Response to Reviewer Penny Mograbi

General comments

1) For me, the hinge-point of this study's methods are that tree crown center points are derived from relative NDVI differences. While this might be valid (and from an eye-ball of Figure 3 it seems to work), there are no references discussing this method. I would suggest this method be backed up by previous references. I would also like to know what the limitations of this method are. I would also like to see some form of validation stats (e.g. Kappa) for the accuracy of the woody cover/forest mask, crown size, crown density outputs. Perhaps some test sites could be manually evaluated and compared with the semi-automated approach. You mention "uncertainty in the accuracy" of your metrics on ln 151 so perhaps the authors have already performed an error test and haven't reported it? It would be interesting for readers to know how well these methods performed (and it would increase your citations!)

   Response: Previous studies have used relative brightness (Bunting & Lucas, 2006) or vegetation indices e.g. NDVI (Karlson et al. 2014) to identify and grow crown segments. We referenced these studies without explaining in detail how they did it, and will expand on the description of these previous methods to better explain how they derive seeds for the crown segments. In terms of limitations and accuracy assessment, the added appendix should hopefully provide information on this. It contains results for a validation assessment using field site data from Kenya.

2) The counterpoint to well-written discussion, is the introduction is not the same quality and reads like a rough draft. The introduction lacks the key "introduction linkage" points made both in the abstract and the discussion. The introduction and discussion should book-end the findings, and the introduction was inadequate in this regard. While the content for the motivation and aims for the study were available if one was looking for it, they were not presented in a clear flow and it felt weak. There were also several lines that would be better suited in the methods section. I have made suggestions on how the introduction could be improved below in the specific comments.

   Response: We will revise and expand the Introduction in response to this comment to improve the flow of the introduction and its link to the discussion.

3) I intuitively felt an important part of this study was mentioned in the discussion for the first time. Ln229-230: The results of your study suggest that increasing woody cover trends from multiple previous research articles are related to increasing crown size, rather than increasing density. This is huge and forms the central finding but is only mentioned once! There are important implications for global carbon cycles (see Poulter et al. 2014 Nature and Liu et al. 2015 Nature Climate Change), bush encroachment etc. This would be a finding that other scientists would explore further. You need to develop this theme. I want to know more!

   Response: We will further emphasize this finding by explaining implications for the global carbon cycle. We do not think, though, that our results implicate that bush encroachment in Africa results from increasing crown sizes instead of more woody plants.

4) PVPs: This aspect of your study is mentioned briefly in the beginning, forms a large chunk of your results and more than half of your discussion. This leaves the manuscript unbalanced and the reader

is left wondering why PVPs are so important and why it was decided to explore it so heavily. If the focus is on PVPs, that needs to be reflected in the abstract (it isn't mentioned once until the end) and introduction (it is mentioned as a phenomenon but no why they are worth exploring or what the question is about them. While I am no specialist in PVPs, I would also suggest that no lit review section of PVPs is complete without a mention of Max Rietkerk's work, particularly Rietkerk & van de Koppel 2008 Trends in Ecology and Evolution. I was also missing mention of Bromley et al. 1997 Journal of Hydrology which specially mentions West African PVP's and 'tiger bands'.

Response: We agree with the reviewer comments and will modify the abstract to increase emphasis on PVPs and explain why PVPs are important to our understanding of drylands. We will also reference the work by Rietkerk.

Specific comments

1. Title: The title has the word "Savannas" in it. Yet, later on the authors mention 'drylands' (ln 40) which contains large areas not typically counted as savannas. In Figure 2 the vegetation area of interest is labelled 'rangelands', as well as in ln 87.

   Why use Ellis & Ramankutty's anthropogenic biome for an abiotic-vegetation study on savannas when you could use a climatic-disturbance based biome which defines savannas? This study does not consider the human component. Whichever term the authors choose require clarification and should be used consistently. Why not provide a map of the savanna extent? For example, the 'rangeland' areas in Morocco, Algeria and Libya are traditionally not considered savannas. The authors could use the extent used by Sankaran et al. 2005 Nature as it is widely accepted. It could even be interesting to see the relative differences in abiotic influences on your sites divided into the "stable" and "unstable" savanna categories, if they agree with Sankaran et al. Just a thought. The other issue with the title is the word "structure" when your metrics measure woody cover and tree density. My understanding is that 'structure' implies height metrics or SCD's.

   Response: We agree with the reviewer's worry that the original manuscript used too many terms: savannas, drylands, and rangelands. Most of the sites are savanna but there are also a few sites without trees in the dataset. We also have humid savanna sites so neither drylands nor savanna is a perfect match. In the revised manuscript we settle on 'savanna' as the most inclusive terminology. We used Ellis & Ramankutty's map as a guideline for sampling across African savannas and avoid sampling in the rainforest, agricultural and urban areas.
   We use the term "structure" describing tree density and crown sizes, i.e. the horizontal vegetation structure. While we are not able to analyze vegetation height, we nevertheless feel the terminology is appropriate. We are not alone in this interpretation as there are many studies on vegetation structure that do not analyze vertical structures.

2. Abstract: PVPs not mentioned until ln 28. They need to be introduced earlier if they are the focus of the study.

   Response: We agree and will introduce PVPs earlier.

3. Ln 12-15 Very concise and clear summary of your introduction and aim in these abstract sentences. This idea also needs to be explicitly stated upfront in the introduction and well referenced. I probably lost the impact of this point in the introduction because of poor flow and structure.

   Response: We agree and will modify the manuscript.

4. ln33-34 "While humans often play a dominant role in many systems. . ." I did not understand the point of this statement and it feels out of place here. Either remove it or expand on it.

   Response: We remove this statement when updating the introduction.

5. ln 38 ". . .future stability and productivity. . ." 'stability is a loaded term in savanna literature. Perhaps rephrase this. This idea would form a nice link to bring up again in your conclusion to tie your manuscript together.

   Response: Will re-phrase this to avoid the term "stability"

6. ln 44-45 Great to bring up fire's influence. Recent work by Smit et al. 2016 Journal of Applied Ecology show that SCD's are affected by high intensity fires, including tall tree (large canopy size?) loss. I understand that fire intensity can't be ascertained with MODIS data, but it does need to be mentioned that intensity plays a role.

   Response: Fire intensity certainly matters and we will add acknowledgement of that in the sentence on line 44.

7. ln 40-50 This may be a personal style preference, but worth a mention (word limit permitting). The first half of the paragraph lists abiotic driver influences on woody veg properties, the 2nd half specifies how these drivers can influence the specific metrics of the study (individual: crown size; population: crown density, woody cover) and provide an example of how the same woody cover can have different ecosystem functioning. This is a natural flow, but I wanted a bit more on both topics. Could these two sections be expanded to their own paragraphs?

   Response: We will take this into account when updating the introduction. Thanks for your suggestion!

8. ln 64-65. Please reference mention of vegetation bands. Rasmussen? Bromley?

   Response: Will add reference.

9. ln 69-70. Both studies the authors cite for "African savannas" are from W Africa. Could other African studies be included?

   Response: Will try to find a similar study from Southern or Eastern Africa.

10. ln +-73-81 This paragraph seems more suited to the methods section. Perhaps you could reduce these details to a sentence or two, linking the methodological processes to the general aim, rather

than mention details here and then details again in the very next paragraph? Figure 1 should also only be mentioned in the methods.

Response: We agree with these comments and will update accordingly.

11. ln 80 The PVPs identified in the study sites, were those sites derived from the literature or were they found by the authors. Please mention this. If the latter, it would be nice for the reader to have image examples of the different kinds of PVPs. Are they very easy to spot?

    Response: They were identified visually by the authors (ln 184-185). We agree it would be clarifying to include images of PVPs and take note of this suggestion.

12. ln 90. Does this mean spring in the northern and southern hemispheres? Could you be more specific?

    Response: We have added wording to the manuscript to explain the approach here. "... when trees were in full leaf (generally in mid to late growing season)"

13. ln 91-92 It's not necessary to mention that another on-going study influenced this one's parameters unless some of the data from that study are included in this paper. Perhaps leave this out.

    Response: We understand the reviewer's comment that it may not be necessary to reference the following study, however, in the end we decided to keep this wording since it impacts site selection shown in Figure 2.

