Patterns in Woody Vegetation Structure across African Savannas

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Abstract. Vegetation structure in water-limited systems is to a large degree controlled by ecohydrological processes, including mean annual precipitation (MAP) modulated by the characteristics of precipitation and geomorphology that collectively determine how rainfall is distributed vertically into soils or horizontally in the landscape. We anticipate

15 that woody canopy cover, crown density, crown size, and the spatial distribution of woody plants in the landscape, will vary across environmental gradients. Exploring these trends can extend our knowledge of how semi-arid vegetation structure is constrained by rainfall regime, soil type, topography, and disturbance processes such as fire. However, a lack of data on woody vegetation structure across African savannas has so far prevented a thorough analysis of their relationships with abiotic factors. Using high spatial resolution imagery, a flexible classification

20 framework, and a crown delineation method, we extracted woody vegetation properties from 876 sites spread over African savannas. At each site, we estimated woody cover, mean crown size, crown density, and the degree of aggregation among woody plants. This enables us to elucidate the effects of rainfall regimes (MAP and seasonality), soil texture, slope, and fire frequency on woody vegetation properties. We estimate trends in mean crown size across the African savanna rainfall gradient and show that previously documented increases in woody vegetation cover with

25 rainfall is more consistently a result of increasing crown size than increasing density of woody plants. We also find a unimodal relationship between mean crown size and sand content suggesting that maximal savanna tree-sizes do not occur in either coarse sands or heavy clays. When examining the occurrence of periodic vegetation patterns (PVPs), we find that the same factors that contribute to the formation of PVPs also correlate with higher levels of woody plant aggregation elsewhere in savannas and that rainfall seasonality plays a key role for the underlying processes.

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1 Introduction

African savannas are complex tree-grass systems controlled by combinations of climate, soil and disturbance processes such as fire and herbivory (Sankaran et al., 2008). While humans often play a dominant role in many systems, it is important to learn how different rainfall regimes, soil types, and topography impact woody vegetation

35 structure. Climate, both rainfall patterns and temperatures, could change in many parts of Africa (Gan et al., 2016), and its effect on vegetation will depend on how those pressures interact with other abiotic and biotic factors. A

thorough understanding of these processes, and how they are influenced by environmental factors, is key to assessing the future stability and productivity of these ecosystems.

40   In drylands, water availability determines the establishment, growth and survival of plants and competitive plant traits are often of a water saving nature (Chesson et al., 2004; Pillay & Ward, 2014). Abiotic environmental factors, such as the rainfall regime, soil type, and topography, impact ecohydrological processes by controlling infiltration rates, runoff generation, and available water capacity, which in turn impact the growth and survival of woody plants in the landscape (Ludwig et al., 2005). Fire regimes, in particular fire frequency, also affect survival of seedlings and juvenile

45   trees, with possible impacts on tree density and size-class distributions (Bond, 2008; Hanan et al., 2008).

Across environmental gradients we therefore expect to see variation in woody vegetation properties, including individual-level characteristics (mean crown size) and population-level characteristics (crown density, woody cover and the spatial distribution of plants in the landscape). These properties are important for ecosystem function and the provision of ecosystem services. Two landscapes with similar woody cover but different sizes of individual trees will

50   sequester different amounts of carbon (Shackleton & Scholes, 2011), harbor different fauna (Riginos & Grace, 2008), and differ in biogeochemical dynamics (Veldhuis, Hulshof, et al., 2016). By studying how woody vegetation properties vary over different environmental settings, we also learn about the impacts of the underlying ecosystem processes.

55   Woody plants increase water infiltration and local accumulation of soil and nutrient resources, as well as altering sub-canopy microclimates (Barbier et al., 2014; Dohn et al., 2016; Gómez-Aparicio et al., 2008). These short-range facilitative effects usually operate at spatial scales of a few meters, but may increase the degree of aggregation among woody plants at larger scales (Scanlon et al., 2007; Xu et al., 2015). Overland flows of water can be especially effective at redistributing resources over longer distances, in some conditions leading to the emergence of periodic vegetation

60   patterns (PVPs; Valentin et al., 1999). Contrasting infiltration rates between bare and vegetated patches lead to redistribution of water and soil resources which reinforces an organized pattern. While soil texture type has been weakly associated with the occurrence of PVPs (Deblauwe et al., 2008), the impervious conditions of the bare patches are generally caused by shallow soil depths, hardpans, or soil crusts (McDonald et al., 2009). On flat ground, PVPs take the form of spotted, labyrinthine or gapped patterns depending on soil water availability. On a gentle slope, they

65   develop into vegetated bands that run parallel to contour lines.

