

Fire regimes and forest resilience: alternative vegetation states in the West African tropics

Francis K. Dwomoh · Michael C. Wimberly

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Abstract

Context Terrestrial ecosystems, including tropical forests, are hypothesized to have tipping points beyond which environmental change triggers rapid and radical shifts to novel alternative states.

Objective We explored the overarching hypothesis that fire-mediated alternative stable states exist in the semi-deciduous tropical forest zone of Ghana, and that increased fire activity has pushed some forests to a new state in which a novel ecosystem with low tree density is maintained by fire.

Methods We combined a 30-year time series of remotely-sensed data with field measurements to assess land cover trends, the effects of fire on forest vegetation, and the reciprocal effects of vegetation change on fire regimes, in four forest reserves. We analyzed precipitation trends to determine if shifts in vegetation and fire regime reflected a shift to a drier climate.

Results Two of the reserves experienced forest loss, were impacted by frequent fires, and transitioned to a vegetation community dominated by shrubs and grasses, which was maintained by fire–vegetation

feedbacks. The other two reserves experienced less fire, retained higher levels of forest cover, and resisted fire encroachment from surrounding agricultural areas. Precipitation remained relatively stable, suggesting a hysteresis effect in which different vegetation states and fire regimes coexist within a similar climate.

Conclusion There is potential for human land use and fire to create novel and persistent non-forest vegetation communities in areas that are climatically suitable for tropical forests. These disturbance-mediated regime shifts should be taken into account when assessing future trajectories of forest landscape change in West Africa.

Keywords Regime shift · Tipping point · Tropical forest ecosystem · Tropical forest fire · Upper Guinean forest

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F. K. Dwomoh (✉) · M. C. Wimberly
Geospatial Sciences Center of Excellence, South Dakota State University, Brookings, SD 57007, USA
e-mail: francis.dwomoh@sdstate.edu

Introduction

There are increasing concerns that human-induced global changes, including climate change, land use change, and habitat loss (Brook et al. 2013), could plunge the Earth system into a divergent regime with severe ecological consequences, including major extinctions and substantial losses of ecosystem function (Barnosky et al. 2012). Connected with these concerns is the idea that the Earth's subsystems,

including ecosystems, have tipping points beyond which environmental change triggers rapid and radical shifts to novel alternative states (Higgins and Scheiter 2012). Tropical forest ecosystems are major components of the terrestrial biosphere that provide vital ecosystem services, including protection of biodiversity and large carbon reservoirs (Cramer et al. 2004). Tropical forests are also important for climate regulation and play a key role in the global water and energy balance. If these forests are susceptible to rapid state shifts occurring at critical thresholds of environmental change, the resulting changes could have severe local, regional, and global implications including threats to ecosystem resilience, ecosystem services and human wellbeing. In this study, we used a long-term dataset of remotely-sensed Earth observations to provide insights into tropical forest resilience and disturbance-mediated tipping points in the West African tropics.

The term “tipping point” describes the critical threshold beyond which changes exceed ecological resilience and the ecosystem shifts radically and nonlinearly into a different state that is potentially irreversible (Scheffer et al. 2009). An important property of systems exhibiting alternative stable states is hysteresis, a term used to describe the difficulty of system recovery once a catastrophic transition is reached (Scheffer 2009). Hysteresis is the net result of both positive and negative feedbacks between the ecosystem state and its rate of change (Scheffer and Carpenter 2003). Positive feedbacks drive rapid state shifts by magnifying small deviations and destabilizing the system, and then negative feedbacks maintain the system once it is shifted into a new state by countering deviations from that state (Boulton et al. 2013). Environmental drivers, including climate variations, nutrient inputs, and land use typically change slowly compared to ecosystem responses (Scheffer et al. 2001; Bestelmeyer et al. 2011). However, these environmental changes can trigger disturbances such as large fires, severe droughts, disease and pest outbreaks, and species invasions that result in rapid transitions to other ecosystem states. When there are strong negative system feedbacks, the ecosystem may not return to the pre-disturbance state even when environmental conditions are similar to those that supported the initial ecosystem condition prior to the disturbance.

Alternative stable states are hypothesized to occur in tropical forests as a result of vegetation interactions

with fuels, microclimate, and fire regimes (Silvério et al. 2013; Brando et al. 2014). Although closed-canopy tropical forests seldom burn because their shaded understories support few herbaceous fuels and maintain high fuel moisture, they become more fire prone once fire or logging opens the canopy, resulting in more fine fuels and drier conditions in the understory (Cochrane et al. 1999; Hoffmann et al. 2012). Frequent, severe, or combined fires limit the establishment of fire-sensitive forest tree species and favor pyrophilic grass and shrub establishment by increasing mortality of seed trees, reducing density and diversity of seedlings, and inhibiting tree seed germination (Silvério et al. 2013; Paritsis et al. 2015). As a result of these positive feedbacks, forest disturbance can lead to rapid overstory canopy loss, resulting in a switch from a fire-resistant forest to fire-dependent vegetation maintained by a self-reinforcing negative fire feedback (Devisscher et al. 2016).

It is extremely difficult, if not impossible, to rigorously test for the existence of multiple stable states using observational data (Petraitis 2013). However, evidence for alternative stable states can be inferred from observations in time and space by detecting characteristic patterns, including surges in time series; multimodal frequency distributions of ecosystem state variables; dual biological response to drivers; and sharp spatial boundaries between contrasting communities (Scheffer and Carpenter 2003). Using these approaches, alternative stable states have been documented in a variety of terrestrial ecosystems. Odion et al. (2010) affirmed the presence of alternative community states of sclerophyll and forest vegetation that are maintained by different self-reinforcing fire feedbacks in northwestern California. Wood and Bowman (2012) similarly concluded that vegetation communities in temperate southwest Tasmania may exist as alternative stable states maintained by fire–vegetation–soil feedbacks. In tropical regions, intense fires associated with droughts can facilitate large-scale grass invasion in tropical forests, prompting the suggestion that such triggers could cause significant portions of the Amazon Forest to be displaced by grass-dominated vegetation (Silvério et al. 2013).

Despite widespread interest in the topic, there is still a dearth of long-term empirical studies focused on fire-driven alternative stable states in tropical forests. Here we utilize a 30-year time series of satellite

remote sensing data to explore fire-mediated alternative stable states in the West African tropical forest (referred to as the Upper Guinean forest). The Upper Guinean forest is a global biodiversity hotspot and has become one of the most human-modified forest ecosystems in the tropics (Poorter et al. 2004; Norris et al. 2010), having lost over 80% of its original forest cover, with the remainder distributed in a fragmented agriculture–forest mosaic (Norris et al. 2010). The Upper Guinean forest is also considered climatically marginal, having the highest temperatures and longest dry seasons of all tropical forest systems worldwide (Malhi and Wright 2004). Moreover, a number of protected areas in this region were impacted by large fire events during the 1980s El Niño-driven droughts (Hawthorne 1994). Thus, the remnant Upper Guinean forests are highly vulnerable to fire and fire-mediated forest loss, and the region provides a suitable testbed for studying alternative stable states established and maintained by fire in tropical forest ecosystems.

This paper addresses the overarching hypothesis that fire-driven alternative stable states exist in the semi-deciduous tropical forest zones of Ghana, and that increased fire activity has compromised forest resilience by pushing the system past a tipping point to an alternative stable state in which a novel ecosystem with low tree density is maintained by fire. We used an exploratory approach in which we quantified patterns of landscape change and fire activity in space and time and then qualitatively assessed whether the observations were consistent with expectations for a system with alternative stable states. We addressed three research questions, each focused on a specific characteristic of systems with alternative stable states: persistent change, feedbacks, and hysteresis (Scheffer 2009; Bestelmeyer et al. 2011; Petraitis 2013).