14. Methods: The sections on preprocessing and classification were thorough. Thanks!

    Response: Thank you!

15. ln 112-115 This section isn't really necessary for the article, although I do understand the feeling of wanting the time and monumental effort taken for analyses to be recognised by the readers!

    Response: We will remove the last two sentences of this paragraph as suggested.

16. ln 132 Is there a reason for the 40 m limitation to crown size?

    Response: We set the upper limit to crown-size at 40m as we thought larger trees would be very rare across our entire sample domain. In reality, the delineation process was very rarely (if ever) affected by this rule as the crown merging procedure seldom resulted in crowns of that size.

17. lns 143-154 This is a well-needed section and I like that the limitations are mentioned. However, it needs bolstering with supporting literature. A quick google search has shown that crown delineation techniques with multispectral, high resolution satellite data exist and it would useful to see a comparison of the trade-offs to back up the method you have used. This ties in with my request to see support for the NDVI crown centre identification method. Accuracy statistics would be a useful addition here.

Response: We agree and will add references to this section. We will also refer to results from the added validation/error Appendix.

18. ln 172 Was a 20 m cut-off used for Ripley's L because that is where the sill occurs on all the curves in Figure 5?

    Response: We chose to evaluate L at 20 m to be at length scales coarser than typical savanna tree crown diameters, and within length-scales of facilitative tree-tree effects. This distance also makes sense from observation of the sills in Figure 7.

19. ln 192 Mentions Figure 4. Figure 3 was never mentioned. Please include it where relevant.

    Response: Will add reference to Figure 4. Thank you.

20. Results: The subheadings seem strange. You have one sentence on vegetation characteristic differences followed by a subheading "3.1. Mean crown size, density and woody cover". Surely the previous paragraph (of one sentence) fits into this subheading? Or was the subheading meant to be related only to BRT results?

    Response: We include the short paragraph at the beginning of the Results section to introduce the reader to Figure 4. Since Figure 4 also contains aggregation we preferred not to include it in Section 3.1

21. ln 194 It was not clear to me from Figure 4 that arid sites had higher levels of aggregation. Perhaps because the colours did not come out well in that panel?

    Response: The three curves overlap considerably for the L-function. However, we infer higher aggregation in the drier systems. The wet sites (>700) have the highest peak close to zero, while the arid sites (<400) have a lower peak at zero and is more spread out over a wider range of values.

22. ln 197 "Woody cover and mean crown size both had strong relationships with the local environment. . ." What factors in the local environment? Could you be more specific?

    Response: We will rephrase this. We were referring to the higher R-squared in general when mentioning strong relationships with the local environment.

23. ln209-211 Nice findings. The sentence that starts " These are factors that influence ecohydrological processes. . ..”at the end of the paragraph is better suited to the discussion section and needs to be referenced.

    Response: Agreed. We will merge this text into the discussion section.

24. ln 219. ". . .aggregation reaching a minimum at around 25 meters." Consistency with meters/m. This sentence also needs a figure reference at the end. Figure 7?

    Response: We will use m instead of meters, and add figure reference.

25. ln 219-220. This is a discussion point.

    Response: Will move to the discussion.

26. “Heading 4.1. Dividing woody cover into density and crown size components” as well as ln 226-228 are concepts that should be addressed in the introduction. This is a key part of what makes this study novel as most research deals with woody cover without addressing density/crown size differences. These lines are the coherent aim and motivation I was missing in the introduction.

    Response: We will modify the Introduction so that this point is more clearly made.

27. ln 229-231 Great finding! Make a meal of it. The authors need to discuss this vs. bush encroachment findings in the literature.

    Response: We will emphasize the novel finding that increasing cover is a function of tree size more than tree density. We are not sure of the reviewer’s point relating to bush encroachment so for now have not addressed this suggestion.

28. ln 243-245 Low woody cover unrelated to rainfall seasonality. This section needs mention of the large role of disturbance agents in “unstable savannas” (sensu Sankaran et al. 2005). The authors do mention elephant impacts in a sentence, but this needs more unpacking and forms part of the caveats to this study’s results as biotic disturbance was not included. Together with acknowledging effects of fire intensity on SCDs.

    Response: We will mention herbivory and other influential factors not captured by the analysis.

29. ln 254 “In accordance with previous literature. . .” There are no references at the end of this sentence. Which literature?

    Response: Will add references.

30. ln 270 “. . .and short-range facilitation through modified microclimate close to nursery plants” needs a reference.

    Response: Will add reference.

Technical corrections

1. ln20-30 Be careful of the change in tenses. Generally, methods and results should be reported in the past tense.

   Response: We will pay more attention to changes in tenses. Good point!

2. Journal editor preference, but Figure mentions should normally be in parentheses, rather than mentioned in the sentence.
   Eg. “Frequency distributions of the four woody properties, separated into three rainfall categories, are shown in Figure 4.” To “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 (Figure 4).”

Response: Will modify text.

3. ln 118 Insert spaces between “240x240” and shouldn’t ‘meter’ be ‘m’. Be consistent throughout the manuscript. Either change previous mention of ‘meter’ to ‘m’ or vice versa.

   Response: Will change to m and add spaces

4. ln 124 ‘ID’ or ‘point’ rather than ‘id’

   Response: Will change to ID

5. ln 241. This is the only occasion a discussion sentence refers to a results Figure. Either include more links to the results where appropriate, or remove this one. Consistency. e.g. ln 228-229 could also use a figure reference?

   Response: Will add more links in the discussion.

Response to Reviewer Sytze de Bruin

Specific comments:

1) Section 2.1 of the paper should include a proper definition of the sampling universe as well as a description of the sampling frame. The section lists sampling criteria, but these seem to address a pragmatic approach for dealing with issues that occurred while preparing the data set rather than a design approach targeting the intended population.

   Response: We have modified the manuscript to clarify that the sampling frame for the analysis was sub-Saharan African savannas with a minimum of anthropogenic disturbances. We also added that within-image site-selection followed a systematic sampling approach and was guided by a 0.04° longitude/latitude grid.

2) Methods section 2.3 (Crown delineation) contains discussion (lines 135-139 and 144-146) which is improperly placed in my view. The methods section should just describe the methods, as used. Alternative methods can be described in the introduction while potential flaws in the results caused by the used methods should be described in the discussion section.

   Response: These lines describe how this delineation method relates to previous delineation approaches, and concerns related to this and other delineation methods. As the purpose is to describe the method and its strengths/weaknesses, we do not think these sentences are inappropriate for the Methods chapter. We understand the reviewer's concerns, but feel that it is better to keep the description of this method in a single section instead of dividing it between Methods and Discussion.

3) Same section (lines 148-150): Is it really enough to balance rates of falsely divided and falsely grouped crowns? I guess one wants to minimize those errors. How was this achieved?

   Response: This is a general statement about the consequences if crowns are systematically falsely divided or falsely merged, which is an issue with all crown delineation methods. Originally, fine-tuning of the delineation method was done by visual inspection of the crown polygons overlaying the high resolution imagery. With the added Appendix, we also refer to the validation of the Kenyan sites.

4) Same section (lines 150-151) The authors seem to have validated the results by visual inspection which showed the results to "look realistic". That is by no means a scientific validation!

   Response: Here we will refer to the validation of the Kenyan sites, which is a quantitative validation. The visual inspection does, however, also play a role since it helped us determine that the delineation was consistently executed across all landscapes. In many scenes, individual trees can be identified from visual inspection.

5) The validation exercise described in the appendix concerns a small dataset in Kenya. In the sample, common large umbrella thorn acacias were claimed to be overrepresented and given their problematic behaviour in determining crown size and crown density they were excluded when computing R2. So, how can the results from this exercise be generalized to the entire dataset?

   Response: The large majority of our sites do not contain this type of trees with particularly large and spread out crowns which are relatively rare across all of African savannas. Since all four sites in Amboseli were dominated by them, we determined they were overrepresented in the field data. We acknowledge that the delineation method underestimates crown sizes for trees with large spread out crowns, and will mention this problem when referring to the appendix.