    To analyze how woody cover, crown size, crown density and the spatial pattern of trees vary with environmental gradients, we need to map the landscape at the level of individual trees. Satellite-based high spatial resolution (HSR; <4 m) sensors have the necessary degree of detail for this task. Papers delineating individual trees from HSR in African

70   savannas have shown promising results (Karlson et al., 2014; Rasmussen et al., 2011), but these studies are generally restricted to small geographical areas. In this paper we present an analysis of woody properties sampled across the diverse water-limited savannas of Africa using a combination of WorldView, Quickbird and GeoEye satellite data (≤ 0.61 m resolution) from 876 sites. To combine data from multiple sensors with varying spectral characteristics and

sun-sensor geometries we developed a flexible classification approach, based on initial unsupervised classification
75 with manual assignment into woody, herbaceous, and bare cover classes. A crown delineation method further divides
the woody areas into individual tree crowns, from which we derive estimates of mean crown size, crown density,
woody cover and the degree of aggregation among woody plants. We then analyze how woody vegetation properties
vary with rainfall regime (MAP and seasonality), soil texture, slope and fire frequency using a boosted regression tree
(BRTs) approach to explore how woody structure varies with the local environment. The dataset contains sites from
80 several areas with PVPs and we also investigate the environmental factors associated with the occurrence of highly
organized periodic patterns. The methodological approach is outlined in Figure 1.

2 Data and Methodology

2.1 Satellite data and sampling strategy

We used data from WorldView-2, WorldView-3, GeoEye-1, and Quickbird-2 satellites, with varying ground
resolutions ≤0.61 meter for panchromatic data and ≤2.44 meters for the multispectral bands. When acquiring data for
the analysis, we adopted a sampling strategy with imagery distributed across Africa in rangelands as defined by the
Anthropogenic biomes product (Ellis & Ramankutty, 2008) (Figure 2). Focus was on selecting recent images (2011-
90 2016) in seasons when trees were in full leaf (green) and avoiding areas of high human population density. The
selection process was also influenced by a second study on change detection where we needed overlapping imagery
from two points in time. We excluded images with view angles >25° or cloud cover >20%. Following these criteria,
we acquired imagery in 48 regions, within which we sampled a total of 876 (240 x 240 m) sites for use in the analysis.
Within-image site-selection was guided by a 0.04° longitude/latitude grid which served as a base for site locations. In
95 some cases, however, the location of sites was adjusted to avoid areas where vegetation structure was clearly
influenced by topography (rocky outcrops, streams and gullies), or anthropogenic activity (settlements, roads, active
or fallow agriculture). Sample locations influenced by topographic or anthropogenic effects were either moved to a
nearby location or eliminated from the analysis. During the later classification process, we found that some sites could
not be classified reliably due to either low image quality, or a lack of contrast between trees and the herbaceous
100 background. These sites were also eliminated. In the end, we ended up with a total of 876 sites (Figure 2).

2.2 Preprocessing and classification of satellite data

Once the locations of sites were established, each site was preprocessed using IDL scripts in ENVI 5.2. This included
Gram-Schmidt pan-sharpening of the blue, green, red, and infrared bands, and orthorectification using embedded
105 RPC-information and an SRTM v2 DEM (Farr et al., 2007). The orthorectified images were resampled using a nearest
neighbor method to a standard 0.6 m ground resolution creating a 400 x 400 pixel (240 x 240m) image centered over
each site. We then ran unsupervised ISODATA classification on the pan-sharpened images to create 18 spectrally
different classes, which were smoothed using a kernel size of 3 pixels. Following preprocessing, the 18 spectrally
distinct classes were manually assigned to woody, herbaceous and bare cover classes using a custom-built software in
110 R. The software includes several tools to facilitate accurate and efficient classifications, including a tool to split a class

into two spectrally different classes if it appears to contain more than one land cover type, and a tool to remove minor inconsistencies such as a single herbaceous pixel in the middle of a tree crown. The sequence of commands used to classify a site were recorded in a log file for future reference and to allow the same commands to be automatically applied on other sites originating from the same satellite image. While these procedures were useful for speeding up

115   the classification process, image classification remained the most time-consuming part of the analysis.

2.3 Crown delineation

After the 240x240 meter image constituting each study site was classified into woody, herbaceous, and bare soil components, a crown delineation process was run to aggregate woody pixels into individual tree crown polygons. The

120   method uses the classified woody layer (as the "forest mask") together with NDVI from the pansharpened imagery and is based on the assumption that woody plants have higher NDVI at the center of the crown, where branches and leaves are dense, and declining NDVI towards the outer edges of the crown where branch and leaf density tend to be lower. The first step in the delineation process is to identify local maxima in NDVI. If the center pixel in the 3x3 pixel neighborhood is a maximum, it is given a unique segment id and serves as a seed for a crown segment. The second

125   step involves iterative growth of segments in all directions, but only to woody pixels with lower NDVI than the neighboring segment pixel. In the third step, neighboring segments are merged if the resulting crown is rounder than both of the two neighboring segments. Since the merging criteria can be fulfilled for several segment neighbors, a segment is only merged once in each iteration and the merging order is based on the roundness of the resulting segments. Here, roundness is calculated as the area of the segment divided by the area of a minimum bounding circle.

