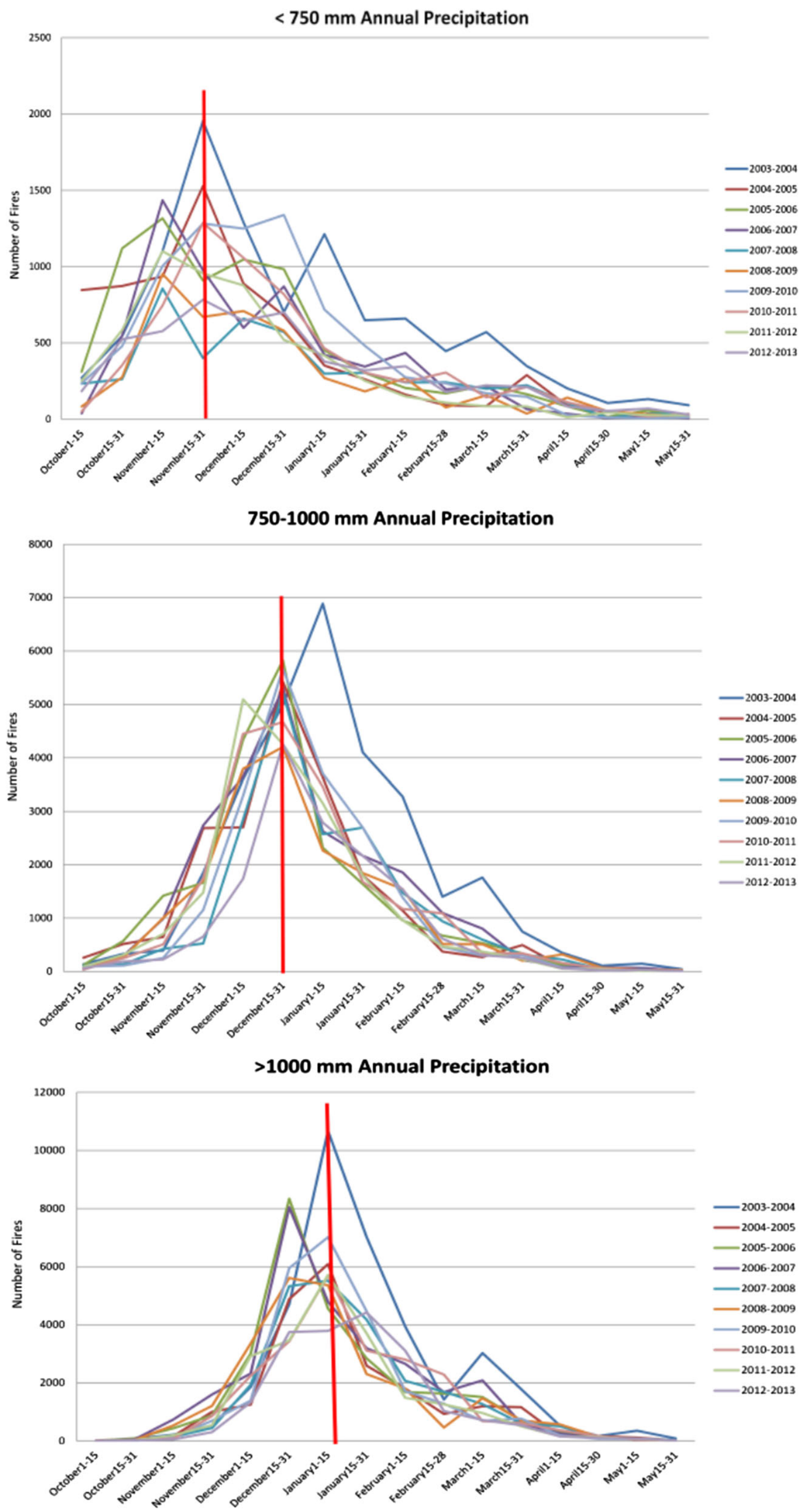

Fig. 5 Fire frequency and peak date by rainfall belt

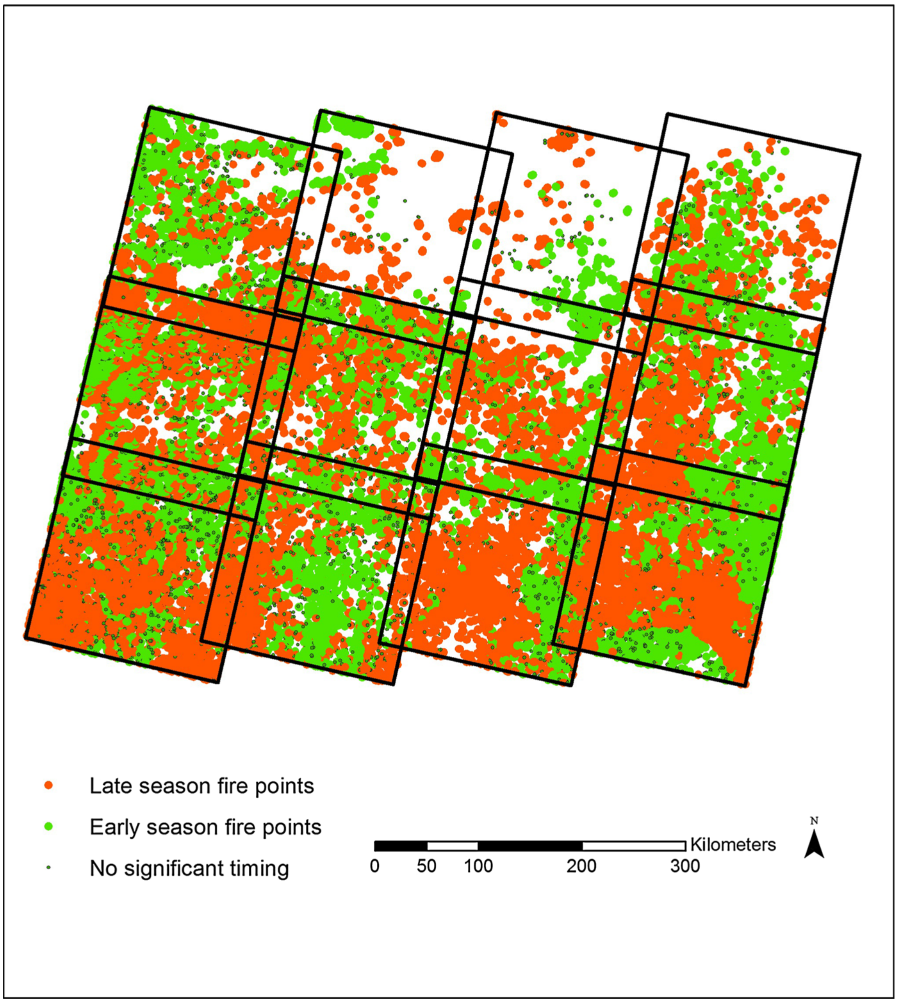

Fig. 6 LISA results for active fires for each sub-area. Points that regularly burn late (LL) are shown in *orange*. Points that regularly burn early (EE) are shown in *green*. (Color figure online)

more consistent regime of burning in the southern belts; that is, fires tend to burn the same locations on the landscape at the same time of year for different years (Table 1).

To visualize the annual monthly pattern of burning for each sub-area, we created CG maps and then combined these to create center of gravity pathways (Fig. 7). These pathways create a "signature" of the spatiotemporal pattern of fires in each sub-area. These pathways allow us to compare the annual trajectory of fires across the landscape for each area and provide a visual assessment of the regularity of the pattern—the more consistent the pathway, the more regular the annual spatiotemporal pattern of burning. If fire regimes were random, there would be no discernable spatiotemporal pattern for multiple years. This is clearly not the case (Table 2).

Finally, we highlight the relationship between land cover and spatiotemporal fire regime for the B1 sub-area which has been documented in previous studies (Laris 2011; Laris et al. 2015). Figure 8 shows the averaged center of gravity maps for the sub-area B1 (overlaid on the fire density map) as well as the vegetation cover fire regime generated from Landsat data. It is evident that fire timing in West African savannas varies by vegetation type (specifically grass type) as can be seen in Fig. 8. A comparison of vegetation cover with the fire regime (both generated from Landsat data) reveals that areas dominated by short-grass savanna (brown in Fig. 8a) consistently burned early (green in Fig. 8b) while those dominated by savanna and woodland (green in Fig. 8a) burn later (red in Fig. 8b). The relationship between the pattern of early fires and vegetation can be seen by comparing