6) It remains unclear to me how vegetation periodicity was characterised. In line 185 (section 2.5), "spotted, labyrinthine, gapped or banded patterns" are briefly referred to (between brackets). This seems to suggest periodicity was identified on a single image. Since periodic behaviour plays an important role in the analyses and conclusions, it is necessary to explicitly describe whether or not multiple images were used and to be very clear on its characterisation.

   Response: We will clarify how sites with periodic patterns were identified. We have also added images of sites with periodic patterns, as suggested by the previous reviewer. We visually inspected each site individually and determined if it had a periodic vegetation pattern. This is straightforward for clear cases of banded and spotted patterns. There were cases where it was less straightforward, e.g. weak gapped patterns, and for those we tried to be consistent with the assessment.

7) The analysis employs a mix of resolutions (support sizes) but I am unsure on how these were integrated. It is mentioned that the TRMM data were resampled by bilinear interpolation, but for the other data sets it remains unclear to me at what resolution the analyses were performed. For example, were average slopes over the 240 x 240 m2 regions used or were patterns within the 240 m cells also considered?

   Response: We only considered the center point of the sites and extracted raster values based on nearest neighbor in all cases except the TRMM where we used bilinear interpolation. We will clarify this in the text.

8) There are several changes of tenses throughout the text (also mentioned in the review of Penny Mograbi). My understanding is that the present tense is reserved for presenting either well-known facts or statistical inferences from sample statistics that are generalised to entire populations. However, in this paper no formal hypothesis testing is performed; all results should thus be in past tense since they concern the used (sample) data set.

   Response: We have modified the text to correct tenses.

9) The previous comment points to a major weakness of the work: One might doubt whether the analyses support drawing general conclusions about woody vegetation properties in response to environmental variation in African savannas. The sampling method would only allow to do so under the assumption that the sample is representative. This should then be explicitly stated and supported by proper argumentation. Furthermore, at some places the authors acknowledge that the used data are not error free. This implies that we are uncertain about the true environmental properties and the woody vegetation characteristics. The question then arrises whether the observed differences or relationships exceed uncertainty bounds. How did the authors decide whether an effect was "clear positive", "weak" or "absent"? The inference mechanism should be described.

   Response: While the sample set was affected by various factors, including image availability, cloud cover in images, and anthropogenic disturbances, we do not see any of these factors creating a bias when relating the woody structure estimates to environmental variables. The inferred “clear positive” or “weak”, relationships were based on the trends in the partial dependence plots. We agree that interpretation of results from boosted regression trees relies to some extent on a qualitative assessment of these trends. When describing the methodology we have added: “The influence of individual predictors was estimated from their relative importance in the BRT models, and the directions of relationships were inferred from their trends in partial dependence plots.”

10) The grey dots in Figures 5 and 6 are claimed to represent fitted values for each of the 876 sites considering a single environmental variable with the other variables fixed at their avarages. For MAP,

rain seasonality, sand content and slope this seems to indicate erratic behaviour at very minor changes of the environmental variable under consideration. For "fire frequency" a vertical banding pattern is observed which suggests the BRT produced multiple outputs for the same fire frequency. How come? This pattern should be explained!

Response: Only the partial dependencies (red lines) account for the average effect of the other variables. We will clarify the text and avoid the term fitted function since it might cause confusion. The erratic behavior (overfitting the data points) is often seen in partial dependency plots of boosted regression trees and is perhaps a weakness of this method. It means we need to focus at the main trend of the response function. Many sites had the same fire frequency (based on the number of fires in the period 2001-2015) which causes the striped pattern. The fitted values are model predictions based on all predictors and will thus vary. We have updated the text to clarify this.

List of relevant changes to the manuscript

General

- Tenses were changed so that our results are referred to in past tense.
- An appendix with results from a validation analysis was added to the main manuscript

Abstract

- PVPs are introduced earlier.
- We added numbers for change in woody properties with increasing rainfall to make it more quantitative.

Introduction

- We improved the link between Introduction and Discussion.
- Some sentences that dealt with methods were removed since those descriptions belonged in the Methods section.

Data and Methodology

- We clarified the description of the sampling frame.
- A figure with images of periodic vegetation patterns was added.

Results

- We added a boxplot with change in woody properties along a rainfall gradient. This provides a more quantitative estimate for how crown sizes, crown density, and woody cover respond to increasing mean annual precipitation.
- Some sentences that were discussing results were moved to the Discussion section.

Discussion

- The finding that crown sizes respond more strongly to rainfall than crown density is explained better.
- The effect of browsing (which we did not estimate) is mentioned.

Patterns in Woody Vegetation Structure across African Savannas

Christoffer R. Axelsson[1] and Niall P. Hanan[2]

[1]Geospatial Sciences Center of Excellence, South Dakota State University, Brookings, SD, USA

[2]Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM, USA

Correspondence to: Christoffer R. Axelsson (christoffer.axelsson@sdstate.edu)

~~Key words: African savannas, vegetation structure, environmental gradients, tree crown delineation, crown size, crown density, tree aggregation, woody cover, rainfall seasonality, periodic vegetation patterns, patchiness~~

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 that woody canopy cover, crown density, crown size, and the level of spatial ~~distribution~~ aggregation among~~of~~ woody plants in the landscape, will vary across environmental gradients. A high level of woody plant aggregation is most distinct in periodic vegetation patterns (PVPs), which emerge as a result of ecohydrological processes such as runoff generation and increased infiltration close to plants. Similar, albeit weaker, forces may influence the spatial distribution of woody plants elsewhere in savannas. 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 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~~ enabled 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~~ found that previously documented increases in woody ~~vegetation~~ cover with rainfall is more consistently a result of increasing crown size than increasing density of woody plants. Along a gradient of mean annual precipitation from the driest (<200 mm/yr) to the wettest (1200-1400 mm/yr) end, mean estimates of crown size, crown density, and woody cover increased by 233 %, 73 %, and 491 % respectively. We also ~~find~~ found 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 PVPs, we ~~find~~ found 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.

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 structure.~~ In dry savannas, 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). Climate, both rainfall patterns and temperatures, could change in many parts of Africa (Gan et al., 2016), and ~~its~~ the effect on vegetation will depend on how those pressures interact with other abiotic and biotic factors. In addition to ecohydrological factors, savannas are heavily influenced by the frequency and intensity of fires (Bond, 2008), as well as herbivore regimes (Sankaran et al., 2008), which often combine to suppress woody cover to levels well below its climatic potential (Sankaran et al., 2005). A thorough understanding of the~~se~~ underlying processes that influence savanna vegetation structure~~, and how they are influenced by environmental factors,~~ is key to assessing the future ~~stability~~ resilience and productivity of these ecosystems.

~~In drylands, water availability determines the establishment, growth and survival of plants and competitive plant traits are often of a water saving nature . 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 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). Woody cover is fundamentally a function of crown sizes and crown density and by studying these components individually, it is possible to attain important insight into the function of ecosystems and what ecosystem services they provide. ~~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 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.~~ The level of spatial aggregation among woody plants can help us understand facilitative and competetive processes determining survival of seedlings and saplings. 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 patterns (PVPs; Rietkerk & van de Koppel, 2008;

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 develop into vegetated bands that run parallel to contour lines (Valentin et al., 1999). While PVPs have been studied extensively, their formative processes are seldom linked to ecohydrological processes in other types of savanna landscapes.

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 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. The woody components of the sites were classified and delineated into individual tree crowns~~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 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 derived estimates of mean crown size, crown density, woody cover, and the degree of aggregation among woody plants. We then analyzed how these 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 several areas with PVPs and we also investigated the environmental factors associated with the occurrence of highly organized periodic patterns. ~~The methodological approach is outlined in Figure 1.~~

2 Data and Methodology

Our methodological approach included a flexible classification approach based on unsupervised classification, tree crown delineation, and boosted regression tree analysis (Figure 1).