130   Round segments thereby get values close to one, while more complex segment forms have lower roundness. This step is re-iterated until rounder segments cannot be formed. We also added a maximum crown size limit so that segments are not merged if the resulting crown is larger than the area of a circle with diameter 40 meters. Before settling on the above rules, we experimented with a larger moving window for identifying local NDVI maxima, different rules for merging segments, and with a minimum bounding ellipse instead of circle. The method was implemented in C code

135   and has several traits in common with previous delineation methods (e.g. Bunting & Lucas, 2006; Karlson et al., 2014; Pouliot & King, 2005) which generally are developed and tuned for a specific landscape type. The method by Bunting & Lucas (2006) is perhaps the most similar since it also identifies segment seeds using local maxima and has iterations of segment merging. That method was developed using the eCognition software and has some additional steps not included in our method, such as post-splitting of segments and the initial generation of a forest mask. In our

140   methodology, the forest mask (woody areas) was already established using the semi-automatic approach described above.

The delineated crowns play an important role in this analysis because they are used for calculating crown density, crown sizes, and woody plant aggregation. We recognize, however, that it is extremely difficult to accurately delineate

145   tree canopies in areas where crowns overlap. In some cases, a large tree crown may be falsely divided into small canopies or a cluster of shrubs may be grouped together into one crown. Another limitation is the difficulty in detecting smaller crowns (~ < 5 m²), especially if their canopy is sparse. The aim here was to delineate crowns over large

environmental gradients across Africa using a consistent methodology. It is important that the rate of falsely divided and falsely grouped crowns is balanced since excessive division of large trees into smaller leads to higher estimates
150   of both woody density and aggregation. The method generates crown layers that look realistic from a visual inspection across all landscape types and different tree densities. Because of uncertainty in the accuracy of the woody properties derived from the delineated crowns, we do not focus on absolute numbers but on how they vary across environmental gradients.

155   **2.4 Environmental variables**

The rainfall data were extracted from the Tropical Rainfall Measuring Mission (TRMM) 3B42 v7 product (0.25° x 0.25°) for the years 1998-2015 (Huffman et al., 2007). In addition to mean annual precipitation (MAP), we use rainfall seasonality represented by the coefficient of variation of mean monthly rainfalls. Due to the relatively coarse resolution of the TRMM data, the rainfall properties for each site were extracted using the bilinear interpolation method. For soil
160   data we used the sand content in the top soil layer (0-5cm) from the ISRIC/AfSIS 250 meter soil property maps of Africa (Hengl et al., 2015). To represent topography we used slope (%) derived from SRTM v2 (3 arc-seconds) elevation data (Farr et al., 2007). Fire frequency (fire events/year) was calculated using the MODIS MCD64A1 collection 5.1 burned area product (500m resolution) for the years 2001-2015 (Giglio et al., 2009). To avoid registering fires identified in adjacent months as separate fires, we counted fire events in consecutive months as a single fire.

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2.5 Statistical analysis of woody vegetation properties and the local environment

We derive four statistical properties of woody vegetation from each image: mean crown size (m²), density (crowns/ha), woody cover (%), and spatial aggregation of woody plants. Aggregation is calculated from the center points of the crown polygons. We use Ripley's K transformed to Besag's L-function to estimate aggregation at distances from 1 to
170   60 meters (Besag, 1977; Ripley, 1977). Calculations were made using the spatstat R package with isotropic edge correction. The L-function was normalized by subtracting the distance so that 0 represents a random pattern and positive values indicate aggregation. For the analysis, we use the L-function at 20 meters to represent aggregation.

We chose boosted regression trees (BRT, in the dismo R package) to relate woody properties to the environmental variables. Its advantages include the ability to model non-linear relationships and to identify interactions between
175   variables (Elith et al., 2008). R^2, calculated through 10-fold cross-validation, is used for evaluating the strength of the relationships. When generating the BRTs, we used family = gaussian, tree complexity = 3, learning rate = 0.01, and bag fraction = 0.5 as model parameters. When analyzing crown sizes and aggregation, we excluded all sites with a woody density of 10 crowns/ha or less due to their low sample size for these metrics.

