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Satellite Remote Sensing of Woody and Herbaceous Leaf Area for Improved Understanding of Forage Resources and Fire in Africa

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SATELLITE REMOTE SENSING OF WOODY AND HERBACEOUS LEAF AREA FOR IMPROVED UNDERSTANDING OF FORAGE RESOURCES AND FIRE IN AFRICA

BY

MILKAH NJOKI KAHIU

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This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy in Geospatial Science and Engineering degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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To the two most wonderful people in my world, Roy and Ryan.

Nawapenda kinyama!

BIOSKETCH

Ms. Kahiu is natural scientist and terrestrial ecologist where she works on use of geospatial technology to understand vegetation dynamics and their interactions with fire and herbivores as well on focusing on biodiversity conservation, land degradation and dynamics of coupled natural-human systems. Her work spans from small to large spatiotemporal scales. For her PhD research she worked under the supervision of Dr. Niall Hanan a community and ecosystem ecologist.

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ABBREVIATIONS

ANOVA	Analysis of Variance
AVHRR	Advanced Very High-Resolution Radiometer
BF	Burn Frequency
BISE	Best Index Slope Extraction
BRT	Boosted Regression Tree
CHIRPS	Climate Hazards Group InfraRed Precipitation with Station data
CO_2	Carbon Dioxide
CRU	Climate Research Unit
DEM	Digital Elevation Model
DOY	Day of Year
DSL	Dry Season Length
FAO	Food and Agricultural Organization
FAOSTAT	Food and Agriculture Organization Corporate Statistical Database
FCC	Fuel, Cure and Connectivity
GADM	Database of Global Administrative Areas
GEB	Global Ecology and Biogeography
GFED4	Global Fire Emissions Database Version 4
GIF	Graphics Interchange Format
GLiPHA	Global Livestock Production and Health Atlas
GLWD-3	Global Lakes and Wetlands Database level 3
HWSD	Harmonized World Soil Database

HPD	Human Population Density
IFP	Intermediate Fire-Productivity hypothesis
LAI	Leaf Area Index
$\mathrm{LAI}_{\mathrm{A}}$	Aggregate Leaf Area Index
$\mathrm{LAI}_{\mathrm{H}}$	Herbaceous Leaf Area Index
$\mathrm{LAI}_{\mathrm{Max}}$	Maximum Leaf Area Index
$\mathrm{LAI}_{\mathrm{Min}}$	Minimum Leaf Area Index
$\mathrm{LAI}_{\mathrm{W}}$	Woody Leaf Area Index
$\mathrm{LAI}_{\mathrm{Winc}}$	In-canopy Leaf Area Index
$\mathrm{LAI}_{\mathrm{W}p\mathrm{inc}}$	Peak within-canopy woody Leaf Area Index
MAP	Mean Annual Precipitation
MISR	Multi-angle Imaging SpectroRadiometer
MODIS	MODerate Resolution Imaging Spectroradiometer
NASA	National Aeronautics and Space Administration
NDVI	Normalized Difference Vegetation Index
NDWI	Normalized Difference Water Index
NMSU	New Mexico State University
NPP	Net Primary Production
PBA	Percentage Burnt Area
PCA	Plant Canopy Analyzer
RS	Remote Sensing
RMSE	Root Mean Square Error
SDSU	South Dakota State University

SSA	Sub-Saharan Africa
TRMM	Tropical Rainfall Measuring Mission
τ_w	Woody Canopy Cover
SI	Support Information
TLU	Tropical Livestock Units
USGS	US Geological Survey
VIIRS	Visible Infrared Imaging Radiometer Suite
VOD	Vegetation Optical Depth
WWF	World Wildlife Fund

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ABSTRACT

SATELLITE REMOTE SENSING OF WOODY AND HERBACEOUS LEAF AREA FOR IMPROVED UNDERSTANDING OF FORAGE RESOURCES AND FIRE IN AFRICA

MILKAH NJOKI KAHIU

2018

In sub-Saharan Africa (SSA) tree-grass systems commonly referred to as savannas dominating drylands, play a critical role in social, cultural, economic and environmental systems. These coupled natural-human systems support millions of people through pastoralism, are important global biodiversity hotspots and play a critical role in global biogeochemical cycles. Despite the importance of SSA savannas, they have been marginalized for years as most governments neglect dryland resources in favor of agricultural research and development assistance. Hence, lack of spatially and temporally accurate information on the status and trends in savanna resources has led to poor planning and management. This scenario calls for research to derive information that can be used to guide development, management and conservation of savannas for enhanced human wellbeing, livestock productivity and wildlife management.

The above considerations motivated a more detailed study of the composition, temporal and spatial variability of savannas, comprising of three components. Remote sensing data was combined with field and literature data to: partition Moderate Resolution Imaging Spectroradiometer (MODIS) total leaf area index (LAI_A) time series into its woody (LAI_W) and herbaceous (LAI_H) constituents for SSA; and application of the partitioned LAI to determine how changes in herbaceous and woody LAI, affect fire regimes and livestock herbivory in SSA.

The results of this analysis include presentation of algorithm for partitioning of MODIS LAI_A from 2003-2015. Biome phenologies, seasonality and distribution of woody and herbaceous LAI are presented and the long-term average 8-day phenologies availed for evaluation and research application. In determining how changes in herbaceous and woody LAI affect fire regimes in SSA, we found that herbaceous fuel-load (indexed as LAI_H) correlated more closely with fire, than with LAI_W, providing more explanatory power than overall biomass in fire activity. We observed an asymptotic relationship between herbaceous fuel-load and fire with trees promoting fires in dry ecosystems but suppressing fires in wetter regions. In the livestock herbivory analysis we found that the more refined forage indices (LAI_H and LAI_W) explained more of the variability in livestock distribution than the aggregate biomass, with livestock favoring moderate to nutrient rich forage resources dependent on animal body size.

CHAPTER 1

Introduction, background and goals of the dissertation

1.0 Introduction and Background

Tree grass systems commonly referred to as savannas are widespread biomes present in all continents except Antarctica, covering ~20% of global terrestrial landscapes, particularly in tropical and subtropical regions between the Tropic of Cancer and Capricorn (White *et al.*, 2000). Various definitions of savanna occur but the common theme is the characterization by a continuous grass layer and a discontinuous trees (Scholes & Archer, 1997). These unique biomes cover >50% of Africa and Australia; ~45% of South America and about 10% in Asia (Solbrig, 1996; Werner, 1991), marked by strong and distinct alternations between wet and dry seasons. Although savannas are characterized by similar traits (two contrasting life forms, comprising of trees and grasses), variations in vegetation structure, including tree canopy cover and density, floristic and faunal composition, occur across the continents and within regions (Shorrocks & Bates, 2015). These variations form the basis of savanna classification, ranging from open savanna grasslands consisting of widely scattered trees, to the closed woodland savanna dominated by trees or forests with a grass layer (San José *et al.*, 1991; Solbrig, 1996).

In Africa, savanna woody vegetation (trees and shrubs) tends to be deciduous, in contrast to the evergreen nature in South America and Australia (Shorrocks & Bates, 2015). The deciduous woody layer generally produces leaves before rains begin, since trees can consume stored food reserves reducing competition with the herbaceous layer (Simioni *et al.*, 2004). In contrast, the continuous herbaceous layer, which consists mainly of perennial C4 grasses (adapted for photosynthetic efficiency in warm environments) and forbs (Shorrocks & Bates, 2015) tends to green up with the onset of rains and senesces soon after the end of the rain season (Borchert & Rivera, 2001; de Bie *et al.*, 1998; Higgins *et al.*, 2011; Simioni *et al.*, 2004).

Savannas occur across a broad range of climate, from cold and dry to warm and wet enough to support forested canopies. In African savannas, temperatures range between 18°-21° with month averages variations caused by low to high sun season Shorrocks & Bates, 2015 (Shorrocks & Bates, 2015). In contrast to the temperatures, moisture patterns are generally very distinct alternating between the wet and the dry season, governed by the annual migration of the intertropical convergence zone across the equator (Maddox, 2006; Shorrocks & Bates, 2015; Solbrig, 1996)

The dynamics of savanna vegetation are not well understood (Lehmann *et al.*, 2011; Murphy & Bowman, 2012; Sankaran *et al.*, 2004; Scholes & Archer, 1997). However, the presence of the two distinct life forms is determined by complex and dynamic interactions including climate, herbivory, fire, topography, soils and geomorphology (Backéus, 1992; Higgins *et al.*, 2000; Shorrocks & Bates, 2015). These interactions have attracted explanations on the co-dominance of the two distinct life forms, which Sankaran *et al.* (2004) summarizes into two broad categories: competition or demographic based mechanisms. Competition based mechanisms include (i) the spatial niche separation hypothesis (Walter, 1939 as cited in Ward et al., 2013) with vertical niche partitioning (rooting depth), which suggests that herbaceous roots in the subsurface are more water-use efficient than trees, that must access deeper water sources to survive (Verweij *et al.*, 2011; Ward *et al.*, 2013); and (ii) the temporal (phenological) niche separation hypothesis Sankaran *et al.* (2004) which posits that woody plants (trees and shrubs) use stored carbon reserves to deploy leaves earlier in the growing season before the herbaceous layer sprouts, allowing trees sole access to early rains, hence minimizing competition with grasses (Borchert & Rivera, 2001; de Bie *et al.*, 1998; Higgins *et al.*, 2011; Simioni *et al.*, 2004). On the other hand, demographic based mechanisms involve facilitation or suppression of one life form, by activities including fire, herbivory, precipitation variability (Lehmann *et al.*, 2011)

2.0 Importance of savannas

Globally, savannas account for ~30% of net primary production (NPP) in terrestrial ecosystems (Archibald & Scholes, 2007; Field *et al.*, 1998), making them important for the rapidly growing human population, livestock and biodiversity conservation for both flora and fauna (Scholes & Archer, 1997). In sub-Saharan Africa savannas, though characterized by low and erratic rainfall (Shorrocks & Bates, 2015), low human populations, and scanty water resources, these unique biomes form a significant part of grazing systems important for survival of humans, livestock and wildlife. Due to the scarce population and perceived low resource base they have been marginalized for decades, if not centuries (Reynolds *et al.*, 2007). However, their economic and environmental significance, particularly their role as foraging lands for livestock and wildlife cannot be underrated (Darkoh, 2003; Hassan & Dregne, 1997; Palmer *et al.*, 2015). Globally livestock is an important source of livelihood for close to a billion human population (Robinson *et al.*, 2014), while in SSA grazing systems comprise a significant source of livelihood, where millions of people depend on pastoralism as a source of food and income. Further, the African savannas support diverse flora and charismatic large herbivore and carnivore guilds, making them among the most important global biodiversity conservation hotspots (Darkoh, 2003; Shorrocks & Bates, 2015; White *et al.*, 2000). In fact African savannas are known to support higher densities of ungulates than any other biome or continent (Du Toit & Cumming, 1999), while in South America only three ungulates are savanna specific, and Australia is characterized by limited numbers of grazing mammals due to poor nutrient forages (Shorrocks & Bates, 2015). Moreover, the vast grasslands and savannas of Africa are important sources and sinks of carbon (Williams *et al.*, 2007) and management of fire and herbivory can significantly alter carbon density in woody biomass (Danell *et al.*, 2006). Additionally, savannas support a rich diversity of termites. As an integral part of savanna ecology, termites create mounds which aerate the surrounding soils coupled with termite droppings that create patches rich in nitrogen and phosphorous hence facilitating growth of grass, shrubs and trees acting as foraging hotspots for herbivores (Sileshi *et al.*, 2010)

African wild fires are almost exclusively from anthropogenic sources (Archibald *et al.*, 2012; Kull & Laris, 2009), with the bulk of fires happening in savannas fueled by the senescent herbaceous layer which is typically flammable throughout the dry season consuming ~10% of savanna net primary production (Lehsten *et al.*, 2009). The recurrent African wild fires are estimated to constitute over 40% of global fire emissions (van der Werf *et al.*, 2017; Williams *et al.*, 2007). Impacts of African savanna fires are not only felt locally, but have far reaching implications, with emissions travelling across the Atlantic to South America, south Pacific and the Indian Ocean (Edwards *et al.*, 2006). Hence utilization and management of African savannas can have important implications for the global carbon cycle.

3.0 Challenges and opportunities of savanna ecosystems in Africa

Despite the benefits accrued from savanna ecosystems they are continually threatened by natural and anthropogenic activities. The current increase in human population, especially caused by migration from overpopulated regions and change in lifestyles, have tremendous impacts on savanna ecosystems. The extractive use of savanna resources, intensification in agriculture (causing ~1% annual conversion of savanna into agricultural production) and livestock grazing, increasing demand for more fuel and land for settlement, have continued to exert pressure on savannas (Grace *et al.*, 2006). Agricultural encroachment is also exacerbated by sedentarisation of nomadic lifestyle, leaving no room for these fragile ecosystems to recover (Weber & Horst, 2011). Furthermore, establishment of road networks and settlements has resulted in fragmentation of savanna landscapes, which impacts vegetation patterns, fire regimes, and biodiversity conservation (Archibald *et al.*, 2009) All these land use /cover changes, and shifts in management, continue to cause degradation through loss of vegetation cover and palatable forage resources (Lambin *et al.*, 2003). Additionally, indigenous hunters and poachers are threatening wildlife and their habitats, leading to abrupt decline in wildlife populations in these unique biomes (Kerr & Currie, 1995). Although savannas have been converted to other land uses, changes in forest ecosystems through intense burning, forest degradation and indiscriminate harvesting of trees has enabled open spaces facilitating herbaceous undergrowth hence introducing savanna like ecosystems in some areas in the forest-savanna transition zone.

Fires are consistent and prominent disturbance factors and agents of change in savanna ecosystems (Roy *et al.*, 2013). Though widely used as management tools to: stimulate pasture growth, clear land for agriculture and reduce fuel hazard (Harrison *et* *al.*, 2010; Pausas & Keeley, 2009), intense and uncontrolled burning can have deleterious effects on savannas and their biodiversity. For instance, intense crown fires in eucalyptus and coniferous trees destroy above ground plant growth causing complete replacement of canopy vegetation (Bond & Keane, 2017). As a "herbivore" consuming net primary productivity (Bond & Keeley, 2005), savanna fires have adverse effects at local scale, impacting land use, productivity, carrying capacity and biodiversity, and global effects that alter hydrological, biogeochemical and atmospheric processes (Bond & Keane, 2017; Crutzen & Andreae, 1990; Harrison *et al.*, 2010).

Naturally, savannas are characterized by low erratic precipitation and recurrent dry spells, but the current increase in intense, severe and prolonged droughts caused by climate change, exacerbated in some areas by overgrazing, are changing the quality and status of vegetation which is slowly leading to degradation (Grainger, 2013; Weber & Horst, 2011). Climate change will have both beneficial and deleterious effects on savannas (Settele *et al.*, 2014). Increased precipitation in arid and temperature rise in cooler ecosystems might create conditions favorable for establishment of savannas. Additionally, projected drying coupled with increased fires could lead to conversion of forest into savannas (Settele *et al.*, 2014). On the other hand, reduced precipitation in some areas across the globe might shift savannas into deserts, a situation exacerbated by poor agricultural practices, overgrazing, soil erosion and deforestation, hence affecting the proper functioning of savannas and global biogeochemical cycles.

Woody encroachment, referring to invasion and increase in trees and shrubs at the expense of perennial grasses, is recognized as a threat to the survival of savannas across the world (Eldridge *et al.*, 2011; Settele *et al.*, 2014 and citations therein). Acting at local to regional scales, various activities are suggested as the drivers of woody encroachment including: suppression of fire, changes in herbivory such as crashes in herbivore numbers; anthropogenic activities that promote woody species with attached economic benefits or even planned and unplanned introduction of alien species. On the other hand, at global scale, proposed drivers include increasing atmospheric CO_2 and changing precipitation regimes associated with global climate change (Settele *et al.*, 2014).

4.0 Remote sensing of savannas

In the recent past the remote sensing (RS) community and earth systems modelers have made substantial progress in developing products to characterize global vegetation traits (Adam *et al.*, 2010; Houborg *et al.*, 2015; Thenkabail & Lyon, 2016; Xie *et al.*, 2008; Xue & Su, 2017). However, despite the importance of savannas, they are not well represented in RS and modeling capabilities (Hill & Hanan, 2010) due to the presence of mixed woody and herbaceous components at scales much finer than most medium and coarse resolution remote sensing data.

Few attempts have been made to partition savanna signals into woody and herbaceous components using RS data. However, these methods are lacking due to the areas covered, data used or approaches applied. Previous attempts to partition LAI into overstory and understory components have been done for boreal, and temperate forests (Huang *et al.*, 2011; Kobayashi *et al.*, 2010; Liu *et al.*, 2017) excluding tropical forests and savanna ecosystems in Africa. In other studies, several authors have tested time series decomposition and spectral unmixing to separate woody, herbaceous and bare soil fractional cover estimates, or photosynthetic, non-photosynthetic and bare components, including works in southern Africa Gessner *et al.* (2013) and Australia (Gill *et al.*, 2017;

Lu *et al.*, 2003; Zhou *et al.*, 2016). Other efforts geared towards refining savanna vegetation into woody and herbaceous components depending on the different phenological traits of the two savanna contrasting life-forms include studies in the Sahel (Brandt *et al.*, 2016), Namibia (Wagenseil & Samimi, 2007) and South Africa (Archibald & Scholes, 2007). Using NDVI and vegetation optical depth retrievals from passive microwave satellite observations, Tian *et al.* (2017) separated leaves from the woody cover in global tropical drylands.

Most of these studies have focused at local scales, or excluded tropical savannas where tree-grass systems dominate (Shorrocks & Bates, 2015). The use of NDVI, fractional cover or photosynthetic versus non photosynthetic components to characterize the contrasting savanna life forms is also challenged by methods requiring an evergreen woody cover, which is not typical for the deciduous African savanna trees (de Bie *et al.*, 1998; Do *et al.*, 2005; Horion *et al.*, 2014; Shorrocks & Bates, 2015). These methods therefore restrict their applicability in African savannas, or provide information that is only indirectly related to ecosystem function, hence limiting their applicability in tropical savanna studies. For instance, NDVI as an indicator of vegetation greenness fails to provide important information about vegetation structure (e.g. leaf area index, LAI) necessary to understand the functioning of terrestrial ecosystems.

LAI, defined as the one-sided area of green leaves (m^2) per unit ground area (m^2) in broadleaf canopies and half total needle surface area per unit ground area in conifers, is considered the most important vegetation structural parameter since leaf surface is the interface where major plant physical and biological process occur (Chen, 2013), including photosynthesis, regulating the rate at which heat, moisture and CO_2 are exchanged between the atmosphere and terrestrial ecosystems. It is therefore a critical parameter in biogeochemical, ecological and meteorological models and remote sensing applications. However, we recognize a major failure of aggregate remote sensing products in the savannas, that fail to separate the primary woody and herbaceous components of the system (Chen, 2013; Garrigues *et al.*, 2008). Separate woody and herbaceous LAI, and other metrics of the density and structure of the main savanna components, would be more meaningful in understanding the separate and distinct role of woody and herbaceous vegetation in mixed tree-grass ecosystems. I argue that appropriate representation of separate woody and herbaceous components of savanna vegetation should be fundamental in global models of vegetation dynamics, competition, land surface-atmosphere interactions and for understanding the spatial and temporal dynamics of consumers of global net primary production (particularly fire and large herbivores).

RS has seen significant application in understanding fire and consequent emissions across the globe, thus beneficial in the management and monitoring of fires and affected resources. RS data have been used in fire research and management at three levels as summarized in Roy *et al.* (2013): i) before the fire occurs to measure the danger of fuel hazard and mapping past burns; ii) real time detection during active fire events to record time, location and intensity; and iii) fire affected area mapping to assess the extent of the burned areas and associated emissions. However, the current remote sensing satellites lack the temporal and spatial characteristics necessary for comprehensive and reliable mapping of fires in savannas, since fires and post fire surface effects can change rapidly (Roy *et al.*, 2013). Roy *et al.* (2013) further state that the available geostationary satellites provide high temporal resolutions images at 15-30 minutes, but limited by spatial resolutions, increasing omission errors for small fires characteristic of tropical savannas. Furthermore, the use of aggregate biomass to assess fire has been confounding, since most fires are either surface fires fueled by herbaceous biomass or crown fires driven by the woody canopy. Thus, there is need to include separate estimates of woody and herbaceous biomass in fire studies.

5.0 Research objectives, hypotheses and expected results

Although savanna systems are recognized as important cultural, environmental and economic resources, their assessment and monitoring has received minimal attention. Hence lack of proper information on the status and trends in forage resources has led to poor planning and management. The situation will be more challenging in the face of climate change, which will increase vulnerability of humans and some ecosystems to impacts associated with climate change and climate related extremes across Africa (Boko *et al.*, 2007; Field *et al.*, 2014). Additionally, the available amount of vegetation in African savannas play a critical role in determining the amount of biomass available for herbivory and combustion. However, there is limited understanding of the role played by each of the savanna components (herbaceous and woody cover) in regulating herbivory and fire in SSA.

The above considerations motivate a more detailed study of the composition, temporal and spatial variability of woody and herbaceous resources in SSA. The overall goal of the research was to use coarse and high spatio-temporal geospatial data to aid in understanding the temporal and spatial variability of herbaceous and woody biomass in savanna (‘tree-grass’) systems to facilitate research and planning for improved utilization and management of these resources. The research comprises three components: (i) partitioning of MODIS total leaf area index (LAI_A) time series into woody (LAI_W) and herbaceous (LAI_H) constituents; (ii) assessing the relationships between herbaceous production and fire regimes in Africa using LAI_W and LAI_H derived in (i); and iii) assessing the relationship between forage quantity and herbivory in sub-Saharan Africa. This involves use of the partitioned time series developed in (i) as an index of forage quantity to determine how forage browse (LAI_W) and grazing (LAI_H) resources determine distribution of livestock in SSA.

The research combines various remote sensing datasets and ancillary data in continental scale analyses. Collated literature data coupled with field data from SSA was used to parameterize and validate key allometric relationships and predictions. Additionally, satellite data were used to generate continent-wide estimates of herbaceous and woody leaf area index which were applied to examine how livestock herbivory and fire vary with temporal and spatial variability in the partitioned LAI estimates. Expected outputs from this research included: gridded time-series of woody and herbaceous LAI estimates covering 2003-2015 epoch for SSA; better understanding of the effects of changes in herbaceous and woody cover components on fire; and improved understanding of the role of forage quantity in distribution of livestock in SSA. The results are compiled in this PhD dissertation document and journal publications. The potential embodied in the overarching goal of this research, that I can develop remote sensing-based approaches to inform and manage savanna resources in Africa, is the common thread motivating the different components of the research outlined below, separated into three substantive analyses.

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CHAPTER 2

Estimation of woody and herbaceous leaf area index in sub-Saharan Africa using MODIS data

Kahiu, M. N., & Hanan, N. P. (2017). Estimation of woody and herbaceous leaf area index in Sub-Saharan Africa using MODIS data. *Journal of Geophysical Research: Biogeosciences*, n/a-n/a. doi: 10.1002/2017JG004105

Abstract

Savannas are widespread global biomes covering ~20% of terrestrial ecosystems on all continents except Antarctica. These ecosystems play a critical role in regulating terrestrial carbon cycle, ecosystem productivity, and the hydrological cycle and contribute to human livelihoods and biodiversity conservation. Despite the importance of savannas in ecosystem processes and human well-being, the presence of mixed woody and herbaceous components at scales much finer than most medium and coarse resolution satellite imagery poses significant challenges to their effective representation in remote sensing and modeling of vegetation dynamics. Although previous studies have attempted to separate woody and herbaceous components, the focus on greenness indices and fractional cover provides little insight into spatio-temporal variability in woody and herbaceous vegetation structure, in particular, leaf area index (LAI). This paper presents a method to partition 1km spatial resolution Moderate Resolution Imaging Spectroradiometer (MODIS) aggregate green leaf area index (LAI_A) from 2003-2015, into separate woody (LAI_W) and herbaceous (LAI_H) constituents in both drought seasonal savannas and moist tropical forests of Sub-Saharan Africa (SSA). In our analysis, we use an allometric relationship describing the variation in peak within-canopy woody LAI of dominant tree species ($\mathrm{LAI}_{\mathrm{W}p\mathrm{inc}}$) across gradients in mean annual precipitation (MAP), coupled with independent estimates of woody canopy cover (τ_{W}), to constrain seasonally changing $\mathrm{LAI}_{\mathrm{W}}$. We present the LAI partitioning approach and highlight the broad spatial and temporal patterns of woody and herbaceous LAI across SSA. The long-term average 8-day phenologies of woody and herbaceous LAI (averaged across 2003-2015) are available for evaluation, research and application purposes.

Keywords:

Africa, Herbaceous, Leaf Area Index (LAI), Phenology, Savanna, Woody

1.0 Introduction

Biomes with vegetation communities consisting of both herbaceous and woody species are widespread on all continents except Antarctica (Solbrig, 1996), including tropical, subtropical and temperate savannas and many regions classified as seasonal woodlands and dry-deciduous woodlands where herbaceous species are also present (Ratnam *et al.*, 2011). These expansive tree-grass or shrub-grass systems, which we will refer to collectively as “savannas”, cover at least 20% of terrestrial ecosystems (Hill & Hanan, 2010). In terrestrial ecosystems, vegetation structure, particularly the relative importance of woody versus herbaceous plants, plays a critical role in regulating the terrestrial carbon cycle, ecosystem productivity, and the hydrological cycle (Franklin *et al.*, 2016). Vegetation structure is also important for human livelihoods and biodiversity conservation as it influences provision of plant products, including fuelwood, wild foods and forage for livestock and wildlife. Ecosystem services provided by the herbaceous and woody layer are distinct in magnitude and seasonality, for example in the provision of fodder for grazers and browsers, respectively, and implications for wild-fire occurrence, fuel wood supply and carbon sequestration (Gessner *et al.*, 2013). Hence, it is important to understand the distinct phenology of the herbaceous and woody layers in terrestrial ecosystems to better understand and model their impacts on productivity, hydrology and biogeochemical cycles, and the spatial and temporal dynamics of fire and herbivory.

During recent decades, the remote sensing community and earth system modelers have made substantial progress in developing products to characterize global vegetation dynamics (Houborg *et al.*, 2015; Thenkabail & Lyon, 2016; Xie *et al.*, 2008; Xue & Su, 2017). However, savanna ecosystems remain a challenge due to the presence of mixed woody and herbaceous components at scales much finer than most medium and coarse resolution remote sensing data. Hence the key characteristics of savannas, including some areas in the moist tropical forests where herbaceous growth is made possible by reduced canopy cover (e.g. due to tree mortality or harvest), are not well represented in earth observation and modeling capabilities (Hill & Hanan, 2010).

Attempts have been made to partition remote sensing products into separate woody and herbaceous components. Liu *et al.* (2017) partitioned understory and overstory LAI in temperate and boreal forests, using MODIS and Multi-angle Imaging SpectroRadiometer (MISR) datasets. However, their method is dependent on the ability to capture realistic forest background reflectivities, and neither tropical savannas nor moist tropical forests were included in their analysis. Similarly, regional studies in temperate and boreal forests of China and Siberia (Huang *et al.*, 2011; Kobayashi *et al.*, 2010) used high spatial resolution and multi-angular data to estimate overstory and understory LAI, but these analyses did not extend to the seasonal savannas or moist tropical forests of Africa.

Several authors have tested methods to separate woody, herbaceous and bare soil fractional cover using time series decomposition and spectral unmixing. For example, Lu *et al.* (2003) developed a time-series decomposition approach (originally proposed by Roderick *et al*., 1999) to separate cover of slowly-varying evergreen tree canopies from ephemeral herbaceous dynamics in coarse-resolution (8 km) AVHRR NDVI data for Australia. However, the method requires that the woody canopy be evergreen, which is not true in many drought-seasonal woody-herbaceous systems. Gessner *et al.* (2013) presented an approach for fractional cover decomposition in Southern Africa using 16-day 250 m resolution MODIS vegetation indices and, in a recent study, Zhou *et al.* (2016) attempted to retrieve herbaceous fractional cover in Australian tropical savannas by linear unmixing of vegetation indices. Other local to regional studies in Africa attempt to tease out woody cover from herbaceous components using the different phenological traits of savanna vegetation (de Bie *et al.*, 1998; Do *et al.*, 2005; Horion *et al.*, 2014), including work in the Sahel (Brandt *et al.*, 2016) and Namibia (Wagenseil & Samimi, 2007). Applying a rather different approach at a larger coverage, Tian *et al.* (2017) used NDVI and vegetation optical depth (VOD) retrievals from passive microwave satellite observations to separate leaves from the woody cover in global tropical drylands covering 35^oN and 35^oS. However, while these studies advanced our understanding of the separate role of woody and herbaceous plants in mixed systems, the focus on fractional cover (Gessner *et al.*, 2013; Lu *et al.*, 2003), and photosynthetic and non-photosynthetic vegetation (Zhou *et al.*, 2016), provides data that is generally only indirectly related to ecosystem function. Leaf area index separated into overstory (woody), and understory (herbaceous) components is, by contrast, directly relevant to models of vegetation dynamics (photosynthesis and growth), tree-grass interactions (competition) and land surface-atmosphere interactions (carbon, water and energy exchange mediated by distinct woody and herbaceous vegetation layers).

Archibald and Scholes (2007) proposed an approach to partition satellite greenness (NDVI) data between woody and herbaceous components for a drought-deciduous African savanna in South Africa. Their approach was based on three characteristic physiological and phenological differences between woody perennials and herbaceous vegetation: (i) many deciduous trees in drought-seasonal systems use water (and nutrients) stored in stems and other storage organs to grow leaves before herbaceous plants; (ii) most of the inter-annual variation in leaf production in mixed woody-herbaceous systems occurs in the herbaceous layer, because the leaf area that trees support is determined primarily by canopy architecture (canopy extent and density of bud initials), whereas tillering in grasses is closely related to inter-annual variability in rainfall; and (iii) that tree green-up rates are relatively constant among years.

In this paper we build on the logic of Archibald and Scholes (2007), who partitioned satellite NDVI measurements, to describe a method for partitioning satellite green LAI estimates into woody and herbaceous components for Sub-Saharan Africa. We present the processing of 8-day interval 1 km spatial resolution MODIS green LAI ("aggregate LAI", denoted LAI_A, because it includes both woody and herbaceous components) time series data (2003-2015) into its woody (LAI_W) and herbaceous (LAI_H) constituents. Per Archibald and Scholes, our method assumes that leaf growth in most African drought-deciduous woody species occurs before herbaceous plant growth in the early rainy season, and that trees generally retain their leaves after senescence of herbaceous plants at the end the growing season. We also assume that seasonal maximum LAI in tree communities is constrained by canopy architecture (canopy cover and bud-density) with relatively little inter-annual variability due to changes in precipitation. To apply the technique at continental scales we introduce two key innovations that constrain the partitioning problem: (1) the use of independent data on woody canopy cover across Africa, and (2) an allometric model describing the relationship between mean annual rainfall (MAP) and peak-season LAI within canopies of dominant trees across Africa.

The objectives of this research were to (i) present the partitioning approach, from algorithm development to generation of the partitioned LAI products for Sub-Saharan

Africa (SSA); (ii) showcase the results of the partitioned woody and herbaceous LAI; and iii) make available the partitioned LAI product for evaluation and applications relating to natural resource management and ecosystem processes across Sub-Saharan Africa.

2.0 Conceptual Approach: Theoretical basis of the LAI partitioning algorithm

Leaf area index (LAI) is a dimensionless variable for characterizing vegetation canopies, defined as the one-sided area of green leaves (m^2) per unit ground area (m^2) in broadleaf canopies and half total needle surface area per unit ground area in conifers. In the context of this paper we distinguish five key LAI terms, as follows: i) Aggregate LAI (LAI_A, m^2 green leaf area per m^2 land area), which is a landscape scale variable comprising the sum of herbaceous and woody leaf area per unit land area; ii) herbaceous LAI (LAI_H, m^2 leaf area per m^2 land area), which is the landscape-scale green leaf area index of grasses and forbs; iii) Woody LAI (LAI_W, m^2 leaf area per m^2 land area), which is the landscape-scale green leaf area index of woody vegetation including trees, shrubs and bushes; iv) In-canopy LAI (LAI_{Winc}, m^2 leaf area per m^2 canopy area), which is a canopy-scale variable describing the amount of green leaf area held within the crown of a woody plant; and v) peak season maximum in-canopy LAI (LAI_{Wpinc}); which is the value of LAI_{Winc} at peak season (i.e. following leaf expansion).

In tree-grass systems, landscape-scale aggregate LAI (LAI_A) is the linear sum of woody (LAI_W) and herbaceous (LAI_H) components (Figure 1), thus we define the identity:

$$LAI_A = LAI_W + LAI_H \qquad \text{Equation 1}$$

Savannas are generally characterized by a more-or-less continuous herbaceous layer and a discontinuous stratum of trees or shrubs (Ratnam *et al.*, 2011). Therefore, for the purposes of this analysis, we assume that the herbaceous vegetation is fully distributed (i.e. herbaceous cover τ_h=1) and this is considered true even if herbaceous biomass is very low or absent. By contrast, woody canopy cover depends on the size and density of individual trees and is often discontinuous ($\tau_w \leq 1$). Additionally, we assume that τ_w varies slowly (at decadal scales assuming no major disturbance), relative to rapidly (i.e. seasonally) varying woody and herbaceous LAI. In mid-growing season (i.e. following full leaf expansion in deciduous trees) LAI_W is therefore composed of τ_w and peak-season within canopy LAI (LAI_{Wpinc}), thus:

$$LAI_W = \tau_w \, LAI_{\mathrm{w}p\mathrm{inc}} \qquad \text{Equation 2}$$

where LAI_{Wpinc} is estimated using an allometric relationship between field measured peak season in-canopy LAI and rainfall (LAI_{Wpinc} = f(MAP); Figure 1a); and using *in situ* in-canopy LAI measurements (Figure 4b). For mid-growing season estimates Equation 1 can then be expanded as:

$$LAI_A = \tau_w LAI_{\mathrm{W}p\mathrm{inc}} + LAI_H \qquad \text{Equation 3}$$

and herbaceous LAI_H determined by difference, Equation 4:

$$LAI_H = LAI_A \quad \tau_w LAI_{\mathrm{W}p\mathrm{inc}} \qquad \text{Equation 4}$$

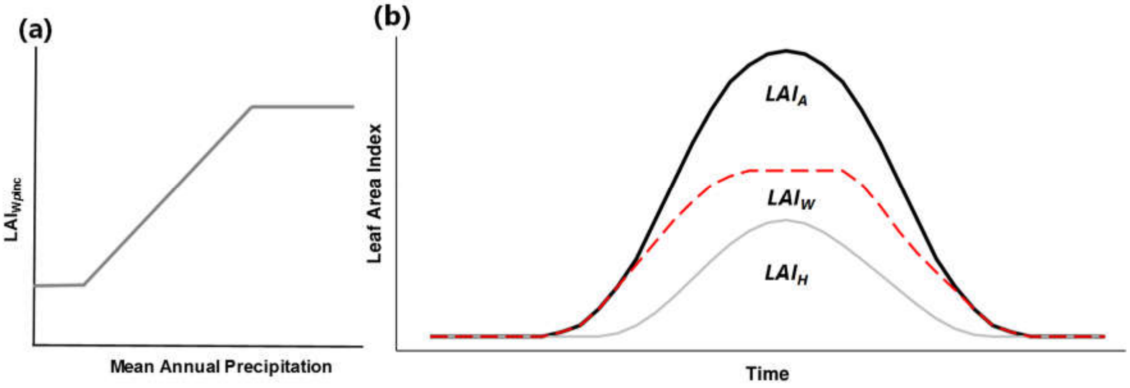


Figure 1: Conceptual basis for the LAI partitioning, with (a) hypothetical increase of peak-season in-canopy LAI (LAI$_{Wpinc}$) as a function of mean annual precipitation (mm/annum), and (b) example for a drought-deciduous woody cover where herbaceous LAI$_H$ (light grey) is computed as the difference between aggregate LAI$_A$ (solid black line) and landscape scale woody LAI (LAI$_W$; dashed red line). In evergreen systems, LAI$_W$ can be maintained year-round. The data-based version of Figure 1a is presented in Figure 4b.