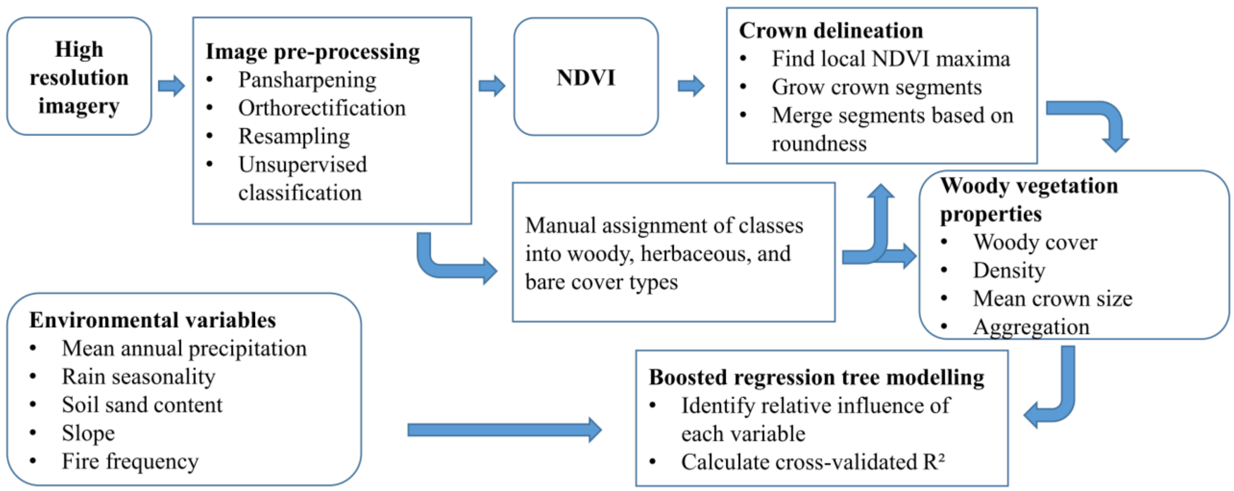


Figure 1. Methodological workflow showing datasets (rounded boxes) and methods (square boxes) used to estimate woody vegetation structure and analyze relationships with environmental variables.

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 m~~eter~~ for panchromatic data and ≤2.44 m~~eters~~ for the multispectral bands). The sampling frame for the analysis was sub-Saharan African savannas with a minimum of anthropogenic disturbances. 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), which helped us identify and avoid areas with high anthropogenic impact. Focus was on selecting recent images (2011-2016) ~~in seasons~~ when trees were in full leaf (~~green~~generally in mid to late growing season) and avoid~~ing~~ 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~~ followed a systematic sampling approach and was guided by a 0.04° longitude/latitude grid which served as a base for site locations. In 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 background. These sites were also eliminated. In the end, we ended up with a total of 876 sites (Figure 2).

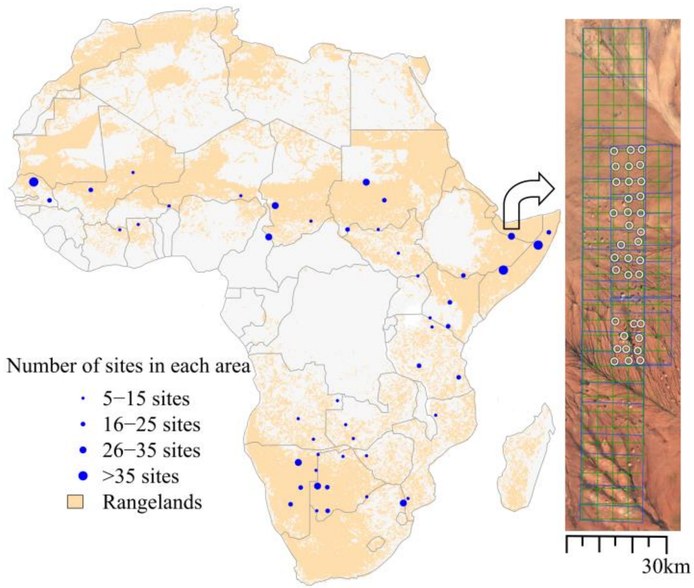


Figure 2: Location of the 48 study areas, containing 876 study sites, spread out over African rangelands. The rangeland areas are from the Anthropogenic biomes product (Ellis & Ramankutty, 2008), and symbol size for study areas is proportional to the number of study sites in each. The map to the right 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 0.04º longitude/latitude grid (green lines) in areas with overlapping older and newer satellite imagery (blue lines).

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 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 240 m) 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 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 the classification process, image classification remained the most time-consuming part of the analysis.~~

2.3 Crown delineation

After the 240 x 240 m~~eter~~ 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 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 3 x 3 pixel neighborhood is a maximum, it is given a unique segment ~~id~~ ID and serves as a seed for a crown segment. The second 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. 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 (Figure 3). 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 m~~eters.~~, as trees larger than this size are very rare throughout the sampling frame. ~~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 and has several traits in common with previous delineation methods (e.g. Bunting & Lucas, 2006; Culvenor, 2002; Karlson et al., 2014; Pouliot & King, 2005) which generally ~~are~~ were 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 of a vegetation index, iteratively expands to neighboring pixels, 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 methodology, the forest mask (woody areas) was already established using the semi-automatic approach described above.

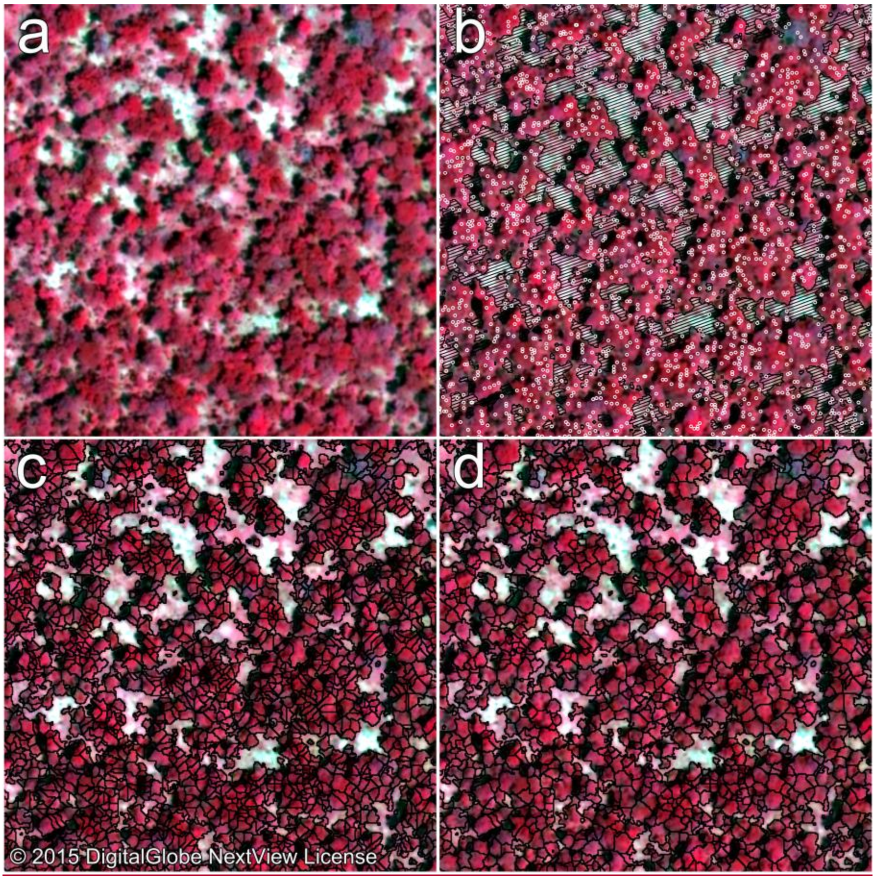


Figure 3: Crown delineation steps for a woodland site in Zambia. (a) Pan-sharpened false-color image, (b) Local NDVI maxima as white points and the non-woody areas shown as striped polygons, (c) Crown segments before merging, and (d) and the final crown polygons following crown merging.

The delineated crowns played an important role in this analysis because they ~~are~~ were used for calculating crown density, crown sizes, and woody plant aggregation. Our analysis of the derived woody properties did not focus on absolute numbers but on how they vary across environmental gradients under the assumption that errors were propagated consistently over space. A visual inspection of all sites indicated that the crown delineation consistently produced crown layers that looked realistic when overlaying the imagery. We recognize, however, that it is extremely difficult to accurately delineate 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 (Rasmussen et al., 2011). 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 of both crown density and aggregation. We evaluated the performance of the classification and delineation methodology using field data from sites in Kenya (Appendix A). This showed that crowns smaller than ~2 m diameter were not reliably detected in the imagery. The validation analysis resulted in relatively strong agreement between estimated and field measured woody properties with R-squares of 0.69 (mean crown size), 0.82 (crown density), and 0.77 (woody cover) when crowns smaller than 2 m diameter were removed from the field data set. We did, however, find that particularly large and spread-out crowns were subdivided, leading to underestimation of crown sizes and overestimation of crown density.