- (i) Is there evidence of persistent forest loss? If the system has shifted to an alternative stable state, then we expect to see a major shift in vegetation structure and composition with no trends of recovery to a forested condition.
- (ii) Is there evidence of fire–vegetation feedbacks? We interpret spatial and temporal associations of high fire activity with low forest canopy cover as evidence of a positive feedback between fire and forest loss. We also contrast fire activity between reserved

areas and the surrounding agricultural matrix to determine whether forests resist the spread of agricultural fires (negative feedback) and whether deforested areas facilitate the spread of agricultural fires (positive feedback).

- (iii) Is there evidence of hysteresis? If persistent shifts to non-forest vegetation and increases in fire activity have occurred over periods when precipitation has remained stable or increased rather than decreasing, then we can infer a hysteresis effect in which the different states can exist under similar climatic conditions.

Methods

Study area

The study area is located between latitudes 7°00′–7°40′ north and longitudes 2°20′–3°00′ west in the Brong Ahafo region of western Ghana (Fig. 1). A forest landscape including four forest reserves was selected for this study. *Pamu Berekum* and *Tain Tributaries Block II* (hereafter called *Tain II*) measure 189 and 509 km², respectively. *Pamu Berekum* is located at the northern edge of the dry semi-deciduous forest type. *Tain II* is located at the southern edge the fire-zone subtype of the dry semi-deciduous forest type. *Asukese* and *Mpameso* measure 265 and 323 km², respectively and are located approximately 60 km to the south near the northern boundary of the moist semi-deciduous northwest forest type (Fig. 1). These sites were chosen because they allow us to compare two sets of reserves in a relatively similar climatic setting but with very distinctive change trajectories following a period of high fire activity associated with the exceptional pan-tropical El Niño-induced droughts in the 1980s (Swaine 1992). In this cloudy and data-poor region, the selected reserves are among the few for which relatively long time series of Earth observation data are available.

Based on data collected from 1976 to 2013 from three meteorological stations located within the study area, mean annual rainfall ranges from 1194 to 1292 mm, and mean daily temperature is about 25 °C in the wet season (April–October) and 27 °C

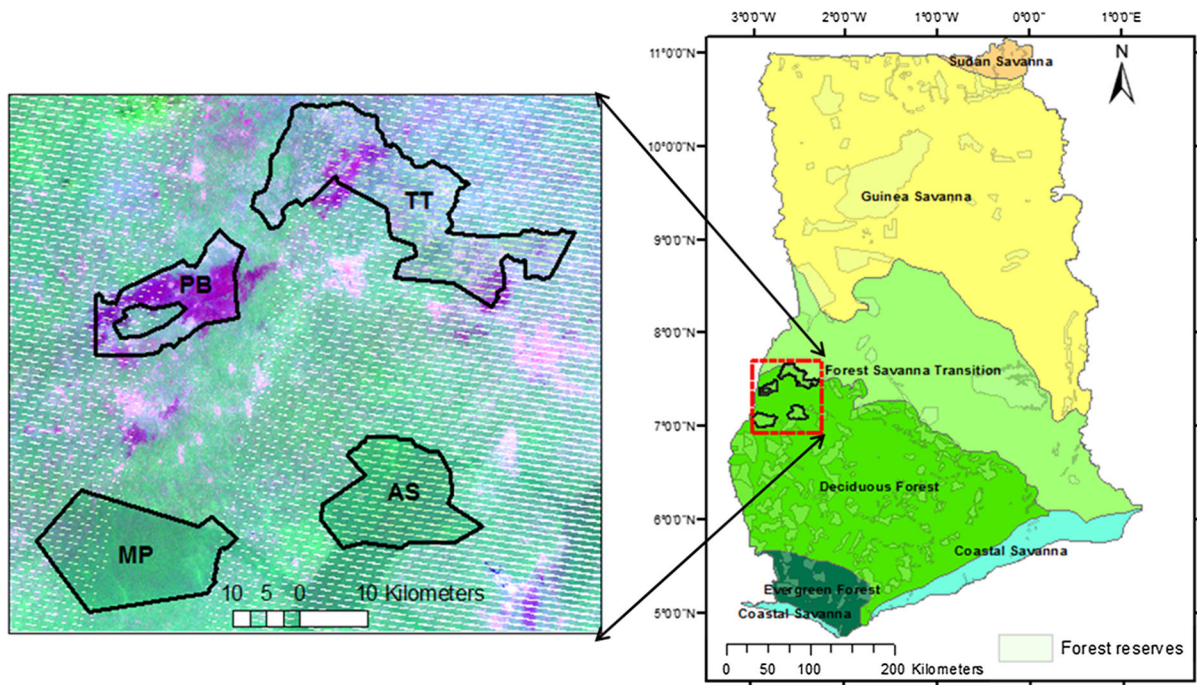


Fig. 1 Vegetation map of Ghana (*right*) with the study area (*left*) on a background Landsat ETM+ image from 5 February 2013 in 743 false color composite. On the *left*, *dark green* represents forest cover, *dark purple* represents recently burned

vegetation, and *white spaces* indicate no data due to Landsat 7 SLC-off data gaps. *AS* Asekese Forest Reserve, *MP* Mpameso Forest Reserve, *PB* Pamu Berekum Forest Reserve, *TT* Tain Tributaries Block II Forest Reserve. (Color figure online)

during the dry season (November–March). The study area is among the most floristically diverse and economically important forest areas in Ghana. Historically, forests in this region were densely stocked and characterized by multi-layered and continuous canopies with abundant lianas and many large, buttressed trees (Hall and Swaine 1981). The most common valuable timber species in the area include *Antiaria toxicaria*, *Triplochiton scleroxylon*, *Khaya* spp., *Entandrophragma* spp. and *Milicia excelsa*.

Currently, the most significant original tropical forests left in the region are those contained in protected forest reserves (Alo and Pontius 2008). Outside of the protected areas, farming represents their primary source of food, income, and security (Blay et al. 2008). The high human population density outside protected areas makes them susceptible to fires because of forest fragmentation and fire spread from agricultural areas. There is also considerable pressure from both legal and illegal logging inside the protected areas to meet high wood demands (Hawthorne 1994; Marfo 2010).

Remote sensing data

We used Landsat TM/ETM+ images acquired during the dry season (November–March) to maximize cloud-free acquisitions and minimize false change detection due to seasonality and phenological differences. A total of 26 images from 1984 to 2015, with cloud cover 25% or lower, were selected from Landsat path/row 195/055. Whenever more than one image was available for a particular dry season, the image with the most conspicuous burn scars and the least cloud contamination was selected. The periods 1984–1995, 1996–2005, and 2006–2015 had nine, seven, and 10 images, respectively. All the images were Level 1 terrain corrected, atmospherically corrected, and converted to surface reflectance using the Landsat ecosystem disturbance adaptive processing system tool (Masek et al. 2006). With the exception of a few images from the European Space Agency, most images were downloaded from the USGS EROS archive (Table S1 in Appendix).

Cloud and cloud shadow masks were obtained through an automated cloud and cloud shadow

detection algorithm, Fmask (Zhu and Woodcock 2012). A separate random forest classification approach, using both the reflective and thermal bands, was used to mask clouds from the 1984 image due to poor performance of the Fmask algorithm. The Carlotto technique for de-hazing implemented in the ImgTools software was used to correct for atmospheric contamination of images affected by haze and smoke (Souza et al. 2013).