For mid-season LAI partitioning, our approach depends on availability of estimates of aggregate LAI$_A$ (e.g. from MODIS, §3.2), tree cover (τ_w, §2.1.3) and peak season in-canopy LAI (LAI$_{Wpinc}$;§3.2.3). In shoulder seasons, we follow Archibald and Scholes (2007) in assuming that trees produce leaves earlier, and retain them later than the herbaceous layer. Thus, in general if $LAI_A < \tau_W LAI_{Wpinc}$ then $LAI_W = LAI_A$ and $LAI_H = 0$. We also follow Archibald and Scholes (2007) in applying a maximum rate for tree-leaf emergence, estimated to be eight weeks for trees in their study site and our field sites in Kenya.

3.0 Materials and Methods

3.1 Methods Overview

Figure 2 provides an overview of the steps used to partition the 8-day 1 km MODIS LAI estimates into woody and herbaceous LAI. In brief, MODIS aggregate LAI is pre-processed to ensure realistic seasonal profiles as inputs to the partitioning algorithm. This is an important step since the partitioning algorithm depends on the previous time-step to allocate woody LAI. Field-measured (*in situ*) LAI measurements include: i) peak season in-canopy LAI (LAI_{Wpinc}) used for the allometric relationship; and ii) a validation set containing landscape scale herbaceous and woody LAI (LAI_H and LAI_W, respectively) for validation of the partitioned products estimated using Equations 2-4. The partitioning procedures are described in more detail below.

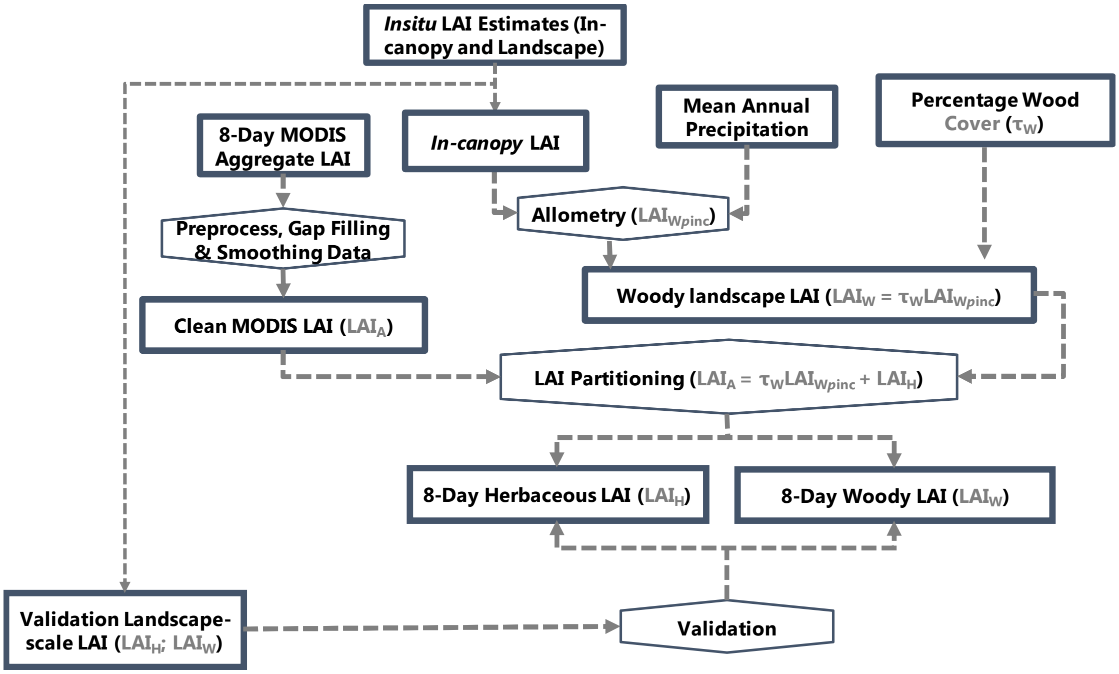


Figure 2: Overview of methods to derive woody and herbaceous LAI estimates from MODIS green aggregate LAI

3.2 Data

3.2.1 MODIS leaf area index (LAI)

Moderate-Resolution Imaging Spectroradiometer (MODIS) has been generating green LAI data for over a decade through Terra and Aqua satellites, timed to cover the globe every 1 to 2 days. MODIS Collection 5 LAI products have an overall good performance with an RMSE of 0.8, and are able to capture realistic seasonality in most biomes, although in evergreen broad leaf forests cloud contamination reduces frequency and quality of retrievals (Yan, Kai,Park, Taejin,Yan, Guangjian,Liu, Zhao*, et al.*, 2016). We used combined MODIS LAI collection 5 (C5) time series from Terra and Aqua satellites (MCD15A2) for years 2003-2015, at 8-day interval and 1 km resolution for SSA. We chose MODIS LAI collection 5 (C5) over the latest collection 6 (C6) due to its resolution that matches our woody cover dataset (§2.1.3), which is a critical input in our partitioning approach. Aside from the increase in spatial resolution from 1 km to 500 m, comparisons indicate relatively small differences in LAI between C5 and C6 (Yan, Kai,Park, Taejin,Yan, Guangjian,Chen, Chi*, et al.*, 2016).

3.2.2 Woody canopy cover and precipitation data for Sub-Saharan Africa

We used the woody canopy cover product developed by Bucini *et al.* (2010) using empirical relationships between MODIS optical data and Ku-band microwave measurements and woody cover estimates at >1000 calibration sites distributed across Africa; Figure 3a. The field and satellite data are centered on year 2005, thus appropriate for the 2003-2015 MODIS LAI era, assuming that woody canopy cover changes slowly, except in locations where a major disturbance event occurs (e.g. savanna tree harvest for charcoal or agricultural clearance). The data was available at 1 km spatial resolution.

When compiling the *in situ* LAI measurements we also recorded reported long-term mean annual precipitation (MAP) for the study sites. In instances where MAP was not reported, it was computed from the gridded global monthly precipitation data from Climate Research Unit, University of East Anglia (CRU-TS v3.24), available at 0.5^0 spatial resolution, covering the period of 1985-2015 (Figure 3b). We chose CRU precipitation to represent long-term bioclimatic conditions across Africa because of its long-term archive (1901-2015), well-defined uncertainties (Harris *et al.*, 2014) and for consistency with earlier analyses e.g. Sankaran *et al.* (2005). To ensure that CRU does not vary significantly from other higher resolution and recently available precipitation datasets, we compared CRU estimates with i) Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) data at 0.05° spatial resolution (Funk *et al.*, 2015); and ii) Tropical Rainfall Measuring Mission (TRMM) Version 7 at 0.25° spatial resolution (Huffman *et al.*, 2007). MAP computed from the two higher resolution datasets has an agreement of >=95% with CRU (see Support Information, Figures S1.1 and S1.2).

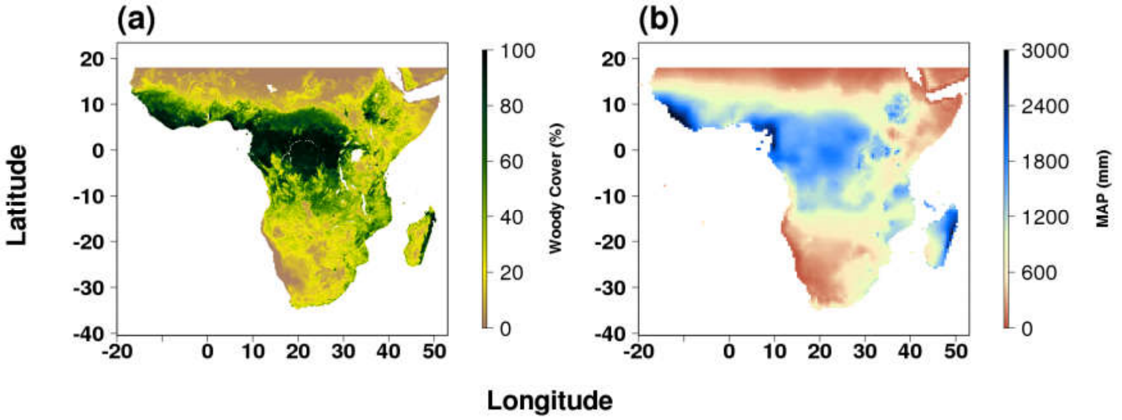


Figure 3: (a) Woody cover estimates for Sub-Saharan Africa, and (b) 30-year (1985-2015) Mean Annual Precipitation (MAP) derived from Climate Research Unit, University of East Anglia (CRU-TS v3.24) data

3.2.3 LAI data for allometry and validation

In African savannas, vegetation production is limited by water availability, where studies show MAP has a close relationship with the seasonal maximum cover and LAI in evergreen and deciduous trees (Archibald & Scholes, 2007; Sankaran *et al.*, 2005). We build on these relationships to develop an allometric relationship between mean annual precipitation (MAP) and peak seasonal within tree canopy ("*in-canopy*") LAI ($\mathrm{LAI}_{\mathrm{W}p\mathrm{inc}}$). To develop the allometric relationship and validate the partitioned LAI estimates we use a combination of our field measurements and literature-derived measurements of woody and herbaceous LAI in a variety of African ecosystems.

We collected LAI data in Kenya during the 2015 October-December "short rains". During the field program, study sites were distributed across a 450-1300 mm yr^{-1} rainfall gradient in central and southern Kenya, including: Tsavo East-West and Amboseli National Parks, Ilngwesi Community Group Ranch and the privately owned Olpejeta Conservancy, both in Laikipia District. Sampling across this rainfall gradient is important for the LAI partitioning allometry, and sampling from dry season to peak LAI allowed us to better characterize the phenological timing of in-canopy LAI up to the peak season LAI ($\mathrm{LAI}_{\mathrm{W}p\mathrm{inc}}$).

Fieldwork for collection of validation data for partitioned LAI involved identification of sites with homogeneous vegetation conditions at the 1 km grid-scale of MODIS LAI data. In each 1 km grid, three parallel north-south transects were laid to guide landscape scale LAI measurements. Each transect was 400 m long, set ~250 m apart and well within the nominal boundaries of the MODIS pixel. Overall, seven 1 km grids were established across the rainfall gradient.

Woody and herbaceous LAI were estimated using the LI-COR LAI-2200 Plant Canopy Analyzer (PCA). On each transect PCA measurements were recorded at three levels: (1) reference measurements made at irregular intervals (20-40 meters) in open areas to record incoming radiation with no influence of vegetation, (2) measurements at 1 meter intervals below woody canopies, but above herbaceous vegetation, to quantify light interception by the woody canopy (and act as reference measurements for the herbaceous measurements) and (3) measurements at 1 meter intervals at ground level (immediately underneath 2) to quantify light interception by herbaceous vegetation. Consistent with manufacturer recommendations (LI-COR Inc, 2012) the time of measurements was generally restricted to twilight hours (dawn and dusk) or during fully overcast skies, with the operator standing with their back to the sun to avoid direct sunlight on the instrument. This ensures uniform sky-illumination conditions and avoids problems of scattering under direct sunlight. However, for logistical reasons measurements were sometimes taken in less ideal conditions (i.e. higher solar angle or under patchy cloud). In these situations, we increased the frequency of reference measurements (1) to reduce impact of variability in incoming radiation on the below-canopy measurements. At each site, dry season measurements of stem area index (made prior to emergence of leaves) were used to correct woody LAI estimates for the stem contribution (Jonckheere *et al.*, 2004).

To develop the in-canopy LAI allometric model we used data from field sites in Kenya supplemented by data from the literature at field sites distributed across Africa. Our approach was to couple landscape scale measurements of seasonal maximum woody leaf area index (LAI_W) with coincident measurements of fractional canopy cover (τ_W) and thus estimate seasonal maximum in-canopy LAI (LAI_{Wpinc}) as:

$$LAI_{Wpinc} = LAI_W/\tau_W \qquad \text{Equation 5}$$

For this purpose, at our field sites in Kenya we took independent PCA readings from plots of ~50m x 50m where we also recorded tree density (> 1-meter height) and measured crown sizes using a tape measure for two crown diameters (the longest and the perpendicular) to estimate canopy areas and total canopy cover (τ_W) within the plot. For in-canopy LAI estimation, incoming radiation measurements were taken in open areas at 5-meter intervals, while below woody canopy measurements, were recorded at 1-meter intervals above the herbaceous vegetation, taken along ten transects laid 5 m apart within each plot. These measurements were used to compute in-canopy LAI (Equation 5).

Our field measurements of landscape-scale and in-canopy LAI were supplemented by literature-based *in situ* LAI estimates from sites across Africa (Figure 4a). Overall, our initial database consisted of ~800 *in situ* LAI estimates, out of these ~370 were for landscape scale LAI (herbaceous LAI_H and woody LAI_W) and 430 for in-canopy LAI (LAI_{Winc}). The in-canopy data included time series measurements where we selected the seasonal maximum, multiple estimates from adjacent locations, which we averaged, and several outliers which we removed, leaving ~150 data points (Figure 4b). The landscape scale LAI data were reserved for validation of the partitioned LAI products (see Supplementary data S3 for field-based LAI datasets).

3.3 Preprocessing of the data

Preprocessing of the aggregate green MODIS LAI was implemented to fill gaps and reduce noise in the time series relating to variable atmospheric effects (aerosols and cloud contamination), sensor defects, variable solar geometry and satellite view angle, changing illumination and differing performance of the main and backup MODIS LAI algorithms (Chen *et al.*, 2004; Kandasamy *et al.*, 2013; Yuan *et al.*, 2011). We used the MODIS LAI quality flags to select non-cloudy pixels from main and backup algorithm. Although the main algorithm is considered the best quality data (Myneni *et al.*, 2003; Yang *et al.*, 2006), here we use both main and back up algorithms since ecosystems in the Congo basin and coastal areas of the Gulf of Guinea had severe reductions in data using the main algorithm alone, as is expected in most tropical Africa ecosystems characterized by persistent clouds (Tchuente *et al.*, 2010).

The quality filtered MODIS LAI data were further corrected using the Best Index Slope Extraction (BISE) method (Viovy *et al.*, 1992), which eliminates contaminated values in the time series for each pixel using an upper enveloping approach, then smoothing and gap filling with spline interpolation. We adopted this approach to reduce the influence of bias introduced into the LAI estimates where atmospheric effects, residual cloud and other sources of error consistently reduce LAI retrievals (Gao *et al.*, 2008). However, the BISE method overlooks overestimation (positive noise) that may be caused by defects such as angular effects (Eklundh & Jönsson, 2015). Additionally, the success of the BISE method is dependent on a sliding window (Viovy *et al.*, 1992) defined by the user, hence can be subjective or limiting where researcher has limited knowledge of an area (Lu *et al.*, 2007). BISE extraction and smoothing of the LAI_A data was implemented in R's *biseVec* Package (Lange, 2012). It is noteworthy that we also tested some of the other commonly used smoothing methods such as Savitzky-Golay (Savitzky & Golay, 1964), but chose the BISE interpolations because of its ability to avoid negative anomalies, while maintaining the integrity of the original MODIS LAI data profile. Gap filling and smoothing was also necessary prior to partitioning since the woody LAI estimate is dependent on phenological increment from the previous date.

Preprocessing of precipitation data involved sub-setting of the global dataset to SSA region, and calculation of annual rainfall totals for the thirty-year period, 1985-2015. We resampled the rainfall data using a spline interpolation to disaggregate the 0.5^0-pixel size to 1 km MODIS LAI resolution and MODIS sinusoidal projection. We did not consider topography in this down-scaling approach due to the relatively low topographic variation across much Africa and because long-term mean annual rainfall varies relatively smoothly in space (relative to much greater spatial variability in individual storm events). Note that, in developing our allometric relationship we used local MAP estimates from the source literature when available and only used CRU precipitation where literature MAP was not reported. The woody cover layer covering the whole of Africa at 1km resolution was also subset to match the MODIS LAI tiles.

3.4 The partitioning allometry

To create the allometry, we developed a piecewise regression model with a knot (change point) at 1650 mm MAP, Equation 6. The general model takes the form:

$$Y = \beta_0 + \beta_1 X + \beta_2 \, (X \quad C)^+ + \varepsilon \qquad \text{Equation 6}$$

Where, β_0 is the intercept, β_1 the slope before the change point C and β_2 the difference in slope after the knot; $\beta_1 + \beta_2$ gives the slope after the knot; $(X - C)^+$ is an interaction term which takes 0 when $C>X$ and $X-C$ when $C<X$; and ε is an error term. We used the *in situ* estimates of the peak season woody in-canopy LAI (LAI$_{\text{Wpinc}}$) and local MAP estimates reported in literature (or CRU MAP where not reported) to fit the model

using ordinary least squares in R, resulting in Equation 7 for the partitioning allometry shown in Figure 4b.

$$LAI_{\mathrm{W}pinc} = 2.5219 + 0.0021 \quad MAP \quad 0.0020 \quad (MAP \quad 1650)^{+}$$

Equation 7

To constrain the model represented by equations 4 and 7, we introduced a low rainfall threshold of 101 mm MAP below which woody cover is assumed to be zero (Sankaran *et al.*, 2005) and thus $LAI_W = 0$ and $LAI_H = LAI_A$ when $\tau_W = 0$. We also assumed that herbaceous vegetation tends to zero under very dense canopies ($LAI_H = 0$ and $LAI_W = LAI_A$ when $\tau_W > 80\%$), since herbage growth on the forest floor is limited by light (Moore, 2008), which is often <5% of light penetrating dense canopies in tropical forests (Bazzaz & Pickett, 1980).

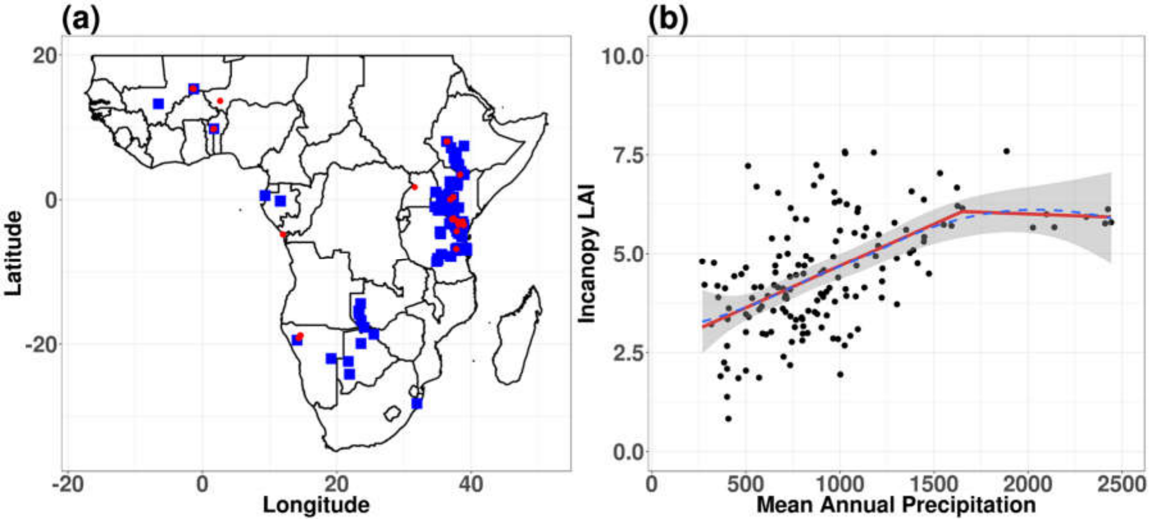


Figure 4: (a) Point locations for *in situ* leaf area index estimates in Sub-Saharan Africa, based on literature and field measurements in Kenya. Displayed in blue and red are in-canopy LAI (LAI_{Wpinc}) and landscape LAI locations respectively; (b) the relationship defining the allometry between mean annual precipitation (MAP) and peak season maximum in-canopy woody LAI (LAI_{Wpinc}), where the red line is fitted using piecewise regression (R-squared=0.3 and RMSE=1.2) while the blue dotted line uses loess fitting.

3.5 Biome map for visualization and assessment of LAI partitioning

To visualize and assess the performance of the partitioned data-set we randomly sampled points in the major biomes of SSA (Figure 5). We use the biome-level samples to visualize mean woody and herbaceous LAI phenologies (at 8-day intervals averaged over the thirteen years of the analysis, 2003-2015) to show the characteristic phenology (climatology) and variability across each biome type. The biome map was generated using White's vegetation map for Africa (White, 1983), aggregated based on rainfall and geography to provide functionally similar regions at scales suitable for visualization in this paper.

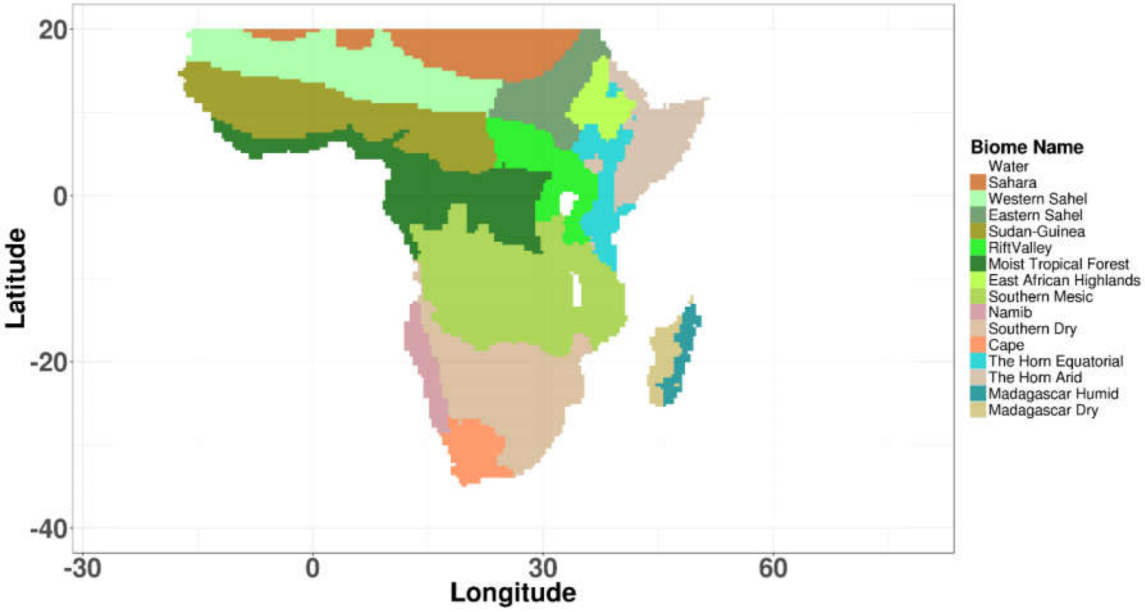


Figure 5: Biome map for Sub-Saharan Africa, based on Whites vegetation map of Africa (White, 1983), aggregated by region and rainfall, used in this analysis to sample partitioned LAI for visualization.

There is need for a comprehensive validation of LAI and its derived products (Garrigues *et al.*, 2008; Jonckheere *et al.*, 2004; Weiss *et al.*, 2004). We attempted to validate the partitioned products with *in situ* LAI measurements, although the total number of data points available for validation is less than recommended (Garrigues *et al.*, 2008; Morisette *et al.*, 2006) and we anticipate additional collection of validation data in future. We used literature data and estimates from our field work in Kenya (§3.2.3). Using the geographic locations of the *in situ* LAI measurements, we extracted the partitioned LAI within the 1x1 pixel and interpolated the 8-day LAI estimates to match *in situ* LAI measurement dates.

4.0 Results

4.1. Validation of partitioned leaf area index products

A comparison of MODIS partitioned LAI with in situ LAI measurements shows an overall agreement of ~50% (Figure 6 and Table 1) but with a tendency to underestimate LAI_W in regions with higher in situ LAI_W. These sites are in savannas and cropland natural vegetation mosaic (Friedl *et al.*, 2010), which we suppose could be either due to: the mismatch in scale of measure between the in situ measurements and MODIS LAI pixel size at 1km resolution; and inadequacy of the generalized allometric equation shown in Figure 4b, suggesting the need for allometries that distinguish different tree functional groups or different bioclimatic regions. We anticipate gradual improvements in validation results in future reanalysis of these LAI re-trievals as more data defining differentiated allometric equations become available.

Table 1: Validation statistics- table showing standard major axis (SMA) regression statistics for the overall and partitioned leaf area index estimates.

LAI group	**Slope**	**Intercept**	**R^2**	**RMSE**	***N***
LAI_W	0.56	0.36	0.43	0.8	358
LAI_H	0.92	-0.11	0.29	0.37	115
$LAI_{(W+H)}$	0.6	0.23	0.49	0.72	473

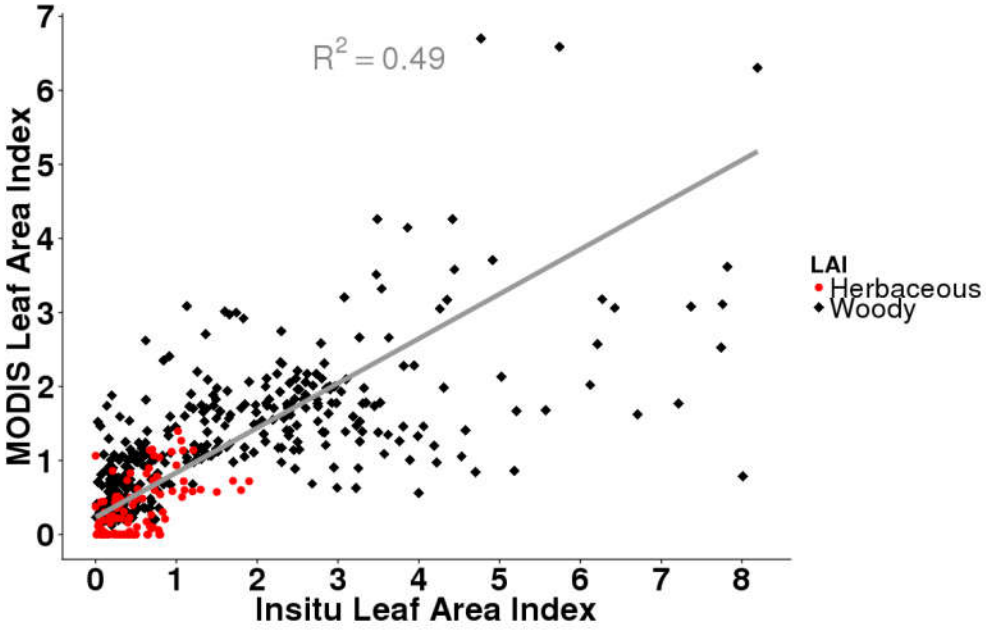


Figure 6: Comparison of MODIS partitioned leaf area index with *in situ* measurements for herbaceous (red points) and woody leaf area index (black points) fitted with a single regression line using standard major axis regression (SMA).

4.2. Maps of partitioned leaf area index

4.2.1. Averaged Annual Maximum LAI

The partitioning approach results in 8-day estimates of herbaceous and woody leaf area index at 1 km resolution for SSA for the period 2003-2015. The 8-day averaged phenologies (i.e. across all years, referred to as LAI climatology in the text) are available as a Supplement (Data S1), and the full resolution time series can be visualized as an animation (Data S2). Full temporal resolution analyses may be obtained by contacting the corresponding author. The 8-day estimates were used to generate annual average maximum LAI (Figure 7) to demonstrate the concentration of woody LAI in the mesic savannas and moist tropical forests, and herbaceous LAI maxima in the mesic savannas.

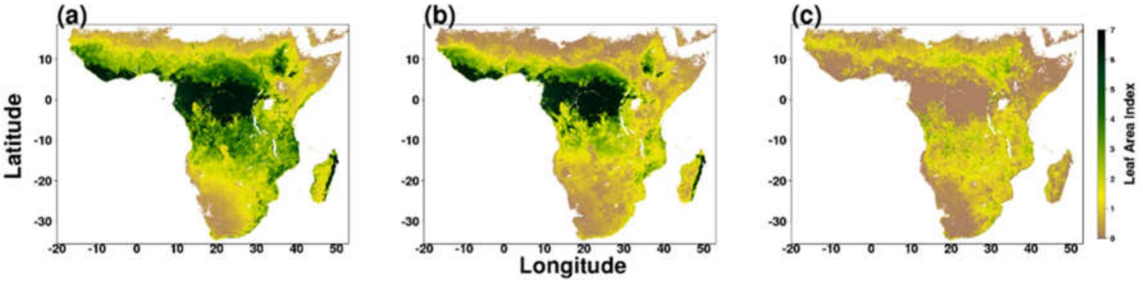


Figure 7: Maximum green leaf area index in sub-Saharan Africa showing (a) aggregate LAI_A from MODIS, (b) partitioned woody LAI_W, and (c) partitioned herbaceous LAI_H. All data were computed as the average of annual LAI maxima for years 2003 to 2015.

4.2.2. Seasonal variability in leaf area index

As a complement to the annual average LAI maxima shown in Figure 7, we computed the ratio of average minimum LAI (LAI_{Min}) to LAI_{Max} to represent the degree of LAI seasonality across the continent (Figure 8). In these data, values close to 0% occur in strongly deciduous regions, while values approaching 100% occur in evergreen and low-seasonality regions. In the aggregate LAI_A, areas with seasonally stable evergreen vegetation occur in the Congo basin, Gulf of Guinea, eastern coast of Madagascar and East African highlands (Figure 8a). The woody LAI seasonality (Figure 8b) emphasizes further the distinctions between evergreen and deciduous woody ecosystems in the moist tropical forest and savannas. Moreover, the woody seasonality also highlights regions of evergreen or weakly deciduous shrublands in drought-seasonal regions of East, Southern and West Africa. These areas are less easily discernable in the aggregate LAI. Herbaceous LAI across most of SSA is highly seasonal (Figure 8c), whether or not the dominant species are annuals (as is the case in most West African savannas) or perennial (as in most East and Southern African savannas). Minor exceptions to the overall high seasonality in LAI_H occur in a few areas on the desert margins (i.e. blue areas in Somalia, Sudan, Chad and Namibia). These may reflect areas of low seasonality herbaceous vegetation as found in parts of the Sahara desert (Yan, Dong *et al.*, 2016), or areas of small semi-deciduous shrubs not detected in the woody cover data set (Figure 3a) and thus wrongly classified as herbaceous vegetation. Note that regions with low woody LAI ($LAI_{Wmax} < 0.5$) or low herbaceous LAI ($LAI_{Hmax} < 0.5$) are excluded from the seasonality estimates in Figure 8. Thus, for example, these figures do not provide data on LAI_W seasonality in areas with few trees in the drier regions, or LAI_H under the dense tree canopies in the tropical forest regions.

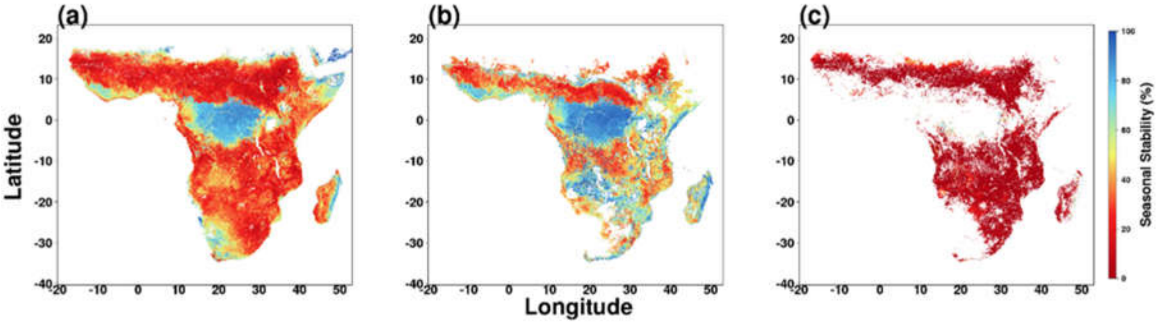
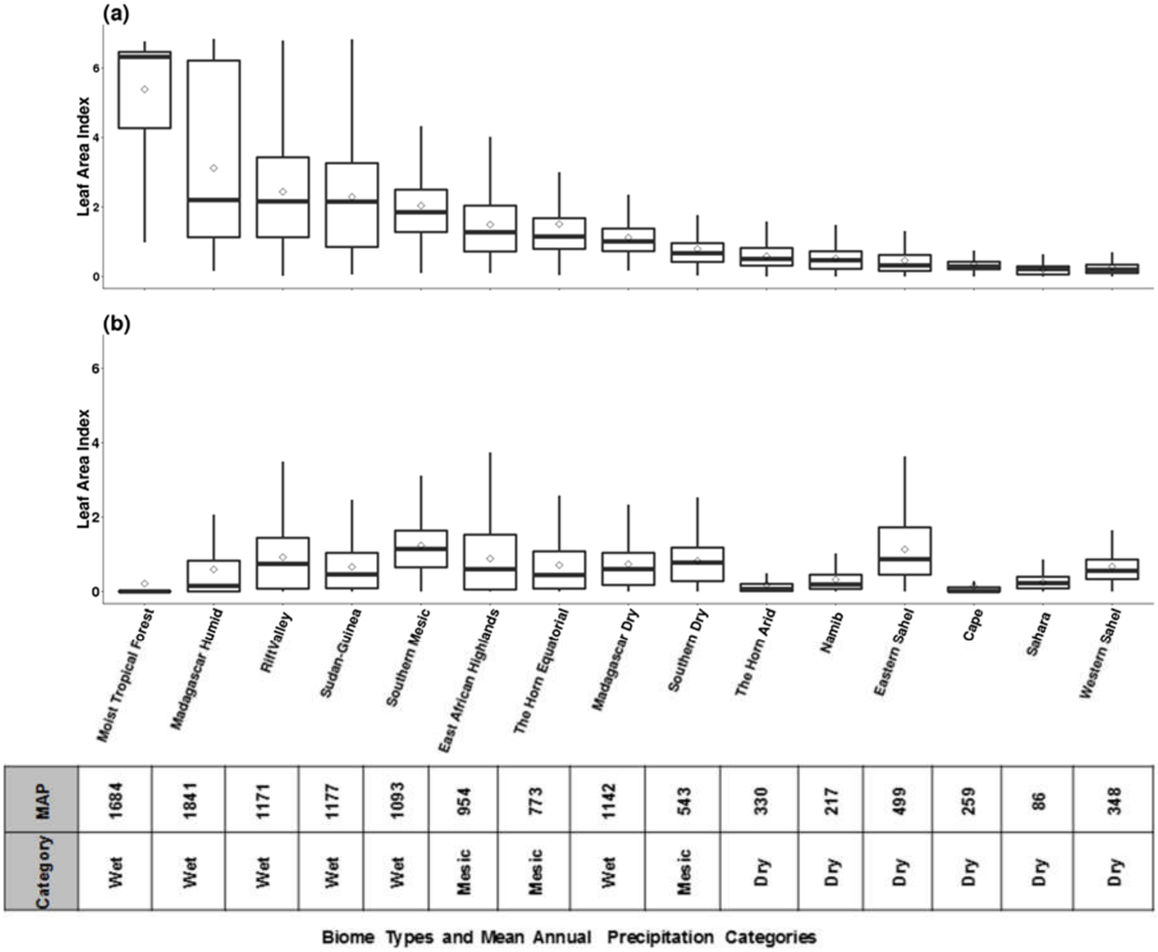


Figure 8: Maps of average LAI_{Min}/LAI_{Max} in sub-Saharan Africa showing (a) aggregate LAI_A from MODIS, (b) partitioned woody LAI_W, and (c) partitioned herbaceous LAI_H. All data were computed as a percentage of the average of 8-day LAI (LAI_{Min}/LAI_{Max}) for years 2003 to 2015. White areas show regions with low LAI maxima (< 0.5) where the seasonality index was not calculated to avoid numerical instability. Blue tones in these maps are evergreen or seasonally stable ecosystems, while shades of red show areas with high seasonality.