~~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 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.~~

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 used 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 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. The extraction of raster values was based on nearest neighbor to the center point of each site in all cases except the TRMM data, for which we used bilinear interpolation due to its coarse resolution.

2.5 Statistical analysis of woody vegetation properties and the local environment

We derived 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~~ was calculated from the center points of the crown polygons. We used Ripley's K transformed to Besag's L-function to estimate aggregation at distances from 1 to 60 m~~eters~~ (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 used the L-function at 20 m~~eters~~ to represent aggregation as this distance is longer than the typical diameter of savanna trees and within length-scales of facilitative tree-tree effects. When analyzing crown sizes and aggregation, we excluded all sites with a ~~woody~~crown density of 10 crowns/ha or less due to their low sample size for these metrics. We ~~chose~~ used 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 variables (Elith et al., 2008). When generating the BRTs, we used family = gaussian, tree complexity = 3, learning rate = 0.01, and bag fraction = 0.5 as model parameters. ~~-~~R^2, calculated through 10-fold cross-validation, ~~is~~ was 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.The influence of individual predictors was estimated from their relative importance in the BRT models, and the directions of relationships were inferred from their trends in partial dependence plots. 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.

The dataset includes several sites with PVPs, which often are treated as a special case because of their striking appearance (Figure 4). 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, Namibia, and Sudan. The separation identificationprocess was based on 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 BRT family parameter was set to “bernoulli”, appropriate for binomially distributed data.

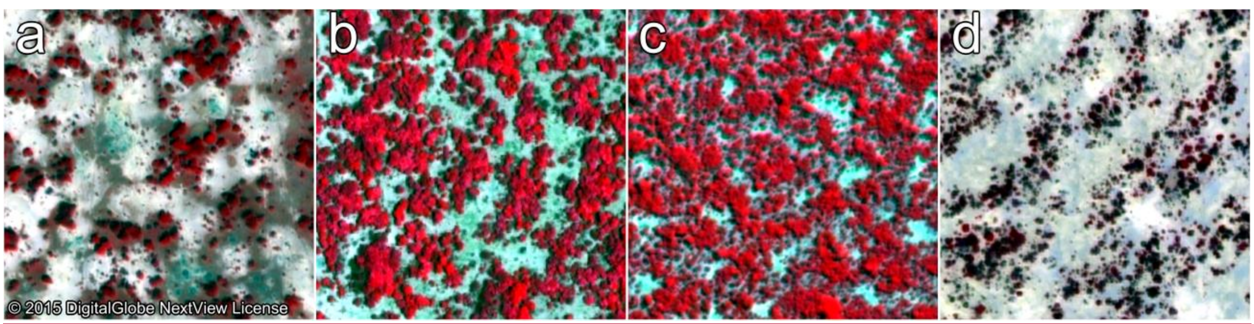


Figure 4: False-color imagery of periodic vegetation patterns identified among the sites: (a) spotted pattern in Senegal, (b) labyrinthine pattern in Mali, (c) gapped pattern in Niger, (d) banded pattern in Somalia. Sites with PVPs were identified visually by the authors.

3 Results

We started by calculating Ffrequency distributions of the four woody properties, separated divided into three rainfall categories, are shown in (Figure 45). The more arid savannas (<400 mm/year) typically featured smaller crown sizes, lower crown density and woody cover, and higher levels of aggregation than sites in the wetter categories.

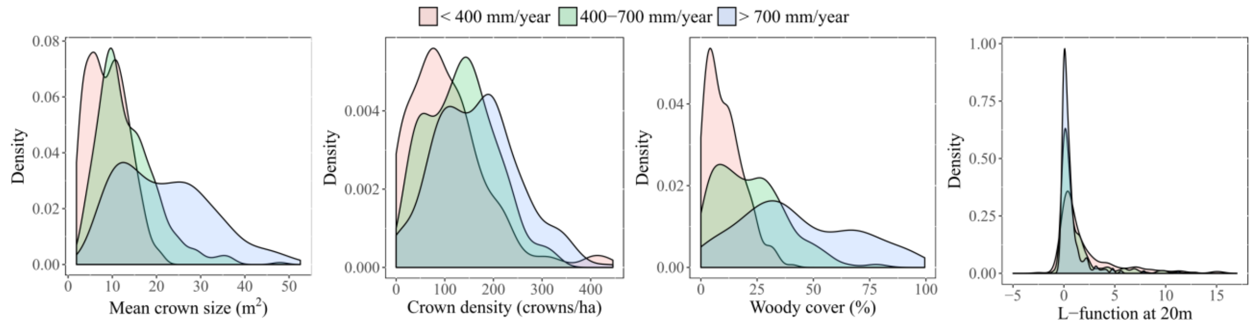


Figure 5: Frequency distributions of mean crown size, crown density, woody cover and aggregation calculated for different MAP ranges.

3.1 Mean crown size, density and woody cover

Boxplots with woody properties divided into MAP bins (Figure 6) show that woody cover and crown sizes increased more sharply with increasing rainfall than crown densities. Along the rainfall gradient from the driest (<200 mm/yr) to the wettest (1200-1400 mm/yr) end, mean estimates of crown size, crown density, and woody cover increased by 233 %, 73 %, and 491 % respectively. The BRT models for ~~W~~woody cover and mean crown size ~~both~~ had high cross-validated R^2 (0.73 and 0.68) ~~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~~ had a clear positive influence on both woody cover and crown sizes, it ~~is~~ was more difficult to interpret the influence of rain seasonality (Figure ~~5~~7). Woody cover ~~has~~ had a weak unimodal response to sand content, that ~~is~~ was driven by ~~a~~ the relationship between crown size and sand content (Figure ~~5~~7). Fire frequency resulted in weak negative responses on all woody properties.

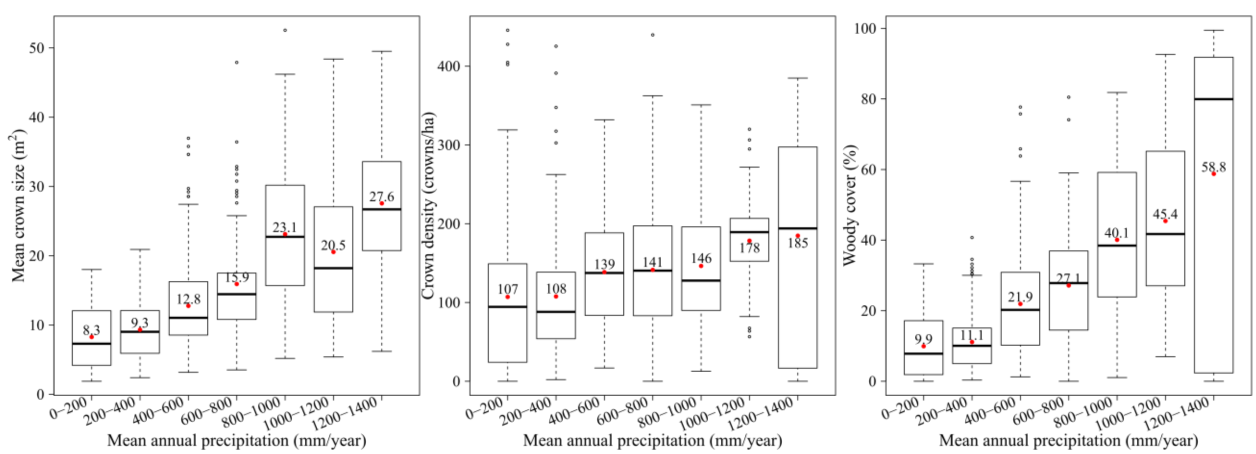


Figure 6: Boxplots of estimates of crown size, crown density, and woody cover along a rainfall gradient. Red points denote the means. Between the driest (<200 mm/yr) and wettest (1200-1400 mm/yr) categories, mean estimates of crown size, crown density, and woody cover increased by 233 %, 73 %, and 491 % respectively.