Mapping fires

The normalized burn ratio (NBR) was used to map burned area in each image. After fire, the reflectance of burned areas typically increases in the middle infrared (MIR) because of soil exposure and decreases in the near infrared (NIR) due to leaf tissue damage. The NBR thus uses MIR and NIR reflectance to map burned areas (Key and Benson 2006). We used NBR thresholds, guided by manual interpretation of the Landsat imagery and field observations, to map fire perimeters in all years with available Landsat imagery with threshold values ranging from 0.06 to 0.18.

The differenced NBR (dNBR) calculates the change between pre- and post-fire NBR estimates as a measure of severity and has been shown to be effective in broadleaf as well as coniferous forest types (Wimberly and Reilly 2007). We mapped fire severity within burned perimeters using the dNBR in 1989 because suitable images for both pre- and post-fire were available only for that year. Because there is no systematic way of generating fire severity classes from continuous values of dNBR, we adopted the approach employed by Numata et al. (2011) using a mean cluster analysis to classify the dNBR values of burned pixels into three classes of fire severity (low, medium and high).

We also obtained MODIS active fire detections at 1-km resolution at the time of Terra (10:30 a.m./p.m. Equatorial nominal overpass time) and Aqua (1:30 p.m./a.m. Equatorial nominal overpass time) satellite overpass from the monthly product MCD14ML, level 3 Collection 6 (Giglio et al. 2016). We characterized the spatial distribution and frequency of active fires for the period 2001–2015. We summarized the active fire detections into an annual active fire density time series (number of active fires per 100 km²) for each forest reserve, as well as the 5-km buffer zone surrounding each reserve.

Mapping forest vegetation change

We used the disturbance index (DI), which is based on the tasseled cap (TC) transformation, to map changes in forest conditions over time (Healey et al. 2005). The TC transformation compresses the data in the six optical-infrared bands of Landsat TM/ETM+ images to three orthogonal indices called brightness (B), greenness (G) and wetness (W; Baig et al. 2014). B is a weighted sum of all the bands, and is often used as a measure of soil exposure. G is a measure of the contrast between the NIR band and the visible bands and is sensitive to the amount of photosynthetically active vegetation (Baig et al. 2014). G is thus analogous to red/NIR-based G indices such as NDVI and EVI. W is a measure of contrast between the NIR and MIR bands and is sensitive to the moisture content of soil and vegetation. In vegetated areas, W can be interpreted as an indicator of canopy structure, soil or surface moisture, or the amount of dead or dried vegetation (Cohen and Goward 2004). TC transformation coefficients were obtained from Crist (1985).

We rescaled the TC indices into normalized B (Br), normalized G (Gr) and normalized W (Wr) by normalizing the respective TC index by the mean and standard deviation of representative forested pixels in each image scene. The reference forest pixels were selected from local image windows containing a mask of stable forest reserves across the entire image scene. This forest mask comprised 14 forest reserves, including national parks that were identified as relatively stable through time in the Landsat images time series. Compared to other vegetated surfaces, dense forest pixels are generally darker in the visible and MIR bands. Therefore, these pixels formed a peak at the lower end of the histograms for these bands (Huang et al. 2008). Our reference forest pixels were selected by identifying the first peak in the histogram of the Landsat red band from our stable forest mask. Even though reflectance values of the reference pixels might change between images due to scene-to-scene variability, the selection approach has been shown to be insensitive to these inter-image variations as long as the histogram peaks can be identified (Huang et al. 2008).

The DI is a linear transformation of the three normalized TC indices derived from Landsat TM/ETM+ images.

$$DI = Br - (Gr + Wr). \quad (1)$$

The DI works on the assumption that disturbed forest exhibits high B, low G and low W. Thus, disturbed areas are spectrally dissimilar to forests and therefore have high DI values. Undisturbed forest has spectral characteristics close to the reference forest pixels and therefore has low DI values (Healey et al. 2005). This approach has been shown to be effective at detecting changes in forested land cover (Hilker et al. 2009; Sieber et al. 2013). Validation of the 2015 DI index with the available Google Earth high-resolution imagery indicated a good separation of forest canopy cover classes by the DI, with a multi-class AUC value of 0.98 (see Appendix S1).

Field inventory

In March 2014 we conducted forest inventory in 11 representative sample plots distributed across the four forest reserves to characterize the conditions shown by the vegetation indices. The numbers of plots sampled in each reserve were two (AS), four (MP), two (PB), and three (TT). In each plot we established belt transects of 100 m × 10 m (0.1 ha). Within these transects, we measured and recorded the diameter at breast height (dbh in cm) of all trees with dbh ≥ 10 cm. Also, we estimated canopy cover (%) at 1 m intervals along each transect. We established three circular subplots of radius 5.65 m (area 100 m²) at every 50 m along the belt transect to measure all small trees of dbh ≥ 2 and < 10 cm. (> 2 m tall). Within each subplot, we took ocular estimates of litter and combined grass/shrub cover. The tree counts were summarized to provide tree density and basal area estimates.

Meteorological data

We analyzed precipitation data from three meteorological stations located in the towns of Bechem, Sunyani, and Wenchi, spanning the latitudinal gradient of the study area (Appendix, Fig. S1). We considered two rainfall metrics: the total annual precipitation (TAP) and the maximum climatological water deficit (MCWD). MCWD estimates accumulated water deficit within a particular year, and this rainfall metric is a useful indicator of the intensity and length of the dry season (Aragão et al. 2007). We computed MCWD using methods described by

Aragão et al. (2007). TAP is a major determinant in the distribution of tropical tree cover and vegetation types, whereas rainfall seasonality (here represented by MCWD) affects fuel moisture and fire regimes in the tropics (Hirota et al. 2011; Staver et al. 2011).

Analysis methods

Question 1: Is there evidence of persistent forest loss?

We graphed time series of mean DI, Br, Gr and Wr indices for each reserve and conducted trend analysis to quantify trajectories of vegetation change. We used the non-parametric Mann–Kendall test to test for increasing monotonic upward or downward trend in forest canopy disturbance after 1989 (Gocic and Trajkovic 2013). We also used the field inventory data collected in March 2014 to provide a more detailed characterization of current vegetation structure and composition in representative plots distributed across the reserves.

Question 2: Is there evidence of fire–vegetation feedbacks?

To determine whether fire regimes were different in reserves that experienced forest loss compared to the intact reserves, we graphed the annual time series of MODIS active fire density and Landsat percent area burned for each reserve. We used Welch's one way ANOVA test and the Games–Howell post hoc test, from the *userfriendlyscience* package in R, to compare mean differences in active fire density and burned area among the four reserves for the entire time series. We used these tests because the data were heteroscedastic and also violated the normality assumption, and therefore did not meet the assumptions for one-way ANOVA or its non-parametric equivalent, the Kruskal–Wallis test. We also compared fire severity in the four reserves in 1989 using the Landsat-derived dNBR measurements.

To assess the interactions between vegetation in the reserves and fire ignited in the surrounding agricultural matrix, we used paired t-tests to evaluate differences in fire activity between the interior and the 5-km buffer surrounding each reserve. This analysis tested whether the vegetation in the reserves generated negative fire feedbacks by resisting the spread of fires ignited in the surrounding agricultural

matrix, or generated positive feedbacks by facilitating fire spread from the matrix.

Question 3: Is there evidence of hysteresis?