4.2.3. Partitioned leaf area index by biome types

We assessed the partitioning performance among wet and dry ecosystems, using the major biomes of SSA as a reference (Figure 5). The 8-day average (climatology for years 2003-2015) partitioned woody and herbaceous LAI, averaged for each biome is shown in Figure 9. The variability in LAI_W within biomes is driven primarily by variability in woody canopy cover (τ_W). Thus, LAI_W is highly variable in the wet biomes, because τ_W can vary between 0 and 1, depending on local land use and disturbance dynamics, while variability in LAIW is constrained in drier biomes by limitations in maximum τ_w (Axelsson & Hanan, 2017), as shown in Figure 9a. By contrast, LAIH tends to be highest in the mesic systems, where rainfall is sufficient for significant herbaceous growth, and where relatively open tree canopies allow sufficient light to pass through for herbaceous (especially C4 grass) growth (Figure 9b). A further assessment of LAI performance by biome type in SSA is available in the supporting materials (Figure S2).



MAP	1684	1841	1171	1177	1093	954	773	1142	543	330	217	499	259	86	348
Category	Wet	Wet	Wet	Wet	Wet	Mesic	Mesic	Wet	Mesic	Dry	Dry	Dry	Dry	Dry	Dry

Figure 9: Distribution by biome of partitioned 8-day average leaf area index (LAI climatology) in (a) woody LAIW, and (b) herbaceous LAIH, with diamond symbols showing the mean within each biome; the lower and upper bounds of the box showing 25th and 75th percentiles respectively; the median denoted by the inner horizontal line, and vertical whiskers showing the full range of data (excluding outliers exceeding 1.5 interquartile range). The order of biomes in both figures is ranked according to median LAIW .

We show the seasonal phenological profiles of partitioned LAI for selected ecosystems in wet, mesic and dry regions of SSA in Figure 10. Here, we not only illustrate the differences among biomes in how total LAI is partitioned between woody and herbaceous components (contrast moist tropical forests with savannas and the Namib desert), but also the distinct differences in timing of growth in the seasonal savannas (northern rainy seasons in northern summer; southern rainy seasons in southern summer), and the bimodal rainy seasons in the Horn of Africa. Peak season herbaceous LAI is higher than woody LAI in the Sahel in contrast to the higher tree LAI in the savannas of southern Africa. Further detailed partitioned LAI profiles are presented in the support information (Figure S2)

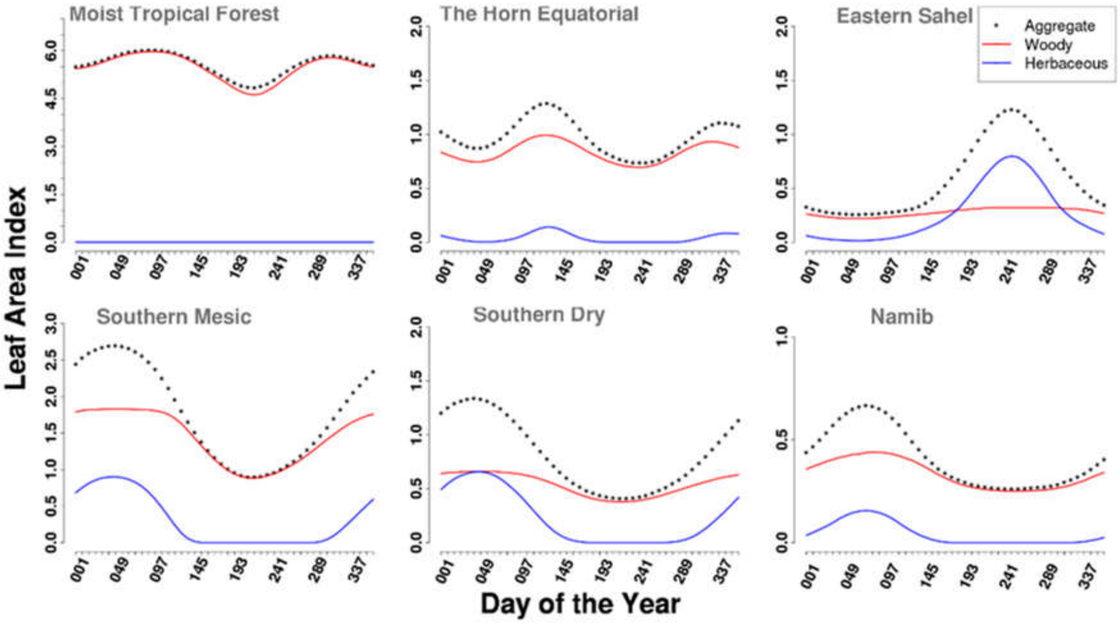


Figure 10: Averaged phenological profiles for aggregate and partitioned LAI for select biomes in sub-Saharan Africa. The profiles are based on biome median LAI values using 8-day average LAI 2003-2015. Note that the y-axes vary to emphasize different patterns of seasonality among the biomes

4.2.4. Relationship between mean annual precipitation and partitioned leaf area index

LAI maxima for various ecosystems is mainly dependent on precipitation and the relative contribution of woody and herbaceous components (Figure 11). Herbaceous LAI has a unimodal distribution with respect to mean annual rainfall (Figure 11c), peaking in the mesic savannas at approximately 900 mm/year, declining in the water-limited arid zones, and declining with light-limitation in the moist tropical forests. Woody LAI, by contrast, initially increases with precipitation, with maximum values (LAI > 6) occurring in regions with MAP > 1200 mm/year, and a striking bifurcation between high LAI forests ($LAI_w > 6$) and moderate LAI savannas ($LAI_w < 5$; Figure 11b). This is consistent with theories of bistability in the forest-savanna transition zones driven by fire and positive feedbacks (D'Odorico *et al.*, 2006; Hanan *et al.*, 2008; Hoffmann *et al.*, 2012), and earlier empirical analyses using the MODIS tree-cover dataset (Hirota *et al.*, 2011; Staver *et al.*, 2011).

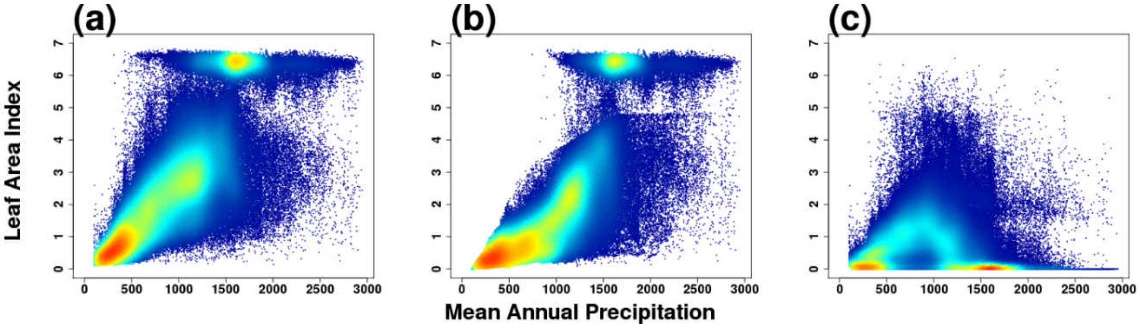


Figure 11: Relationship between mean annual precipitation and leaf area index in sub-Saharan Africa. (a) Aggregate LAI_A, (b) Woody LAI_W, and (c) Herbaceous LAI_H. LAI data in these figures show average annual LAI maxima for the years 2003-2015 for a random sample of 500,000 points across sub-Saharan Africa.

Hanan *et al.* (2014) questioned whether the bistability apparent in the MODIS tree-cover data between open grassland and savanna in drier regions, and between savanna and forest in wetter regions, might be an artifact of the statistical approach used to predict tree cover from MODIS (classification and regression trees). In this analysis, however, bifurcation between high LAI 'forests' (>6 LAI) and lower LAI 'savannas' (<5 LAI) appears in the MODIS aggregate (Figure 11a), and is reinforced in the partitioned woody LAI following removal of the herbaceous LAI component (Figure 11b). We questioned if the apparent LAI bifurcation might reflect parameter-differences between MODIS land cover classes. However, we find that both forest and savanna classes occur above and below the bifurcation, suggesting that the pattern is not algorithm-dependent (Figure 12). The potential causes of this forest-savanna LAI bifurcation (the extent to which it may be caused by the MODIS and partitioning algorithms, or reflect real differences relating to forest-savanna woody traits and ecology) will be explored in more detail in a subsequent paper.

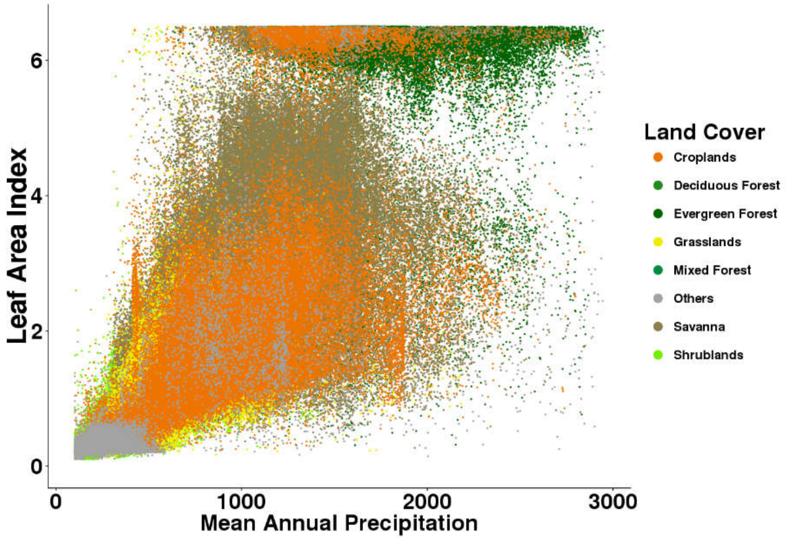


Figure 12: Relationship between mean annual precipitation and MODIS aggregate LAI color-coded by land cover classes (Friedl *et al.*, 2010)

5.0 Discussion

In this paper, we have presented an approach for separating MODIS LAI into woody and herbaceous constituents across sub-Saharan Africa (SSA) where ~65% of terrestrial biomes are savanna ecosystems with woody-herbaceous mixtures (Archibold, 1995). While several authors have developed methods for LAI partitioning in temperate and boreal regions (Huang *et al.*, 2011; Kobayashi *et al.*, 2010; Liu *et al.*, 2017), and woody cover separation from herbaceous cover at local to regional scales in Africa (Brandt *et al.*, 2016; Gessner *et al.*, 2013; Wagenseil & Samimi, 2007), our analysis is unique in providing long-term woody and herbaceous LAI phenologies for tropical Africa. Separated woody and herbaceous LAI allow users to understand the separate and distinct phenology and function of woody and herbaceous vegetation in ecosystem processes across SSA.

Our analysis relies on the quality and consistency of the MODIS aggregate LAI product. Early assessments identified relatively larger errors in seasonal LAI retrievals (de Bie *et al.*, 1998; Palmer *et al.*, 2015). However, there has been a recorded improvement of LAI retrievals through various collections and validation efforts. Intercomparison of MODIS collection 5 and 6 (C5 and C6) shows good agreement, consistency and continuity for all biomes (Yan, Kai,Park, Taejin,Yan, Guangjian,Liu, Zhao*, et al.*, 2016). For this analysis we used C5 LAI estimates because the 1km spatial resolution corresponds with our tree cover product. Validation of partitioned woody and herbaceous LAI products based on field measurements across Africa indicate root mean square errors of 0.72, 0.37 and 0.80 LAI units for overall partitioned, herbaceous and woody LAI, respectively, as shown in Table 1.

We recognize the limitation of our partitioning approach, which is dependent on input MODIS LAI, the woody LAI allometry and the woody cover products, each with associated errors and uncertainty. Overall, however, the potential benefits to our understanding of ecosystem processes made possible through availability of partitioned woody and herbaceous phenologies, make the partitioning exercise worthwhile. In some areas we observed unrealistic LAI seasonality, particularly in evergreen forest regions with persistent cloud cover (Chen *et al.*, 2004; Kandasamy *et al.*, 2013; Tchuente *et al.*, 2010; Yan, Kai,Park, Taejin,Yan, Guangjian,Liu, Zhao*, et al.*, 2016), although on a regional basis the evergreen characteristics of the moist tropical forests are clear (see Supplementary Information Figure S2). Additionally, the use of a static woody cover product (Bucini *et al.*, 2010) centered on 2005 to constrain the woody LAI, while appropriate for most slowly-changing systems, will not capture change in woody-herbaceous LAI partitioning in landscapes undergoing rapid change (e.g. deforestation for agricultural expansion, fuelwood or timber). For this initial analysis, we ignore this potential source of error, assuming that deforestation is relatively localized. In future re-analysis we anticipate progressive improvements to our methodology with collection of additional data to refine allometric relationships and woody cover datasets updated at 1-5 year intervals. Future improvements in the partitioned LAI products will also be achieved via feedback from user community; updates and improvements in the MODIS and later VIIRS aggregate LAI retrievals.

The averaged phenology product, which we make available at 1 km spatial resolution and 8-day temporal resolution for all of sub-Saharan Africa (see Supporting information Data S1), provides users with LAI “climatologies” (in the sense of long-term averages) defining the seasonal variations in the woody and herbaceous functional groups common to most terrestrial biomes. The averaged phenology data also reduces errors relating to cloud contamination and other sources of LAI retrieval variability, although inter-annual variations in LAI (particularly in herbaceous LAI relating to rainfall variability) are suppressed in the long-term averages. Partitioned woody and herbaceous LAI datasets can contribute to improved understanding of terrestrial ecosystem processes, including the land-surface atmosphere, biogeochemical and ecological interactions that define the role of vegetation communities in the biosphere and the provision of natural and anthropogenic services. In particular, these partitioned products at landscape to continental scales provide opportunities for parameterization and validation of models that represent the crucial functional separation between woody plants (trees and shrubs) and herbaceous vegetation, and the potential for terrestrial remote sensing and associated ecosystem models to move beyond aggregated (so-called big-leaf) representation of the terrestrial biosphere.

Data Accessibility Statement

Datasets associated with this paper are available in the Dryad data portal (https://datadryad.org). The datasets include: i) gridded LAI averages presented in a zipped netcdf file format, containing MODIS aggregate, woody and herbaceous LAI with averages computed for every 8-day time-step from 2003-2015 (46 time-steps x 3 LAI type, described in support information Data S1); ii) Aggregate and partitioned LAI animations for years 2003 to 2015, uploaded in a zipped Graphics Interchange Format (GIF) format. The file shows LAI time-series per 8-day interval for years 2003 to 2015 (Support information Data S2). Part of the animation can also be viewed here:

https://globalmonitoring.sdstate.edu/content/modis-lai-partitioning; and iii) the *in situ* LAI measurements used for developing the partitioning allometry and validation of the partitioned herbaceous LAI_H and woody LAI_W (Supporting information Data S3)

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SUPPLEMENTARY MATERIAL

Supporting Information for

Estimation of woody and herbaceous leaf area index in Sub-Saharan Africa using MODIS data

1.0 Introduction

The supporting information includes data used in developing the partitioning allometry models and additional results for the MODIS LAI partitioning process presented in the main manuscript.

2.0 List of supporting datasets

Data S1: Gridded 8-day averages (climatology) leaf area index (LAI) at 1 km for years 2003 to 2015, presented in netcdf format. There are three zipped netcdf file containing 8-day averages for aggregate (*MCD15A2.2003_15.Africa.V02.LAIA.Climatologies.nc.zip*), woody (*MCD15A2.2003_15.Africa.V02.LAIW.Climatologies.nc.zip*) and herbaceous (*MCD15A2.2003_15.Africa.V02.LAIH.Climatologies.nc.zip*) LAI (i.e. total of 46 time periods x 3 LAI estimates) representing an average year for each 1 km location in sub-Saharan Africa. We have also provided the metadata and example R-Script on how to process the data (*KahiuMN.HananNP_JGR_10.1002-2017JG004105.txt*) in R-Programming (https://www.r-project.org/). The data, metadata and R-script are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v5s0j.

Data S2: LAI animation for years 2003 to 2015 contains aggregate, woody and partitioned LAI mosaicked for sub-Saharan Africa, presented in gif format. The animation shows the estimates of aggregate LAI and partitioned woody and herbaceous LAI estimates for each 8-day interval during the entire 13-year time-period, Filename: MCD15A2.2003_2015.Africa.V02.Animation.gif. An online version of the animation can be accessed here: https://globalmonitoring.sdstate.edu/content/modis-lai-partitioning and https://www.savanna-lab.com/research_kahiu.html. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v5s0j

Data S3: The in situ LAI measurements are provided in Microsoft Excel format containing measurements for sub-Saharan Africa collated from literature and field measurements in East Africa. The file contains three worksheets: i) description of the files and data variables; ii) *in situ* in-canopy LAI used to develop the partitioning allometry; and iii) LAI estimates used for the validation of the partitioned herbaceous and woody LAI. Filename: *Insitu.incanopy.LandscapeScale.LAI.FINALtoJGR.20170707.xlsx.*

3.0 List of Supporting Figures

Figure S1.1: Shows maps comparing mean annual precipitation from three global products for sub-Saharan Africa from 1998 to 2015

Figure S1.2: Scatterplot displaying statistical relationship between CRU, CHIRPS and TRMM mean annual precipitation for sub-Saharan Africa from 1998 to 2015.

Figure S2: Biome level phenology in panels A through O showing 8-day LAI averages for aggregate, woody and herbaceous components for different biome types in Africa. The biomes are based on Africa vegetation types (White, 1983), with locations sampled randomly across sub-Saharan Africa (total of 500,000 points), thus the data density varies between regions in proportion to their area.

4.0 List of supporting tables

Table S1: Zonal and seasonal biome averages for mean annual precipitation (MAP), aggregate, woody and herbaceous LAI, providing additional information on the biome level LAI by mean annual precipitation

Table s2: Metadata describing the contents of the MS Excel file containing in-canopy and landscape scale *in situ* LAI measurements

5.0 Text for supporting information

Text S1: Inter-comparison of mean annual precipitation from three global products for sub-Saharan Africa

Here we compare three gridded global monthly rainfall products for mean annual precipitation estimates for sub-Saharan Africa (SSA), namely: i) Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) with global coverage spanning the latitudes 50°S to 50°N, available from 1981 to present at 0.05° spatial resolution (Funk *et al.*, 2015); ii) Tropical Rainfall Measuring Mission (TRMM) Version 7 covering the region within the latitudes 50°S to 50°N at 0.25° spatial resolution from 1998 to present (Huffman *et al.*, 2007); and iii) Climate Research Unit precipitation time series by University of East Anglia (CRU-TS v3.24) available at 0.5° spatial resolution from 1901 to 2015 temporal coverage (the rainfall data used in this analysis) (Harris *et al.*, 2014). To compare the three products, mean annual precipitation (MAP) was computed for the period 1998-2015 (the TRMM data period) for SSA and spatially aggregated to 0.5° to match CRU-TS precipitation. MAP computed from the two higher resolution datasets has a good agreement with CRU MAP ($R^2 >= 0.95$; Figures S1.1 and S1.2). In this analysis we used CRU data because it provides long-term averages (30-year climate) that are at the appropriate temporal scale for the in-canopy LAI allometry which depends on tree community adaptation to local climate averages, rather than inter-annual variability.

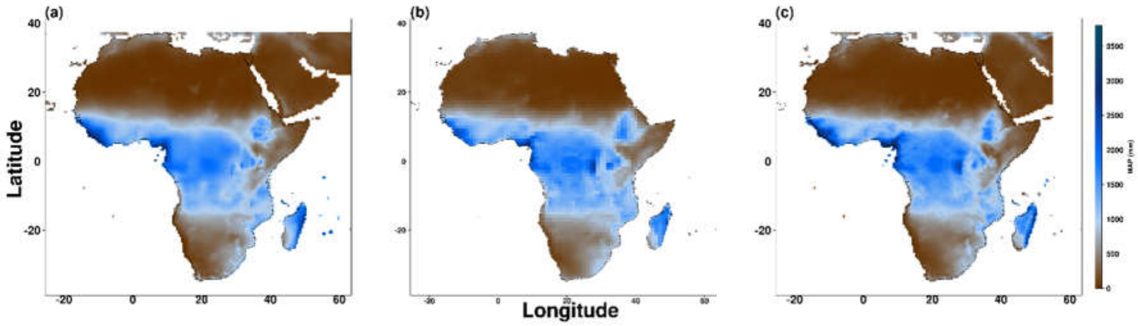


Figure S1.1: Comparison of mean annual precipitation for sub-Saharan Africa from (a) CRU-TS, (b) TRMM and (c) CHIRPS for years 1998 to 2015, aggregated to half degree spatial resolution.

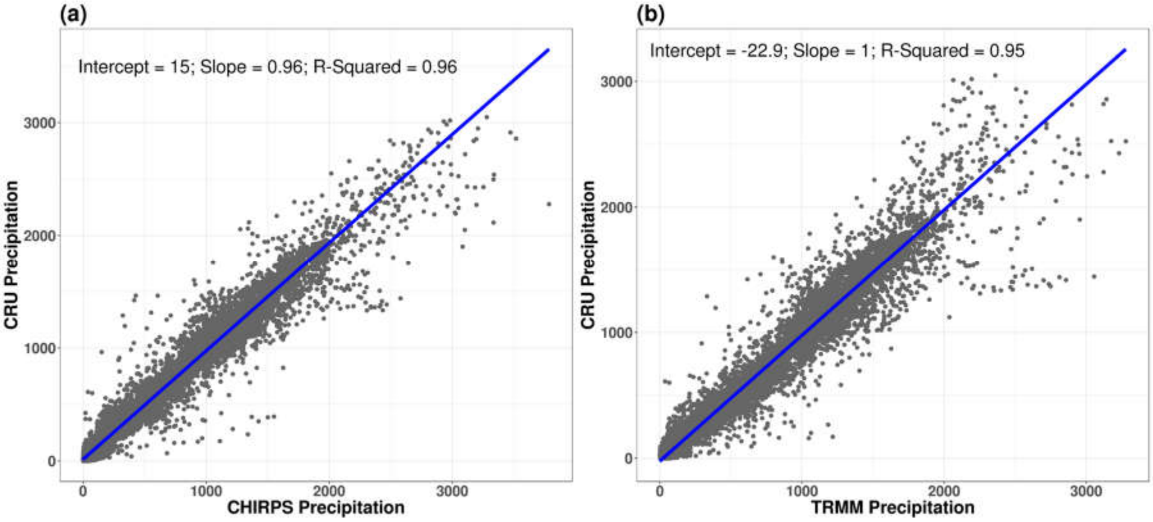


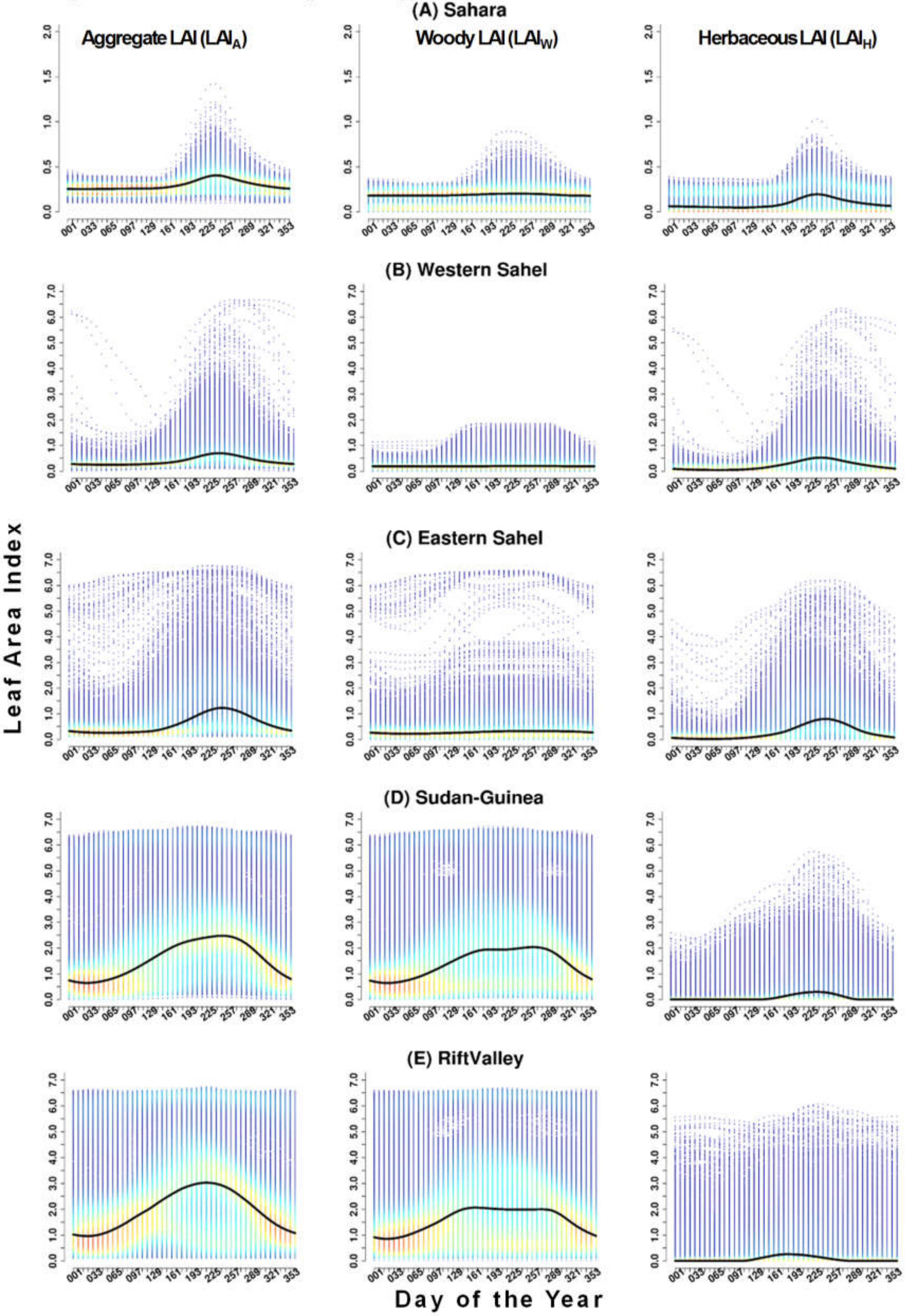
Figure S1.2: Scatterplots to compare CRU-TS mean annual precipitation with (a) CHIRPS (b) TRMM for all the data after spatial aggregation to half degree.

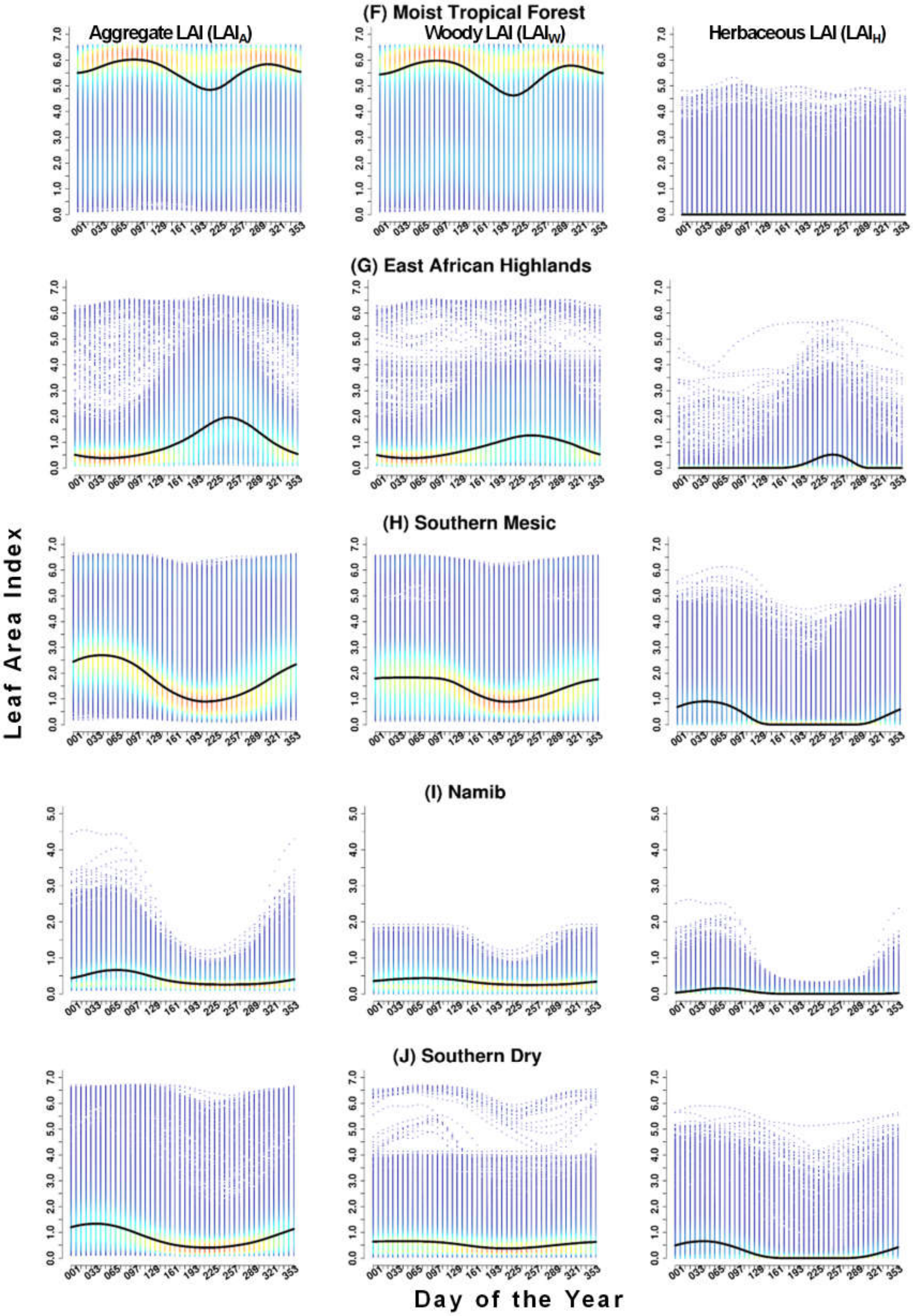
Text S2: Biome level phenology

In this section, we show biome-level 8-day phenologies of aggregate, woody and herbaceous LAI randomly sampled at a total of 500,000 points across Africa from the 13-year average time-series (2003-2015). The randomly-selected points allow us to visualize the median and variability in woody and herbaceous LAI phenology in each biome (Figure S2) with the density of points varying as a function of the spatial extent of each biome. In most biomes, we see a clear central tendency relating to the magnitude of growth and seasonality, but considerable spatial variability reflecting the large spatial extent of the biome map, with inherent variability in climate, soils and vegetation, but in many cases also reflecting human impact within biomes, including agricultural activities, forest clearance for timber, urban expansion, etc.