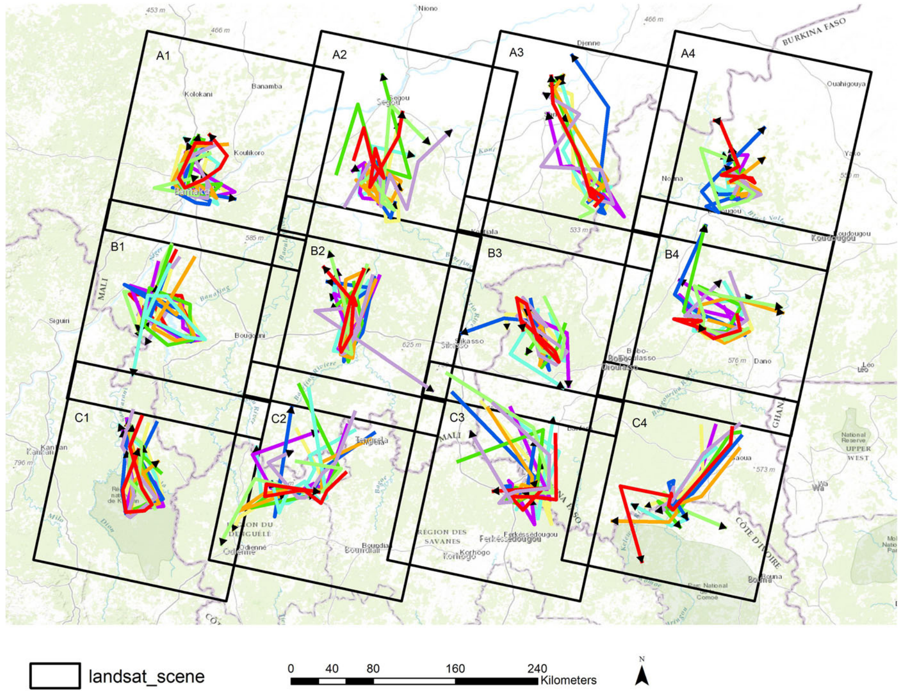

Fig. 7 Center of gravity fire maps for each sub-area

Table 2 Average distance of separation between fires from different years based on LISA analysis by zone and sub-area (A1–C4)

	Average distance (m)				Mean
North (zone A)	1439	2536	2791	1774	2135
Central (zone B)	999	1413	1584	1312	1327
South (zone C)	796	1065	1128	951	985

the vegetation and fire regime maps with the CG pathway image for Mali (Fig. 8c). The center of gravity of burning begins in the north and west and then, following the pathway, shifts slightly west corresponding to the high concentration of short-grass savanna found in this zone (sub-area A). Later, in December and January, burning shifts to the southeast where there is far less short-grass savanna and where larger fires occur in open savannas dominated by taller grasses (sub-area B). In late January, fires shift back to the northwest where valley areas, which are wooded and too moist to burn in the early dry season, are burned. Finally, the fires move further south to the moister and more densely wooded savanna and along some riverine flood plains and riparian areas in the southwest.

Discussion

Our findings support the hypothesis that the regularity of the fire regime increases from north to south in the study area. The frequency and number of total annuals fires also increases from north to south while the timing of the peak fire date shifts later. In general, these findings support our overarching hypothesis that the fire regime in the southern savanna belts (precipitation > 750 mm) theoretically creates a stronger buffering mechanism, than that of the northern belt (precipitation < 750 mm).

The data presented indicate the spatiotemporal patterns of fire vary widely in West Africa. While there are clearly hotspots where fires are more frequent and cool spots where there is little or no fire, there is no discernable geographic pattern (i.e., north–south) at the broad scale of fire density analysis. Each sub-region appears to have a unique pattern of hot and cool spots (Fig. 3). In contrast, the graphs of fire frequency and timing indicate that the temporal pattern of fires and peak burn dates are highly regular especially for the two southern (mesic) belts of analysis. The southern-most sub-areas have the most regular temporal patterns of fire with peaks occurring on or near the same date each year in contrast to the northern-