We analyzed TAP and MCWD from 1990 to 2013 using the non-parametric Mann–Kendall test and breakpoint analysis to determine whether or not the changes in vegetation and fire regime after 1990 could be explained by a shift to a drier climate. Breakpoints in time series are points at which the mean changes, and such analyses are useful for determining when abrupt transitions occur and thus identifying potential regime shifts (Bestelmeyer et al. 2011). Cumulative sum plots, residual sums of squares, Bayesian information criterion and F-statistic analyses were used for abrupt change point detection in the precipitation time series (Bestelmeyer et al. 2011).

Results

Question 1: Is there evidence of persistent forest loss?

The time series of DI, B, G, and W showed varied responses across the study sites (Figs. 2, 3). From

1990 onward, DI was higher and exhibited a significant increasing trend in PB (0.1 significance level) and TT (0.05 significance level), but remained low with no significant trend in AS and MP (Table 1). No significant increasing or decreasing trend in G was detected in any of the reserves. There were significant decreasing trends in W in the northern reserves (PB and TT), but no significant trends in the southern reserves (AS and MP). There was a significant increasing trend in the B index in TT, but no significant trends in PB and the southern reserves. Based on these results and visual inspections of the trends, there was no evidence of recovery of forest conditions in PB and TT, and no evidence of increasing forest disturbance in AS and MP.

The forest inventory data from 2014 indicated that most of PB and TT lacked a forest canopy (Table 2). We also sampled one small remnant forest patch in TT, which had a relatively high basal area but also had lower tree density and canopy cover than the other plots located in unlogged forests. In contrast, the representative plots in AS and MP had higher tree densities, basal areas and canopy cover, although canopy cover tended to be lower in plots with evidence of recent logging.

The inventory data showed that shrub/grass cover was generally lower in the AS and MP plots than in the

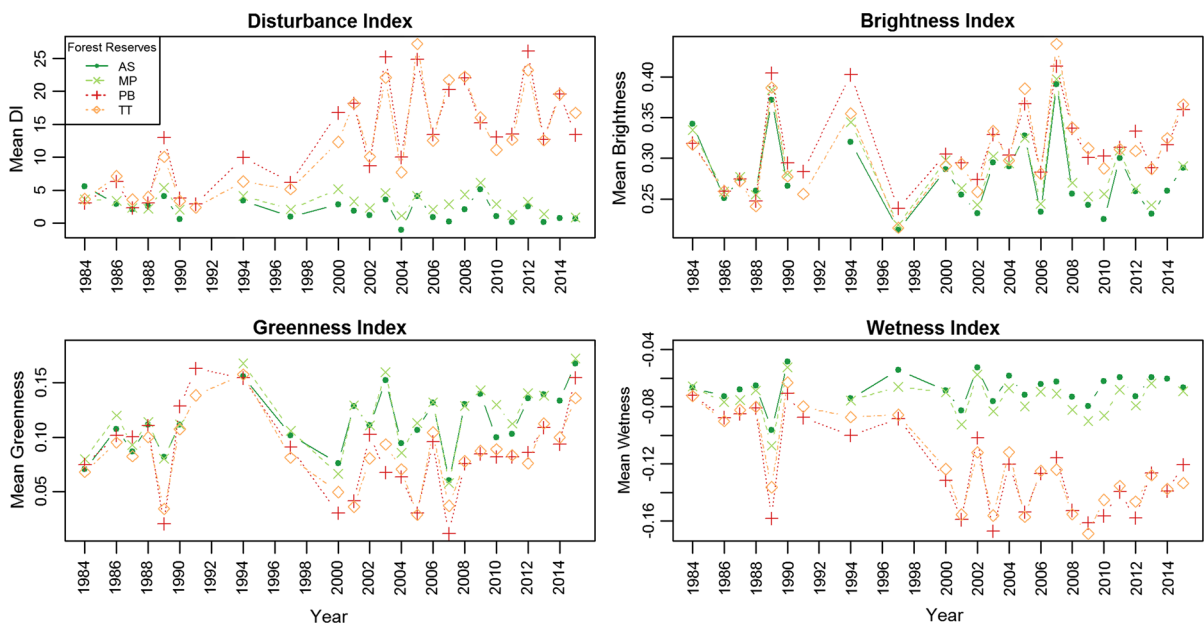


Fig. 2 Time series of disturbance index and tasseled cap brightness, greenness and wetness indices across the four reserves

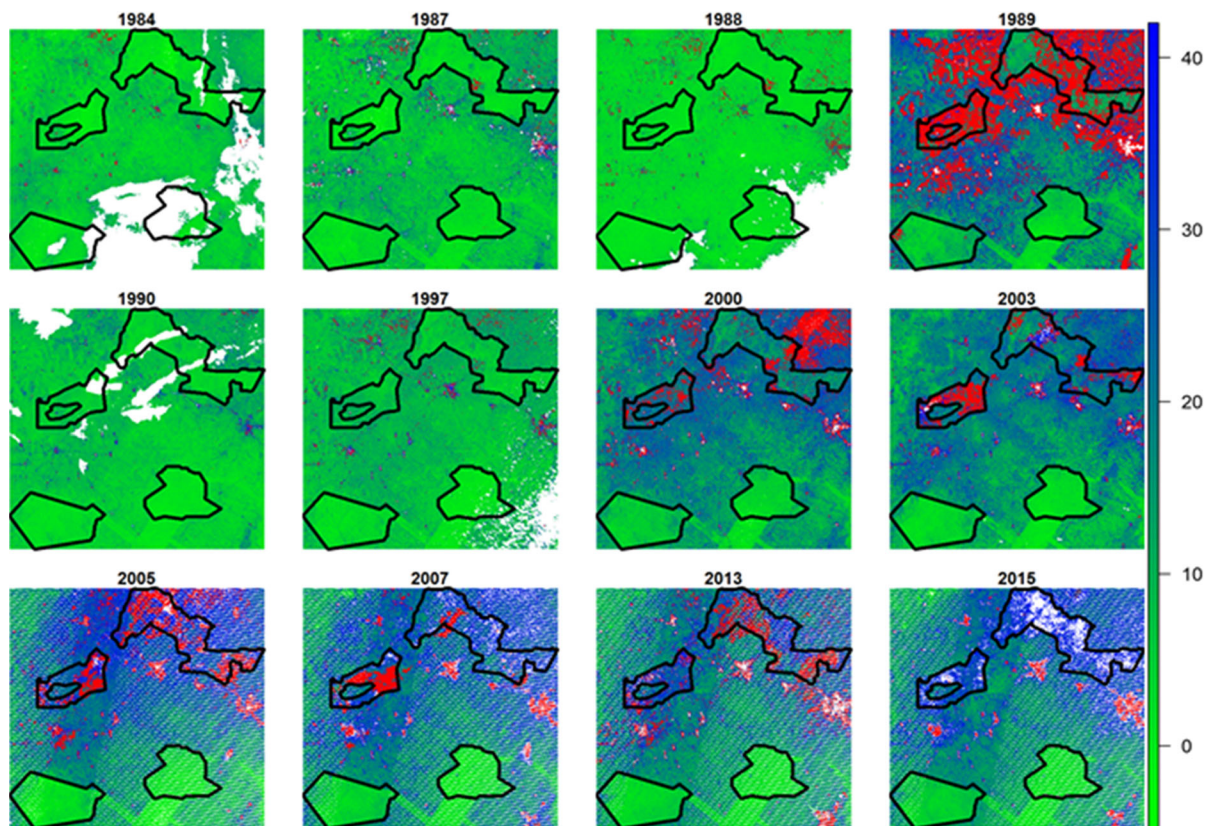


Fig. 3 Disturbance index time series maps showing vegetation cover changes within the forest reserves. Colors represent a gradient from closed forest (green) to degraded forests or low

vegetation cover (blue). Red represents recently burned sites, white spaces indicate non-vegetated surfaces or no data. (Color figure online)