Table S1 shows partitioning performance grouped into three rainfall categories: wet, mesic and dry. In the low rainfall areas (MAP <500mm) comprising of Sahara, Namib, Cape, the Horn arid and the Sahel (Eastern and Western Sahel), the low tree cover leads to low woody LAI, with mean and median <0.5 (Table S1 and Figure S2). In the Sahara biome, which in our analysis only includes a small area mainly in the southern region at the border with the Sahel, the spatial aggregate LAI is low (range 0.1 and 1.26 for minimum and maximum respectively) which peaks during the wet season from early July to late September. With a generally low vegetation cover, both herbaceous and woody LAI get small fractions of the aggregate LAI (Table S1 and Figure S2). In the Sahel region (eastern and western), the seasonal maximum LAI is reached in June to October. The wetter Eastern Sahel gets a higher woody and herbaceous LAI at a mean of 0.38 and 0.40 compared to the Western Sahel with means at 0.23 and 0.25 for LAI_W and LAI_H respectively. In the Namib biome, LAI peaks in the wet season beginning from November to April, where the LAI_A seasonal average 0.51 and the partitioned LAI_W and LAI_H at 0.4 and 0.12 respectively. The Cape, characterized by low MAP and a short growing season from January to March, has average maximum LAI_A of 0.34, while the partitioned LAI_W and LAI_H are 0.28 and 0.10

Figure S2: Biome level phenology




(F) Moist Tropical Forest
Aggregate LAI (LAI$_A$)
Woody LAI (LAI$_W$)
Herbaceous LAI (LAI$_H$)
(G) East African Highlands
(H) Southern Mesic
(I) Namib
(J) Southern Dry
Leaf Area Index
Day of the Year
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
001
033
065
097
129
161
193
225
257
289
321
353

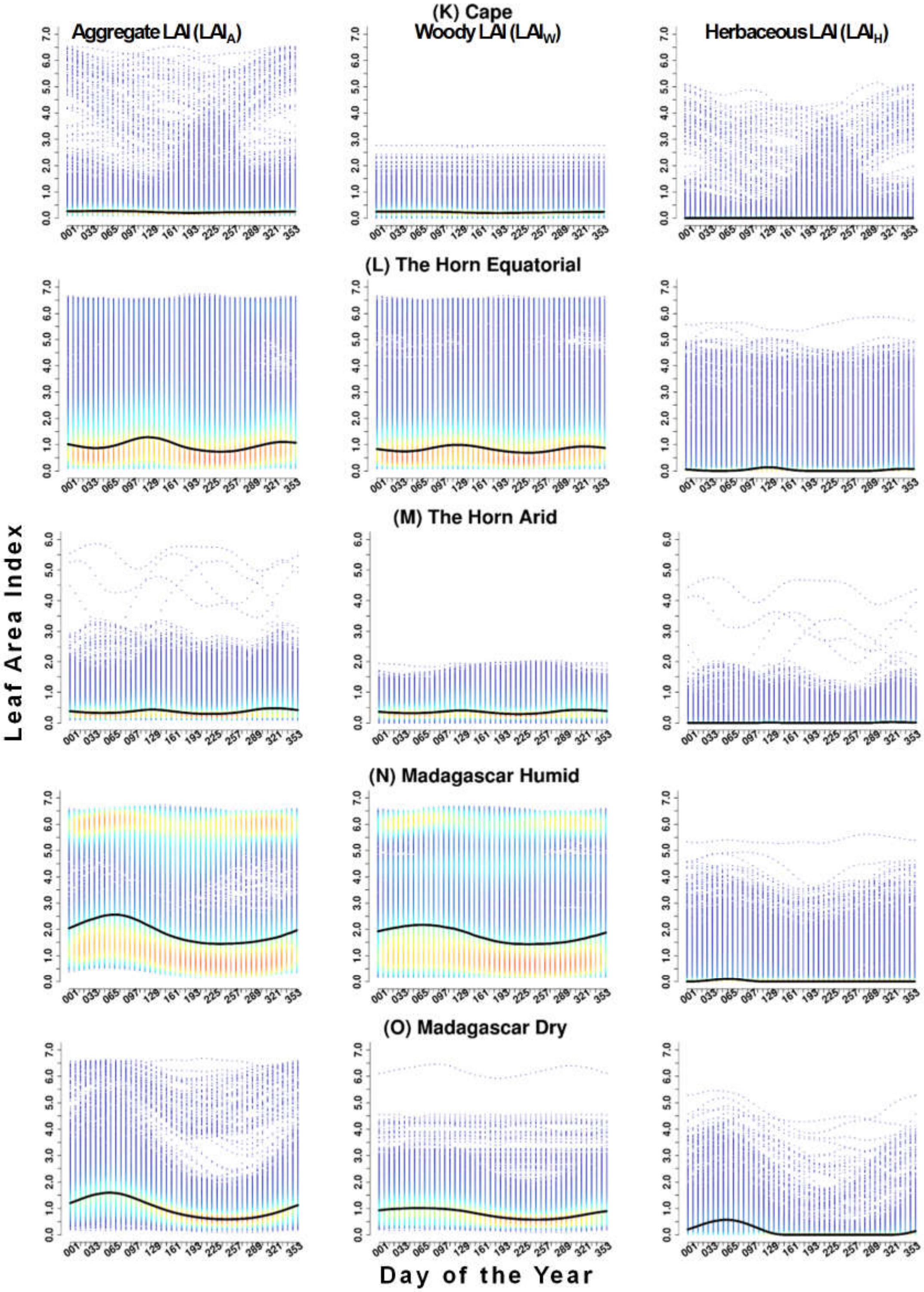


Figure S2: 8-day time series leaf area index averages (i.e. 46 LAI estimates averaged across years 2003-2015) for different biome types in Africa, showing the median response (black line) and the range of individual pixel values, for the MODIS aggregate LAI (LAI$_A$), partitioned woody LAI (LAI$_W$) and herbaceous LAI (LAI$_H$). Locations were sampled randomly across Africa with a total of 500,000 points, thus the data density varies between regions in proportion to their area.

The mesic ecosystems (500mm - 1000 mm MAP) are found in the Horn Equatorial, Southern Dry and East African Highlands biomes, with mean woody LAI in the range 0.5 to 1.0, while LAI_H is between 0.2 and 0.3 (Table S1 and Figure S2). The horn equatorial is characterized by bimodal precipitation, with long rains in March to June and short rains in November to December, which are apparent in the aggregate and partitioned LAI profiles, with seasonal averages are 1.31, 1.05 and 0.30 for LAI_A, LAI_W and LAI_H respectively. In Southern Dry biome, LAI peaks in the months of November to April, where seasonal average maximums are 1.48, 0.78 and 0.70 for LAI_A, LAI_W and LAI_H. In the East African Highlands, the seasonal average maximums are 1.21, 0.98 and 0.23 for LAI_A, LAI_W and LAI_H, observed during the wet months between June and November. Here, our partitioning allocates higher LAI to LAI_W due to the presence of woodlands and shrublands around Ethiopian highlands. Generally, in these mesic ecosystems, the tree cover and woody LAI is higher than in drier regions.

The regions we define as wet ecosystems (1000 mm < MAP) include the Southern Mesic, Madagascar (dry and Humid), Rift Valley, Sudan-Guinea and Moist Tropical Forest biomes. The mean zonal LAI is high (1.0 - 5.0). In this category, the partitioning allocates LAI mainly to the LAI_W, while LAI_H is relatively small (~0.1-0.5). In the Southern Mesic biome, LAI peaks from December to March. The seasonal average maxima are 2.97, 1.98 and 1.0 for LAI_A, LAI_W and LAI_H (Table S1).

The Rift Valley observes a May to September surge in LAI, where LAI_A seasonal average maxima is at 2.92, while partitioned LAI_W is 2.32 and LAI_H at 0.63. In Sudan-Guinea the growth season falls between the months of June to October, where seasonal average maxima are at ~ 2.68, 2.13 and 0.55 for LAI_A, LA_W and LAI_H respectively. In the Moist Tropical Forest biome where MAP is the highest, LAI remains consistently high throughout the year, although a small deep is observed from June to September, Figure S2F. The partitioning has seasonal average LAI_W remaining above 4.0 throughout the year while LAI_H remains low at an average of ~0.2. In Madagascar, the growth season runs from December through March. The eastern wetter area classified as Madagascar humid has high LAI_A which remains significantly high throughout the year. Partitioning allocates LAI mainly to LAI_W, which has a mean of 2.75 while LAI_H remains low with a mean of ~0.30. In the western drier Madagascar, classified here as Madagascar dry, LAI increase follows the precipitation regime, with seasonal average maxima observed at ~ 1.80, 1.10 and 0.70 for LAI_A, LA_W and LA_H respectively (Table S1).

Biome Name	Precipitation		Aggregate LAI (LAI$_A$)				Woody LAI (LAI$_W$)				Herbaceous LAI (LAI$_H$)				Seasonal Average Max		
	MAP	Category	Min	Median	Mean	Max	Min	Median	Mean	Max	Min	Median	Mean	Max	LAI$_A$	LAI$_W$	LAI$_H$
Sahara	86	Dry	0.10	0.28	0.29	1.26	0.00	0.19	0.16	0.91	0	0.09	0.13	0.88	0.42	0.20	0.22
Namib	217	Dry	0.10	0.35	0.51	3.81	0.00	0.31	0.40	1.89	0	0.02	0.12	2.13	0.79	0.51	0.28
Cape	259	Dry	0.10	0.24	0.34	6.47	0.00	0.22	0.28	2.44	0	0.00	0.06	5.09	0.37	0.31	0.09
The Horn Arid	330	Dry	0.10	0.36	0.48	5.09	0.00	0.35	0.43	2.15	0	0.00	0.05	4.27	0.60	0.50	0.10
Western Sahel	348	Dry	0.04	0.33	0.48	6.69	0.00	0.19	0.23	1.89	0	0.17	0.25	6.19	0.91	0.27	0.64
Eastern Sahel	499	Dry	0.02	0.44	0.78	6.78	0.00	0.26	0.38	6.63	0	0.16	0.40	6.34	1.48	0.46	1.03
Southern Dry	543	Mesic	0.07	0.72	0.95	6.74	0.05	0.53	0.65	6.65	0	0.09	0.30	5.69	1.48	0.78	0.70
The Horn Equatorial	773	Mesic	0.09	0.93	1.31	6.68	0.09	0.81	1.05	6.63	0	0.03	0.26	4.82	1.61	1.20	0.41
East African Highlands	954	Mesic	0.07	0.79	1.21	6.76	0.07	0.68	0.98	6.76	0	0.00	0.23	5.27	2.27	1.48	0.79
Southern Mesic	1093	Wet	0.12	1.77	2.12	6.63	0.10	1.40	1.67	6.61	0	0.10	0.45	5.64	2.97	1.98	0.99
Madagascar Dry	1142	Wet	0.13	0.92	1.14	6.72	0.13	0.76	0.88	4.44	0	0.01	0.26	6.05	1.78	1.10	0.68
Rift Valley	1171	Wet	0.10	1.77	2.25	6.76	0.10	1.42	1.89	6.67	0	0.01	0.36	6.04	2.92	2.32	0.63
Sudan-Guinea	1177	Wet	0.02	1.49	1.88	6.76	0.02	1.20	1.68	6.65	0	0.00	0.20	5.81	2.68	2.13	0.55
Moist Tropical Forest	1684	Wet	0.15	5.63	4.80	6.60	0.15	5.56	4.69	6.61	0	0.00	0.11	5.30	5.15	5.02	0.13
Madagascar Humid	1841	Wet	0.11	1.92	3.05	6.76	0.11	1.77	2.75	6.76	0	0.00	0.30	6.04	3.48	2.98	0.50

Table S1: Zonal and seasonal biome averages for mean annual precipitation (MAP), aggregate, woody and herbaceous leaf area indices. For the aggregate, Woody and herbaceous columns, the statistics are spatial averages for every biome. The seasonal average maxima represent the spatial temporal maximum, averaged for each biome, derived from the median fit in Figure S2

Item	**Description**
Files included	
Metadata	Description of the data included in the dataset
IncanopyLAI	*In situ* LAI measurements used in the development of the MODIS leaf area index partitioning model
validation LAI	Insitu LAI measurements used for the validation of the partitioned MODIS leaf area index
Data Column Names	
CrownArea	Woody cover crown area
insituLAI	*In situ* leaf area index measurements from literature and Kahiu MN et al 2015 fieldwork in Kenya
incanopyLAI	Within woody canopy leaf Area Index
MODISLAI	MODIS estimates of leaf area index
DateMeasure	Date of measurement (format DD/MM/YYYY)
Day	Calendar date of measurement
Month	Calendar month of measurement
YYYY	Year of measurement
Julian	Julian day of measurement
Biome	Broad categorization of the vegetation type
VgtClass	Vegetation functional type i.e. herbaceous and woody component classes
MeaScale	Vegetation scale of measure (within canopy woody estimates or at landscape scale)
Species	Species type at site of measurements
MAP	Mean annual precipitation (mm/annum) for the site of measurements
Temperature	Temperature for the site where measurements were taken
Altitude	Altitude (meters above sea level) for the site where measurements were taken
Latitude	Geographical location from equator in decimal degrees
Longitude	Geographical location along the longitudes in decimal degrees
Site	Local name where measurements were taken
Country	Country where measurements were taken
Method	Reported type of measurement for estimating *in situ* leaf area index
Citation	Source of the data
Comment	Additional notes provided in literature
Data	
Missing Data	-999

Table S2: Metadata for the in-canopy and landscape scale *in situ* LAI measurements for the data provided in MS Excel format for Data S3.

Supplementary References

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CHAPTER 3

Fire in sub-Saharan Africa: the Fuel, Cure and Connectivity hypothesis

Kahiu, M. N., & Hanan, N. P. (*in press*). Fire in sub-Saharan Africa: the Fuel, Cure and Connectivity hypothesis. *Global Ecology and Biogeography*

Abstract

Aim Past analysis of satellite-based fire activity in tropical savannas support the intermediate fire-productivity hypothesis (IFP) which posits a close correlation with estimates of total net primary productivity in drier savannas and declines towards the extremes. However, these analyses ignore the distinct roles played by herbaceous and woody vegetation on fire ignition and spread. We hypothesize that, since herbaceous vegetation provides the primary fuel, fire activity in African savannas is asymptotically correlated with herbaceous production. Conversely, woody production affects fires indirectly through effects on herbaceous production and its connectivity. In contrast to IFP, we propose the Fuel, Cure and Connectivity (FCC) conceptual model for tropical fire activity. FCC makes explicit the distinct role of herbaceous and woody fuels, avoiding the confounding interpretation of the role of total production, while providing opportunities to quantify fuel curability, tree effects on herbaceous fuel growth and connectivity, and human management.

Location Sub-Saharan Africa (SSA).

Time 2003-2015

Taxa Woody and herbaceous vegetation

Methods We used boosted regression tree analysis to test competing models explaining fire activity: (i) Aggregate fuel-loads; and (ii) partitioned woody and herbaceous fuel-loads; both derived from MODIS leaf area index.

Results Herbaceous fuel-load was consistently most influential, providing more explanatory power than overall biomass in fire activity. Fuel curability rated second, then human population density (HPD), and woody biomass least important. We observed an asymptotic relationship between herbaceous fuel-load and fire activity consistent with FCC; trees promote fires at low densities but suppress fires at higher densities; fires were rare in wetter regions, emphasizing the need for fuel to cure; fires were concentrated in low human population areas underscoring the critical role of land management.

Conclusions The proposed FCC framework provides a more nuanced understanding of fire activity in tropical ecosystems, where herbaceous biomass is the key determinant of fire activity.

Keywords*:* Africa, Fire, Fuel Cure and Connectivity hypothesis, Herbaceous, Intermediate Fire Productivity hypothesis, MODIS Leaf Area Index (LAI), Woody

1.0 Introduction

Fire is a widespread and recurrent phenomenon that plays a critical role in global biogeochemical cycles, altering atmospheric chemistry, determining the distribution and structure of global biomes, and altering the ecological function of terrestrial ecosystems (Bond, 2001; Bowman *et al.*, 2009). Fire can be both a source of carbon and a facilitator of carbon sinks (Yue *et al.*, 2016). As a source of carbon, fires burn standing vegetation biomass causing rapid release of carbon which may have taken many years to accumulate (Mouillot & Field, 2005). Tropical savannas are responsible for about 30% of net primary production (NPP) in terrestrial biomes, equivalent to that of tropical forests (Grace *et al.*, 2006). However due to frequent and extensive burning, contributing ~62% global carbon emissions (van der Werf *et al.*, 2017), tropical savanna fires reduce the capacity of terrestrial ecosystems to sequester carbon (Yue *et al.*, 2015) . Conversely, fires promote vegetation growth, hence facilitate uptake of atmospheric carbon dioxide through photosynthesis (Bond, 2001). Wild fires also influence atmospheric chemistry and radiative forcing through emission of trace gases and aerosols (Crutzen & Andreae, 1990; Harrison *et al.*, 2010).

Fire is also important in changing soil properties and in turn influences cycling of elements such as potassium and phosphorous through wind erosion as ash, volatilization and leaching (Bond, 2001; Harrison *et al.*, 2010). For millenia, fire has shaped global biomes such as savannas, and many savanna plants have evolved fire resistant or fire-dependent traits (Bond, 2001; Bond & Midgley, 2012; Bowman *et al.*, 2009; Murphy & Bowman, 2012). At regional and global scales, fire-tree cover feedbacks define vegetation patterns, where frequent fires limit tree canopy growth and promote open savannas dominated by the herbaceous layer and fires in an amplifying feedback that may contribute to alternate savanna and forest stable states (Hanan *et al.*, 2008; Hirota *et al.*, 2011; Hoffmann *et al.*, 2012; Staver *et al.*, 2011).

For millenia, fire has been a universal natural phenomenon, found in almost every vegetation type across the globe (Archibald *et al.*, 2013; Giglio *et al.*, 2013). However, natural fire regimes have been altered by humans through ignition and suppression (Archibald, 2016; Harrison *et al.*, 2010). Today, fire is used for ecological and economic benefits (Bowman *et al.*, 2009; van der Werf *et al.*, 2010). As a management tool fire is used to clear old and new land for cultivation, reduce hazardous fuel loads, facilitate forest regeneration, improve pasture quality and control pests (Harrison *et al.*, 2010) and as a hunting tool for poachers and traditional hunters (Pausas & Keeley, 2009). On the other hand fire has been widely suppressed to minimize deleterious effects associated with uncontrolled fires e.g. property damage, loss of human lives, human health and biodiversity loss (Archibald, 2016)

Fire is most predominant and frequent in tropical savannas, particularly in African savannas (Archibald *et al.*, 2013; Giglio *et al.*, 2013). Tropical savanna fires are almost exclusively surface fires, fueled by senescent herbaceous material (Bond & Midgley, 2012; Frost & Robertson, 1985; Murphy & Bowman, 2012), with crown fires being rare since trees are scattered with their crowns high above the ground (Bright *et al.*, 2012). In African savannas fires consume ~10% of NPP (Lehsten *et al.*, 2009), constituting >60% of total global burnt area (Bistinas *et al.*, 2013; Giglio *et al.*, 2013; van der Werf *et al.*, 2010). According to the pyrome classifications of Archibald *et al.* (2013), African fires fall mainly into two main pyromes: frequent-intense-large and frequent-cool-small.

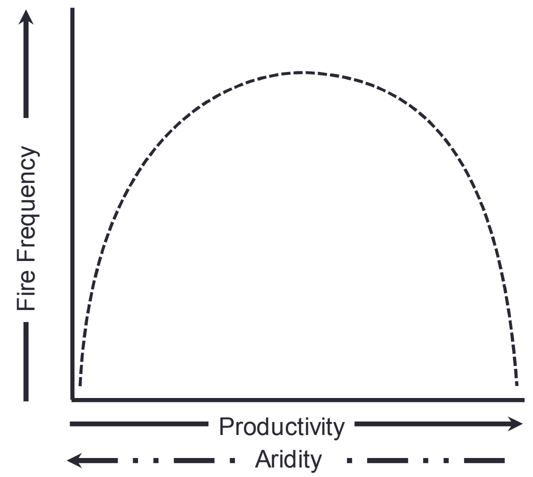

Figure 1: The Intermediate Fire-Productivity (IFP) model showing a hump shaped ('unimodal') relationship between fire frequency and productivity/aridity, peaking at intermediate levels and declining in highly productive but wet environments and arid but low productivity ecosystems. Adapted from Pausas and Bradstock (2007).

Four conditions must be met for a fire to ignite, persist and propagate in a landscape (Bradstock, 2010): sufficient biomass, adequately dry to burn ("cured"), favorable atmospheric conditions for combustion and the presence of natural or anthropogenic ignition sources (Krawchuk & Moritz, 2011). A widely cited phenomenological model for the frequency and extent of fire in terrestrial systems is the "intermediate fire-productivity" hypothesis (IFP; Pausas & Ribeiro, 2013). In the IFP model, fire activity peaks at intermediate productivity (and aridity) and declines towards the extremes (Figure 1). Highly productive areas tend to be limited by fuel moisture ("too wet to burn"), while xeric ecosystems are limited by lack of sufficient and well-distributed fuel ("too little to burn"). The resulting unimodal distribution of fires with respect to productivity and aridity has empirical support from both regional and global scale analyses (Archibald *et al.*, 2013; Bowman *et al.*, 2014; Pausas & Ribeiro, 2013). However, the IFP model, particularly when tested using satellite measurements of total net primary production, fails to disentangle the important distinctions between herbaceous and woody vegetation in promoting and/or suppressing fire ignition and spread in tropical ecosystems.

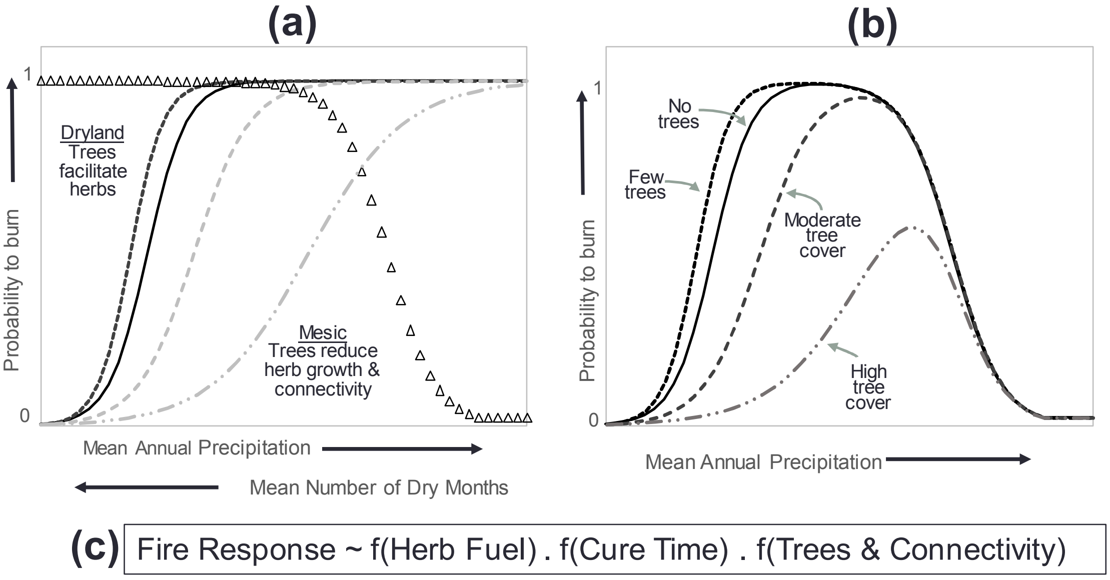

Figure 2: Conceptual diagrams outlining the "Fuel, Cure and Connectivity" (FCC) model for tropical wildfires controlled by joint probabilities of sufficient herbaceous fuel availability (P(Fuel), solid and dotted lines) and sufficient length of dry season for fuel to cure (P(Cures), Δ symbols). (a) shows hypothesized probability that fuel-load will be sufficient to carry a fire with increasing mean rainfall, and the effect of increasing tree cover from no trees (solid line), to low tree cover in dry savannas (dashed), to potentially high tree cover in mesic savannas (dotted), assuming that trees facilitate herbaceous growth in drylands, but reduce herbaceous growth and connectivity in mesic savannas (Dohn *et al.*, 2013). Thus trees may increase fire prevalence in drier savannas but decrease in mesic savannas; (b) shows hypothesized joint probability that landscapes with varying herbaceous-woody vegetation structure will have sufficient fuel, that is suitably cured and spatially contiguous, to carry a fire; (c) summarizes the FCC model as a functional equation relating fire variables (frequency or average burn area) to fuel load, cure probability, tree effects on herbaceous fuel and connectivity, and management.

Our proposed savanna Fuel, Cure and Connectivity (FCC) conceptual model (Figure 2) is based on the premise that, in tropical savannas, wild-fires are generally fueled by herbaceous materials, with crown fires being rare. Therefore, at continental scales, the frequency, burn intensity and average burned area of tropical fires will tend to increase with herbaceous biomass, perhaps reaching an asymptote above a certain biomass where fuel is no longer limiting. We anticipate that average herbaceous fuel availability increases near-linearly with mean annual rainfall (Deshmukh, 1984; Shorrocks & Bates, 2015). However, the availability of sufficient time for fuels to cure (i.e. to dry enough to burn following an ignition event) will be correlated with dry season length (DSL) and thus inversely proportional to mean annual rainfall. Woody biomass, by contrast, may facilitate herbaceous growth in drier environments, but tends to suppress herbaceous growth and reduce connectivity in wetter environments (Archibald *et al.*, 2012; Dohn *et al.*, 2013). Thus, in contrast to the IFP model that posits a unimodal response of fire to total productivity, the FCC model posits a family of positive sigmoidal relationships (depending on the variable influence of trees) between mean annual precipitation (MAP) and the probability of herbaceous fuel being sufficient for a successful fire (Figure 2a). Simultaneously, however, we anticipate a negative sigmoidal response in the probability that available fuel will have time to cure, and it is the product of P(Fuel) and P(Cures) that defines the overall probability that an ignition event will successfully light a fire that is persistent and large enough to be observed in satellite imagery (Figure 2b). The probability of an ignition event is not represented in the conceptual diagrams (Figure 2a and b). However, since most wild-fires in Africa are intentionally set as part of management practices (Kull & Laris, 2009), we introduce human population density into the empirical model (Figure 2c). Bistinas *et al.* (2013) found the direction of human population density (HPD) influence in SSA depends on land use systems, with rangelands experiencing a positive relationship, while higher human populations in agricultural areas suppress fire through agricultural expansion and intensification (Andela *et al.*, 2017). We therefore anticipate an overall negative relationship between HPD and fires. We note that, in contrast to Bradstock (2010) and others, we do not include atmospheric conditions in our conceptual or empirical model (Figure 2): while an important variable in temperate and boreal systems we assume that dry season air temperatures and humidity in tropical Africa are almost always favorable for fire, to the extent that it is assumed not to be a limiting factor in this analysis.

While the FCC conceptual model might be viewed as a simple refinement of the IFP, we highlight two important distinctions that provide potentially important new insight into tropical wild fire processes: (a) the decline in fire frequency in wetter high-productivity tropical biomes is conceptually linked only to fuel wetness in the IFP, but to either or both fuel-wetness and lack of herbaceous fuel-load under dense tree canopies in the FCC; and (b) where the IFP posits a general increase in fire with productivity, the FCC distinguishes the direct role of herbaceous fuel-load and the indirect role of woody canopies in facilitating or competing with herbaceous growth and thus reducing fuel load and spatial connectivity.

Our objectives in this study were to: i) understand how two characteristics of fire regime (fire frequency and average percent burned area) vary with changes in herbaceous and woody fuel components; ii) explore the role of dry season length in promoting curing of fuels prior to burning, and humans in providing ignition sources, and (iii) quantify and evaluate the applicability of the FCC hypothesis relative to the IFP across sub-Saharan Africa. We use the conceptual model illustrated in Figures 2a-b as the basis for our a priori hypotheses, and a Boosted Regression Tree (BRT) approach to quantify the form and magnitude of fire responses to the contributing factors shown in Figure 2c. The satellite fire products include the MODerate Resolution Imaging Spectroradiometer

(MODIS) active fire detection product (MCD64A1) Collection 6, commonly referred to as burnt area and the Global Fire Emissions Database Version 4 (GFED4, without small fires) burnt fraction as complementary estimates of fire return frequency and annual average percent burned area, respectively. The partitioned LAI time series developed in Kahiu and Hanan (2017) are used to derive estimates of average annual maximum leaf area index (LAI) as proxies for fuel load. The probability that fuel has time to dry sufficiently to burn (Krawchuk & Moritz, 2011) is indexed using estimates of dry season length (DSL). A spatially disaggregated human population density (HPD) dataset is also used as an indicator of anthropogenic influences, including sources of ignition and land management practices. A summary of the data used is presented in the support information (SI) in Appendix 1, Table S1.1. We tested two basic BRT model formulations: (i) aggregate LAI models, where the aggregate (MODIS) LAI is used to represent available fuel, as in earlier studies; and (ii) partitioned LAI models, using separate constituents of woody and herbaceous LAI, based on the refined FCC model.

2.0 Materials and Methods

Environmental variables were selected to represent the primary drivers of fire hypothesized in Figure 2, including direct estimates or proxy indices for fuel load, fuel curing, the impacts of tree canopy, and anthropogenic ignition/management shown in SI, Table S1.1.

2.1 Data and preprocessing steps

2.1.1 Satellite fire products

The study covers the whole of sub-Saharan Africa (SSA)

Percentage burned area

We used Global Fire Emissions Database version 4 (GFED4 without small fires) burned area product (Giglio *et al.*, 2013) to compute the percentage burnt area (PBA) per 0.25^0 spatial resolution pixel in SSA. The data, provided as a monthly global product from mid-1995 to 2016, was downloaded (fuoco.geog.umd.edu) for years 2003-2015, spatially subset for the SSA region and used to compute annual cumulative burnt area in each pixel, from which long-term (13-year) average percentage burned areas were calculated (Figure 3a).

Burn frequency

To determine burn frequency (BF) the MODIS Terra and Aqua combined MCD64A1 collection 6 monthly burn product was used (Giglio *et al.*, 2016). MCD64A1 dataset derived using MODIS collection 6 (C6) surface reflectance coupled with MODIS active fire data, includes a monthly level 3 product at 500m spatial resolution, summarizing the date of burn (presented as Julian day of burn in the range 1-366) covering the period November 2000 to November 2016 (Giglio *et al.*, 2015) at the time of this analysis. The MCD64A1 tiled dataset for years 2003 to 2015 was downloaded for SSA region. We extracted the burn date and quality assurance flags which we used to mask out water cells then computed the annual average burn frequency for the study period (Figure 4b). According to the product user guide (Giglio *et al.*, 2013) MCD64A1 C6 product includes an improved mapping algorithm, reduced error of omission, better mapping of small fires, enhanced classification accuracy, increased spatial coverage and improved quality assurance.

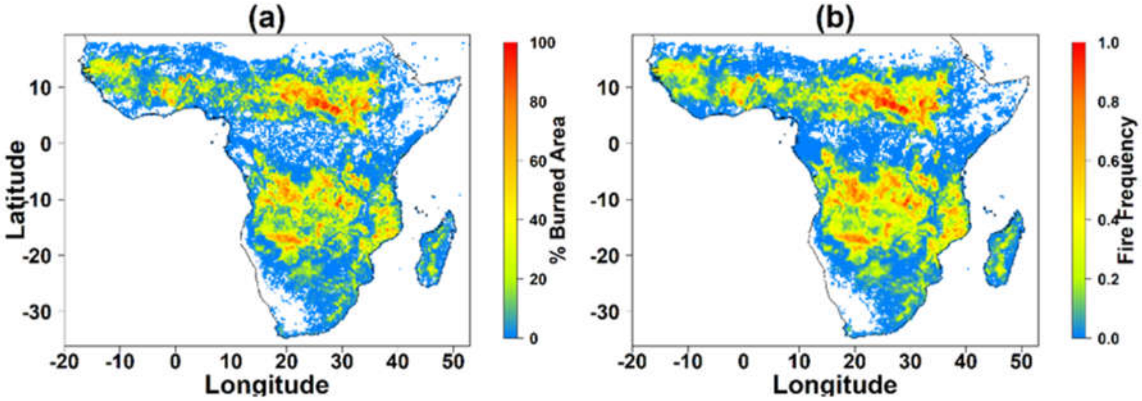

Figure 3: Percentage annual average burnt area derived from Global Fire Emissions Database version 4 (GFED4) in (a) and (b) annual average fire frequency computed from MODIS burnt area product (MCD64A1) scaled between 0 and 1; both covering the study period 2003-2015

2.1.2 MODIS aggregate and partitioned woody and herbaceous leaf area index

Average annual maximum green LAI is used in this analysis as a proxy for fuel load, based on the logic that, in tropical savannas burning senescent leaves rather than wood, there is very little carry-over of leaf biomass between years (i.e. it is generally eaten, burned or decomposes at annual time-scales), thus peak leaf area during the rainy season will be closely correlated with the amount of leaf biomass that senesces and cures to constitute fuel during the subsequent dry season. MODIS aggregate (total) leaf area index (Myneni *et al.*, 2015), and a recently-derived woody-herbaceous partitioned LAI product (Kahiu & Hanan, 2017) were used as proxies for fuel load, analogous to the IFP approach (total biomass) and the FCC approach (herbaceous only), respectively.

Aggregate MODIS leaf area index

MODIS aggregate leaf area index (LAI_A) for SSA was downloaded from combined MODIS LAI (Terra and Aqua satellites) collection 5 (C5) time series (MCD15A2) for years 2003-2015, at 8-day interval and 1km resolution. LAI_A was preprocessed to fill missing data and reduce noise in the time series caused by atmospheric contamination, sensor and solar geometry issues (Chen *et al.*, 2004). The preprocessing steps are further detailed in Kahiu and Hanan (2017). The preprocessed LAI_A was used to derive annual average maximum LAI (LAI_{Amax}, Figure 4a).

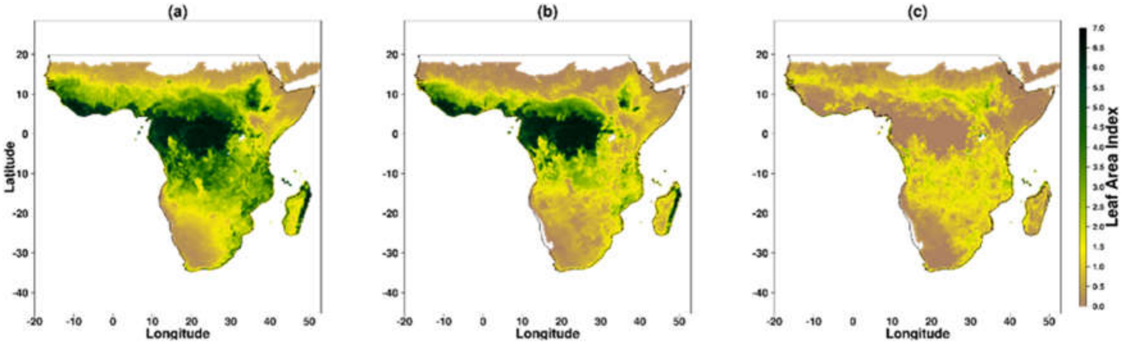

Figure 4: Maps of annual average maximum leaf area index in sub-Saharan Africa, (a) aggregate LAI_{Amax} from MODIS, (b) partitioned woody LAI_{Wmax}, and (c) partitioned herbaceous LAI_{Hmax}. The data were derived as the per pixel average of annual LAI maxima for years 2003 to 2015

Partitioned leaf area index

The partitioned LAI products are generated using the 8-day LAI_A at a spatial resolution of 1 km for the time period 2003-2015. As detailed in Kahiu and Hanan (2017), LAI_A is separated into woody (LAI_W) and herbaceous (LAI_H) constituents in

SSA, using independent tree cover estimates and an allometric relationship between mean annual precipitation and seasonal LAI maxima for dominant woody species in SSA. From the partitioned product, we computed the per pixel annual maximum LAI which was then averaged for the 13 years of our study (Figure 4 b-c). A small number of pixels with herbaceous LAI > 3 LAI units were found to be concentrated in wetlands and seasonally flooded grasslands and were eliminated from this analysis.

2.1.3 Indicators of vegetation moisture content

Vegetation moisture condition is an important variable that dictates the potential for fuels to burn (Cochrane & Ryan, 2009). Here we estimate the average number of dry season months as a proxy for vegetation moisture status and the time available for biomass to cure. The dry season length (DSL) for SSA was computed using Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk *et al.*, 2015). The dataset has a global coverage spanning the latitudes 50°S to 50°N, available from 1981 to present at 0.05° spatial resolution. CHIRPS incorporates satellite and ground station precipitation estimates to derive gridded precipitation products. We used the monthly precipitation product for years 2003-2015, computed the monthly average precipitation, then set a 30 mm threshold below which a month was considered to be dry. We then computed the average annual maximum number of cumulative dry months, taking into account that the dry season in much of Northern and East Africa traverses one calendar year to another. The computed DSL was then aggregated to 0.25^o to match the spatial resolution of the PBA (Figure 5a).

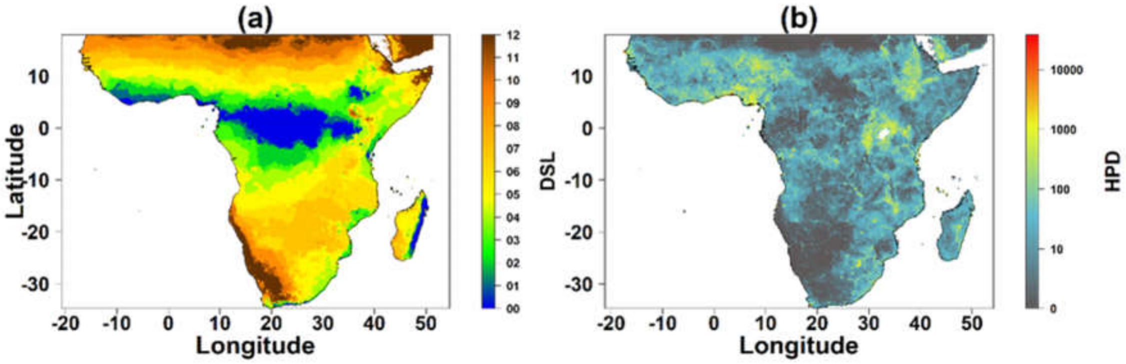

Figure 5: Seasonality and anthropogenic drivers of fire activity in Africa. (a) The dry season length (DSL) computed using CHIRPS precipitation estimates with a threshold of 30 mm precipitation defining dry months, averaged for years 2003-2015. (b) Human population density (HPD, people/km^2; Bhaduri et al., 2002). Note that urban areas with HPD > 500 people/km^2 were eliminated in the analysis.