180   The dataset includes several sites with PVPs, which often are treated as a special case because of their striking appearance. It is of interest to examine the environmental conditions associated with the occurrence of PVPs as well as those associated with aggregated woody populations in savannas without PVPs. We therefore separated sites with periodic vegetation from the rest and generated an additional set of models. The category with periodic vegetation contained 149 sites situated in Somalia, Senegal, Chad, Mali, Niger, and Sudan. The separation process was based on

185   visual inspection and all sites with traits of periodic patterning (spotted, labyrinthine, gapped or banded) were put in
        the PVP category. We created one model for predicting aggregation among all sites, one for predicting aggregation
        among sites with no PVPs, and a third for predicting the occurrence PVPs. In the latter model, all PVP sites were
        given the value 1 and the rest 0, and the model family parameter was set to "bernoulli", appropriate for binomially
        distributed data.

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3 Results

Frequency distributions of the four woody properties, separated into three rainfall categories, are shown in Figure 4.
The more arid savannas (<400 mm/year) typically feature smaller crown sizes, lower crown density and woody cover,
and higher levels of aggregation than sites in the wetter categories.

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3.1 Mean crown size, density and woody cover

Woody cover and mean crown size both had strong relationships with the local environment and the same
environmental factors that control woody cover also had a large influence over crown sizes (Table 1). In both cases,
MAP had the largest relative influence followed by rain seasonality. While MAP has a clear positive influence on

200   both woody cover and crown sizes, it is more difficult to interpret the influence of rain seasonality (Figure 5). Woody
        cover has a weak unimodal response to sand content that is driven by a relationship between crown size and sand
        content (Figure 5). Fire frequency resulted in weak negative responses on all woody properties.

3.2 Woody plant aggregation

205   Our estimates of aggregation are based on the L-statistic (at 20 meters) minus the distance, meaning positive values
        signal aggregated woody populations and negative values indicate dispersed populations (Figure 6). The large majority
        of sites had positive values, indicating a rarity of dispersed woody populations in African savannas. There is little
        difference in the results for aggregation when sites with periodic patterns are included or not (Table 2). Higher levels
        of aggregation are generally associated with high seasonality, low MAP, fine-textured soils, and relatively flat terrain.

210   These factors are also influential in determining the areas where periodic vegetation patterns occur. In fact, periodic
        patterns are absent in areas with MAP above 750mm, rain seasonality below 1.1, a sand content above 75%, and slopes
        steeper than 3.8%. These are factors that influence ecohydrological processes such as the propensity to form overland
        flows during rainfall events. Fire frequency had no effect on the level of aggregation.

215   Additional insight can be drawn from Figure 7 which shows estimates of aggregation for distances up to 30 meters
        for the sites divided into five categories: sites with periodic patterns and subdivisions based on MAP and soil texture.
        All categories are dispersed at short distances because each crown takes up space and there is bound to be a short
        distance between the center points of crowns even for adjacent plants. Sites with PVPs have the highest levels of
        aggregation reaching a maximum at around 25 meters. The combination with wetter climes (≥600 mm MAP) on

220   coarse-textured soils (≥60% sand) stands out with lower levels of aggregation than the other categories.

4 Discussion

4.1 Dividing woody cover into density and crown size components

Numerous authors have investigated how woody canopy cover varies across African savannas in response to variations
in environmental variables (Good & Caylor, 2011; Sankaran et al., 2005; Staver et al., 2011). Woody cover is
fundamentally a function of crown sizes and crown density, and by separating these components we can analyze
whether they respond differently to environmental factors and how they combine to drive landscape-scale canopy
cover changes across the continent. Our results indicate that crown sizes respond more strongly to rainfall than woody
density. The commonly observed relationship of increasing woody cover with MAP in African savannas (e.g.
Sankaran et al., 2005) is thus mainly a result of increasing size of trees rather than tree density, at least in savannas
with MAP < 700 mm. We also found a unimodal relationship between crown sizes and soil texture that was not present
in the results for woody densities. Soil properties have a considerable effect on the water cycle and a few studies have
noticed that woody growth is suppressed on clayey soils in drylands (Lane et al., 1998; Sankaran et al., 2005; Williams
et al., 1996). Recently, Fensham et al. (2015) showed that the effect is likely due to the higher wilting point on clays
which limits the soil moisture available for plants to extract. A combination of low rainfall and fine-textured soils can
lead to very low soil water potentials and impact the vegetation in a way reminiscent of even dryer conditions. In our
results, the relationship appears unimodal with suppression on both the clayey and the sandiest end. Woody growth is
then controlled by available soil moisture which can be limited by either a high wilting point on clayey soils or low
field capacity on sandy soils. Our results indicate that these constraints affect the size of woody plants and not their
abundance. Woody densities were most strongly influenced by rainfall seasonality and appears to have a unimodal
response function (Figure 5). The sites with very low rainfall seasonality (<0.8) are all situated in the western part of
East Africa (Serengeti, Masai Mara, and northern Uganda) in a region with bi-modal rainfall distributions and far
lower seasonality that further east. Many of these sites had low woody densities and cover but likely for other reasons
than rainfall seasonality. Elephant densities are thought to be a key driver of woody cover in the Mara-Serengeti
ecosystem (Morrison et al., 2016). If we focus on sites with rainfall seasonality above 0.8, there is a more linear
relationship with lower woody densities in areas with high rainfall seasonality which could be associated with higher
water stress in more seasonal systems. Overall, the estimated woody properties were more strongly influenced by
rainfall amounts and seasonality than by soil, slope, and fire. Fire frequency had a weak negative association with
both woody cover, crown sizes, and densities. Fire has, however, an interactive relationship with vegetation structure
(Archibald et al., 2009) and this analysis cannot separate the effect of fire on vegetation from impacts of vegetation
structure on the fire regime.