Table 1: Relative influence of each environmental variable and the cross-validated R^2 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 R^2	0.68	0.49	0.73

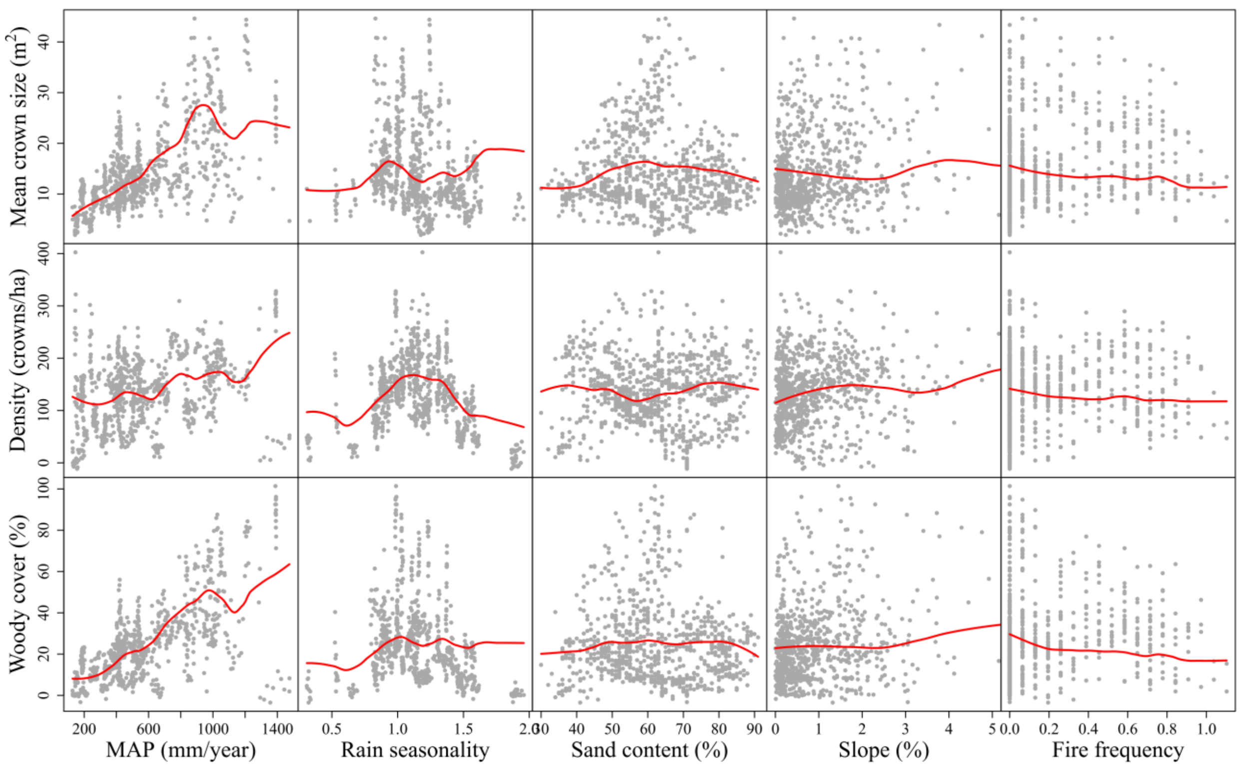


Figure 7: Modeled BRT responses ("partial dependencies") of woody canopy properties to each environmental variable when accounting for the average effect of the other four variables. The red lines are smoothed representations of the responses, with fitted values (model predictions based on the original data) 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.

3.2 Woody plant aggregation

Our estimates of aggregation ~~are~~ were based on the L-statistic (at 20 m~~eters~~) minus the distance, meaning positive values signal aggregated woody populations and negative values indicate dispersed populations (Figure ~~6~~8). The large majority (82 %) of sites had positive values, indicating a rarity of dispersed woody populations in African savannas. There ~~is~~ was little difference in the results for aggregation when sites with periodic patterns ~~are~~ were included or not (Table 2). Higher levels of aggregation ~~are~~ were generally associated with high seasonality, low MAP, fine-textured soils, and relatively flat terrain. These factors ~~are~~ were also influential in determining the areas where periodic vegetation patterns occur. In fact, periodic patterns ~~are~~ were 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.~~

Table 2: Relative influence of each environmental variable and the cross-validated R^2 from the BRT models when modeling woody aggregation (L-function at 20 m) 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 R^2	0.31	0.29	0.83

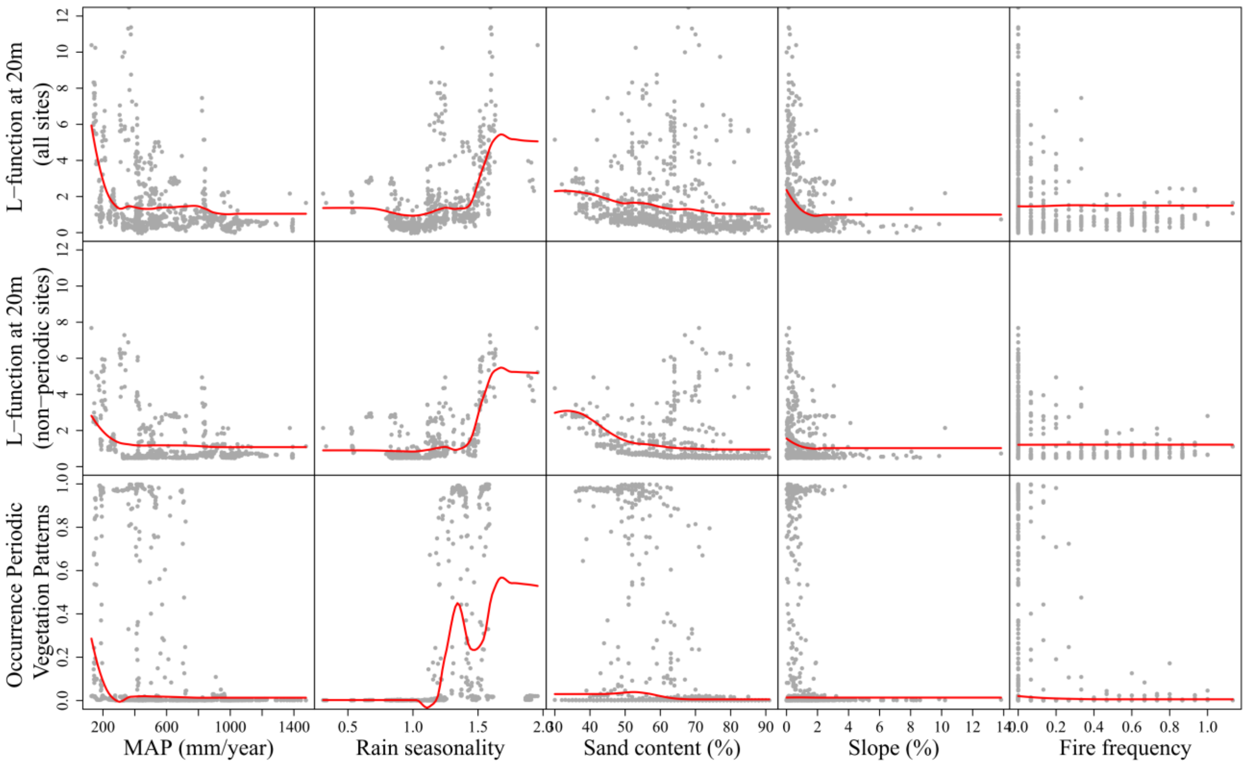


Figure 8: Modeled BRT responses ("partial dependencies") for predictions of under what conditions PVPs occur (top), and woody aggregation (L-statistic at 20 m) for all sites not categorized as having periodic patterns (bottom). The response for each environmental variable accounts for the average effect of the other four variables. The red lines are smoothed representations of the responses overlaying the fitted values (model predictions based on the original data; grey dots).

Additional insight ~~can~~ was~~be~~ drawn from analyzing aggregation along distances and with the data categorized into PVPs and ~~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 (Figure 9). All categories ~~are~~ were 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~~ had the highest levels of aggregation reaching a maximum at around 25 m (Figure 9)~~eters~~. The combination with wetter climes (≥600 mm MAP) on coarse-textured soils (≥60% sand) ~~stands out with~~featured lower levels of aggregation than the other categories.