2.1.4 Human population density

We used year 2015 human population density (HPD) estimates for SSA from the Gridded Landscan population dataset developed by US Oak Ridge National Laboratory, available at ~1km spatial resolution (Bhaduri *et al.*, 2002). The HPD data was aggregated (using the mean) to match the spatial resolution of other analysis datasets at 0.25^0. To avoid high density urban locations, we restricted our analysis to human population density <500 persons/km^2.

2.2 Boosted regression tree analysis

To test the hypotheses illustrated in Figure 2, we used Boosted Regression Tree (BRT) analysis. BRTs are statistical machine learning methods which combine i) a boosted technique that improves model accuracy through bagging predictions and iterative fitting, and ii) a regression model which relates a response variable to predictors through recursive binary splits. We chose BRT due to their advantages over traditional statistical modeling methods, as outlined by Elith *et al.* (2008), including their ability to fit linear and complex nonlinear relationships, accommodate missing data and outliers, with no need to transform data or remove outliers; handle predictor variable interaction; and work with a variety of response variable types including Gaussian, Poisson and Binomial.

We tested two basic models, analogous to the IFP and FCC conceptual models, describing spatial variation in percent burned area and fire frequency across Africa with respect to (i) aggregate LAI (LAI_A), and (ii) partitioned herbaceous LAI (LAI_H; Table 1).

Table 1: Models used to explore burnt area and fire frequency in sub-Saharan Africa using boosted regression tree analysis

Response variable (Fire activity)	**Explanatory Variables**	
	Model 1: Aggregate model	*Model 2: Partitioned model*
Percentage Burnt Area (GFED4 Data)	Aggregate LAI + Dry Season Length + Human Population Density	Herbaceous LAI + Woody LAI + Dry Season Length + Human Population Density
Mean Annual Burn Frequency (MCD64A1)	Aggregate LAI + Dry Season Length + Human Population Density	Herbaceous LAI + Woody LAI + Dry Season Length + Human Population Density

3.0 Results

3.1 Fire patterns and boosted regression analysis

Initial bivariate analysis of the relationships between fire activity (percent burnt area, PBA, and burn frequency, BF) and the potential driver variables are shown in the SI Appendix S2 and Figures S2.1 and S2.2.

3.1.1. Fire relationship with vegetation productivity

BRT analysis results are shown in Figure 6-7 and Table 2. Results from the aggregate LAI model indicate several patterns of fire with environmental covariates. LAI_A has a unimodal relationship with PBA (Figure 6a) and BF (Figure 6d) consistent with bivariate analysis (Figures S2.1a and d) and the IFP conceptual model for fire activity (Figure 1). Fire is low in the low LAI areas (fuel limitations in arid ecosystems), peaking at intermediate LAI_A values (intermediate productivity) then declines towards high LAI_A ecosystems (too wet to burn).

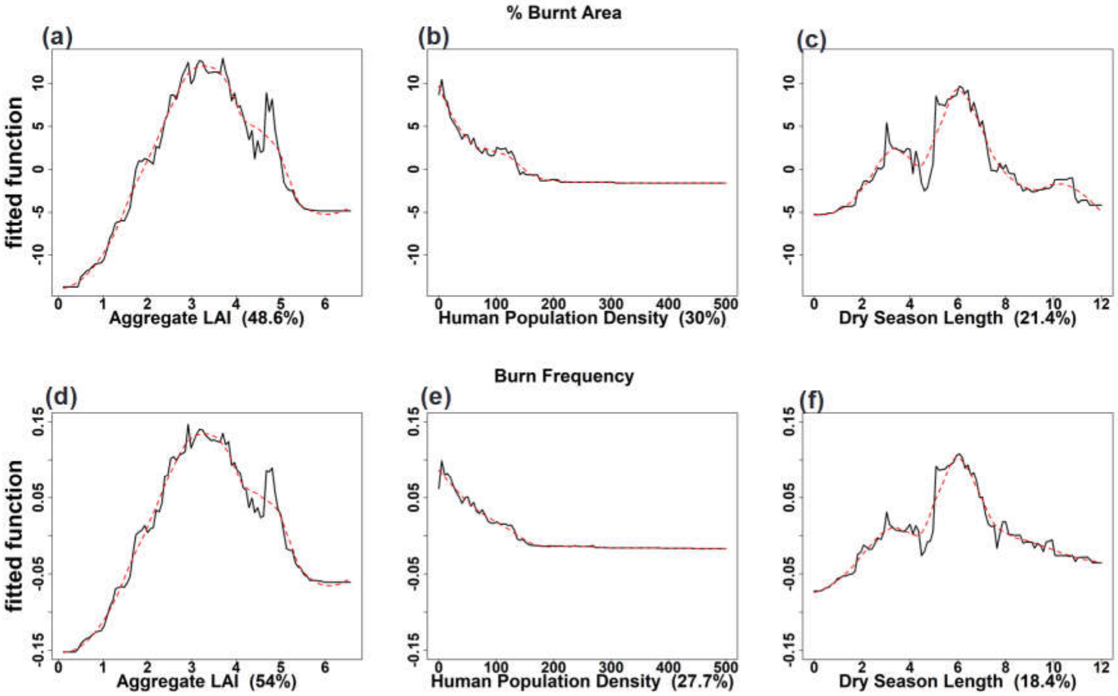

Figure 6: Partial dependency plots from boosted regression tree analysis for aggregate model (Model 1; Intermediate Fire productivity hypothesis) for (a to c) percentage burnt area and (d-e) burn frequency showing fire responses to aggregate leaf area index , human population density (HPD) and dry season length (DSL). The red lines are fitted using a loess smoothing and the variables are ranked in order of their relative importance (%) which is shown beside the x-axis labels

In the partitioned LAI model where total leaf area index (LAI_A) is separated into LAI_W and LAI_H estimates, we observe an asymptotic response of fire with LAI_H, reaching an asymptote at LAI ~2.5 for both PBA and BF, consistent with the FCC hypothesis that herbaceous biomass is the primary fuel for tropical fires (Figures 7a and e), but that above a certain threshold of biomass ($LAI_H>2.5$; indexed here using peak herbaceous LAI) fires are no longer limited by fuel availability. In this model, the influence of woody LAI is relatively low (ranked 4th among the driver variables fitted, Figures 7d and h), with a unimodal form. Fire activity initially increases with increasing woody leaf area index peaking at LAI_W~2.5 before declining at higher LAI_W. The patterns in fire activity with LAI_W are consistent with the FCC model where trees facilitate herbaceous productivity (and thus fuel availability) in drier environments, but tends to suppress fires through reduced herbaceous fuel connectivity in wetter (high tree cover) environments. Further results to assess fire sensitivity to increasing herbaceous and woody biomass based on mean annual precipitation categorization are shown in SI, Appendix S4, Table S4.2 and Figures S4.5.

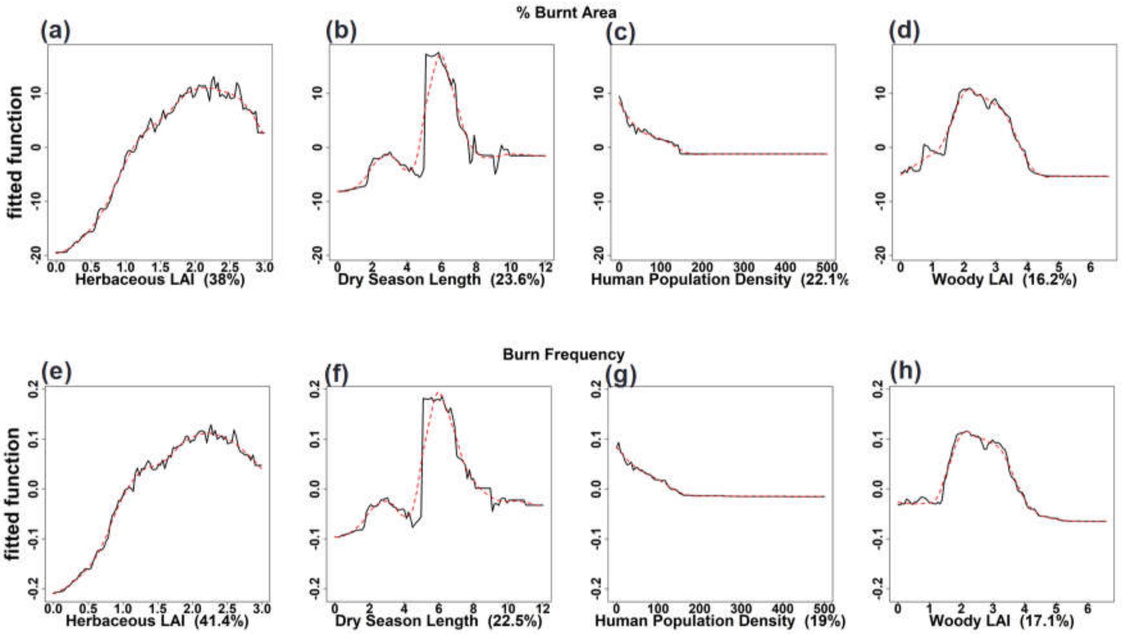

Figure 7: Partial dependency plots from BRT analysis for partitioned model (Model 2; Fuel, Cure and Connectivity hypothesis) for (a to d) percentage burnt area and (e to h) burn frequency, showing fire responses to partitioned herbaceous leaf area, dry season length (DSL) and human population density (HPD) and woody leaf area index (LAI_W). The red lines are fitted using a loess smoothing. The variables are ranked in order of their relative importance (%) which is shown beside the x-axis labels

3.1.2. Fire relationship with indicators of moisture availability

The influence of dry season length (DSL) on fire activity is consistent with the FCC hypothesis that a minimum dry season length is required for fuel to cure (Figures 6 and 7). In these analyses, it appears that at least 2 dry months are necessary for fires to be common, with a major increase in fire frequency and burn area in systems with >5 dry months. Contrary to our expectation of an asymptotic relationship, however, we see an apparent decline in fire frequency at DSL>7, perhaps reflecting interactions with fuel availability that the BRT approach is not able to fully separate (i.e. fire declines at high DSL may reflect fuel limitations in these very dry systems that was not fully characterized using the LAI_H estimates).

3.1.3. Fire relationship with human population

The results indicate that humans tend to suppress fires, with a negative exponential relationship, with fires most common at low HPD (< 50 persons/km^2) and declining fire frequency and average burn area in more densely populated regions (Figures 6b and e and 7c and g). Fires were concentrated in pastoral zones (HPD < 50) and low intensity agricultural zones (HPD<100), and rare in locations with HPD > 200 people.

3.2 Explanatory power and rank of driver variables

We observed varying importance ranking and explanatory power for the different environmental covariates used in both the aggregate and partitioned models. In the aggregate models, LAI_A has the best explanatory power, followed by HPD and DSL (Table 2 and Figure 6). Overall, the aggregate model explains ~52% of the spatial variability in average burnt area and 58% fire frequency across SSA. The ranking of independent drivers of fire activity changes for both PBA and BF in the partitioned models (Table 2). As hypothesized, herbaceous LAI has the most substantial influence on fire in SSA, followed by DSL, HPD and finally LAI_W. Overall the partitioned model explains slightly more (R^2 ~62%) of fire activity in SSA, than the aggregate model (R^2 ~55%).

Table 2: Boosted regression tree analysis results for the variability in average burnt area and fire frequency for aggregate and partitioned leaf area index models in sub-Saharan Africa

	Relative Influence (%)		
	Aggregate Model		
Variable	% Burnt Area	Fire Frequency	Averages
Aggregate LAI	47.54	49.65	48.59
HPD	31.13	28.40	29.76
DSL	21.34	21.95	21.64
R-Squared	0.52	0.58	0.55
	Partitioned Model		
Herbaceous LAI	38.16	38.84	38.50
DSL	24.69	23.53	24.11
HPD	22.32	21.00	21.66
Woody LAI	14.82	16.63	15.73
R-Squared	0.59	0.65	0.62

DSL= dry season length; HPD = human population density; LAI = average annual peak leaf area index

3.3 Comparison of model predictions and observed burnt area and fire frequency

We used the partitioned LAI BRT models to predict fire patterns across SSA to facilitate spatial comparison with the original data and identify region where the models perform particularly well or poorly (Figure 8). In general, the spatial patterns agree, showing the hotspots of burning in savannas within southern Chad and Sudan, in south eastern Sahel and Southern African miombo; regions of relatively low fire occur in the drier zones in the horn of Africa, the Namib/ Kalahari areas and northern Sahel; and low fire frequency in wet areas including the Congo Basin, West African coast and highlands. We notice some areas of disagreement where over-prediction is evident e.g. a strip along the east African coast which coincides with the DSL peak burning range (compare

Figures 8 and Figure 5a). Under-prediction is also apparent in fire hotspots areas in southern and northern Africa. It is noteworthy that the BRT results are similar for PBA and BF where we observe similar spatial patterns in the difference images.

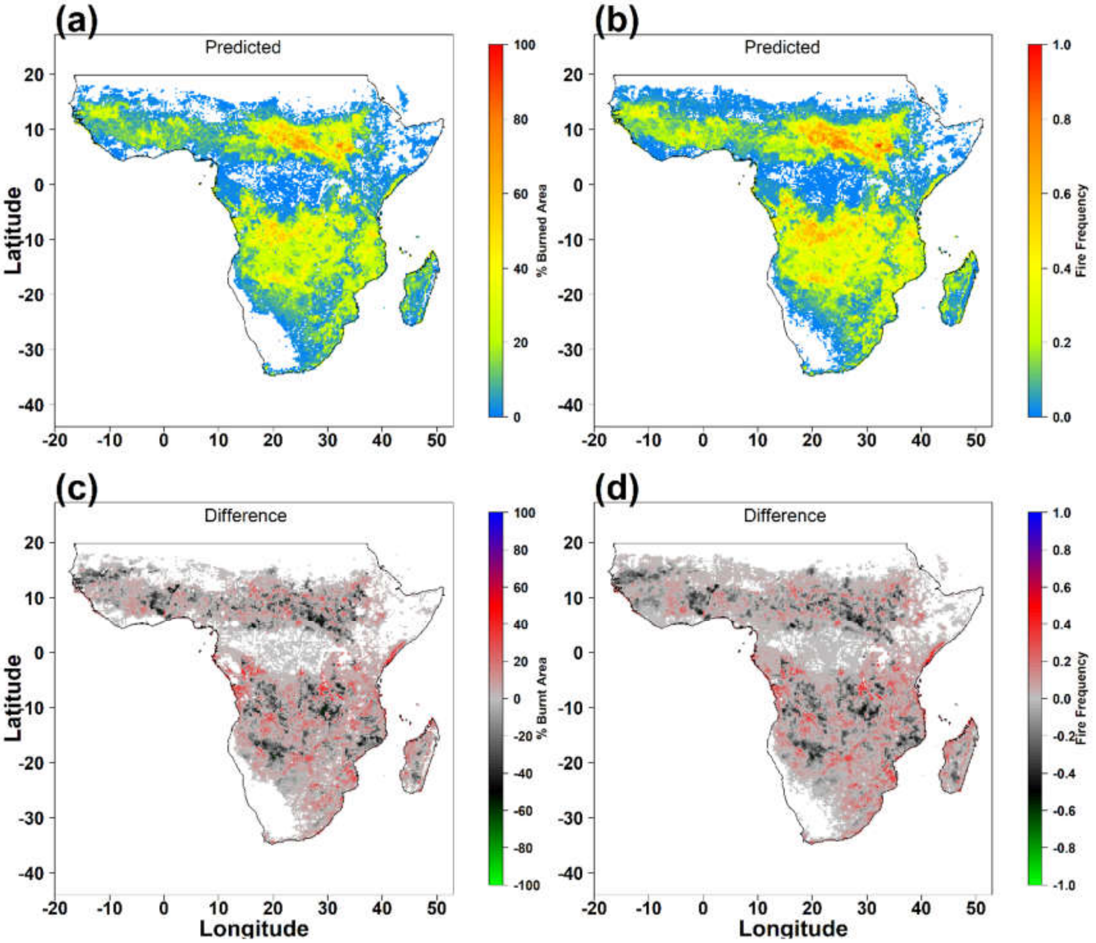

Figure 8: Comparison of predicted and satellite observed fire activity in sub-Saharan Africa using the partitioned leaf area index model. (a) Predicted burnt area and (b) Predicted fire frequency scaled between 0 and 1 both derived from Boosted regression tree analysis. The differences between observed and predicted are shown in (c) burnt area and (d) fire frequency.

We compare the observed and predicted PBA and BF statistics in Table 3. Overall the fitted partitioned model performs better for PBA (R^2=0.53) and BF (R^2=0.63) than the aggregate model for PBA (R^2=0.49) and BF (R^2=0.59). Both aggregate and partitioned models tend to under-predict fires at high observed fire activity, but partitioned models

(Figure 8) outperformed the aggregate models shown in SI, Appendix S3 and Figures S3.3 and S3.4.

Table 3: Summary statistics for observed versus predicted fire activity (percentage burnt area and fire frequency) for the aggregate model (intermediate fire productivity hypothesis) and the partitioned model (the fuel, cure and connectivity hypothesis) in sub-Saharan Africa

Model	**Fire Activity**	**Intercept**	**Slope**	**R-Squared**
Aggregate	*Burnt Area (PBA)*	5.18	0.66	0.49
	Fire Frequency (BF)	0.06	0.70	0.59
Partitioned	*Burnt Area (PBA)*	4.11	0.72	0.53
	Fire Frequency (BF)	0.05	0.74	0.63

4.0 Discussion

4.1. Summary of main results

In our analysis we: i) explored how fire frequency and average percent burned area vary with changes in herbaceous and woody fuel components; ii) assessed the role of dry season length in promoting curing of fuels prior to burning, and humans in providing ignition sources, and (iii) quantified and evaluated the applicability of the Fuel Cure Connectivity hypothesis (FCC) relative to the intermediate fire productivity hypothesis (IFP) across SSA. Fire frequency and burned area are influenced by multiple environmental and social factors in Africa but fuel load, indexed as maximum herbaceous LAI (LAI_H), was consistently most influential and provided more explanatory power than overall biomass, indexed as maximum aggregate LAI (LAI_A; i.e. herbaceous + woody). DSL was the second most important fire explanatory variable followed by HPD, and LAI_W least important in the partitioned model. While the BRT modeling approach remains sensitive to variable interactions, some clear patterns emerged: (i) the relationship between herbaceous fuel-load and fire frequency/extent was asymptotic rather than unimodal, contrasting the IFP, but consistent with the FCC; (ii) trees, may promote fires at low densites through facilitation of grass growth, but they suppress fires at higher densities, presumably by reducing fuel bed connectivity; (iii) fires were rare in regions with DSL < 2 months, peaking at 5-7 months, emphasing the need for fuel to cure; (iv) fires were also concentrated in areas with low human population, underscoring the critical role of land management, with fires concentrated in pastoral zones (< 50 people) and low intensity agricultural zones (<100 people), and rare in locations with

HPD > 200. These findings point to the need for disentangling fuel load types in fire analysis and the need to consider management practices and fuel cure time (DSL).

4.2. How fire activity changes with herbaceous and woody fuel components

We observed varying importance ranking and explanatory power for the different environmental covariates used in both the aggregate and partitioned models to explain fire frequency and spatial extent in SSA. From the analysis of the partitioned model, herbaceous biomass is the most important determinant of fire in SSA (Table 3), since it fuels fires in tropical savannas where most of the burning occur on the surface with crown fires being rare. These results are in agreement with our hypothesis that herbaceous biomass (LAI_H) has the most significant influence on fire in SSA, compared to woody fuel components (LAI_W). Overall the partitioned model has the best explanatory power of fire activity ($R^2 = 0.62$) in SSA compared to the aggregate model ($R^2=0.55$), as summarized in Table 2. The burnt area and fire frequency product show high fire activity in southern Chad, the Central African Republic, and South Sudan. Previous authors (Giglio *et al.*, 2013) suggested that the conspicuous hotspot in fire activity in this region can be tied to hot Harmattan trade winds. Our results however, show that the principal cause of fire activity in this region is related to relatively low tree cover and associated high herbaceous fuel load that supports frequent and extensive fires.

4.3. Role of seasonality and human management

Dry season length (DSL) and human population density (HPD) also exert important controls on fire activities within SSA. DSL is an important proxy of fuel load moisture status and the time required for curing fuel. Fuel moisture is considered a strong determinant of fire spread rates and intensity of surface fires (Cochrane & Ryan, 2009). In the partitioned model, our results suggest DSL is the second most important variable in explaining fire frequency and burn extent in SSA. The influence of DSL on fire activity is consistent with the FCC hypothesis that a minimum dry season length is required for fuel to cure. Further, our results suggest that at least 2 dry months are necessary for fires to be common, with a major increase in fire frequency and burn area in systems with 5-7 dry months. Contrary to our expectation of an asymptotic relationship, however, we see an apparent decline in fire frequency at DSL>7, perhaps reflecting interactions with fuel availability that the BRT approach is not able to fully separate.

HPD is ranked as the third most important variable to explain fire activities in the partitioned model. Our results suggest that human populations tend to suppress fires, with a negative exponential relationship, with fires most common at low HPD (< 50 persons) and declining fire frequency and average burn area in more densely populated regions. In SSA, fires are anthropogenic in nature (Kull & Laris, 2009), but the influence is dependent on land use management. Bistinas *et al.* (2013) found that increasing human population in rangelands leads to increasing fire, while agricultural areas experience a decline with increase in human population. This is in concert with our findings where we see a high fire occurrence in areas with HPD <50, then declines exponentially towards denser populations with fires being rare in HPD >200. A recent analysis (Andela *et al.*, 2017) concluded that there has been a decline in fires in Africa and elsewhere in the globe, associated with higher human populations suppressing fire through agricultural expansion and intensification. These findings agree with an analysis in southern Africa, where Archibald *et al.* (2009) found burnt area declined with increasing HPD. HPD has a further influence on fire by affecting biomass connectivity since human settlements and agricultural fields are often largely cleared of burnable surface vegetation while artificial barriers and land fragmentation breaks fire spread (Archibald *et al.*, 2009; Bowman *et al.*, 2011).

4.4. Applicability of the fuel, cure and connectivity hypothesis relative to the intermediate fire productivity across sub-Saharan Africa.

IFP hypothesis has been used to explain the relationship between fire and overall productivity across the globe. Here we tested its applicability in SSA tropical fires characterized by surface fires fueled by herbaceous biomass. In our aggregate biomass (LAI_A) model, we observe a unimodal relationship with percentage burnt area and fire frequency in SSA in accordance with IFP hypothesis (Bowman *et al.*, 2014; Pausas & Ribeiro, 2013). However, the pattern changes in the partitioned biomass model, where herbaceous biomass (LAI_H) increases linearly with both PBA and BF, reaching an asymptote at $LAI_H > 2$, consistent with the FCC hypothesis. On the other hand, the pattern of woody LAI_W controls on average burn area and fire frequency are distinct from the asymptotic relationship observed for LAI_H, following the unimodal pattern previously reported for the IFP framework (Figure 7). We interpret the form of the woody LAI partial dependence plots as follows: that modest LAI_W (< 2) indirectly supports fires (SI, Figure S4.5a), possibly through facilitation of herbaceous growth that is commonly observed in drier environments (Dohn *et al.*, 2013). However, as woody LAI increases above 2 LAI units, trees begin to suppress fires (SI, FigureS4.5c-d), perhaps through the combination of fuel suppression (competition for light and water) common in wetter zones (Dohn *et al.*, 2013) and through their effect on spatial distribution of herbaceous biomass and connectivity (Archibald *et al.*, 2012). These relationships between herbaceous and woody biomass in our models lead us to accept the applicability of our proposed savanna FCC hypothesis that in tropical savanna wild-fires (generally fueled by herbaceous materials) tend to increase linearly with herbaceous biomass reaching an asymptote above a certain biomass where fuel is no longer limiting. Further the BRT analysis and relative ranking of explanatory drivers tends to confirm our hypothesis that herbaceous biomass estimated indirectly using LAI_H is the most important determinant of fire in SSA, with LAI_W being less important overall, and exerting their effect indirectly via herbaceous fuel-load and connectivity.

It is noteworthy, we also tested the fire models with other environmental variables known to influence fire activity and spread in a landscape. Slope was included in initial model testing, but eliminated as 'non-informative' during the model simplification process as recommended for BRT (Elith *et al.*, 2008). The lack of statistical significance of the terrain variable slope in the fire models can perhaps be explained by the nature of SSA fires, which happen in savannas, characterized mainly by flat plains. We also tested applicability of Normalized Difference Water Index (NDWI) as an indicator of fuel moisture but was omitted due to its high collinearity with the remote sensing based estimates of leaf area index. We also note the limitation of the existing satellite based fire activity products which are surrounded by uncertainties and tend to underestimate fires (Chuvieco *et al.*, 2016). However, over time there has been improvement in the data, for instance MCD64A1 C6 product used in this analysis is now better compared to previous versions (Giglio *et al.*, 2013). Therefore, we believe the fire activity products used in this analysis, were able to capture the general fire activity patterns in SSA.

4.5. Implications of the research

The current paradigm contends that climate change will result in increased fire risk in various global ecosystems (Jolly *et al.*, 2015), necessitating a better understanding of fire activity and regimes across the globe. From this analysis, it is evident there is need for disentangling fuel load types in fire analysis and modeling. We also found that the role of seasonality, providing sufficient time for fuels to cure, was very influential in the fitted BRT models and will be important to consider in future projections. Consistent with our findings, Barros and Pereira (2014) found that some land cover types are more prone to fire than others. In particular, the overall negative exponential relationship between fire frequency and HPD provides strong evidence that in SSA, HPD is less about the availability of ignition sources, and much more about the specific land management approaches adopted in pastoral and agricultural regions, where local customs relating to the use of fire (it's acceptability or otherwise) may lead to significant regional differences in fire activity both now and into the future.

Data Accessibility Statement

The datasets used for this analysis can be accessed online most of which are freely available, as described below:

i. Percentage burnt area product from Global Fire Emissions Database version 4 (GFED4 without small fires) - at the time of this analysis, the data was accessed through - fuoco.geog.umd.edu. We used summaries derived from GFED4 burnt area product for years 2003-2015, see §2.1.1.1 in the main text

ii. Burned frequency derived from MODIS collection 6 burned area monthly product described in §2.1.1.2 in the main text can be availed here: https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd64a1_v006 -

iii. Aggregate and partitioned leaf area index data (§2.1.2 in main text) are described in Kahiu and Hanan (2017). Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v5s0j

iv. Rainfall data used for computing dry season length (DSL) are described and can be accessed here http://chg.geog.ucsb.edu/data/chirps/

v. Human population density data, Landscan developed by US Oak Ridge National Laboratory, which we are not at liberty to share due to the data use privacy policy, see their website for further details: http://web.ornl.gov/sci/landscan/landscan_data_avail.shtml.

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SUPPLEMENTARY MATERIAL

Supporting Information for

Fire in sub-Saharan Africa: the Fuel, Cure and Connectivity hypothesis

Appendix S1: A summary of the data used is in the analysis

The data used in the analysis presented in the main text are presented in Table S1.1.

Table S1.1: Environmental variables used in the fire analysis model that directly or indirectly affect fire patterns. All data types were aggregated at 0.25^{O} x 0.25^{O} to match the fire burnt area product.

Fire drivers	**Environmental variables**	**Derived statistics**
Fuel load	Aggregate LAI (IFP model)	Mean annual maximum (2003-2015)
	Herbaceous LAI (FCC model)	Mean annual maximum (2003-2015)
Tree canopy effects on herbaceous connectivity	Woody LAI	Mean annual maximum (2003-2015)
Fuel wetness (cure time)	Dry season length (DSL)	Average number of months with no rain (2003-2015)
Anthropogenic ignition and/or management	Human population density	Population density (people/km^2 for year 2015)

Appendix S2: Exploratory results

We note that, while simple bivariate plots provide some insight into underlying relationships, they can be misleading in multivariate systems with interacting processes. Thus, multivariate BRT analyses (Section 3.2 in the main text) are necessary to fully explore these datasets.

Plots of annual average percent burnt area (PBA) and burn frequency (BF) against fuel-loads, indexed using the aggregate (i.e. total) LAI, reveal the unimodal relationship, with fire activity highest at intermediate LAI, observed previously and identified as the intermediate fire-productivity (IFP) pyrogeographic framework (Figure 1, main text). While the range of PBA and BF includes some locations with very high annual burn fraction and annual fire occurrence, the majority of locations, shown by the loess curves, have lower annual-scale PBA and BF. Interestingly, the response of PBA and BF to variations in partitioned woody (LAI_W) and herbaceous (LAI_H) seasonal maximum leaf area index (Figure S2.1) are more consistent with the FCC framework, shown in Figure 2 (main text). In particular, the loess curves indicate near-linear increase in fire with herbaceous fuel (Figure S2.1c and f), and a unimodal relationship between fire activity and LAI_W (Figures S2.1b and e), consistent with tree facilitation of herbaceous growth in drier (low tree cover) regions, followed by suppression of fires through reduced connectivity in wetter (high tree cover) environments.

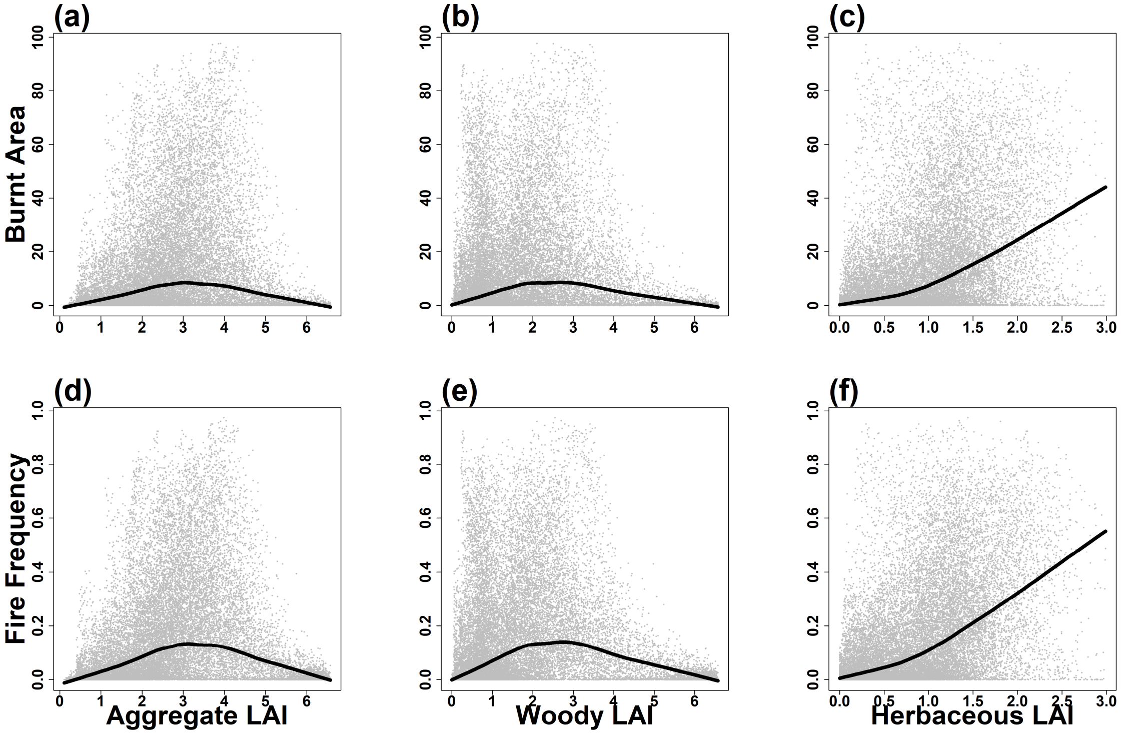

Figure S2.1: The relationship between fire activity and leaf area in sub-Saharan Africa. (a to c) percentage burnt area (PBA) and (d to f) burn frequency (BF), plotted against mean annual leaf area index (LAI) maxima for aggregate (a and d), woody (b and e) and herbaceous leaf area index (c and f). Fire activity and leaf area averages were computed for the 2003-2015 period. The solid black line is a smooth spline fit for the data.

Bivariate plots of fire responses to dry season length (DSL; Figure S2.2a and c) suggest a unimodal relationship, where the FCC model would predict an initial increase (low DSL locations being too wet to burn) followed by an asymptote (all locations with more than a threshold number of dry months, sufficient for fuel to cure, and are able to burn). Given that these are unimodal plots of bivariate relationships we conclude that the apparent decline in fire in drier locations (high DSL) may reflect interactions among drivers (e.g. fuel-load) that mask the expected effect of dry season length. These interactive effects are separated in the multivariate analysis (Section 3.2 of the main paper).

The apparent response of fires to human population density (HPD, Figs S2.2b and d) suggests an initial increase then a negative exponential prevalence of fires with increase in human populations. This pattern in the data is consistent with management differences among the pastoral zones, where human population is low and fires are often set for range improvement and hunting, compared to more densely populated areas where fire is used at more local scales for agricultural purposes and in landscapes where connectivity and fire spread is restricted.

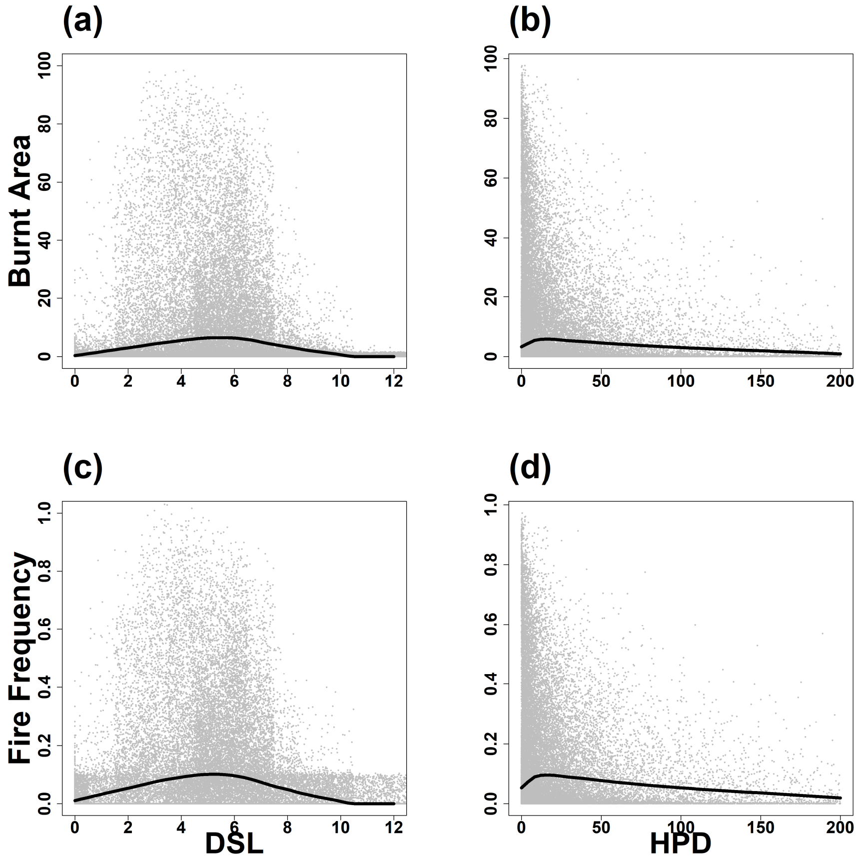

Figure S2.2: Relationships between fire activity, fuel moisture and human management. Top panel percentage burnt area versus (a) dry season length (DSL) and (b) human population density (HPD); and bottom panel fire frequency with (c) DSL and (d) HPD. The regression lines represented as black solid lines were fitted using loess smoothing function. The HPD data in the plot were restricted to <= 200 for viewing purposes but analysis restricted to <=500 to remove dense urban areas.