4.2 Woody plant aggregation and the occurrence of periodic vegetation patterns

In accordance with previous literature, we found that the formation of highly aggregated PVPs is associated with
specific environmental conditions. Periodic patterns are most likely to occur in areas with high rainfall seasonality,
low mean annual rainfall, on fine-textured soils, and on flat or gently sloping terrain. These results are in agreement
with a global study on the biogeography of PVPs by Deblauwe et al. (2008) who found similar effects in regions with
strong seasonal variation in temperature and more constant rainfall (Australia and Mexico) and in regions with distinct

rainfall seasonality but more constant temperatures (Africa). Our analysis further shows that the same factors that
260   contribute to PVP emergence are associated with higher levels of aggregation among woody plants elsewhere in
African savannas. PVPs thus appear under conditions that naturally favor local facilitation and patchiness. However,
the vegetation at many sites with these conditions do not exhibit highly organized periodic patterns which could be
related to soil properties other than texture. The dominant process in the formation of PVPs is a significant overland
flow from bare to vegetated patches which requires near impervious soils. This property is typically associated with
265   shallow soil depths, physical crusts, or hardpans (Leprun, 1999; McDonald et al., 2009), is not strongly dependent on
soil texture, and is not available as a reliable data product.

So, what are the mechanisms that influence local aggregation and patchiness in savannas? Some proposed factors
include fire frequency (Veldhuis, Rozen-Rechels, et al., 2016), seed dispersal (Pueyo et al., 2008), runoff-erosion
270   processes (Ludwig et al., 2005), and short-range facilitation through modified microclimate close to nurse plants. With
increasing abiotic stress, we expect stronger tree-tree facilitation in accordance with the stress gradient hypothesis (He
et al., 2013). In our analysis, the most influential predictor for modeling aggregation was rainfall seasonality, a factor
that could influence plant dynamics in more than one way. The pronounced dry season associated with highly seasonal
systems exerts a strong abiotic pressure, especially on juvenile trees with less developed root systems. Juvenile
275   survival through the dry season is likely higher in the shelter of nearby trees. Over time, a bias in survival rates may
lead to higher aggregation among adult trees. Once the wet season arrives, it often comes in heavy downpours which
can quickly saturate the top soil leading to overland flows. This leads to both redistribution of water resources to
woody patches with higher infiltration rates, and redistribution of litter and soil resources (Ludwig et al., 2005). The
more concentrated rains may also alleviate competition for water during the growing season leading to facilitation
280   being the dominant force in highly seasonal drylands. There was also a clear relationship between fine-textured soils
and higher aggregation. Fine-textured soils increase runoff through lower infiltration rates, and may also amplify stress
during the dry season through their higher wilting point. We found no link between fire frequency and aggregation
and a weak relationship with slope favoring aggregation on flat or gently sloping terrain. This relationship can also be
explained in terms of overland flows. Steeper slopes tend to create drainage rills leading the water downhill which
285   break up the local patch-interpatch redistribution of resources (Saco & Moreno-de las Heras, 2013).

5 Conclusions

Using high spatial resolution imagery, a flexible classification framework, and a crown delineation methodology, we
estimated several key woody vegetation properties in African savannas and analyzed how these vary with local
290   environmental conditions. We find that woody cover, crown sizes, and woody plant densities are more strongly
influenced by rainfall amounts and seasonality than by soil texture, slope and fire frequency. Of specific interest is
that mean crown sizes respond more strongly to mean annual rainfall than plant densities, and has a unimodal
relationship with soil sand content. Maximal tree sizes were associated with mid-textured soils and appeared
suppressed on both clays and very sandy soils. The level of aggregation among woody plants was most strongly related
295   to rainfall seasonality, as was the occurrence of PVPs. Similar processes that influence patchiness in savannas also

contribute to the formation of PVPs, with impermeable soil conditions being a possible difference maker between a patchy savanna landscape and highly organized periodic vegetation.