Table 1 Nonparametric Mann–Kendall test to detect trends in DI, brightness, greenness, and wetness indices from 1990 to 2015

Vegetation index	Statistics	AS	MP	PB	TT
Disturbance index	tau	−0.158	−0.15	0.316	0.432
	p-value	0.363	0.405	0.056*	0.009**
Brightness index	tau	−0.018	−0.072	0.221	0.284
	p-value	0.944	0.705	0.183	0.086*
Greenness index	tau	0.205	0.268	0.032	0.053
	p-value	0.234	0.13	0.871	0.77
Wetness index	tau	−0.018	−0.111	−0.326	−0.4
	p-value	0.944	0.544	0.048**	0.015**

Positive Kendall's tau statistic values indicate increasing trends, whilst negative values indicate decreasing trends

** Significant at 0.05 significance level, * Significant at 0.1 significance level

PB and TT plots (Table 2). In AS and MP the shrub and herbaceous layers were dominated by species typical in forest gaps and the forest understory, including herbs in the genus *Afromomum* and the family *Marantaceae*. However, in PB and TT the

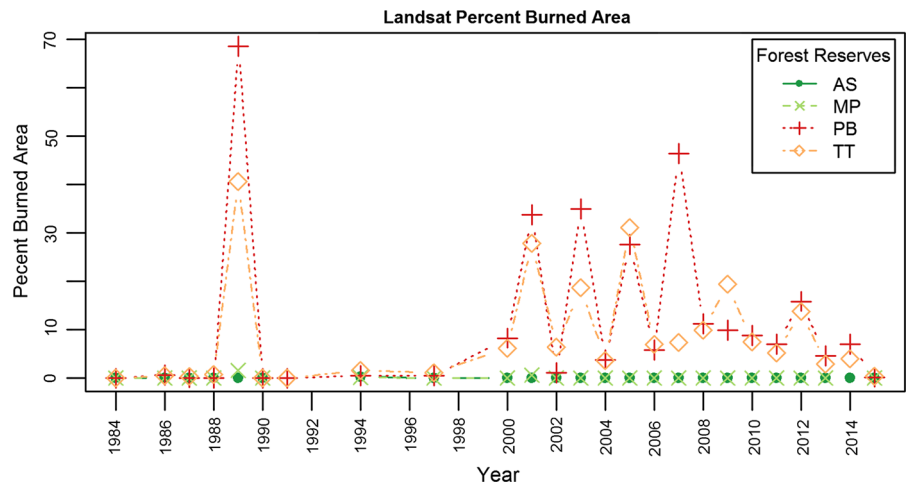
shrub and herbaceous layers were dominated by heavy thickets formed by a mixture of *Pennisetum purpureum* (elephant grass), the shrubs *Chromolaena odorata* and *Solanum erianthum*, and copious regeneration of *Ficus* spp. The percentage of the forest floor

Table 2 Summary of vegetation characteristics of representative field plots sampled in March 2014

Reserves	Logging status	Tree density (stems ha ⁻¹)		Basal area (m ² ha ⁻¹)		Canopy cover (%)	Shrub cover (%)	Litter cover (%)
		Trees	All tree	Trees	All tree			
		5–10 cm dbh	≥5 cm dbh	5–10 cm dbh	≥5 cm dbh			
AS	Recent logging ^a	67	137	0.28	4.7	27	100	100
AS	No recent logging	500	900	2.18	30.99	64	0	53
MP	Recent logging	767	1067	3.07	34.87	45	47	50
MP	No recent logging	533	953	2.01	22.39	73	5	72
MP	Recent logging	200	470	0.74	8.38	27	53	45
MP	Recent logging	433	863	1.68	27.75	70	5	90
PB	No forest	0	0	0	0	0	100	85
PB	No forest	167	207	0.47	1.71	1	100	85
TT	No forest	67	67	0.15	0.15	0	98	100
TT	No recent logging	0	230	0	27.15	40	68	85
TT	No forest	0	10	0	4.36	5	100	100

^a Recent logging indicates field evidence of logging activity at least in the recent two decades

Fig. 4 Time series of burned area mapped from Landsat TM/ETM+ imagery



covered by litter varied widely among all the sampled locations, but was generally higher in PB and TT and in plots with recent logging.

Question 2: Is there evidence of fire–vegetation feedbacks?

The time series of Landsat burned area showed that the largest annual burned area was recorded in 1989 and that this fire in this year was more widespread in the two northern reserves, PB and TT, than the southern reserves, AS and MP (Fig. 4). During that year, 66.0% of PB and 39.0% of TT were burned at moderate to high severity (Fig. 5). In contrast, only 2% of MP and

less than 0.10% of AS were burned at moderate to high severities.

There were significant differences in Landsat burned area ($F = 8.67, p < 0.001$, Welch’s one-way ANOVA; Fig. 4) and MODIS active fire density ($F = 21.92, p < 0.001$, Welch’s one-way ANOVA; Figs. 6, 7) across all the reserves. For both the Landsat burned area and the MODIS active fire annual time series, there was more fire activity in the two northern reserves that had minimal forest cover (PB and TT) than in the two southern reserves that retained a mostly intact forest canopy (AS and MP, Figs. 4, 6). The Games–Howell post hoc tests confirmed that for both fire variables, there were no significant differences

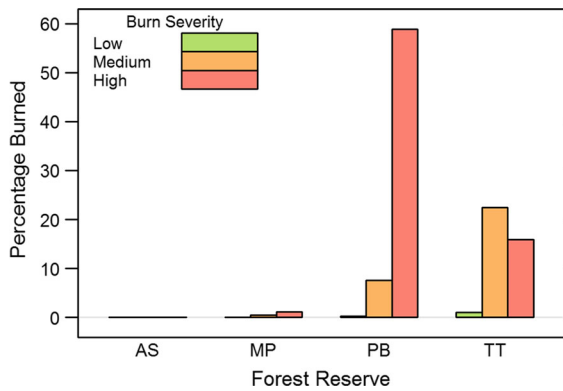


Fig. 5 Immediate (7-weeks) post-fire burn severity measured by the differenced normalized burn ratio (dNBR) summarized across four forest reserves in 1989

(0.05 significance level) between TT and PB, or between AS and MP (Appendix, Fig. S4). However, mean values in TT and PB were significantly higher than in AS and MP.

There were more active fires in the reserve interiors than in their corresponding buffers in the highly disturbed northern reserves (Figs. 7, 8; paired *t* test, $p = 0.002$ and <0.001 in PB and TT, respectively). In contrast to the northern reserves, there were more active fires in the buffer zones of each reserve than within reserve interiors in the less disturbed southern reserves (Figs. 7, 8; paired *t*-test, $p < 0.0001$ in both AS and MP). Overall active fire densities were lower both in the reserves and buffer of AS and MP compared to PB and TT. We inferred that the non-forest vegetation in PB and TT exhibited positive

feedbacks that facilitated the growth and spread of agricultural fires ignited in the surrounding matrix, whereas the forest vegetation in AS and MP exhibited negative feedbacks and resisted spread of fires from the surrounding matrix. This inference is supported by the fire patterns shown in Fig. 3, in which fire scars in PB and TT after 2000 tend to be adjacent to the edge of the reserve and extend into and sometimes through the entire reserve, whereas no substantial fire scars are seen in AS and MP.