Appendix S3: Comparison of aggregate model predictions and observed burnt area and fire frequency

We further compare the observed and predicted PBA and BF in Figures S3.3 and S3.4. Both aggregate and partitioned models tend to under-predict fires at high observed fire activity, but partitioned models (Figure 8, main text) outperformed the aggregate models (Figure S3.3 and S3.4). Overall the fitted partitioned model performs better for PBA (R^2=0.59) and BF (R^2=0.63) than the aggregate model for PBA (R^2=0.49) and BF (R^2=0.53).

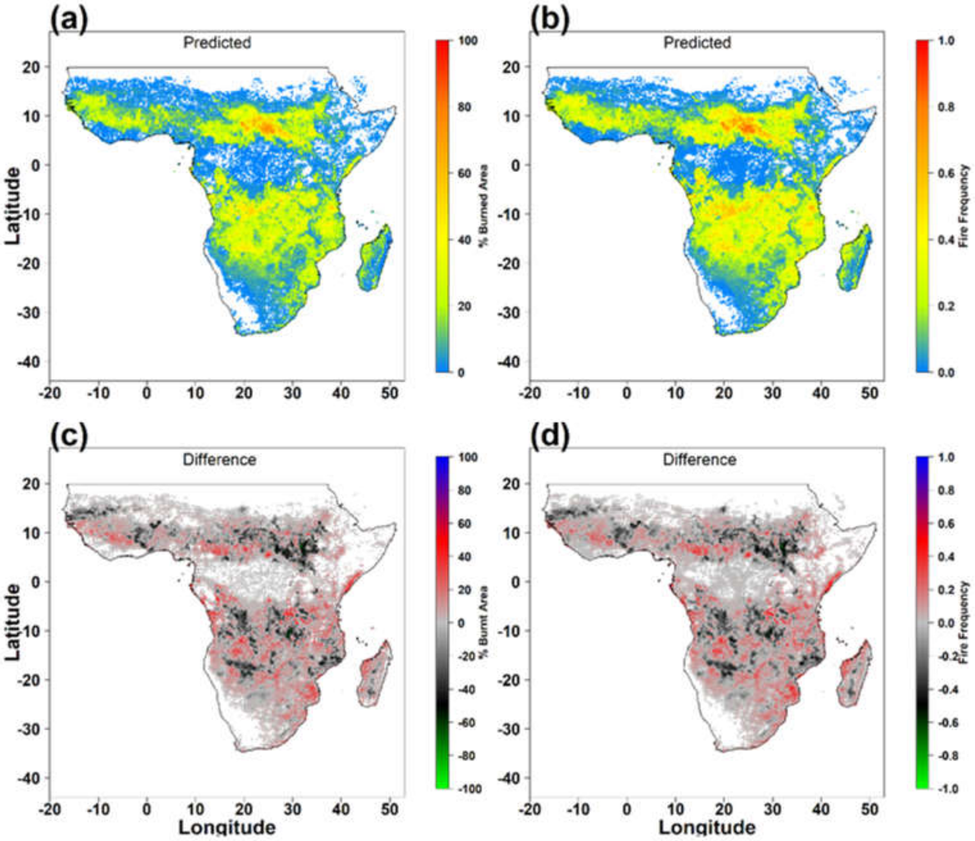

Figure S3.3: Comparison of predicted and satellite observed fire activity in sub-Saharan Africa using the aggregate leaf area index model. (a) Predicted burnt area and (b) Predicted fire frequency scaled between 0 and 1 both derived from Boosted regression tree (BRT) analysis. The differences between observed and predicted are shown in (c) burnt area and (d) fire frequency.

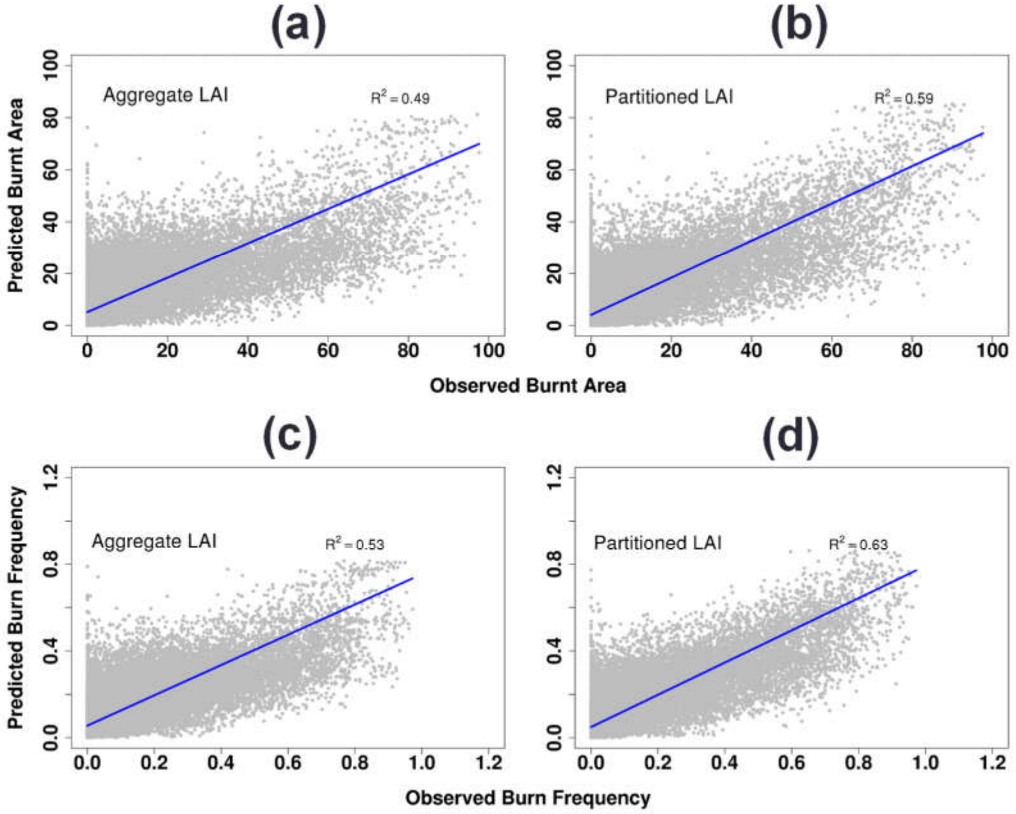

Figure S3.4: Scatter plots for predicted and observed fire activity in sub-Saharan Africa. (a, b) Percentage burnt area for aggregate LAI and partitioned LAI; (c, d) fire frequency for aggregate and partitioned LAI, respectively. Regression lines were fitted using standard major axis (SMA).

Appendix S4: Analysis of fire sensitivity to increasing herbaceous and woody biomass within various precipitation ranges

We grouped fire and partitioned leaf area index estimates according to mean annual precipitation (MAP) by separating data into four bins: arid (0-300 mm/y), semi-arid (300-600 mm/y), mesic (600-900 mm/y) and wet (> 900mm/y). To determine the changes in fire response to LAI_H and LAI_W in different rainfall zones, we fitted linear regression models within each bin with fire activity (burnt area and fire frequency) as the response variable and herbaceous and woody leaf area index as explanatory variables, as summarized in Table S4.2. We compared the fitted slopes to test the sensitivity of fire to increasing herbaceous (LAI_H) and woody biomass (LAI_W).

Table S4.2: Summary statistics for multiple linear regression models to assess sensitivity of fire (burnt area and fire frequency) to increasing seasonal maximum herbaceous (LAI_H) and woody (LAI_W) leaf area index within discrete precipitation ranges across sub-Saharan Africa.

Regression Model	**MAP Category**	**Variable**	***Burnt Area Coefficients***	***Fire Frequency Coefficients***
Formula = Fire ~ Herbaceous LAI + Woody LAI)	0 < MAP < 300 mm	Intercept	-0.619*	-0.010*
		LAI_H	3.428*	0.046*
		LAI_W	1.784*	0.032*
		R-squared	0.107*	0.048*
	300 < MAP < 600 mm	Intercept	-0.126	0.001
		LAI_H	8.713*	0.093*
		LAI_W	-0.568	-0.010
		R-squared	0.137*	0.092*
	600 < MAP < 900 mm	Intercept	0.578	0.001
		LAI_H	16.668*	0.200*
		LAI_W	-6.397*	-0.075*
		R-squared	0.241*	0.174*
	900 < MAP	Intercept	13.863*	0.179*
		LAI_H	9.924*	0.111*
		LAI_W	-1.983*	-0.025*
		R-squared	0.217*	0.159*
LAI- Leaf Area Index; MAP- Mean Annual Precipitation (millimeters per annum); the asterisks indicate the results were statistically significant at p-value <0.05				

We observe relationships that support the FCC model (Figure 2) as shown in Figure S4.5 and Table S4.2. Fire sensitivity to woody LAI (LAI_w) changes from positive for low rainfall to negative for high rainfall (Table S4.2 and Figure S4.5a-d). This supports our inference that the presence of shrubs and trees may facilitate herbaceous undergrowth (and thus increase fires) in arid environments (positive slope), changes to near neutral in semi-arid systems (Figure S4.5b), before competing with herbaceous growth and reducing connectivity (and thus decrease fires) in mesic and wet systems(Figures S4.5c-d; (Dohn *et al.*, 2013). On the other hand, we observe an increasing slope with LAI_H as mean annual precipitation changes from low to high (Table S4.2 and Figure S4.5e-h). These results reinforce the boosted regression tree (BRT) analysis and conclusions in the main text (Figure 7).

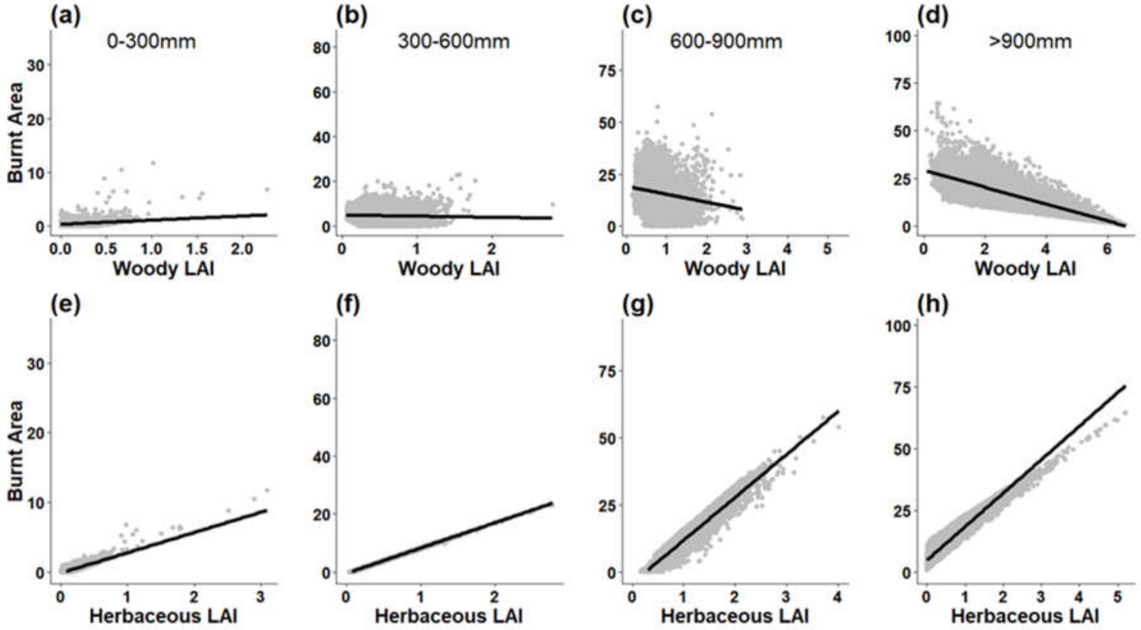

Figure S4.5: Scatter plots for relationship between average burnt area and partitioned fuel biomass (indexed using seasonal maximum LAI) in sub-Saharan Africa categorized according to mean annual precipitation (MAP in millimeters per annum) domains defined as arid (0-300 mm), semi-arid (300-600mm), mesic (600-900mm), and wet (> 900 mm). The scatterplots show multiple regression predictions (Table S4.2) for fire responses to herbaceous and woody biomass. Panels (a-d) show fire responses to woody LAI, with high scatter reflecting that woody LAI is not the primary fuel for fires (relatively low sensitivity to woody LAI as shown in Table S4.2), but instead highlighting a trend for trees to increase fires (slightly) in drier systems, and decrease fires in wetter systems, consistent with tree-grass facilitation-competition patterns (Dohn *et al.*, 2013) and the importance of fuel connectivity (see explanation in the main text). Panels (e-h) show all positive relationships between average burnt area and LAI_H, reflecting the importance of herbaceous fuel, with low scatter reflecting the much greater sensitivity of fire to LAI_H than to LAI_W (compare slopes in Table S4.2). The black lines are linear fits through plotted data.

Data used in the analysis are freely available online. Further details are provided in the data availability statement.

Supplementary References

Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K. A., & Hanan, N. P. (2013). Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. *Journal of Ecology, 101*(1), 202-209.

CHAPTER 4

Assessing the relationship between forage resources and livestock distributions in sub-Saharan Africa

Abstract

Aim The aim of this paper was to explore major correlates of livestock distribution in Africa with key emphasis on the relative influence of woody and herbaceous biomass as proxies of forage quantity for browsers and grazers respectively. Specifically, we tested the value of newly available partitioned woody (LAI_W) and herbaceous (LAI_H) biomass in understanding livestock distributions across sub-Saharan Africa (SSA); quantified the emergent sensitivity of livestock distribution patterns to patterns of forage and other environmental covariates; and evaluated the scale-dependence of locally established ecological relationships and patterns of herbivores and environmental variables at continental scale.

Location Sub-Saharan Africa (SSA).

Time period Livestock data centered on year 2007, with forage estimates derived as averages of years 2003 to 2015

Methods New estimates of available herbaceous forage and browse were analyzed using a combination of boosted regression tree (BRT) and analysis of variance (ANOVA) to explore major correlates of livestock distributions across SSA. Herbaceous (LAI_H) and woody (LAI_W) leaf area index used as proxies of grazing and browsing forage resources were coupled with other environmental covariates to infer herbivore distribution at continental scales.

Results Different environmental covariates had varying influences on livestock distribution in SSA, with water availability generally being the most critical

variable (>60% influence), except for goat distributions which were less sensitive to water availability. Forage biomass was the second most important variable in livestock distribution, with herbaceous and woody LAI rating either second or third in all models for cattle, sheep and goats. Herbaceous LAI had a positive correlation with grazers (sheep and cattle) reaching an asymptote for LAI>2. Human population density (HPD) was the most important variable in the distribution of smaller body mass animals (sheep and goats) with a relative influence of 26% for goats and 27% in sheep. Herbaceous production influenced livestock grazers more than woody production in the partitioned biomass model. LAI_H had a relative influence of ~17% and 16% compared to ~6% and 5% in LAI_W for grazers. Confounding results were observed in sheep (primarily grazers) and goats (primarily browsers) models, with both herbaceous and woody biomass negatively influencing their distribution. In sheep the relative influence of LAI_W was 25% compared to LAI_H at 12%. This influence is reversed in the predominantly browser goats with herbaceous biomass influence at 26% and woody biomass at 23%. Livestock generally favored regions with moderate to high soil nutrient availability. However, this relationship varied with animal body size, with larger body-size livestock (cattle) being less sensitive to forage nutrient status than small ruminants (sheep and goats). In agreement with our hypothesis that slope constrains animal movement, livestock preferred gentler slopes.

Conclusion These findings point to the need for including separate woody and herbaceous biomass in understanding herbivory. While the general patterns of established ecological relationships between livestock density and environmental variables are broadly consistent with expectations, the detailed rankings of variable

may not be perfect e.g. soil class effects in the BRT models is not always in strict order of increasing/decreasing nutrient status. This may be caused by uncertainties in the data on livestock distributions and environmental covariates rather than representing actual patterns. Better and finer spatio-temporal scale datasets and broadening of herbivore categories to include wildlife could improve the performance of our models.

Key words: Africa, Cattle, Forage resources, Goats, Herbaceous biomass, Herbivory, Remote sensing, Sheep, Woody biomass

1.0 Introduction

Large mammal herbivory plays a critical role in shaping and determining the structure and function of global vegetation, particularly in tropical savannas (Archibald & Hempson, 2016; Charles *et al.*, 2017; Staver *et al.*, 2009). Conversely, the distribution and abundance of large herbivores is determined by both ‘bottom-up’ and ‘top-down’ mechanisms. These mechanisms and controls apply for both wild and domestic herbivores. Bottom-up processes that jointly determine livestock herbivore distribution and densities usually relate to resource availability and accessibility (food quantity, quality, water, topography and weather; Bailey & Provenza, 2008; Hopcraft *et al.*, 2010), while top-down controls involve natural enemies (disease, parasites and predators; Grange & Duncan, 2006). To understand the determinants of herbivore abundance and distribution within these complex interactions, researchers have simplified them by breaking the various factors into biotic factors (forage quality and quantity, animal body size and disease) and abiotic factors (water, climate, topography), each of which have specific and interacting roles in herbivore distribution and abundance (Fritz & Duncan, 1994; Hopcraft *et al.*, 2010).

According to the species energy hypothesis, higher abundance and richness of heterotrophs should occur where available food energy is higher, readily and consistently available (Hobi *et al.*, 2017). In large mammalian grazing systems, however, herbivore distributions are also determined by the interaction of forage nutritional quality and herbivore body size, that impacts energy requirements, gut residence time and herbivore ability to process low-quality forage (Clauss *et al.*, 2013). Larger herbivores require large amounts of biomass, but can cope with relatively low nutrient concentrations, hence they tend to occur in wetter ecosystems characterized by high productivity and low quality forage. In these wetter ecosystems herbaceous plants in particular, allocate more energy to structural development, resulting in vegetation with high biomass but low nutritional quality. Thus in the grazing lands, larger herbivores tend to occupy areas of high plant biomass availability and low soil nutrients, while smaller herbivores are more limited by forage quality and tend to be more common in areas with low plant productivity, but higher soil fertility and plant nutrient status (Fritz & Loison, 2006).

Human population density (HPD) is also important in determining herbivore distribution. Studies show a positive correlation between productivity and human density, as humans tend to settle in moderate to high productivity areas (Luck, 2007). This scenario creates competition between agricultural activities and herbivores, and studies have linked human colonization of terrestrial ecosystems to loss of wild herbivores (Burney & Flannery, 2005). On the other hand, humans dictate the distribution of domestic herbivores, with wetter ecosystems favored for crop production while drylands are left for pastoralism, particularly in Africa. We therefore anticipate a negative correlation between livestock and HPD or likely an initial increase in low HPD then a decline in higher HPD areas especially in the wetter crop production areas.

Although various biotic and abiotic factors control spatiotemporal distribution, abundance, and density of livestock herbivores, forage resources (quality and quantity) remain the principal determinant, especially in Africa where extensive studies on large herbivores have shown productivity regulates herbivore populations through bottom-up mechanisms of resource limitation (Fritz & Loison, 2006 and citations therein; Hopcraft *et al.*, 2010). African dryland and savanna ecosystems support among the richest and most diverse communities of wild herbivores (Anderson *et al.*, 2016; Du Toit &

Cumming, 1999; Shorrocks & Bates, 2015). However, as in other parts of the world, most larger wild herbivores are now confined within protected areas (Shugart, 1998), leaving vast landscapes dominated by pastoralist land use systems and livestock. Understanding the biotic and abiotic factors that determine livestock distribution and abundance is key to best management practices and for better understanding of how livestock systems may respond to future environmental changes, including shrub encroachment, changing patterns of rainfall and temperature, and habitat fragmentation/loss to agriculture.

Despite many advances in our understanding of the ecology, abundance and distribution of herbivores, research is limited by lack of detailed observations at large spatial scales (Sagarin *et al.*, 2006). Here we use FAO census data on livetock distribution and abundance across Africa to explore the drivers of pastoral practices in the rangeland ecosystems in Africa, which comprise over 50% of the land area of sub-Saharan Africa (SSA) and provide sustainable livelihoods and protein to African populations (African Union, 2010). Although sometimes ignored, pastoralism directly supports ~300 million people in SSA, and contributes significantly to African economies through supply of animal products to domestic, regional and international markets (African Union, 2010).

Previous research has focused on understanding large wild herbivore abundance, distribution and density at local level (Ganskopp, 2001; Schoenbaum *et al.*, 2017), with few studies using remote sensing data. Our novel approach uses continental scale satellite derived forage estimates, coupled with environmental variables, to analyze the large scale biogeographical determinants of livestock distribution, abundance and density in SSA. In addition to the biological and physical constraints on large herbivore distributions cited earlier, livestock distributions also depend on complex combinations of socio-economic and political factors that may limit the ability of pastoralist communities to raise livestock in areas where they can optimize on forage quantity and quality. We explored the distinct roles played by herbaceous and woody forage availability, anticipating that herbaceous production influences grazers, while woody production influences browsers. We anticipated positive linear or asymptotic relationships between forage resources (LAI_H for grazers and LAI_W for browsers) and livestock biomass. Additionally, larger livestock (cattle) have the ability to process high quantity-low quality food, while smaller herbivores are more limited by forage quality and thus tend to dominate areas with low plant productivity but higher nutrients. Hence, we hypothesized large herbivores will be more common in high forage production areas irrespective of forage quality, while smaller livestock including sheep and goats will favor nutrient-rich areas. Water also constrains livestock distribution (Bailey & Provenza, 2008; Peden *et al.*, 2007), therefore we posit that livestock density will be sensitive to the local availability of water, but quickly reach an asymptote as small water bodies can provide drinking water to animals foraging over a much larger geographical area. Human management systems regulate livestock distribution through agricultural expansion, urbanization and infrastructural development. We hypothesized an initial rapid increase of livestock with human population density, declining in more densely populated agricultural areas. Terrain constrains animal movement and livestock prefer gentle slopes (Bailey, 2005), hence we expected an inverse relationship between livestock abundance and slope.

To test our hypotheses we used herbaceous (LAI_H) and woody leaf area index (LAI_W) retrievals for all of sub-Saharan Africa at 1 km spatial and 8-day temporal resolutions (Kahiu & Hanan, 2017) to compute annual average maxima leaf area index (LAI_{max}) as proxies for forage quantity for domestic herbivore grazers and browsers, respectively. Our aim was to test whether these remote sensing estimates of separate grazing and browsing forage resources and other environmental covariates can be used to infer the drivers of herbivore distribution at continental scales. Forage quality and accessibility vary with vegetation type and soil nutrients. Broadly speaking, since soil nutrients influence forage quality (Archibald & Hempson, 2016), we included soil nutrient availability as an index of forage nutritional status.

Our research objectives were to: i) test the value of newly available partitioned woody (LAI_W) and herbaceous (LAI_H) biomass in understanding livestock distributions across sub-Saharan Africa; ii) quantify the emergent sensitivity of livestock distribution patterns to patterns of forage and other environmental covariates, and (iii) evaluate the scale-dependence of locally established ecological relationships and patterns at continental scale.

2.0 Materials and Methods

2.1. Data and preprocessing steps

2.1.1. Herbivore datasets and sub-Saharan Africa administrative boundaries

Sub-Saharan Africa (SSA) administrative boundaries were accessed through the Database of Global Administrative Areas (GADM; http://gadm.org/version2) in ESRI shapefile format. Country livestock estimates were sourced from Global Livestock Production and Health Atlas (GLiPHA; Clements *et al.*, 2002; FAO, 2018) downloaded from http://kids.fao.org/glipha/# which provides census estimates at sub-national administrative district scales. Manual disambiguation was required in cases of spelling differences and administrative district name changes. We elected not to use the spatially interpolated data of Robinson *et al.* (2014), instead deciding to use the original census data from GLiPHA cross-matched to corresponding administrative districts in the SSA administrative boundaries shapefile. This decision to use original census data also avoided circularity in modeling livestock distributions that were interpolated, in part, based on environmental variables (Robinson et al., 2014). In a few countries where no recent livestock data estimates were available through GLiPHA we used national estimates available from the Food and Agriculture Organization Corporate Statistical Database (FAOSTAT; http://www.fao.org/faostat/en/#data/QA). All livestock numbers were converted to Tropical Livestock Units (TLU; i.e. 250 kg of live animal weight) using tropical Africa conversion factors for cattle at 0.70 TLU, sheep and goats at 0.10 TLU (Jahnke & Jahnke, 1982). The resulting TLU was used to compute TLU density/km^2

within each administrative block. In total we had 528 administration units across SSA (Figure 1).

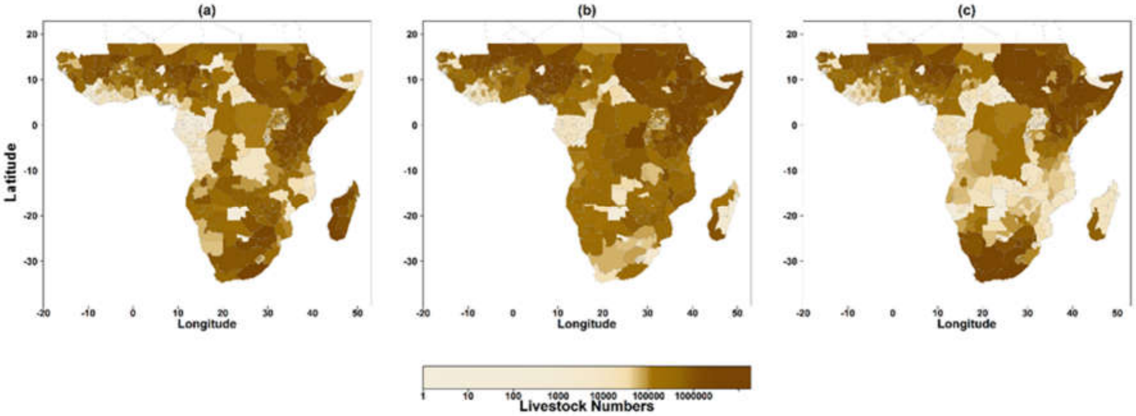

Figure 1: Livestock distribution maps (in tropical livestock units, TLU) in sub-Saharan Africa, (a) Cattle, (b) goats and (c) sheep. The data are based on original census data within sub-national administrative units, as reported by the Global Livestock Production and Health Atlas (GLiPHA; Clements *et al.*, 2002)

To conduct analysis of variance (ANOVA) for the different biomes, we further regrouped the administrative zones into biome classes using a summarized version of White’s vegetation map of Africa (White, 1983), shown in Table 1. All the variables were summarized based on the majority biome class.

Table 1: Biome class, mean annual rainfall and mean nutrient status for bio-climatic regions across sub-Saharan Africa.

	Biome Class	MAP (mm/annum)	Nutrient Status
1	*Rift-Sudano Guinea*	1180	No Limitations
2	*Sahel*	487	No Limitations
3	*Southern Dry*	610	No Limitations
4	*Moist Tropical Forest*	1874	Severe limitations
5	*East African Bimodal*	879	No Limitations
6	*Southern Mesic*	1102	Moderate limitations
7	*Sahara*	130	No Limitations
8	*The Horn Arid*	317	Moderate limitations
9	*Southern Arid*	238	Moderate limitations
10	*Madagascar Dry*	1330	No Limitations
11	*Madagascar Humid*	1887	Severe limitations

MAP - Mean Annual Precipitation; mm- millimeters

2.1.2. Forage resource estimates: MODIS aggregate and partitioned woody and herbaceous leaf area index

We used Collection 5 (C5) MODIS total (aggregate) leaf area index (Myneni *et al.*, 2015) and its woody and herbaceous constituents as proxies for forage biomass (Figure 2).

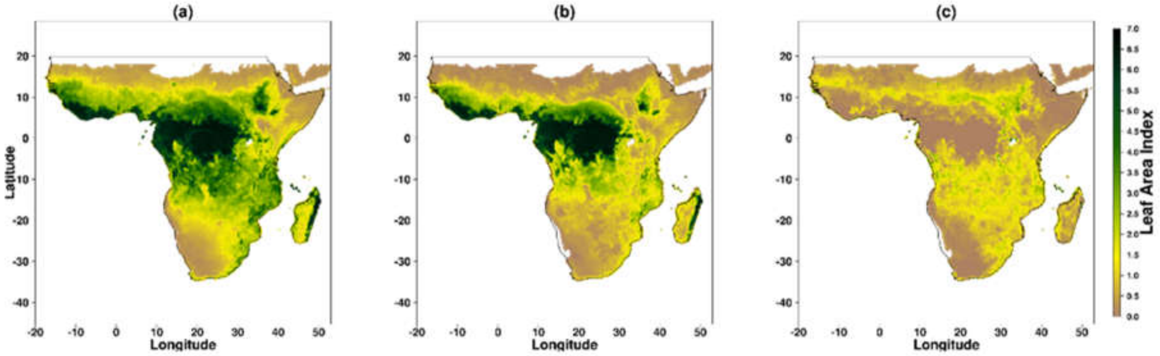

Figure 2: Maps of annual average maximum leaf area index in sub-Saharan Africa, (a) aggregate LAI_{Amax} from MODIS, (b) partitioned woody LAI_{Wmax}, and (c) partitioned herbaceous LAI_{Hmax} (data from Kahiu & Hanan, 2017). The data were derived as the per pixel average of annual LAI maxima for years 2003 to 2015

The partitioned LAI products were generated using the dataset described by Kahiu and Hanan (2017). In summary, the partitioning of aggregate LAI (LAI_A) from the MODIS satellite is dependent on an allometric relationship between precipitation and seasonal LAI maxima for dominant woody (trees, shrubs and bushes) species in Africa. From the aggregate and partitioned LAI product at 8-day and 1km spatial resolution we computed the per pixel yearly maximum LAI then averaged over the 2003-2015 study epoch (Figure 2). These estimates were used to derive the average regional woody and herbaceous LAI estimates for the livestock administrative zones generated in section 2.1

2.1.3. Topography

We used the GTOPO30 Global digital elevation model (DEM) at 30 Arc-Second (approximately 1km at the Equator) from the US Geological Survey (USGS; https://lta.cr.usgs.gov/GTOPO30) to estimate topographic relief and slope for SSA (Figure 3a). The derived slope was used to determine the average topography for the livestock administrative zones used in this analysis.

2.1.4. Soil nutrient availability

Soil nutrient status was estimated using the Food and Agricultural Organization (FAO) soil nutrient availability index from the Harmonized World Soil Database v 1.2 (HWSD; Figure 3b). The dataset comprises four qualitative categories on soil nutrient limitations coded 1 to 4, namely: No or slight limitations (1); Moderate limitations (2); Severe limitations (3) and Very severe limitations (4). The HWSD meta-data classify growth potential for these qualitative classes whereby class 1 is rated 80 -100%, class 2 has 60 - 80%, class 3 with 40 - 60%, and class 4 has less than 40%. Within each administrative zone we extracted the majority nutrient availability index class.

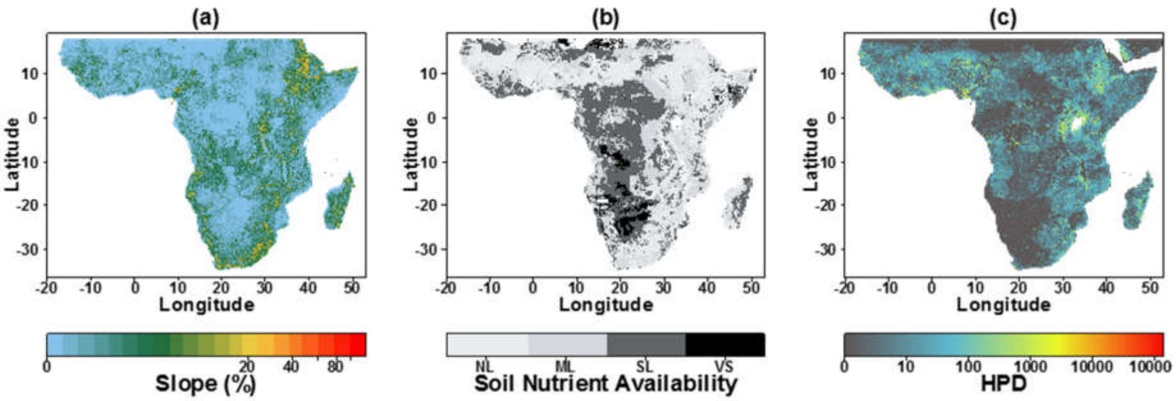

Figure 3: Maps of sub-Saharan Africa for (a) topography using slope estimates; (b) soil nutrient availability status from the Harmonized World Soil Database v 1.2, where NL, ML, SL and VS represent Non-or Slight Limitations; Moderate Limitations; Severe Limitation and Very Severe Limitations respectively; and (c) human population density (HPD; humans per km^2) based on gridded Landscan population estimates for year 2015.

2.1.5. Water resources

The availability of surface water for livestock was estimated using the World Wildlife Fund (WWF) gridded Global Lakes and Wetlands Database level 3 (GLWD-3) at 30-second spatial resolution (Lehner & Döll, 2004; Figure 4b). We computed the fraction of each administrative zone covered by water (or wetland). The wetland classes comprise of open water to fractional wetland areas.