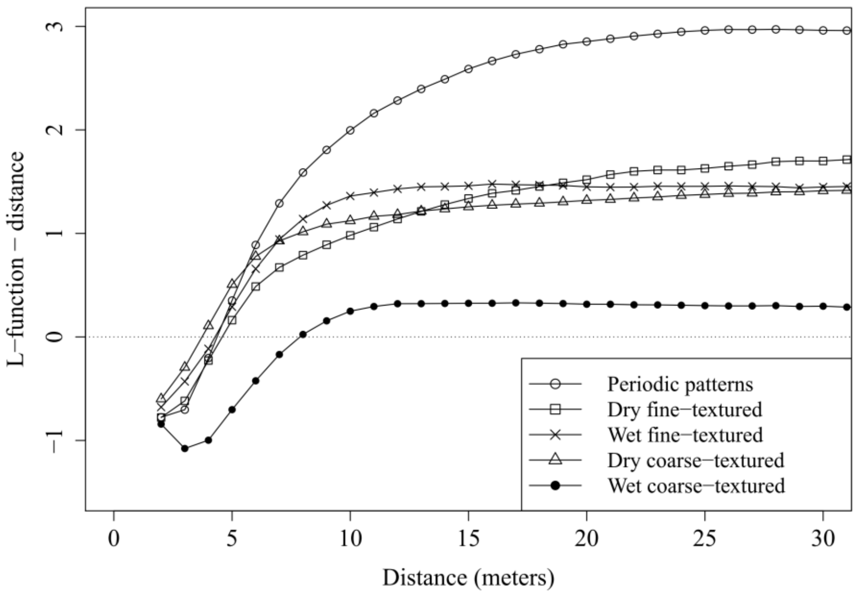


Figure 9: Level of aggregation among tree crowns calculated using Ripley's K transformed to Besag's L-function. The figure shows the mean values of five categories: sites with periodic vegetation patterns, and four subdivisions based on mean annual precipitation and soil texture. Sites classified as 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.

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 variation~~s~~ in environmental variables (Good & Caylor, 2011; Sankaran et al., 2005; Staver et al., 2011). Given that tropical savannas cover about an eighth of Earth's land surface (Scholes & Archer, 1997) and contributes heavily to the global carbon cycle (Poulter et al., 2014), it is important to understand the makeup of these variations in terms of crown sizes and tree densities.~~Woody cover is fundamentally a function of crown sizes and crown density, and b~~By separating woody cover into mean crown size and density ~~these components~~ we ~~can~~ were able to analyze whether they respond differently to environmental factors and how they combine to drive landscape-scale ~~canopy~~ woody cover ~~changes~~ across the continent. Our results ~~indicate~~ suggest that crown sizes respond more strongly to rainfall than ~~woody~~ crown density (Figure 6). ~~The~~ This indicates that the commonly observed relationship of increasing woody cover with MAP in African savannas (e.g. Sankaran et al., 2005) is ~~thus mainly~~more a result of increasing size of trees ~~rather~~ than increasing 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~~ crown densit~~y~~~~ies~~ (Figure 7). 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~~ suggest these constraints affect the size of woody plants and not their abundance. ~~Woody~~ Crown densities were most strongly influenced by rainfall seasonality and appears to have a unimodal response function (Figure ~~5~~7). The sites with very low rainfall seasonality (<0.8) ~~are~~ were 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). Browsing, especially by elephants, has a great impact on woody structure (Sankaran et al., 2013) and is a key factor we did not capture in this analysis. If we focus on sites with rainfall seasonality above 0.8, there is a more linear relationship with lower ~~woody~~ crown ~~densities~~ density and cover in areas with high rainfall seasonality which could be associated with the long periods of high~~er~~ water stress in more seasonal systems. Lehmann et al. (2014) found that high rainfall seasonality can constrain canopy closure and is an important predictor for the presence of savanna. 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~~research (Deblauwe et al., 2008), 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 (Figure 8). These are factors that influence ecohydrological processes such as the propensity to form overland flows during rainfall events (Valentin et al., 1999). The~~se~~ 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 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 shallow soil depths, physical crusts, or hardpans (Leprun, 1999; McDonald et al., 2009), and is not strongly dependent on soil texture~~, and is not available as a reliable data product~~.

Previous literature have linked ~~So, what are the mechanisms that influence l~~local aggregation and patchiness in savannas~~? Some proposed factors include~~ to fire frequency (Veldhuis, Rozen-Rechels, et al., 2016), seed dispersal (Pueyo et al., 2008), runoff-erosion processes (Ludwig et al., 2005), and short-range facilitation through modified microclimate close to nurse plants (Holmgren & Scheffer, 2010). 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 (Table 2), 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 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 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. Sites with the combination of coarse-textured soils (≥60% sand) and wetter climes (≥600 mm MAP) stood out in the analysis by being far less aggregated (Figure 9). This points to the interactive effects of these variables. 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 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 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 size~~s~~ responded more strongly to mean annual rainfall than plant densities, indicating that the commonly observed relationships between woody cover and rainfall (e.g. Sankaran et al., 2005) is more a result of increasing crown sizes than changes in crown density~~and has a unimodal relationship with soil sand content~~. ~~Maximal~~ Larger ~~tree~~ crown 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 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~~ the possible difference ~~maker~~ between a patchy savanna landscape and highly organized periodic vegetation.

Acknowledgements

The satellite data were provided through a NASA agreement and under NextView license. ~~Thanks to~~We thank Jamie Nickeson, Njoki Kahiu, Sujan Parajuli, and Dinesh Shrestha for assistance with data retrieval, field work, and image classification. The project was funded by the National Science Foundation (Coupled Natural-Human Systems Program) and the NASA Terrestrial Ecology Program. CRA was also supported by a Graduate Research Fellowship through the Geospatial Sciences Center of Excellence at South Dakota State University.

Appendix A: Validation of Estimated Woody Vegetation Properties using Field Data from Kenya

This appendix describes a validation analysis of estimated mean crown size, crown density, and woody cover using field data collected in southern Kenya during September-October 2015. Plots were established in five protected areas: Tsavo West NP, Tsavo East NP, Amboseli NP, Ol Pejeta wildlife conservancy, and Il Ngwesi group ranch (Figure A1). In total, we established 28 plots with at least four plots in each protected area. The size of plots varied with the density of trees and shrubs, ranging from 350m^2 to 8000m^2 with a median at 1450m^2 (38x38m). The position of plot corners were determined with a GPS and the positions of trees and shrubs within each plot were measured with a laser rangefinder from the plot corners. Using measuring tape, we determined the diameter of crowns along the longest axis and on the perpendicular. From these two measurements, we later calculated crown sizes assuming elliptic crown shapes. We acquired the best available high resolution imagery covering the sites from 2012 or later. In some cases, this resulted in imagery of lower quality (few green leaves on the trees) than the imagery used in the continental analysis.

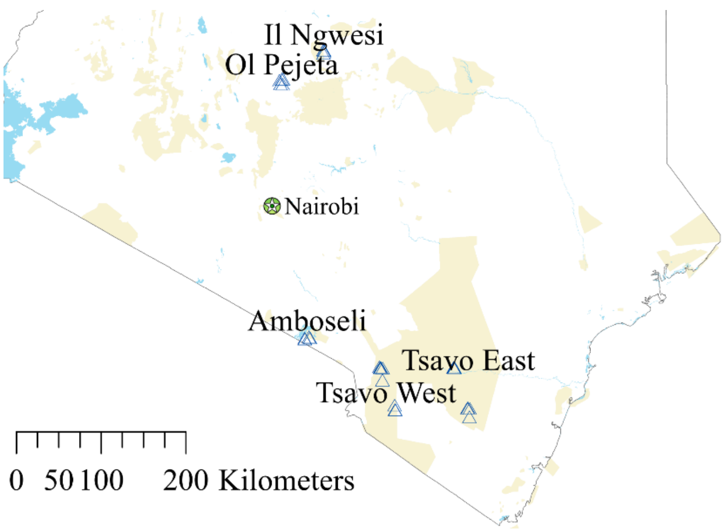


Figure A1: Map of the five protected areas in southern Kenya where field work was conducted. The positions of individual plots are marked with blue triangles.