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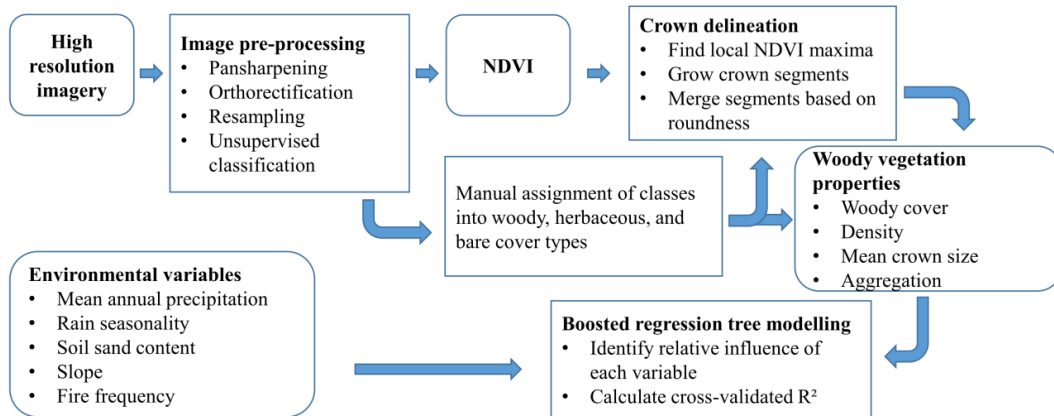


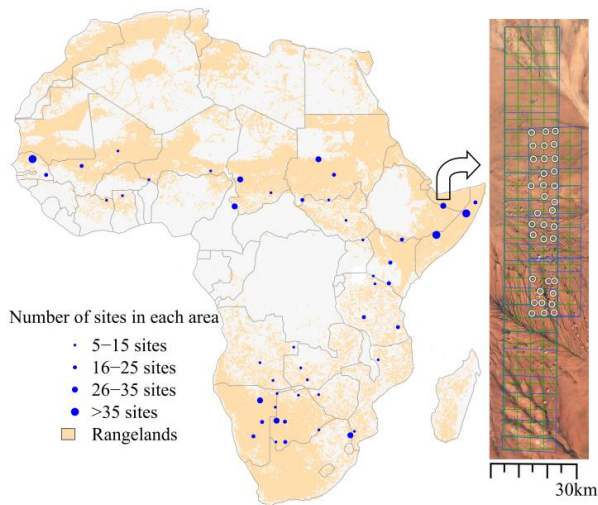
Figure 1. Methodological workflow showing datasets (rounded boxes) and methods (square boxes) used to measure woody vegetation structure and analyze relationships with environmental variables.

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Figure 2: Location of the 48 study areas, containing 876 study sites, spread out over African rangelands. The rangeland areas are from the Anthropogenic biomes product (Ellis & Ramankutty, 2008), and symbol size for study areas is proportional to the number of study sites in each. The map to the right shows a study area on the border between Somalia and Ethiopia and exemplifies the sampling strategy for study sites (white rings). The placement of sites was guided by a

415   0.04º longitude/latitude grid (green lines) in areas with overlapping older and newer satellite imagery (blue lines).
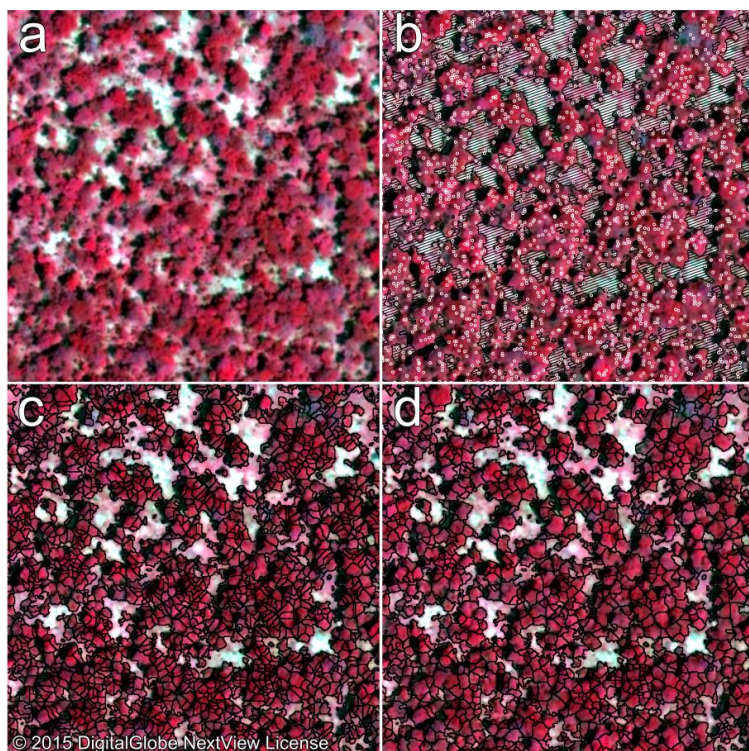
Figure 3: Crown delineation steps for a woodland site in Zambia. (a) Pan-sharpened false-color image, (b) Local NDVI maxima as white points and the non-woody areas shown as striped polygons, (c) Crown segments before merging, and (d) and the final crown polygons following crown merging.