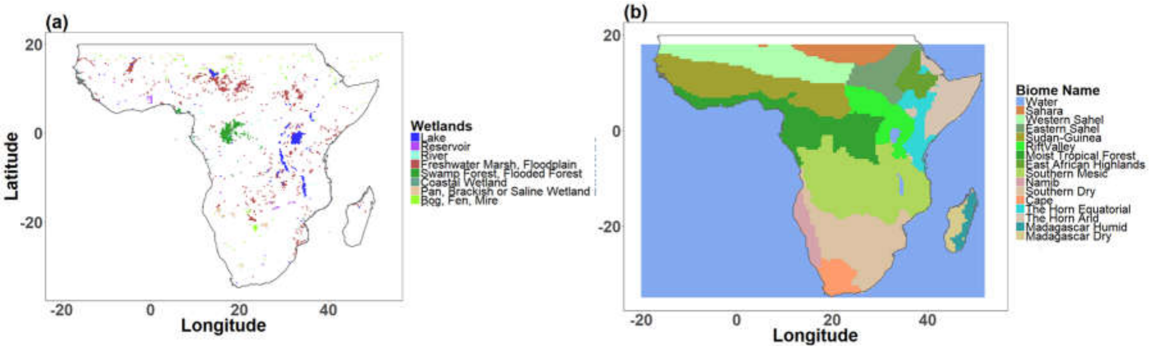

Figure 4: (a) Water resources map for sub-Saharan Africa derived from World Wildlife Fund gridded Global Lakes and Wetlands Database Level 3; and (b) Biome map based on Whites vegetation map of Africa (White, 1983), aggregated by region and rainfall, used for summarizing livestock numbers within the various regions in Africa

2.1.6. Human population density

We computed the 2015 Human Population Density (HPD) from gridded Landscan population dataset developed by US Oak Ridge National Laboratory, available at ~1km spatial resolution (Bhaduri et al., 2002; Figure 3c). We eliminated urban area pixels where HPD>1000, then extracted the zonal statistics using means for the SSA administrative boundaries.

2.1.7. Biome map for summarizing regional livestock distribution

To assess livestock distribution across SSA we summarized the numbers and TLUs in the major biomes of SSA (Figure 4b). To generate the biome map we used White's vegetation map for Africa (White, 1983) to aggregate the classes based on rainfall and geography to provide functionally similar regions for ease in display.

2.2. Modelling criteria

To test our hypotheses, we used Boosted Regression Tree (BRT) analysis, which are statistical machine learning methods that combine regression and classification for better model performance. BRTs are advantageous over traditional statistical methods since they combine the strengths of regression trees with boosting, hence can handle various types of response and predictor variables (numerical, categorical, census) can fit linear and complex nonlinear relationships, are able to handle missing data and outliers with no need to transform data or remove outliers, and allow users to quantify and visualize interactions between predictors (De'ath, 2007; Elith *et al.*, 2008). To fit the BRT models we used the 'gbm.step' function in R dismo package (Hijmans *et al.*, 2017) and set the parameters as follows: nature of the error structure (family) = 'poisson', learning rate = 0.001, tree complexity = 5, bag fraction = 0.5, and retained the default number of trees = 50.

We tested two basic models (Table 2) describing how livestock distribution is determined by forage biomass in sub-Saharan Africa with respect to (i) aggregate LAI (LAI_A), and (ii) partitioned LAI (herbaceous and woody LAI).

Table 2: Aggregate and partitioned models used for the herbivory analysis using boosted regression trees

Response variable **(Livestock TLU km^{-2})**	***Explanatory Variables*** Model 1: Aggregate model	Model 2: Partitioned model
Total Livestock	Aggregate LAI (LAI_A) + Human Population Density (HPD) + Nutrients + Water Coverage + Slope	Herbaceous LAI (LAI_H) + Woody LAI (LAI_W) + Human Population Density (HPD) + Nutrients + Water Coverage + Slope
Cattle		
Sheep		
Goats		

Using biome classes shown in Table 1 we assessed the variations in livestock distribution using multiple linear regression models and analysis of variance (ANOVA) using log-transformed predictor and dependent variables to satisfy the assumptions of linear regression. The aggregate model was of the form: $\log(\text{Herbivore} + 1) \sim \log(LAI_A+1) + \log(HPD+1)$ + Biome Types + $\log(\text{Water Coverage}+1) + \log(\text{Slope}+1)$ while in the partitioned model we substituted the aggregate biomass with the separate woody and herbaceous forage biomass: $\log(\text{herbivore}+1) \sim \log(LAI_W+1) + \log(LAI_H+1) + \log(HPD+1)$ + Biome Types + $\log(\text{Water Coverage} +1) + \log(\text{Slope}+1)$. To compare means between the variables we derived ANOVA statistics for the individual aggregate and partitioned models. Additionally, we assessed whether inclusion of partitioned forage estimates adds value to the understanding of herbivore distribution, by comparing the regression results of aggregate and partitioned models.

3.0 Results

3.1. Livestock distribution in sub-Saharan Africa by biome type

Across the entire SSA, total livestock numbers vary by groups. Considering the 'raw' livestock numbers, goats were most numerous, followed by cattle then sheep (Figure 5a). After converting to a biomass proxy using tropical livestock units (1 TLU = 250 kg live weight), the ranking changed with cattle highest and sheep the least (Figure 5b).

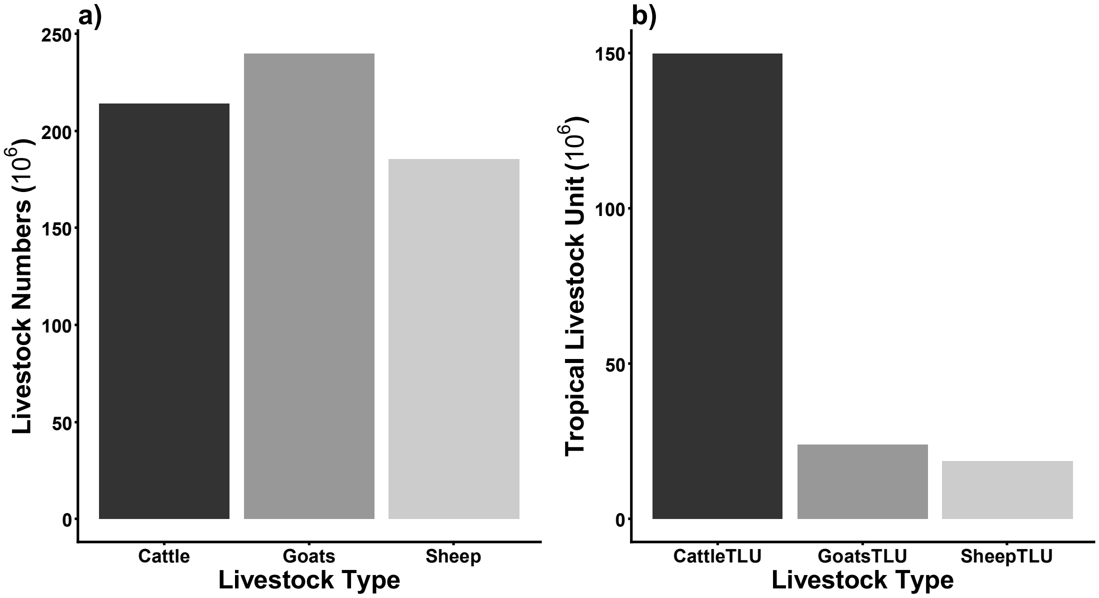

Figure 5: Livestock numbers in all of sub-Saharan Africa. In (a) total livestock numbers for cattle, goats and sheep and (b) total tropical livestock units (TLU), based on average African livestock weights of 175 kg (cattle, TLU=0.7) and 25 kg (goats and sheep, TLU=0.1).

According to biome classifications, East African bimodal region had the highest livestock density, while the desert fringes of the Sahara and Namib ("southern arid") and the moist tropical forest had the lowest livestock density (Figure 6). In non-desert regions, while livestock densities generally decline with increasing rainfall, the patterns also reflect local land use systems and livestock-herding practices.

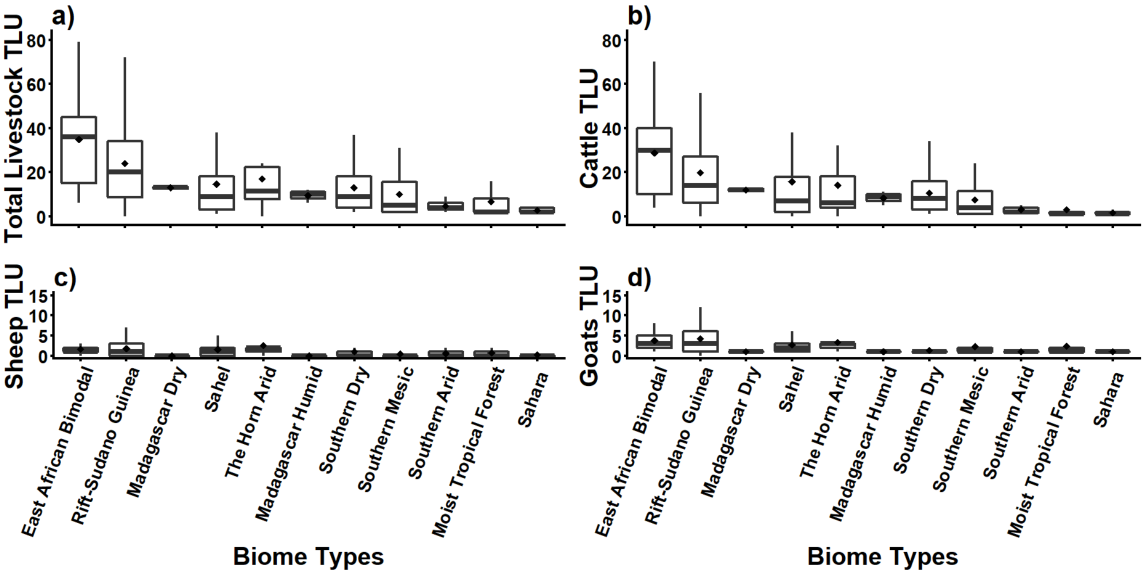

Figure 6: Distribution of livestock biomass by biome type in sub-Saharan Africa using the tropical livestock units (TLU km^{-2}). The boxplots show (a) total livestock, (b) cattle, (c) sheep and (d) goats. Diamond black dots are the means, boxplot lower and upper bounds show 25th and 75th percentiles respectively; the inner horizontal line denotes median, and vertical whiskers showing the full range of data (excluding outliers exceeding 1.5 interquartile range). Biomes are ordered according to total livestock median.

3.2. Model performance and relative influence of environmental covariates on livestock distribution

To compare the performance of both aggregate and partitioned models, we conducted BRT, multiple linear regression and ANOVA. The partitioned model performed better in the regression analysis with model explanatory power from the R^2 statistic slightly higher than the aggregate model (Supplementary Table S1). ANOVA analysis for both models show inclusion of the separate woody and herbaceous forage biomass added value to understanding herbivore distribution in SSA, with F-values for all the models statistically significant at p-value <0.05 (Table 3). However, in the BRT models the explanatory power in both the aggregate and partitioned models were similar (Table 4).

Table 3: Analysis of variance (ANOVA) results comparing multiple linear regression for aggregate and partitioned models for total livestock, cattle, goats and sheep

Herbivore	**Model**	**Res.DF**	**RSS**	**DF**	**Sum.of.Sq**	**F-value**	**p-value**
Total TLU	Aggregate	513	327.179				
	Partitioned	512	322.044	1	5.134	8.163	0.004
Cattle TLU	Aggregate	513	396.704				
	Partitioned	512	389.635	1	7.070	9.290	0.002
Sheep TLU	Aggregate	513	195.959				
	Partitioned	512	189.578	1	6.381	17.232	0.000
Goats TLU	Aggregate	513	172.901				
	Partitioned	512	171.361	1	1.540	4.601	0.032

TLU-Tropical Livestock Unit

In the aggregate model, water fraction was the most influential independent driver for total livestock distributions, while HPD rated second, aggregate biomass third, slope fourth and soil nutrient availability the least influential. The importance of water in the overall livestock model was driven primarily by cattle distributions (Figure S1-S3), a pattern which may reflect cattle heavy dependency on water (Figure 5b). Conversely, HPD had the most influence on small ruminant numbers (sheep and goats), as summarized in Table 4. In the aggregate models, forage availability indexed by LAI_A, also appeared to be far more influential in the distribution of small ruminants (sheep and goats; Figures S4 and S5) than cattle (Table 4 and Figure S3). Soil nutrient status had a generally small role in aggregate models, with the exception of the sheep model at 15%, compared to 5% for goats and at <1.5% for total livestock and cattle models (Table 4; Figure 8).

Table 4: Relative influence of explanatory variables for the aggregate and partitioned model in explaining livestock distribution in sub-Saharan Africa derived from boosted regression tree models developed with cross-validation on data from 528 observations and a tree complexity of 5

	Aggregate Model			
Variable	*Total Livestock*	*Cattle*	*Goats*	*Sheep*
HPD	12.0	10.5	33.3	32.8
Aggregate LAI	9.3	6.4	27.7	24.8
Nutrients	1.1	0.7	4.2	14.6
Slope	7.1	5.2	15.4	9.5
Water Fraction	70.4	77.1	19.3	18.3
SE	0.04	0.04	0.05	0.06
R-Squared	0.1	0.1	0.2	0.3
	Partitioned Model			
HPD	10.8	7.9	28.2	27.9
Herbaceous LAI	15.3	16.5	25.3	13.0
Woody LAI	8.2	4.5	21.8	25.3
Nutrients	0.5	0.3	1.8	5.3
Slope	3.9	3.0	11.7	6.7
Water Fraction	61.2	67.7	11.2	21.8
SE	0.04	0.05	0.06	0.09
R-Squared	0.1	0.1	0.2	0.3
SE-Standard Error				

In the partitioned model, where we used separate estimates of woody (LAI_W; for browsers) and herbaceous (LAI_H; for grazers) forage availability, we also observed water as the main determinant of herbivore distributions in the total livestock and cattle models (Table 4), but the more refined indices of forage availability explained more of the variability than in the aggregate model. The critical importance of water on livestock models was also evident in the total livestock and cattle models influencing >60% livestock distribution, while reducing in the smaller ruminants at 23% for sheep and 12% for the drought resistant goats. Livestock responded to water presence as long as it is available within a certain threshold, above which no observable change was apparent in both aggregate and partitioned models. We argue that water is the first requirement for water-dependent domestic animals (i.e. no water, no livestock). Once water is available, the other variables become important. Nutrient availability had relatively little influence on the fitted BRT models for total livestock and cattle models, although in the small livestock (sheep and goats), the percentage level of influence was slightly higher in both the aggregate and partitioned models.

3.3. Livestock relationship with biotic and abiotic factors

The spatial distribution of cattle, sheep and goats was sensitive to the presence of water, with livestock densities low in areas with little or no surface water, increasing rapidly to an asymptote above which no further effect was observable in both aggregate (Figures S1 to S6) and partitioned (Figures 7 to 10) models. HPD had a sigmoidal relationship with livestock distribution, increasing with human population and reaching an asymptote in areas HPD >200 confirming our hypothesis that HPD is strongly correlated with livestock to a certain threshold. The increase corresponds with rangelands where we anticipated high livestock numbers.

In the aggregate models (Figures S1 to S6), forage biomass indexed using LAI_A showed high numbers in areas with moderate LAI values but then declining beyond LAI_A of 3, in contrast to our hypothesis of unimodality. As expected livestock correlated negatively with slope, declining with increasing slope, since livestock (and pastoralists in general) avoid areas of high elevations and slope.

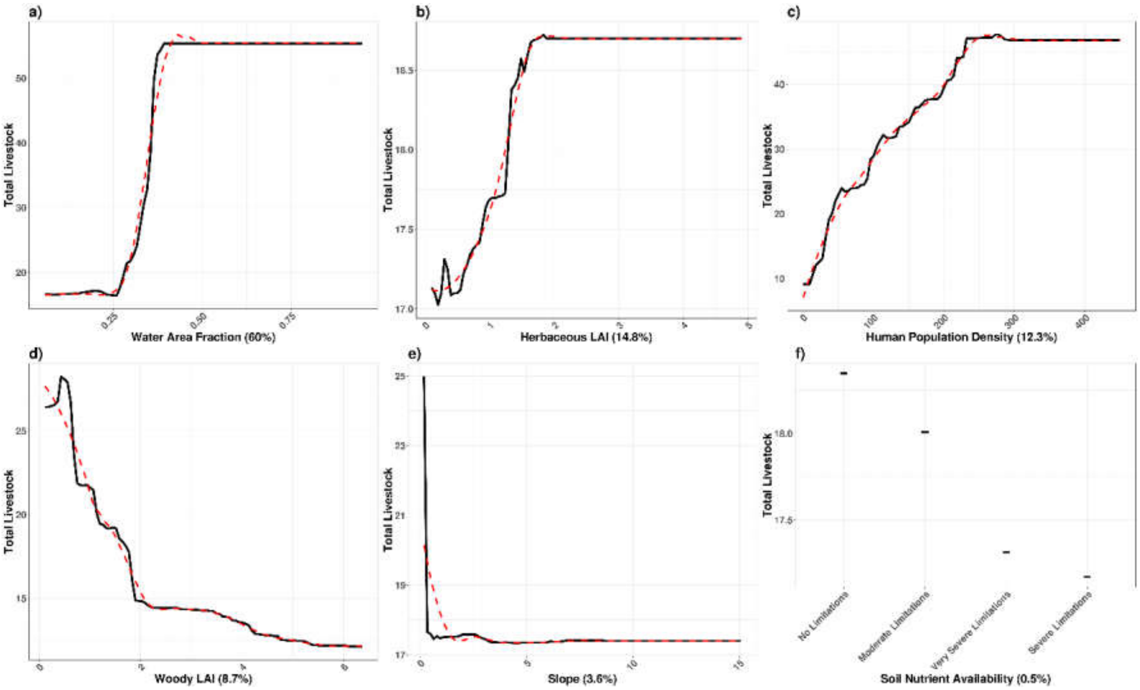

Figure 7:Partitioned boosted regression tree model response of total livestock (cattle, goats and sheep, in TLU km^{-2}) to spatial distribution of environmental covariates, including (a) water coverage, (b) herbaceous LAI (LAI$_H$), (c) human population density, (d) woody LAI (LAI$_W$), (e) slope, and (f) soil nutrient availability status. The relative influence of each variable is shown along the x-axis labels (in brackets).

In the partitioned model, the herbaceous biomass (LAI$_H$) which ranks as the second most important variable in livestock distribution for the total livestock, and cattle models had a strong positive correlation with livestock biomass consistent with our hypothesis. On the other hand, the negative relationship between LAI$_H$ and the predominantly grazing sheep is unexpected as sheep decline with both LAI$_H$ and LAI$_W$ (Figure 8). The negative relationship between LAI$_H$ and goats (Figure 9) confirmed our hypothesis that goats that are characteristically browsers will favor regions with higher woody biomass. The negative relationship between woody biomass (LAI$_W$) and total livestock is realistic and in line with our expectation since the largest part of the livestock biomass, were grazers (sheep and cattle, Figure 5) that mainly depend on the herbaceous forage biomass.

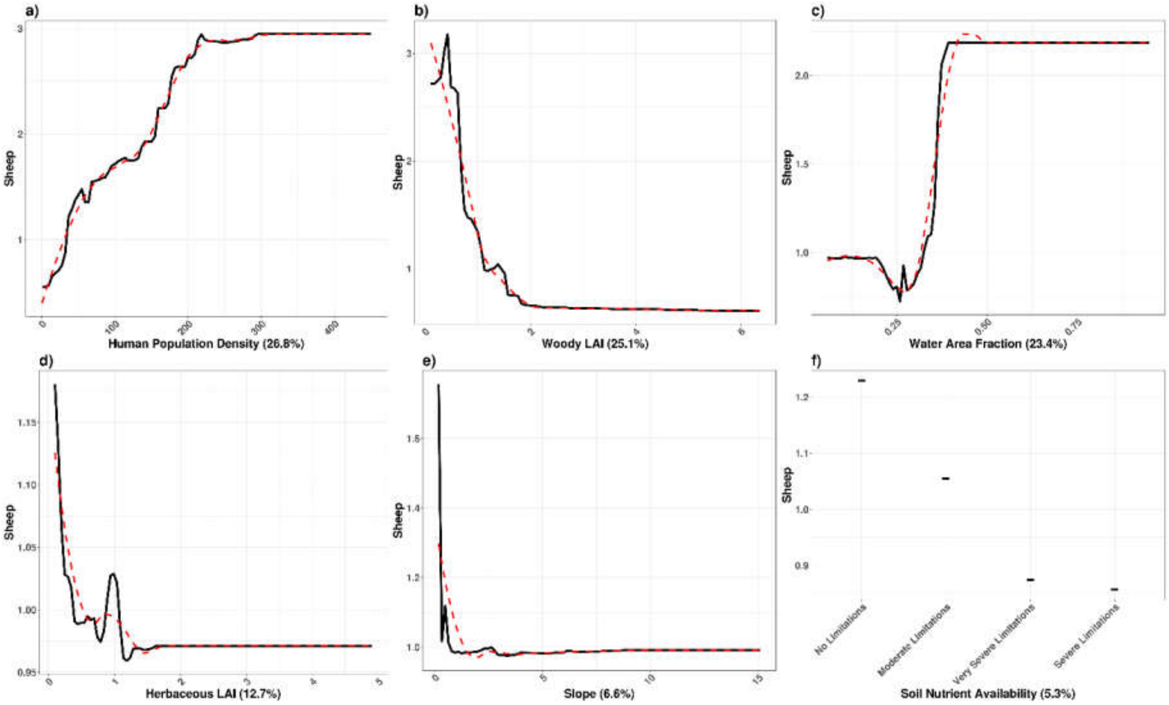

Figure 8: Partitioned BRT model marginal response of sheep (in TLU km^{-2}) to spatial distribution of environmental covariates, including (a) human population density, (b) woody leaf area index, (c) water coverage, (d) herbaceous leaf area index, (e) slope, and (f) soil nutrient availability. Quoted in brackets within the x-axis labels are relative influence of the explanatory variables on sheep.

In goats, which are primarily browsers (Figure 9), we observe somewhat comparable patterns to the sheep model (Figure 8), though differences were evident in the explanatory power of the variables. In the aggregate model, HPD, total biomass (LAI_A) and water remained the three most important variables in that order, Figures S5. LAI_W ranking higher than LAI_H is rather confounding and in contrast with our expected relationship that woody biomass would have rather a more significant role in distribution of the largely browser goats than the herbaceous vegetation.

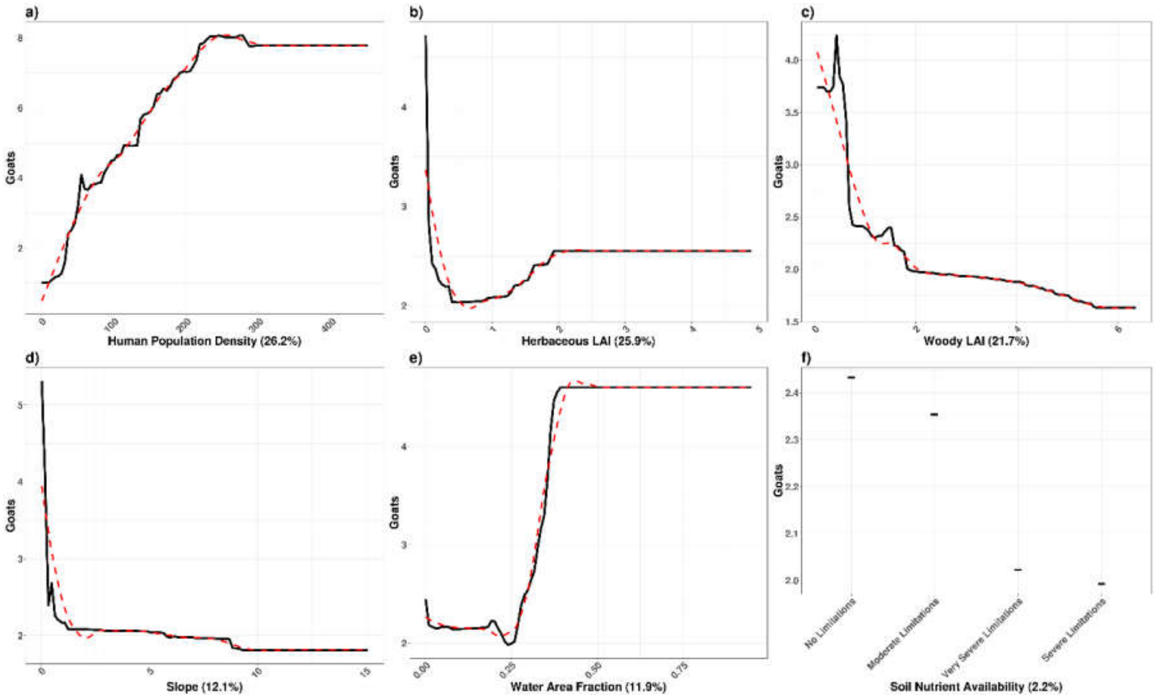

Figure 9: Partitioned BRT model marginal response of goats (predominantly browsers, in TLU km^{-2}) to spatial distribution of environmental covariates, including (a) human population density, (b) herbaceous leaf area index, (c) woody leaf area index, (d) slope, (e) water coverage, and (f) soil nutrient availability. The relative influence of each variable is quoted in brackets within the x-axis labels

3.4. Herbivore distribution contrasting livestock diet types and body size categorizations

In the analysis, we assessed relationships for individual livestock type but also for feeding type categories to assess the differences between browsers and grazers and animal body sizes. We observed similar patterns for cattle and total livestock in both aggregate and partitioned LAI models perhaps due to the large cattle biomass, Figure 5b. However, slight differences were evident in the relative influence of the environmental variables used, Table 4

3.4.1 Browsers versus grazers

Here we compared livestock grazers (cattle and sheep) with browsers (goats). Cattle had a negative relationship with woody LAI in contrast to the positive relationship with herbaceous biomass ($\mathrm{LAI_H}$), which was also the second most important variable in their distribution, Figure 10. This relationship was somewhat different in the sheep model (Figure 8), as expected a negative relationship with woody biomass emerged but rather unclear pattern with herbaceous biomass estimates. Diverging from our expectations, we observed a negative nonlinear relationship with goats (largely browsers) and woody biomass. We suppose this relationship perhaps could be due to our partitioned woody and herbaceous estimates with forbs and smaller shrubs that goats mainly feed on being classified as herbaceous LAI estimates.

3.4.2 Variations with body biomass

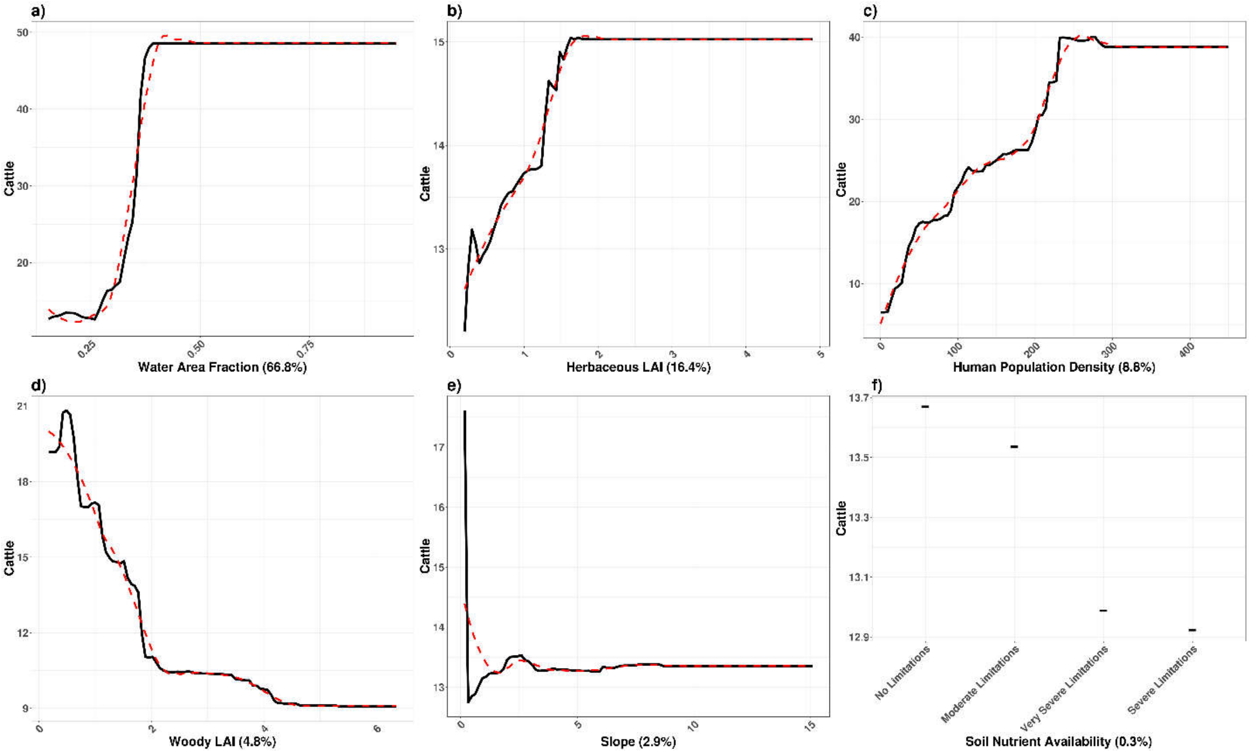

Figure 10: Relationship and relative influence of environmental covariates on larger feeders (cattle) in the partitioned model in relation to (a) water coverage, (b) herbaceous leaf area index, (c) human population density, (d) woody leaf area index, (e) slope, and (f) soil nutrient availability. The relative influence of each variable is quoted in brackets within the x-axis labels. Red lines were fitted using loess smoothing

We compared large (cattle) with smaller (sheep and goats) feeders to assess the influence of body biomass on herbivore distribution in SSA. In the large feeders (Figure 10), water was the most important followed by herbaceous LAI, while in the smaller feeders, HPD ranked the most important variable followed by either herbaceous biomass in goats or woody biomass in sheep. Nutrients in both feeders were the least important in the partitioned models. In general, livestock densities were higher in the more nutrient rich systems relative to the nutrient poor systems. The relative influence of soil nutrients in small feeders was higher at 5.3% for sheep (Figure 8f) and 2.2% for goats (Figure 9f) compared to the large feeders at 0.3% (Figure 10f). These results indicate that smaller herbivores favor higher nutrient resources compared to larger animals requiring large forage quantities regardless of their nutritional status. While the general patterns of livestock density to variations in soil nutrients were broadly consistent with expectations, the detailed ranking of soil class effects in the BRT models was not always in strict order of increasing/decreasing nutrient status. We conclude that this may be caused by uncertainties in the data (both soil and livestock distributions), rather than representing actual patterns.

4.0 Discussion

4.1. The value of newly available partitioned woody (LAI_W) and herbaceous (LAI_H) biomass in understanding livestock distributions across SSA

To understand whether inclusion of separate woody and herbaceous forage biomass would improve our understanding of livestock distribution, we tested aggregate (LAI_A) and partitioned forage biomass (LAI_H and LAI_W) models. Based on regression analysis and ANOVA the partitioned model was superior over the aggregate model (Table S1) in explaining livestock distribution in SSA. We therefore conclude that inclusion of the separate woody and herbaceous forage biomass adds value to understanding herbivore distribution in SSA. However, in the BRT models the explanatory power based on R^2 statistic were similar (Table 4).

4.2. The emergent sensitivity of livestock distribution patterns to patterns of forage and other environmental covariates

Different environmental covariates have different influences on livestock distribution in SSA. Water was a critical variable for livestock in the total livestock and cattle models, influencing over 60% of livestock distribution in both the aggregate and partitioned models. However, in individual models of sheep and goats, water rated third and fifth at 23% and 12% in that order. On the other hand, HPD ranked highest in the smaller livestock with a relative influence of 26% for goats and 27% in sheep. Forage biomass was the second most important variable in livestock distribution, with herbaceous and woody LAI rating second or third across the individual livestock types (cattle, sheep and goats) in the partitioned models. The significant influence of water and herbaceous biomass as the two most critical determinants of cattle confirms the fact that cattle consumes ~70% of forage and water resources compared to that of goats and sheep at 10% each (King, 1983), hence dominating the wetter ecosystems while goats are more drought resistant inhabiting the drier ecosystems (Vrieling et al 2016). In the total livestock biomass, we suppose the similarity with the results in cattle model was due to the high influence of cattle biomass (Figure 5b).

In support of our hypothesis, herbaceous production influenced cattle more than woody production in the partitioned biomass model. LAI_H had a relative influence of ~15% compared to ~9% woody biomass. To our surprise woody biomass had higher influence on sheep (primarily grazers) distribution with LAI_W at ~25% compared to LAI_H at ~13%; a pattern reversed in goats (predominantly browsers) with herbaceous biomass influence at ~26% and woody biomass at 22%.

Most ungulates daily activities are divided into feeding, watering and resting. On an average day a cattle spends about one third of its time resting (George *et al.*, 2007), pointing to the importance of shade for livestock. Herbivores dominate (or pastoralists will guide their animals in) areas where they can find adequate forage, water and shade. Conceivably, this can be explained by the initial peak of livestock in areas with LAI_W between 0.5 and 2, characteristic of open savannas.

The influence of nutrients in all the partitioned models shows livestock favored moderate to nutrient rich forage resources corresponding with moderate to non-limitation soil nutrient availability status. However, the influence of soil nutrients varied among the large (cattle) and smaller feeders (goats and sheep), with relatively little influence on large feeders, but higher influence on the distribution of small livestock, (Table 4).

4.3. The scale-dependence of locally established ecological relationships and patterns at continental scale.

We observed varying relationships between livestock and environmental variables. Livestock increased linearly with water reaching an asymptote at ~0.3 water coverage. The importance of herbaceous production in livestock distribution was evident in the total livestock and cattle models showing a positive relationship reaching an asymptote beyond $LAI_H>2$, while woody biomass was inversely correlated with livestock biomass, a pattern expected for grazers, but unforeseen for browsers (goats). Consistent with our hypothesis, we observed a positive correlation between livestock and HPD, confirming earlier results suggesting strong correlations between livestock densities and HPD where livestock tends to increase with agricultural intensification (Peden *et al.*, 2007). Our results point to the important threshold of HPD above which no observable difference is evident. We assume this is tied to management where HPD <=250 are rangeland areas and moderately productive ecosystems unlike the densely populated wetter ecosystems characterized by crop husbandry. In agreement with our hypothesis, livestock was inversely related with slope, preferring gentler slopes <=10% for watering and grazing George *et al.* (2007).

4.4. Challenges and opportunities

Our research has focused on the main factors that determine distribution and abundance of livestock in Africa. However, it does not exhaust the factors that determine herbivore distribution. Ideally, our analysis should have included finer scale livestock distribution numbers, perhaps even telemetry GPS data and inclusion of larger wild herbivores, but such data are rarely available in Africa. Although there is available gridded livestock (Robinson *et al.*, 2014) at 1km resolution centered around year 2007 and wild herbivore (Hempson *et al.*, 2015) data, we did not include them in our analysis since they were modelled using vegetation and other environmental variables which would likely introduce circularity in our analysis. We also acknowledge the limitation with the soil nutrient availability data which are not good enough to resolve more detail than we have shown in our analysis. A better approach would be to have direct estimates of forage nutrients but was limited by data availability.