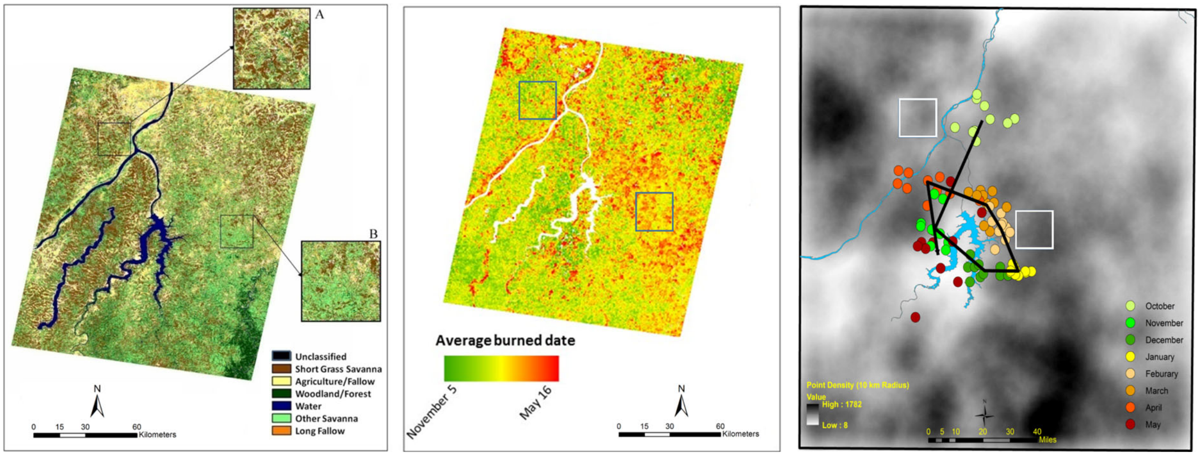

Fig. 8 Land cover (**a**) fire regime (**b**) (generated from Landsat imagery) and CG pathway (from MODIS) for sub-area *B1*. Highlighted areas *A* and *B* illustrate two contrasting vegetation cover types and corresponding fire regime and relation to CG pathway. (Color figure online)

most study areas which have the most varied peak dates. It is also clear that the number of fires detected is higher in the southern belts than in the northern one (Fig. 4). The CV values show that variation in the fire peaks decreases from north to south for each sub-area of analysis. Average variation in the peak date declines from a high of 0.39 in the north, to 0.12 in the central zone to 0.06 in the south. There is also very little variation of fire peaks between the southern sub-areas ($0.0 < CV < 0.09$) and little variation in the central areas ($0.08 < CV < 0.15$) while the variation in north is greatest ($0.23 < CV < 0.61$). The higher values in the north indicate greater inter-annual variability and a more chaotic fire regime.

This north–south variation in temporal pattern is most clearly visible at the scale of the regional savanna belts. The timing of the onset of burning and peak fire is earliest in the north (late November). This broad pattern is to be expected as the ITCZ retreats from the north first resulting in an earlier end to the rains and earlier start of the fire season. However, the northern peak is 1 month prior to the peak for the central region (end of December) which is only 15 days prior to the southern peak (Mid-December). If the shifting ITCZ were the main reason for the difference in the dates of fire peaks, we would expect a more even distribution by date, the reason that there is less of a difference in peak date for the two southern regions is not clear, but is likely a function of human burning practices. It is also evident at this scale of analysis that the number of annual fires increases from north to south as does the overall regularity of the fire regime. The regime is clearly most regular in the south, as indicated by the CV values and peaks in the fire curves.

The LISA analysis also shows that fire patterns in the southern two zones are significantly more regular than those in the north. Fires tend to follow a very regular annual pattern in the southern zones. Importantly, there is a clear spatiotemporal pattern—*early* fires tend to regularly burn specific areas of the landscape while *late* fires burn others especially in the southern belts (Fig. 6). The LISA analysis also supports our overarching hypothesis. This analysis finds that average distance between fires (for all years) is progressively smaller moving from the northern belt to southern one indicating a more consistent spatial regime of burning in the south. The average distance decreases from 2.1 km in the north to 1.3 km in the central zone to less than 1.0 km in the south (Table 1). Here again, it is evident that the pattern is more similar between the southern two zones than between the northern and central zone, for example.