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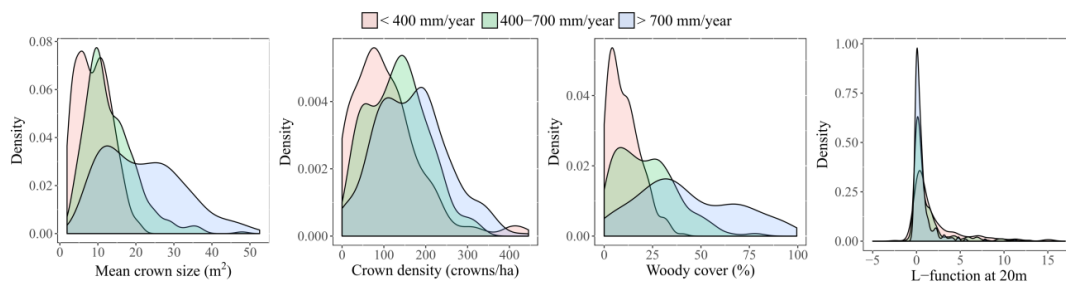
Figure 4: Frequency distributions of mean crown size, crown density, woody cover and aggregation calculated for different MAP ranges.

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Table 1: Relative influence of each environmental variable and the cross-validated R² from the BRT models when modeling woody cover, crown density, and mean crown size.

Variables	Mean Crown Size	Crown density	Woody cover
MAP	45%	33%	47%
Rain seasonality	21%	37%	23%
Sand content	17%	13%	10%
Slope	11%	13%	10%
Fire frequency	6%	4%	11%
Cross-validated R²	0.68	0.49	0.73

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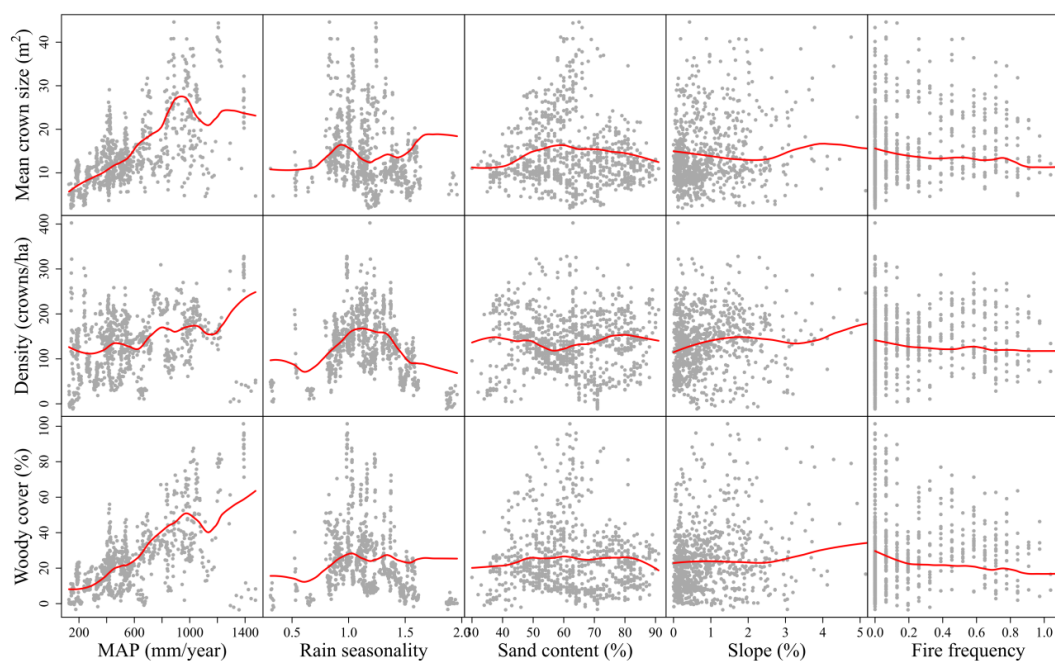
Figure 5: Modeled BRT responses ("partial dependencies") of woody canopy properties to each environmental variable when accounting for the average effect of the other four variables. The red lines are smoothed representations of the fitted functions, with fitted values for each of the 876 sites shown as grey dots. The x-axis for the slope predictor was truncated at 5% to highlight the response in the bulk of the data.