Question 3: Is there evidence of hysteresis?

Precipitation was similar along a north–south gradient throughout the study area. Mean annual precipitation (\pm standard deviation) from 1976 to 2013 ranged from 1244 ± 171 at Wenchi in the north to 1194 ± 171 at Sunyani between the northern and southern reserves to 1282 ± 228 at Bechem in the south.

Precipitation trends indicated a gradual increase in TAP in all the weather stations punctuated by some dry years in 1990s and the 2000s (Fig. 9). These increases were statistically significant in all the weather stations (p -value <0.01), except at Wenchi. The MCWD trend did not show evidence of worsening drought stress during the dry season (Appendix, Fig. S3). Instead there was a statistically significant improvement in moisture conditions in Bechem (p -value <0.05), and no statistically significant change in Sunyani and Wenchi. No abrupt changes in precipitation were detected in any of the time series. Thus, the non-forested conditions in PB and TT have been

Fig. 6 MODIS active fire density time series

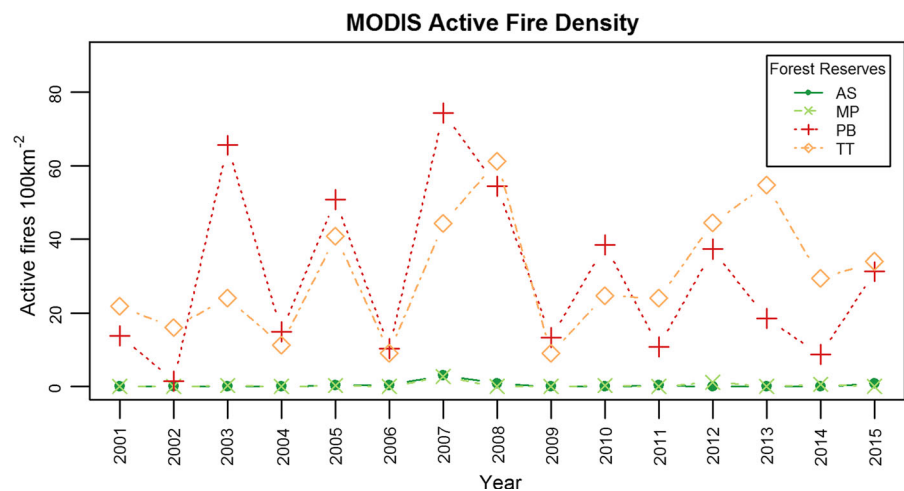


Fig. 7 Spatial distribution of MODIS active fires, 2001–2015, within forest reserves and 5 km buffer zones around the reserves

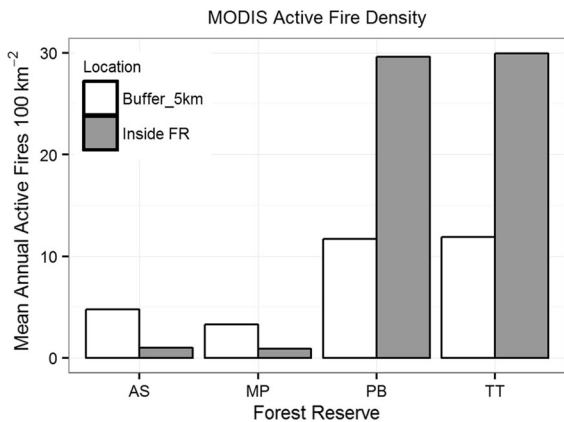
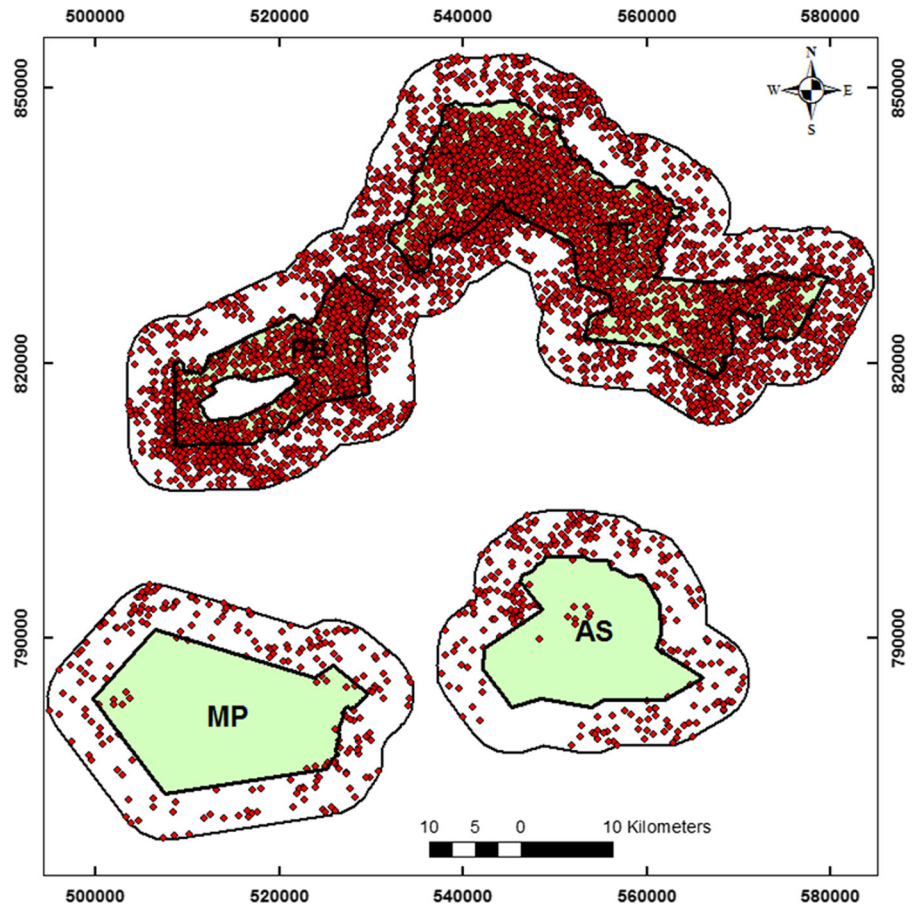


Fig. 8 Mean annual MODIS active fire density within reserves and 5-km buffers around each reserve

maintained throughout a time period during which precipitation has generally been stable or increasing, and thus climatic suitability for forests has also been stable or increasing.

Discussion

Although our time series of Landsat observations encompassed more than 30 years from 1984 through 2015, the results need to be interpreted in the context of longer-term trends. Mentions were made of historical fires in the reserves in our study area for several decades before the 1980s, noting that they were mainly occasional forest-floor fires which did not cause severe damage to the forest (Hall and Swaine 1981). A study of historical fire records in Ghana’s forest zone from 1910 to 1993 showed that periods of widespread fires coincided with droughts, but also found a sharp rise in fire frequency beginning in the early 1980s (Orgle 1994). Swaine (1992) also observed this trend of increasing fire incidence in the 1980s and argued that a coupled interaction between human land use changes and climatic changes were responsible. Forest assessments conducted between 1986 and 1988 indicated that widespread burning had