Other factors influencing herbivore distribution that would have been important to consider include: predation which in some instances has been found to be a more important factor than forage availability in some wild ecosystems in Africa (Grange & Duncan, 2006), while some herbivores choice of foraging sites is determined by fear of predation (Preisser *et al.*, 2005; Sinclair *et al.*, 2003); land tenure which is important especially among nomadic pastoralists; vegetation seasonality which affects forage quality (Mueller & Orloff, 1994); migratory nature of animals and nomadic lifestyle of African pastoralists though we believe the large polygons data used in our analysis act as a range within which herders/animals travel in search of water and forage resources; open water used in the analysis is not sufficient since in rangelands small water bodies and installed boreholes avail water for livestock but are difficult to capture with remote sensing applied for open water mapping. Elsewhere it has been reported elephants dig dried up river beds and edaphic grasslands (Dudley *et al.*, 2001) which provide water for other wild species and livestock in some areas; dietary changes especially during droughts where pastoralists use twigs to feed livestock observed in some of our previous works in Eastern Africa. However, we believe the use of averages in our analysis is able to capture some of the variabilities within the data; disease and disease vectors since pastoralists and humans in general avoid tsetse and other disease infested areas, for instance tsetse infestation in humid ecosystems in West, Central and East African regions limit livestock production (Ford, 1973); fire has both positive and deleterious effects on herbivores. They facilitate high nutrient herbaceous regrowth which is an attractant to many herbivores especially the smaller body animals that favor high nutritious forage (Eby *et al.*, 2014). On the other hand, fires consume most of the senescent or dry biomass (Lehsten *et al.*, 2009) which could be forage reserves for herbivores in the dry season. It is noteworthy, that we included crop area as a proxy for land use management on livestock distribution in our models. However, no significance changes were observed in the results, since crop production had the same impact on livestock as HPD, hence omitted in our final models.

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SUPPLEMENTARY MATERIAL

Supporting Information for

Assessing the relationship between forage resources and livestock distributions in sub-Saharan Africa

Appendix 1: Multiple linear regression and analysis of variance (ANOVA)

All the multiple linear regression model results were statistically significant with p-value <0.05. The partitioned models were better suited for explaining livestock distribution compared to the aggregate models (Table S1). Furthermore, ANOVA analysis for the aggregate and partitioned model to determine whether including the refined forage resources added value to the models other than using the aggregate biomass, shows the addition had a significant contribution to the models, as shown by the statistically significant F-value with p-value <0.05 in Table 3, in main text. The means between the variables were different as shown by the large high F-values that were higher than the critical value in almost all the model variables, Table S1. Given that there were 10 degrees of freedom (DF) for biome types and 1 DF for other explanatory variables against 513 DF for all observations the critical value for biomes was 1.85 and other variables at 3.86 derived using: qf(.95,10, 513) and qf(.95,1, 513), respectively, derived in R-Programming.

Table S3: Multiple linear regression and ANOVA analysis results for the livestock herbivory models. The models were run based on the various livestock groupings including total, cattle, sheep and goats. The Overall p-value for the linear regression models were statistically significant p-value <0.05. The columns represent: Herbivore -the livestock category; Sum.Sq- error sums of squares; DF-Degrees of Freedom; F-statistic and p-value of each model explanatory variable

	Aggregate Models						**Partitioned Models**					
Herbivore	**Variable**	**Sum.Sq**	**DF**	**F-value**	**p-value**	**R^2**	**Variable**	**Sum.Sq**	**DF**	**F-value**	**p-value**	**R^2**
	LAI$_A$	33.81	1	53.01	0.000		LAI$_W$	37.72	1	59.96	0.000	
	HPD	127.33	1	199.65	0.000		LAI$_H$	5.08	1	8.07	0.005	
	Biomes	41.16	10	6.45	0.000		HPD	123.62	1	196.53	0.000	
	Water	2.41	1	3.78	0.052		Biomes	39.53	10	6.28	0.000	
	Slope	0.19	1	0.30	0.583		Water	2.34	1	3.72	0.054	
Total TLU						0.517	Slope	0.02	1	0.04	0.848	0.524
	LAI$_A$	21.99	1	28.44	0.000		LAI$_W$	29.06	1	38.19	0.000	
	HPD	111.44	1	144.10	0.000		LAI$_H$	1.13	1	1.48	0.224	
	Biomes	76.30	10	9.87	0.000		HPD	106.59	1	140.06	0.000	
	Water	4.75	1	6.14	0.014		Biomes	62.05	10	8.15	0.000	
	Slope	0.02	1	0.03	0.861		Water	4.25	1	5.58	0.019	
Cattle TLU						0.489	Slope	0.86	1	1.13	0.288	0.497
	LAI$_A$	55.29	1	144.74	0.000		LAI$_W$	58.63	1	158.35	0.000	
	HPD	22.28	1	58.32	0.000		LAI$_H$	10.01	1	27.02	0.000	
	Biomes	20.55	10	5.38	0.000		HPD	20.97	1	56.65	0.000	
	Water	1.50	1	3.93	0.048		Biomes	20.26	10	5.47	0.000	
Sheep TLU	Slope	0.46	1	1.20	0.273	0.397	Water	1.44	1	3.88	0.049	0.416

							Slope	0.00	1	0.01	0.937	
	LAI$_A$	15.87	1	47.08	0.000		LAI$_W$	14.09	1	42.10	0.000	
	HPD	57.70	1	171.19	0.000		LAI$_H$	6.25	1	18.67	0.000	
	Biomes	10.00	10	2.97	0.001		HPD	57.54	1	171.90	0.000	
	Water	0.08	1	0.23	0.635		Biomes	8.68	10	2.59	0.005	
	Slope	1.83	1	5.42	0.020		Water	0.15	1	0.44	0.506	
Goats TLU						0.407	Slope	1.61	1	4.80	0.029	0.412

HPD- Human Population Density; LAI$_A$-Aggregate Leaf Area Index; LAI$_H$- Herbaceous Leaf Area Index; LAI$_W$-Woody Leaf Area Index; TLU-Tropical Livestock Unit

Appendix 2: Livestock relationships with environmental variables in the aggregate models

Livestock distribution had different relationship with various environmental variables.

Here we show partial dependency plots for the aggregate models from Figures S1 to S4

Appendix 2.1: Total Livestock relationship with environmental variables in the aggregate model

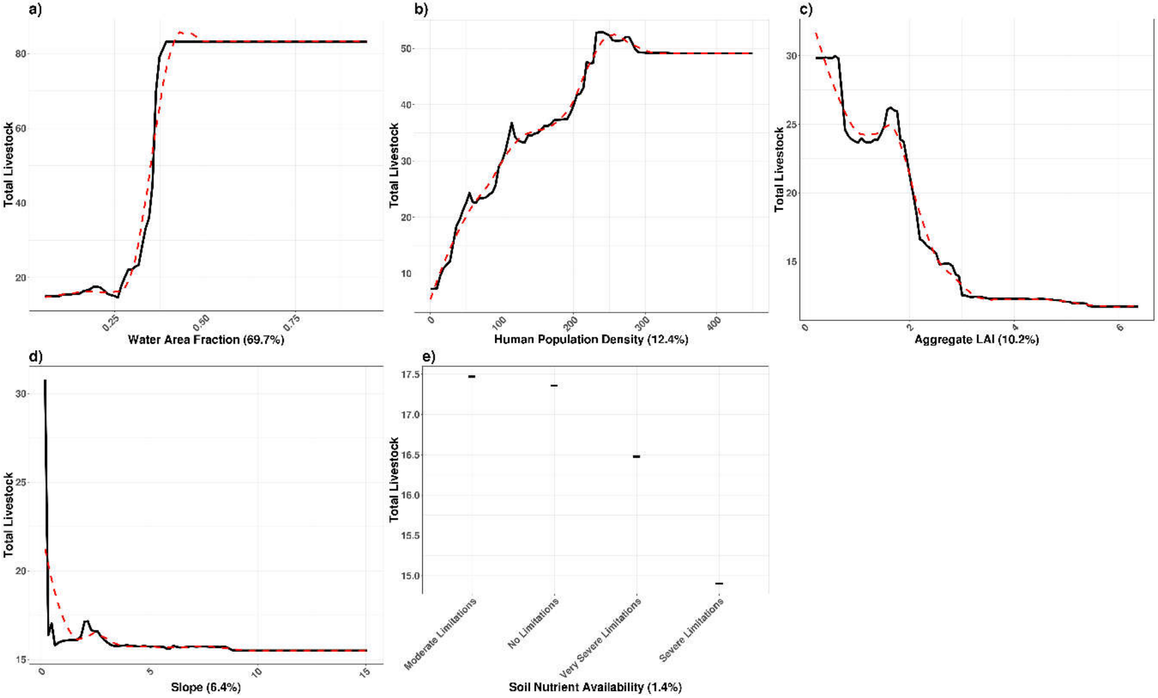

Figure S3: Predicted livestock patterns in the aggregate model for all the livestock (cattle, goats and sheep) using tropical livestock units against (a) water coverage, (b) human population density, (c) aggregate leaf area index (LAIA), (d) slope, and (e) soil nutrient availability status. The relative influence of each variable is shown along the x-axis labels (in brackets) and red lines fitted with loess smoothing.

Appendix 2.2: Cattle relationship with environmental variables in the aggregate model

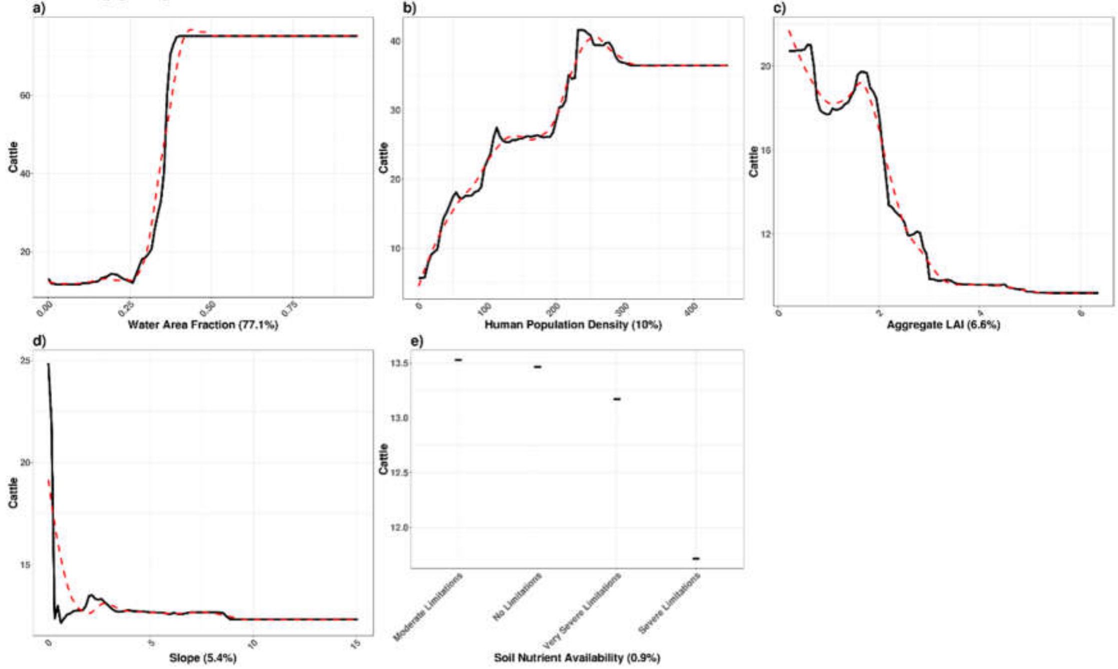

Figure S4: Predicted livestock patterns in the aggregate model for cattle using tropical livestock units against (a) water coverage, (b) human population density, (c) aggregate leaf area index (LAI_A), (d) slope, and (e) soil nutrient availability status. The relative influence of each variable is shown along the x-axis labels (in brackets) and red lines fitted with loess smoothing

Appendix 2.3: Sheep relationship with environmental variables in the aggregate model

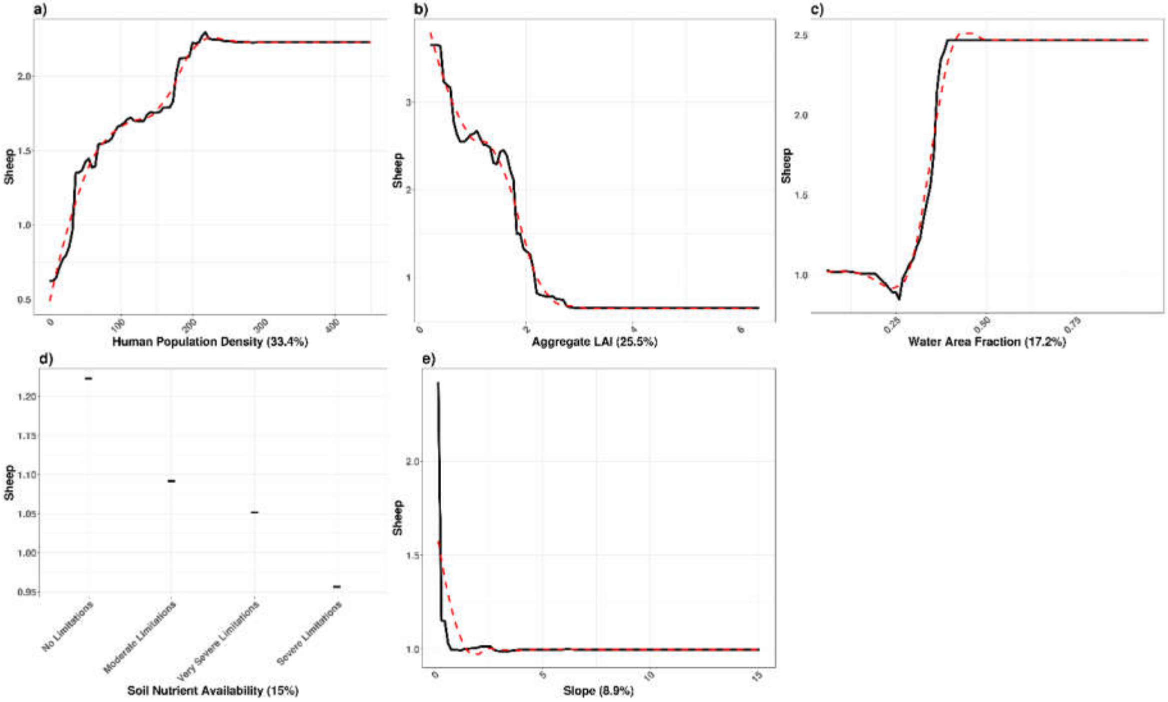

Figure S5: Predicted livestock patterns in the aggregate model for sheep using tropical livestock units against (a) human population density, (b) aggregate leaf area index, (c) water coverage, (d) soil nutrient availability and (e) slope. The relative influence of each variable is shown along the x-axis labels (in brackets) and red lines fitted with loess smoothing

Appendix 2.4: Goats relationship with environmental variables in the aggregate model

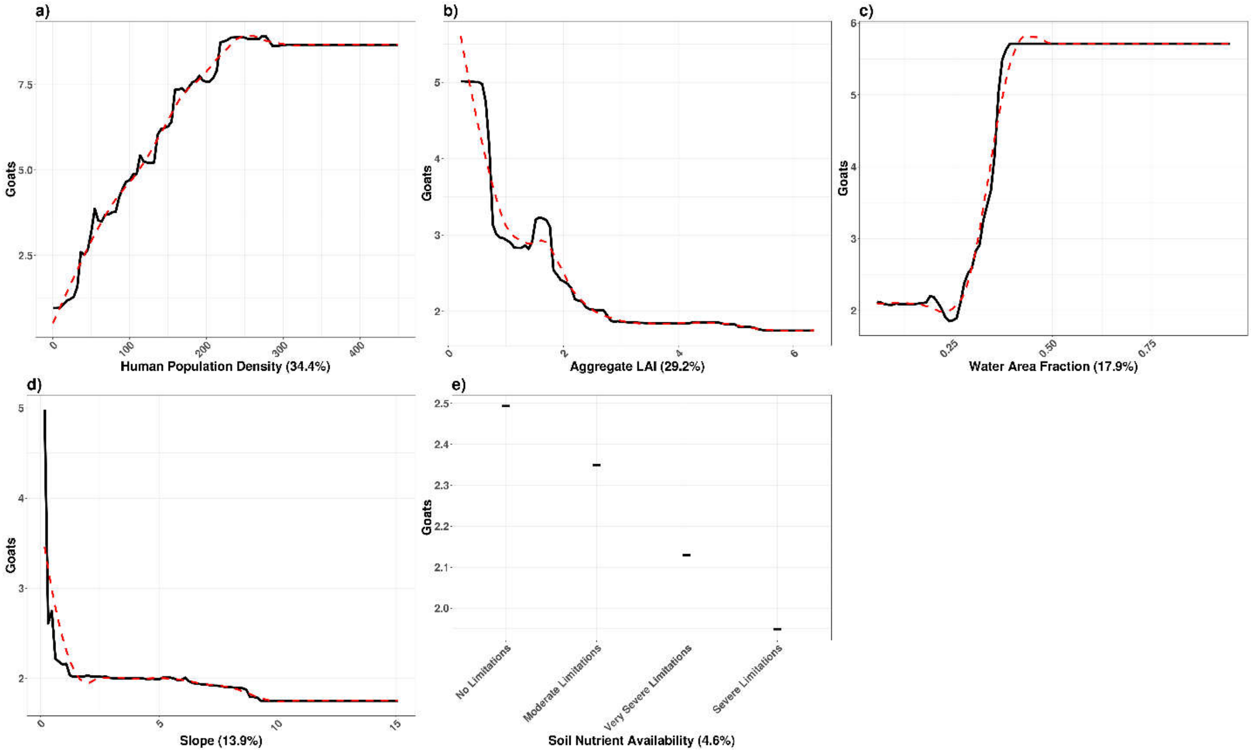

Figure S6: Predicted livestock patterns in the aggregate model for goats using tropical livestock units against (a) human population density, (b) aggregate leaf area index, (c) water coverage, (d) soil nutrient availability and (e) slope. The relative influence of each variable is shown along the x-axis labels (in brackets) and red lines fitted with loess smoothing

CHAPTER 5

Summary, synthesis and recommendations

1.0 Summary of research and key results

The work presented in this dissertation advances our understanding of the distribution and phenology of woody and herbaceous leaf area index (LAI) in Africa and how these key elements of vegetation structure impact fire activity and livestock distribution in tropical savannas. In my research, I incorporated known vegetation phenological traits with remote sensing signals to separate aggregate LAI for the two contrasting life-forms in savanna ecosystems (‘tree-grass systems’) and further applied the separate LAI estimates to understand how woody and herbaceous biomass influences fire activity and herbivory in Africa.

In chapter 2, I attempted to address the challenge often facing ecologists and the remote sensing community in representing the contrasting savanna life-forms in medium resolution satellite data. With realization that greenness indices and aggregate LAI used previously to represent savannas provides little insight into spatio-temporal variability in woody and herbaceous vegetation structure, I used the 8-day MODIS leaf area index at1km spatial resolution from 2003-2015 to separate woody from herbaceous LAI in sub-Saharan Africa (SSA). I developed an allometric relationship describing the variation in peak within-canopy woody LAI of dominant tree species across mean annual precipitation gradients, coupled with independent estimates of woody canopy cover, to constrain the rapidly changing woody LAI. I generated 8-day woody and herbaceous LAI estimates for years 2003-2015, which I used for further analysis in understanding fire behavior and livestock herbivory in SSA. I have made available the partitioned LAI estimates as 8-day averages of the 2003-2015 epoch for user community to test and use them in various applications. LAI phenology is also availed as an animation file for the user community to visualize the contrasting woody and herbaceous phenology across SSA and assess performance of the partitioning approach. This analysis also included interesting plots showing bifurcation between high LAI in forests and moderate LAI savannas and the degree of seasonality (evergreen versus deciduous) in woody and herbaceous vegetation across Africa.

In chapter 3, I showed how the use of aggregate biomass to understand tropical savanna fires using the intermediate fire-productivity hypothesis (IFP; Pausas & Ribeiro, 2013) ignores the separate and distinct roles played by herbaceous and woody vegetation on fire ignition and spread in tropical savannas. I proposed the ‘Fuel, Cure and Connectivity (FCC)' conceptual model that recognizes the important and separate roles of herbaceous vegetation in tropical savanna fires. The model combines other important environmental covariates including dry season length necessary for fuel to cure, human population density as a proxy for ignition sources and land management. I hypothesized that since tropical savanna fires are almost exclusively surface fires, fueled by herbaceous biomass, fire activity in SSA will be asymptotically correlated with herbaceous production. From this analysis it is apparent that herbaceous fuel-load is the predominant control of tropical savanna fires, while the need for fuel to cure rated second in fire ignition and spread in SSA. In contrast to the unimodal relationship promoted by IFP, an asymptotic relationship between herbaceous fuel-load and fire activity is evident, consistent with FCC. The novelty in the FCC model is the inclusion of partitioned woody and herbaceous fuel biomass and tree facilitation of herbaceous undergrowth which, to my knowledge, has not been explored in relation to fire activity in the African context. The partitioned fuel-load estimates and tree facilitation of herbaceous undergrowth forms the basis of the FCC model where, in particular, it is not total production that matters in the tropical savanna fires, but herbaceous production, since fires in this region are surface fires fueled by the herbaceous biomass. I have shown herbaceous vegetation tends to burn more frequently than woody vegetation hence concluding that the large fire hotspot found in southern Chad, the Central African Republic and South Sudan is related to the particularly low tree cover and associated high herbaceous biomass in this region. This contrasts previous work (Giglio *et al.*, 2013) that suggested these fire hotspots can be explained by the hot Harmattan trade winds. Although the FCC model does not include fire weather factors, making this observation open to debate, I argue that patterns in herbaceous fuel load are a more logical explanation of this fire activity in the hotspots, a phenomenon that is also evident in the southern Africa mesic savannas. In this analysis, I have shown that FCC model avoids the confounding interpretation of the role of total production, while providing opportunities to quantify fuel curability, tree effects on herbaceous fuel growth and connectivity, and human management, emphasizing the need to separate woody and herbaceous biomass in fire models for better understanding of tropical savanna fires.

In chapter 4 I explored major correlates of livestock distribution in Africa, with key emphasis on the relative influence of woody and herbaceous LAI as proxies of forage quantity for browsers and grazers respectively. I tested the value of the partitioned LAI estimates (developed in chapter 2), coupled with water, human population density, topography, and soil nutrients status in understanding livestock distributions across SSA and evaluated the scale-dependence of locally established ecological relationships and patterns of herbivores and these environmental covariates at continental scale. I hypothesized that herbaceous production influences grazers, while woody production influences browsers and the relationship is positive linear or asymptotic in LAI_H for grazers and LAI_W for browsers. Animal body size plays a role in their distribution, hence I hypothesized large herbivores will be more common in high forage production areas irrespective of forage quality, while smaller livestock including will favor nutrient-rich areas. Water resource availability often constrain pastoral activities and livestock distribution thus I anticipated livestock density will be sensitive to the local availability of water, but quickly reach an asymptote as small water bodies can provide drinking water to animals foraging over a much larger geographical area, while human population density will cause an initial rapid increase of livestock then decline in more densely populated agricultural areas. Terrain constrains animal movement and livestock prefer gentle slopes thus I hypothesized an inverse relationship between livestock abundance and slope. Results show inclusion of refined forage biomass improves our understanding of domestic livestock distributions. Water availability is a critical variable in determining livestock distribution, but once available further increase does not matter. Cattle increased with herbaceous LAI more than woody LAI in the partitioned model. However, the negative influence of herbaceous LAI on sheep that are predominantly grazers and woody LAI on the predominantly browsing goats was a confounding result in the analysis. HPD has a positive influence on livestock distribution reaching an asymptote in moderate human population areas indicating the increase corresponds with rangelands where we anticipated high livestock numbers, levelling out in highlands where HPD and agricultural activities are high. Overall, it was apparent that livestock distributions generally favor regions with moderate to high soil nutrient availability, a relationship that varies with animal body size, with larger body-size livestock (cattle) being less sensitive to forage nutrient status than small ruminants (sheep and goats). These findings point to importance of including separate woody and herbaceous biomass in understanding herbivory.

2.0 Limitations of the research

The performance of aggregate LAI partitioning is dependent on the quality and consistency of the MODIS LAI product. Previous versions of MODIS LAI identified relatively larger errors in LAI retrievals (de Bie *et al.*, 1998; Palmer *et al.*, 2015), but over the years improvements have been achieved through various collections and validation efforts. Here we used MODIS Collection 5 LAI which provides reliable and reasonably well characterized dataset for global LAI estimates. Notable problems with the LAI were cloud cover in the tropical and coastal forest ecosystems, lowering the value of LAI. Although I corrected these problems through removal of low LAI data caused by contamination and later smoothing to have realistic LAI seasonality, remnant errors were evident in some pixels. This could have introduced errors in the partitioned LAI estimates. Since this was a beta product, in the revised partitioning, I hope the partitioning estimates will get better with use of MODIS Collection 6 and Visible Infrared Imaging Radiometer Suite (VIIRS) LAI datasets.

Other possible sources of uncertainty and errors in the partitioning analysis were the woody cover, precipitation and *in situ* LAI estimates and errors introduced through preprocessing steps, therefore propagating errors in the partitioned LAI. Particularly the use of a static woody cover product centered on year 2005 (Bucini *et al.*, 2010) to constrain the woody LAI, while appropriate for most slowly-changing systems, is unable to capture changes in woody-herbaceous LAI partitioning in landscapes exposed to rapid changes/disturbance e.g. deforestation, fire. However in this initial analysis where I derive the beta version of the partitioned LAI, I ignored this potential source of error, assuming that deforestation is relatively localized. Future versions of this analysis should use improved estimates of woody cover, updated at regular intervals (e.g. at ~5year intervals).

The partitioning allometry was based on a limited and dispersed number of *in situ* LAI measurements, hence requires recalibration with additional data for better representation of all vegetation types across Africa. Thus far, validation of partitioned LAI estimates based on field based LAI estimates shows an overall agreement of ~50%, with root mean square errors of 0.72, 0.37 and 0.80 LAI units for overall partitioned, herbaceous and woody LAI, respectively. These statistics indicate the need for refinement of the partitioning allometry through inclusion of additional field based LAI data for herbaceous and woody LAI and for further validation. Gradual improvements will be possible in future reanalysis and operationalization phase of this product as more validation and model calibration data become available and following feedback from users.

In the fire and herbivory analysis in chapters 3 and 4 respectively, I acknowledge the limitations of the data used. I applied the partitioned LAI in these two analysis which coupled with other datasets used may propagate errors and introduce uncertainties in the analyses. The current satellite based fire activity products are surrounded by uncertainties and tend to underestimate fires (Chuvieco *et al.*, 2016), especially with most moderate resolution satellite based burned area and active fire products, that tend to have limited ability to detect fire activity in tropical forests while underestimating small fires (Roy *et al.*, 2013). However, over the years, there has been a significant improvement in satellite fire activity products, for instance MCD64A1 Collection 6 product used here is now better compared to previous versions (Giglio *et al.*, 2013). Therefore, I believe the shortcomings with the data used in the fire analysis would not affect the general fire activity patterns and the general findings in the analysis.

Carry over biomass dependent on rains from the previous season is a very important variable in understanding fire activity (Bond & Keane, 2017). However, the FCC model does not incorporate this variable, but I believe the use of annual average maxima is somewhat able to capture this variability. I recognize the limitations in FCC model with potential for collinearity between number of dry months (dry season length; DSL) and the LAI terms used as proxy for fuel load. However, inclusion of DSL provides additional insight on the curability of fuels an important variable worth including.

While the general patterns of established ecological relationships between livestock density and environmental variables are broadly consistent with expectations, I observed inconsistencies with variable rankings, which may be due to errors and uncertainties in the data on livestock distributions and environmental covariates rather than representing actual patterns. The resolution at which I applied the livestock models captures a lot of variability which might have affected the results. Landscapes are very heterogeneous containing topographic and other variable environmental characteristics that may impact herbivory, but which the level of this analysis may not have captured. I believe better results would be evident with finer spatio-temporal scale datasets, herbivore movement data, forage quality maps or improved soil maps, vegetation maps and water availability data. Additionally, the herbivore distribution analysis could be better with inclusion of the often lacking and unreliable wildlife herbivore estimates.

3.0 Synthesis and recommendations for future research

My research has contributed to a new quantification and understanding of spatiotemporal patterns of woody and herbaceous LAI a challenge often facing ecologists and the remote sensing community in representing the contrasting savanna life-forms in medium resolution satellite data. As evident in my analysis on fire activity and herbivore distribution in SSA, this unprecedented information could be used for future applications in utilization and management of savanna resources and broader research themes in savanna science.

Shrub encroachment in savannas has been document not only in Africa but globally, in the Americas, Australia and Asia, a phenomenon induced by human activities such as grazing, fire suppression, introduction of woody species for economic purposes, planned or unplanned introduction of alien species and recently tied to increasing atmospheric CO_2 and changing precipitation regimes associated with global climate change (Settele *et al.*, 2014). Its impacts are beneficial in biogeochemical cycles especially carbon sequestration (Hughes *et al.*, 2006) but also threatens the survival of savanna biomes and is detrimental to grazing systems (Eldridge *et al.*, 2011; Settele *et al.*, 2014 and citations therein). Increased canopy cover increases above ground net primary productivity thus increasing carbon storage per unit land area, while declining herbaceous undergrowth (Hughes *et al.*, 2006; Moleele *et al.*, 2002), which is the main source of forage for wild and domestic herbivores. Human induced changes that will increase growth such as water, nutrients, fire suppression, reduced herbivory, and impacts associated with climate change will continue to cause canopy closure causing changes in savanna biomes (Murphy & Bowman, 2012). Therefore estimating and monitoring inter and intra annual $\mathrm{LAI_W}$ seasonality is essential for understanding the dynamics of changing woody cover components in global savannas.

Bifurcation is also an important topic in savanna ecology with varying views on its manifestation theoretically and with empirical observations. In ecological literature studies have shown the theoretical basis of bistability (D'Odorico *et al.*, 2006; Hanan *et al.*, 2008; Hoffmann *et al.*, 2012), while others have attempted to quantify their prevalence in global biomes in empirical analysis (Favier *et al.*, 2012; Hirota *et al.*, 2011; Ratajczak & Nippert, 2012; Staver *et al.*, 2011). I derived estimates of woody and herbaceous LAI maxima to show its relationship with mean annual precipitation (MAP), since LAI maxima for various ecosystems is mainly dependent on precipitation and the relative contribution of woody and herbaceous vegetation. Woody LAI, initially increases with MAP, then a conspicuous bifurcation evident between high LAI forests and moderate LAI savannas, consistent with theories of bistability in the forest-savanna transition zones (D'Odorico *et al.*, 2006; Hanan *et al.*, 2008; Hoffmann *et al.*, 2012), and empirical analyses based on MODIS tree-cover product (Favier *et al.*, 2012; Hirota *et al.*, 2011; Ratajczak & Nippert, 2012; Staver *et al.*, 2011). However Hanan *et al.* (2014) questioned whether the bistability apparent in the MODIS tree-cover data between medium LAI savanna in drier regions, and between savanna and forest in wetter regions, might be an artifact of the classification and regression trees approach used to predict tree cover from MODIS. In the partitioning of MODIS LAI, I have shown evidence of bifurcation in the MODIS aggregate LAI maxima, further reinforced in the partitioned woody LAI. I hope this will invoke an interesting discussion within the savanna ecology and the remote sensing community on bistability driven by fire and positive feedbacks in savanna-forest transition zones. Furthermore LAI$_W$, provides data necesary for assessing the bistability of woody cover which is essential for future predictions on impacts of global change on terrestrial biomes.

From the partitioning analysis, I derived a product showing the degree of evergreen versus deciduousness in SSA ecosystems, something that I believe has not been available before or at the scale of this analysis. My product shows seasonally stable evergreen ecosystems, with the woody LAI seasonality further highlighting the distinctions between evergreen and deciduous woody ecosystems in the moist tropical forest and savannas, and woody seasonality in weakly deciduous shrublands in drought-seasonal regions of SSA. On the other hand, herbaceous LAI across most of SSA is highly seasonal, regardless of whether the dominant species are annuals or perennials. With changing precipitation regimes and human induced modifications the seasonality product is important to monitor and quantify how these alterations may or will affect vegetation seasonality, thus biogeochemical cycles and resource provision in the continent.

In the fire analysis, derived estimates of partitioned LAI, were used to explore the distinct and separate roles woody and herbaceous biomass in fire activity in the tropical ecosystems of Africa, also applicable in other tree-grass ecosystems across the globe. The current paradigm contends that climate change will result in increased fire risk in various global ecosystems (Jolly *et al.*, 2015; Moriondo *et al.*, 2006; Scholze *et al.*, 2006; Settele *et al.*, 2014), necessitating a better understanding of fire activity, behavior and regimes across the globe. Herbaceous biomass fuels fire in tropical savannas while woody biomass has indirect effects through facilitation of herbaceous undergrowth in drier environments while suppressing fire in wetter biomes by suppressing herbaceous undergrowth and connectivity. Furthermore, fire activity is dependent on land cover type with some more prone to fire than others (Barros & Pereira, 2014). As demonstrated in my analysis it is imperative to refine and disentangle fuel load types in fire analysis and modeling.

Savannas are a source of forage and fuelwood supply in many parts of Africa, where rangelands cover over 60% of the continent. Tropical savannas are some of the most densely populated ecosystems, and in SSA woody biomass the main source of fuelwood (Arnold *et al.*, 2006; Bailis *et al.*, 2005; Delmas *et al.*, 1991; Levine, 1991), thus quantifying and monitoring the composition of herbaceous and woody biomass in Africa is vital. As an indicator of available forage resource in SSA, the partitioned LAI product will go a long way in addressing impacts of climate change (Settele *et al.*, 2014) and some of the challenges faced by pastoralists in this part of the world. For instance, within the frame work of index-based livestock insurance (Vrieling *et al.*, 2016) in Kenya, Ethiopia and Uganda (later expanding to other parts of Africa), NDVI which is just an estimate of vegetation vigor (Tucker, 1979), is used to monitor forage anomalies to be used as the basis for insurance payouts. The application of the partitioned LAI product would be a better proxy for estimating forage resources. Furthermore, the invasion of alien species in some grazing ecosystems that remain evergreen year-round could be misleading when using NDVI to assess vegetation anomalies as they will indicate normal seasonality despite failed rains affecting herbaceous undergrowth which is the main forage resource. Therefore, estimates of seasonal and annual variations in woody and herbaceous LAI and quantification of probable changes associated with climate change will aid in understanding and predict how societies will be affected in Africa.

Savannas are rich biodiversity conservation hotspots globally (Darkoh, 2003; Shorrocks & Bates, 2015; White *et al.*, 2000). In Africa alone most of the protected areas dominate savanna/rangeland biomes. The composition of flora and fauna in these biomes is dependent on the structure and composition of woody and herbaceous layers. For instance the big cats and various large herbivore species prefer inhabiting the open savannas. Therefore, Shifts from savanna to forest or savanna to grassland or desert have far reaching implications for biodiversity conservation, more so when the changes impact survival of various flora and fauna. To manage savanna biomes for successful biodiversity conservation efforts there is need to monitor the status and trends of woody and herbaceous vegetation. Using seasonal and interannual estimates of woody and herbaceous LAI has the potential to provide information on the savanna structure and general composition for informed biodiversity conservation efforts.

Arguably the importance of representing separate savanna constituents in RS has many benefits to ecologists, scientific community and environmental managers. However, while there are still many challenges the research presented in this dissertation has significant potential to improve our understanding of current anthropogenic changes and probable impacts of climate variability and change. I believe future improvements in understanding vegetation variability among and within biomes is an important step as I have shown here using remote sensing data to understand spatio-temporal variations of woody and herbaceous biomass in Africa and how these constituents can be applied in various applications including fire, herbivory, and climate change modelling.

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