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445   **Table 2: Relative influence of each environmental variable and the cross-validated R² from the BRT models when modeling woody aggregation (L-function at 20 meters) and occurrence of PVPs. In the latter model, all sites with PVPs were given the value 1 and the rest the value 0.**

Variables	Aggregation (all sites)	Aggregation (non-periodic sites)	Occurrence PVPs
MAP	28%	16%	20%
Rain seasonality	44%	51%	46%
Topsoil Sand	14%	16%	21%
Slope	14%	17%	1%
Fire frequency	1%	0%	10%
Cross-validated R²	0.31	0.29	0.83

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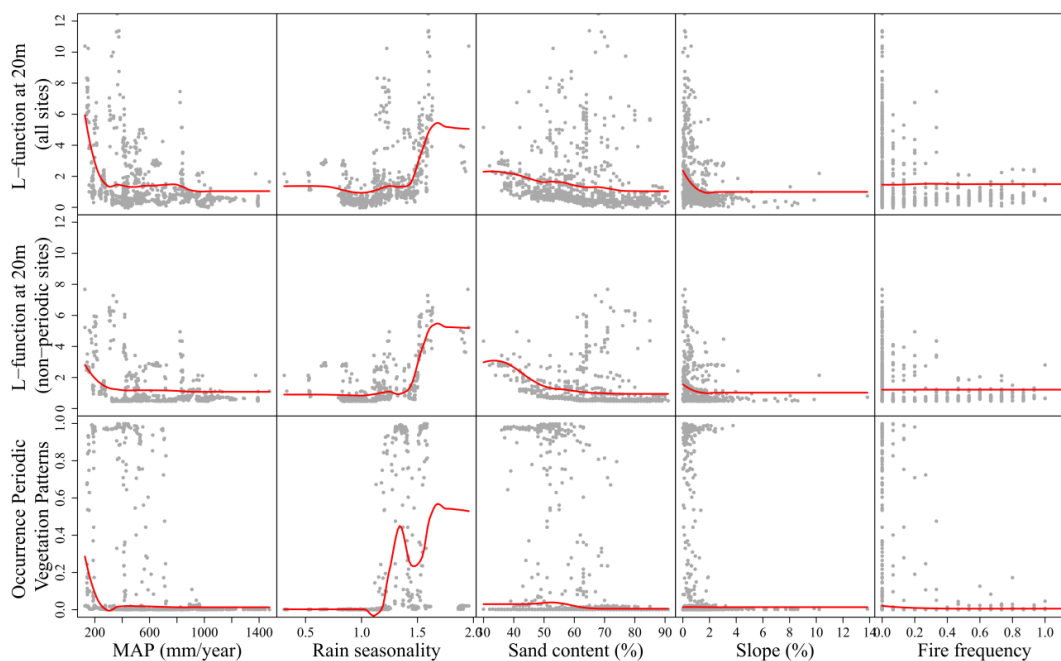
Figure 6: Modeled BRT responses for predictions of under what conditions PVPs occur (top), and woody aggregation (L-statistic at 20 m) for all sites not categorized as having periodic patterns (bottom). The response for each environmental variable accounts for the average effect of the other four variables. The red lines are smoothed representations of the fitted functions overlaying the fitted values (grey dots).

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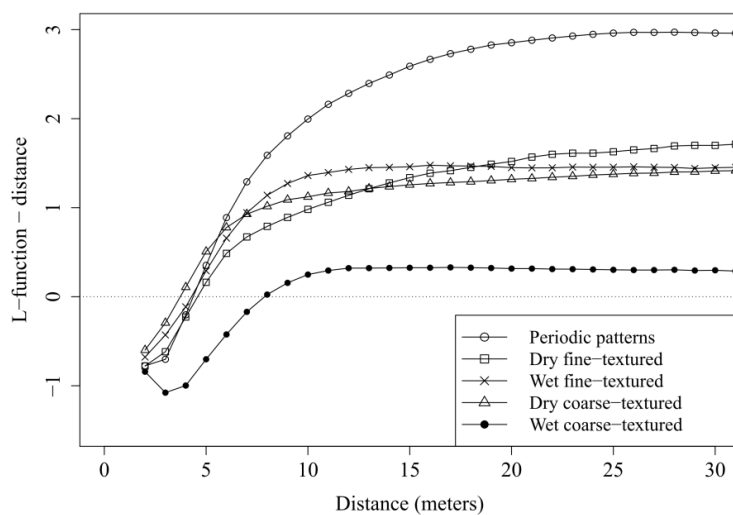
Figure 7: Level of aggregation among tree crowns calculated using Ripley's K transformed to Besag's L-function. The figure shows the mean values of five categories: sites with periodic vegetation patterns, and four subdivisions based on mean annual precipitation and soil texture. Sites classified as having periodic patterns were not included in the latter subdivisions. Sites with MAP below 600 mm were categorized as dry whereas sites with a sand content below 60% were categorized as fine-textured.

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