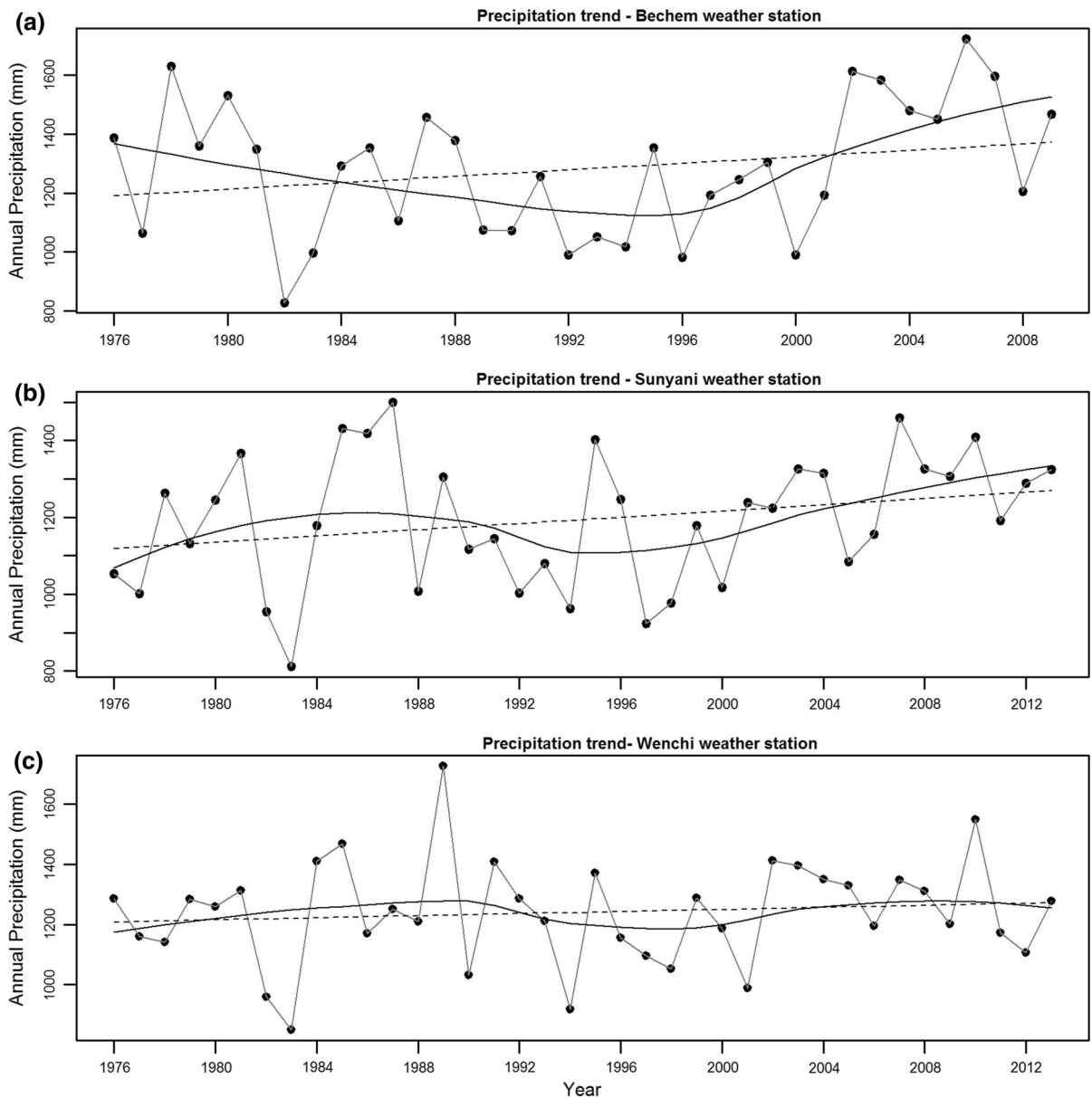


Fig. 9 Time series of annual precipitation from three meteorological stations spanning the latitudinal gradient of the study area. Data cover the periods **a** 1976–2009, **b** and **c** 1976–2013. *Dashed lines* represent linear trends, *solid lines* represent locally smoothed trends

occurred in numerous reserves in the semi-deciduous forest zone, and that large portions of the reserves that we studied burned in the early 1980s (Hawthorne 1994), although we did not detect these fires in the Landsat record. However, only PB and TT were reburned by the extensive and severe fires that we observed in 1989.

These repeated fires in the 1980s played a key role in a shift from forest to grass and shrub-dominated

vegetation in the two northern reserves. Even though the spectral indices showed rapid recovery in 1990, these reserves likely became more susceptible to subsequent fires because of reduced canopy cover, increased fuel loads, and decreased fuel moisture following multiple disturbances (Cochrane et al. 1999; Brando et al. 2014). Therefore, we strongly suspect that PB and TT experienced additional fires that were not detected in the sparse Landsat record of the

1990s. Generally, large canopy trees have thicker bark and are better able to survive fires than smaller trees, but they succumb to fire upon repeated burns (Balch et al. 2015). It is also possible that fire damage to canopy trees during the 1980s could have led to delayed mortality of the injured trees over the subsequent decade. Based on our satellite observations combined with information from the historical record and knowledge of tropical forest fire ecology, we suggest that the most likely scenario is that repeated fires gradually eroded the resilience of the two northern reserves.

From 2000 onward, the deforested northern reserves burned more frequently than the forested southern reserves, and these frequent fires have maintained grass and shrub-dominated vegetation in the northern reserves by limiting the establishment of fire-sensitive forest tree seedlings. Results from experimental and field-based studies in the Amazon affirm that repeated fires significantly impede successful regeneration of woody forest species, but foster the spread of invasive grasses (Silvério et al. 2013; Balch et al. 2015). In the northern reserves, the fire-maintained vegetation is mainly a mosaic of the invasive and fire-prone shrub, *C. odorata* and tall grasses such as *P. purpureum* (elephant grass), and *Panicum maximum* (Swaine 1992; Amisshah et al. 2011) with low densities of forest tree species (Fig. 10). The grasses and shrubs tend to be very aggressive competitors, curtailing seedling establishment and growth of forest tree species. In an experimental study in Ghana, Honu and Dang (2000) recorded that decreased seedling growth and survival was associated with *C. odorata* infestation, and that tree regeneration was significantly enhanced following removal of this invasive shrub. Loss of overstory trees due to fire also reduces seed sources and limits seedling establishment due to the absence of nurse trees, reduced competitive advantage, and harsh environmental conditions (Paritsis et al. 2015).

Our results showing more fires in the interiors than outside the northern reserves suggest that fires ignited in the surrounding landscape matrix and subsequently burned into these reserves, where the pyrophilic grasses and shrubs facilitated their spread. Fire is the main land preparation tool for agriculture in the area, and fire spread from agricultural areas is one of the main sources of fire ignition in the forest reserves (Appiah et al. 2010). We infer a positive feedback whereby the vegetation in these reserves amplified the

effect of these ignitions through rapid spread rates and propagated fires through the reserve and back into the surrounding landscape. Contrasting results showed fewer fires in the interiors than in the buffers of the relatively intact southern forest reserves, suggesting a negative feedback, whereby the closed canopy forests inside the reserves prevented fire spread from the adjacent agricultural matrix because of less live fuels and higher fuel moisture in the shaded understory.