The CG analysis reveals several broad patterns. First, it is clear from these maps that precipitation is not the main driver of the burning regimes—if this were the case then the annual burn pattern for the sub-areas would progress directly from north to south following the shifting ITCZ. In fact, only a single sub-area follows this pattern—the southeast corner (C4). Indeed, several sub-areas have a "counter" patterns in which fires generally begin in the south and then move in a northerly direction (A3 and C2).

As can be seen in the close-up of B1 from Mali, the center of burning shifts from the north to the south via a spiraling pattern whereby center point of fires move south, the east, then northwest, and finally ends in the south. Note that the fire regime is highly regular during the middle (peak) months of fire season (December–January) as indicated by the tight clustering of the CG points for all years in the study (Fig. 8). Driving the spatiotemporal pattern of burning at the sub-area scale of analysis is the vegetation pattern on the landscape which has been well documented elsewhere (Devineau et al. 2010; Laris 2011; Laris et al. 2015; Caillault et al. 2015).

What is most striking about the CG maps is how regular the annual burning pattern is for most of the study regions especially those in the southern belts. It is clear that the areas with the least regular spatiotemporal patterns are those in the most northern areas where precipitation tends to be less than 750 mm annually. According to theory, these dryer areas are soil moisture-driven savannas as opposed to fire-driven ones (Sankaran et al. 2005; Ward et al. 2013).

This study has several possible limitations. First, MODIS active fire data does not capture all fires because many savanna fires are small and burn quickly which may result in them being missed by the satellite during overpass. We note, however, that previous research finds that MODIS active fire produces a very good representative sample (and hire number of fire points) for spatiotemporal analysis of burning (lower error than other products except for Landsat scale analyses, for example, for which data are not available for all years) (Caillault et al. 2015). Second, our selection of "belts" and sub-areas for analysis are only approximations of actual savanna types. Nonetheless, we find that are hypothesis is supported by findings at both belt and sub-area scale of analysis. Third, in terms of our argument that the spatiotemporal patterns of burning are related to vegetation patterns and people's burning practices, while our past work, and that of others, have documented this linkage for two of the case study areas, it may well be that other factors cause the unique burning patterns for other parts of the broad study area. Finally, we do not at this time have sufficient data to argue that the fire intensity in the southern savanna zones annually causes a sufficiently severe burn to prevent trees from overcoming grasses, although numerous experimental results suggest that this is the case (e.g., Louppe et al. 1995). According to preliminary results from our field studies based on the analysis of over 200 burned plots in areas where precipitation varies between 900 and 1100 mm, we have found that mid-season fires are sufficiently intense to create a "fire trap" by burning juvenile trees back to the main stem or roots.

Conclusions

This study finds that in mesic savannas of West Africa, the fire regime follows a regular annual spatiotemporal pattern. The two southern-most belts of the study region (where precipitation is above 750 mm) have more regular fire regimes than the northern belt where precipitation is lower. This is true for both the temporal and spatiotemporal patterns of fire as was hypothesized. We thus conclude that the anthropogenic fire regime in the southern savannas of West Africa provides a mechanism to support Jeltsch's buffering model; that is, a regular annual fire regime which maintains or buffers the savanna and prevents a shift to a more wooded environment. Our findings add a human-ecological mechanism to support the work of Staver et al. (2011a, b) and Sankaran et al. (2005) who have shown that mesic savannas are disturbance driven (or *maintained* as we prefer) systems. Finally, our findings support the notion that the broad regional spatiotemporal pattern of fire is a function of both human practice and landscape cover pattern (Laris 2011).

Our findings also support those of Archibald et al. (2010) who found that, although most global models assume strong links between fire and climate, this appears to be less true in the African savannas where human impact on fire regimes is substantial and acts to limit the responsiveness of fires to climatic events. We concur that the fire regimes of the mesic savannas of West Africa are at least partly decoupled from the effects of climate, thus the striking regular fire regimes.

Finally, our finding that the fire regime is a function of the human ecology of the region strongly suggests that future changes in fire regimes will be a function of changes in vegetation cover and specifically grass cover because the human burning regime is tied to grass species. As such, more research is needed to determine the specific mechanisms that cause change in grass species in savannas. We suggest that changes in grass species will be a function of both human land uses and climate change and research should focus on determining how these two factors in combination cause shifts in grass cover which will ultimately produce modifications to the fire regime.

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