These interactions between the reserves and the surrounding landscapes emphasize the important effects of human land use on fire regimes. Forest reserves in Ghana have mostly been protected against conversion to cropland and other agricultural land uses. However, forest rehabilitation and plantation activities, such as the *Taungya* agroforestry system, do occur inside some reserves and have been cited as sources of forest fires in Ghana (Orgle 1994). Most forest reserves in Ghana are logged, primarily through selective logging of individual trees (Adam et al. 2006), and illegal logging is also widespread (Marfo 2010). Logging disturbs the forest canopy and result in fragmented forests that are more vulnerable to fire (Hawthorne et al. 2012). Many forests in Ghana were subjected to heavy timber exploitation beginning in the early 1960s and continued into the early 1980s (Treue 2001; Adam et al. 2006). All the reserves in our study area are known to have experienced heavy logging prior to the 1980s, and this logging is believed to have led to increased fire susceptibility following the severe drought of 1982–1983 (Hawthorne 1994; Orgle 1994; Hawthorne and Abu-Juam 1995). Thus, human activities such as agriculture and timber extraction helped to create the conditions that resulted in increased fire susceptibility and led to the observed regime shifts in the northern reserves.

Our finding of divergent fire regimes associated with contrasting vegetation types in areas with similar rainfall suggests that fire–vegetation feedbacks can maintain distinctive vegetation and fire regimes in areas with similar climate, a finding also confirmed by Dantas et al. (2013). This result also fits the conceptual model of Staver et al. (2011), who concluded that in climates with intermediate annual rainfall (1000–2500 mm) and a dry season shorter than 7 months, fire is a major determinant of alternative vegetation states. Another recent assessment of Afrotropical vegetation similarly concluded that fire has the potential to maintain tropical forests and

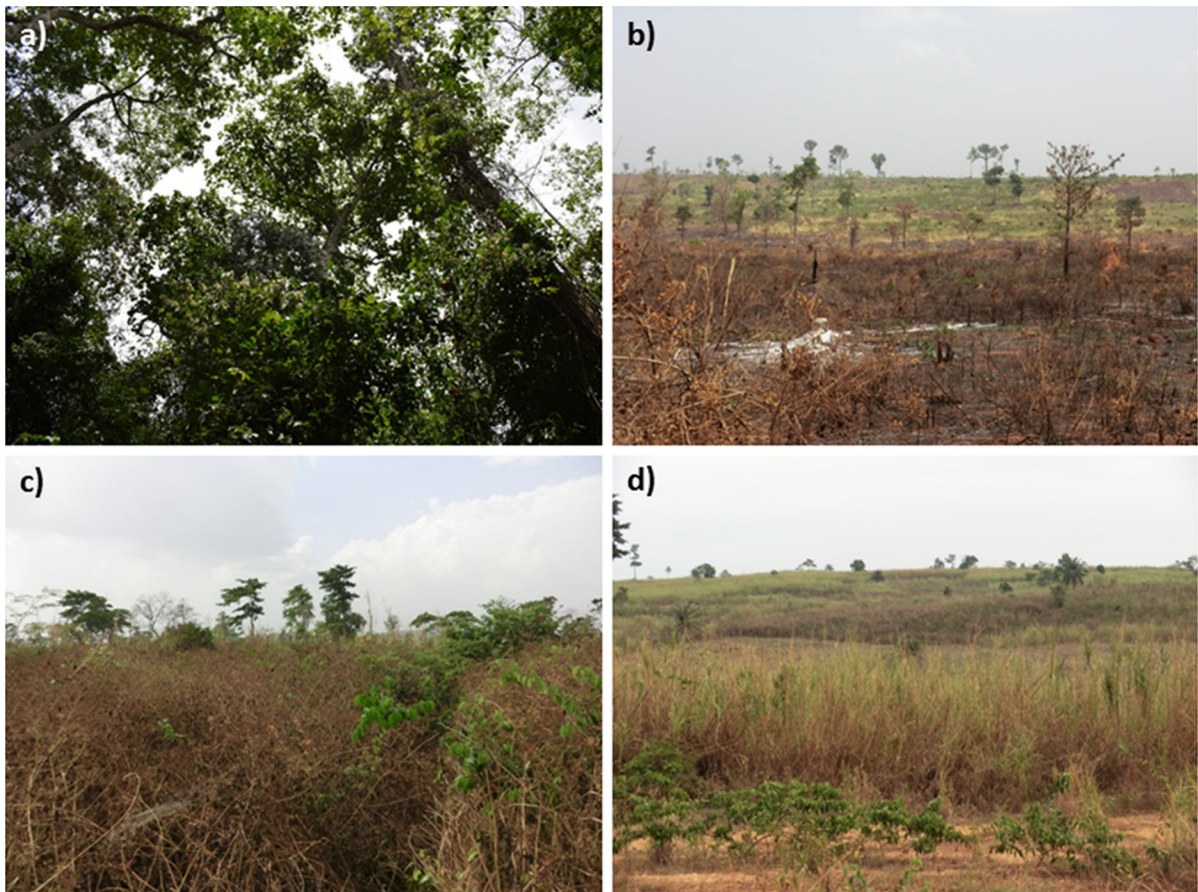


Fig. 10 Pictures showing conditions of **a** canopy cover in unburned forest in AS, **b** a degraded and recently burned area in PB with few isolated trees, **c** frequently burned vegetation in TT

dominated by *Chromolaena odorata*, and **d** frequently burned vegetation in PB dominated by *Pennisetum purpureum* (elephant grass)

savannas as alternative biome states under a broad range of environmental conditions (Dantas et al. 2016). Our results thus suggest a hysteresis effect, in which a disturbance-driven state change was followed by maintenance of a new, non-forested vegetation community under levels of precipitation that continued to support forests at nearby locations. Even though the variability in soils, topography, and other climatic conditions across our study area is not large, there is also the potential for fire–vegetation feedbacks and the resulting hysteresis to magnify relatively small environmental differences into much larger disparities in disturbance regimes and vegetation characteristics (Beisner et al. 2003).

It is important to note several challenges associated with the present study. Like most tropical regions, there are few historical data documenting changes in

the landscape, so we gleaned pieces of evidence from multiple sources to arrive at our conclusions. We acknowledge that persistent cloud cover and missing image data constrained our remote sensing analyses to years when cloud-free Landsat images were available. In particular, Landsat acquisitions in our study area were rare in the 1990s due to downlinking problems as well as the commercialization of the Landsat program during that era (Goward et al. 2006). Our Landsat record did not go far back enough to capture earlier fires associated with the 1982–1983 severe droughts. There are also areas of missing data in images acquired after May 2003 due to failure of the Landsat 7 ETM+ scan line corrector (SLC-off). It is also recognized that MODIS hotspot detections may be limited by unfavorable observing conditions and the timing of the satellite overpass (Giglio et al. 2016). The coarse

spatial resolution of MODIS also means that we may have missed lower intensity and smaller fires, especially understory fires. Hence, total numbers of fires are likely underestimated, although spatial and temporal comparisons of relative numbers of hot spots are still valid.

Whilst there are few empirical studies on alternative stable states in terrestrial ecosystems, such studies on tropical forests are even rarer. Although the use of remotely sensed data in the study of alternative stable states is not new, previous studies have often neglected the temporal component by substituting time for space in their analyses (Hirota et al. 2011; Staver et al. 2011). Our approach combining field measurements and multiple spectral vegetation indices from long-term time series Landsat imagery is thus a unique contribution. This study demonstrates the potential for land use change and fire to create novel and persistent non-forested vegetation communities in regions that are climatically suitable for forests. These changes were not immediate, but occurred slowly because of delayed tree mortality, continued impacts of human disturbances such as logging, and gradual erosion of forest resilience due to repeated fires. A critical implication is that assessments of future vegetation dynamics in the region will need to consider land use, fires, and their dynamic landscape–scale interactions in the context of broader drivers related to climate change and human population growth. In particular, further research focused on elucidating the drivers and mechanisms of forest degradation and fire encroachment may allow for the detection of early warning signals and the development of strategies to prevent further forest loss in tropical West Africa.

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