Our analysis of detection ratios (Figure A2) indicated a detection threshold of ~ 2 m below which smaller trees and shrubs were not reliably detected, while most individuals with crown diameter > 3 m were detected. The detection ratios were likely negatively influenced by the sometimes low quality of the imagery and the time difference between image acquisition and field work (often 2-3 years).

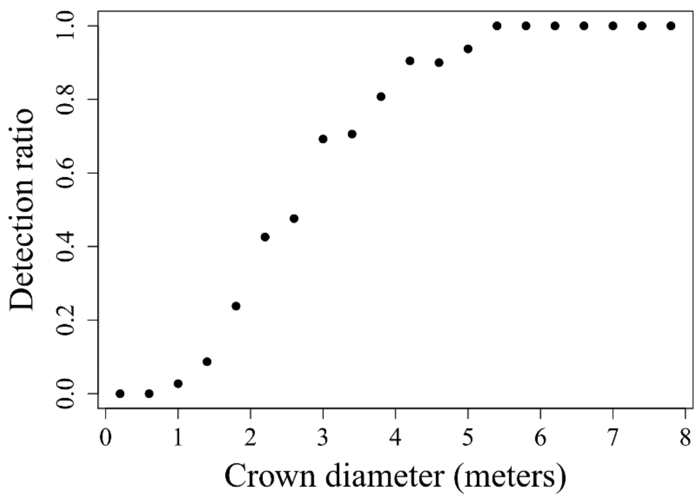


Figure A2: Detection ratios of woody plants in classified imagery at field work sites. The values were calculated as mean detection ratios for trees divided into bins of width 40 cm.

When calculating the relationship between estimated and field measured woody properties (Figure A3), we excluded all field measured trees and shrubs with a diameter less than the 2 m detection threshold. Estimates of the woody properties then fall relatively close to the one-to-one line. The four sites in Amboseli were dominated by large umbrella thorn acacias (*Vachellia tortilis*) with particularly large and spread out crowns (Figure A4). The spread-out architecture of these crowns make them appear as several distinct crowns from above, and the delineation algorithm did not identify them as single trees. The large majority of our sites in the continental analysis do not contain this type of trees which are relatively rare across all of African savannas. Since they dominated all four sites in Amboseli, we determined they were overrepresented in the field data set and therefore chose to exclude the Amboseli sites when calculating R^2 for mean crown size and crown density. We also excluded one site in Ol Pejeta (OLP3) where the smaller trees lacked green leaves in the imagery and could not be detected.

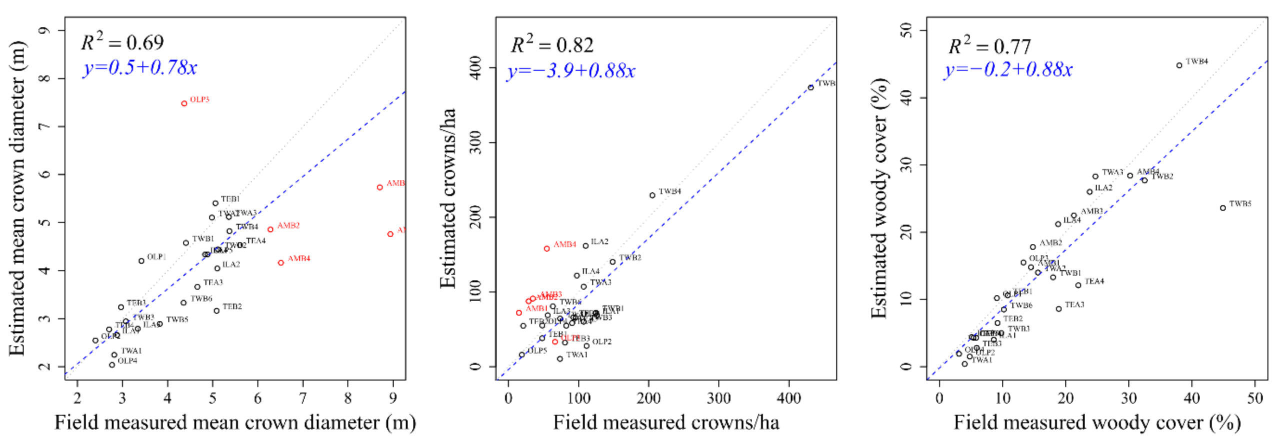


Figure A3: Validation of estimated mean crown size, crown density, and woody cover. The Amboseli sites and one site in Ol Pejeta were excluded when calculating R^2 for mean crown size and crown density. These sites are shown in red color.

Figure A4. Vachellia tortilis at a field work site in Amboseli NP, Kenya. The left image shows two trees with overlapping crowns, with the second being further back on the left. The right image shows the same trees in false color satellite imagery. The spread out architecture of the canopy make them appear as several distinct crowns. The camera symbol roughly indicates the position from which the ground photo was taken.

References

Archibald, S., Roy, D. P., van Wilgen, B. W., & Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in southern Africa. *Global Change Biology, 15*(3), 613-630.

Barbier, N., Bellot, J., Couteron, P., Parsons, A. J., & Mueller, E. N. (2014). Short-Range Ecogeomorphic Processes in Dryland Systems *Patterns of Land Degradation in Drylands* (pp. 85-101): Springer.

Besag, J. (1977). Comments on Ripley's paper. *Journal of the Royal Statistical Society B, 39*(2), 193-195.

Bond, W. J. (2008). What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics, 39*, 641-659.

Bunting, P., & Lucas, R. (2006). The delineation of tree crowns in Australian mixed species forests using hyperspectral Compact Airborne Spectrographic Imager (CASI) data. *Remote Sensing of Environment, 101*(2), 230-248.

Chesson, P., Gebauer, R. L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M. S., . . . Weltzin, J. F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia, 141*(2), 236-253.

Culvenor, D. S. (2002). TIDA: an algorithm for the delineation of tree crowns in high spatial resolution remotely sensed imagery. *Computers & Geosciences, 28*(1), 33-44.

Deblauwe, V., Barbier, N., Couteron, P., Lejeune, O., & Bogaert, J. (2008). The global biogeography of semi-arid periodic vegetation patterns. *Global Ecology and Biogeography, 17*(6), 715-723.

Dohn, J., Augustine, D. J., Hanan, N. P., Ratnam, J., & Sankaran, M. (2016). Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna. *Ecology*.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology, 77*(4), 802-813.

Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment, 6*(8), 439-447.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., . . . Roth, L. (2007). The shuttle radar topography mission. *Reviews of Geophysics, 45*(2).

Fensham, R. J., Butler, D. W., & Foley, J. (2015). How does clay constrain woody biomass in drylands? *Global Ecology and Biogeography, 24*(8), 950-958.

Gan, T. Y., Ito, M., Hülsmann, S., Qin, X., Lu, X., Liong, S., . . . Koivusalo, H. (2016). Possible climate change/variability and human impacts, vulnerability of drought-prone regions, water resources and capacity building for Africa. *Hydrological Sciences Journal*, 1-18.

Giglio, L., Loboda, T., Roy, D. P., Quayle, B., & Justice, C. O. (2009). An active-fire based burned area mapping algorithm for the MODIS sensor. *Remote Sensing of Environment, 113*(2), 408-420.

Gómez-Aparicio, L., Zamora, R., Castro, J., & Hódar, J. A. (2008). Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores? *Journal of Vegetation Science, 19*(2), 161-172.

Good, S. P., & Caylor, K. K. (2011). Climatological determinants of woody cover in Africa. *Proceedings of the National Academy of Sciences, 108*(12), 4902-4907.

Hanan, N. P., Sea, W. B., Dangelmayr, G., & Govender, N. (2008). Do fires in savannas consume woody biomass? A comment on approaches to modeling savanna dynamics. *The American Naturalist, 171*(6), 851-856.

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecology letters*.

Hengl, T., Heuvelink, G. B., Kempen, B., Leenaars, J. G., Walsh, M. G., Shepherd, K. D., . . . Tamene, L. (2015). Mapping soil properties of Africa at 250 m resolution: Random forests significantly improve current predictions. *PloS one, 10*(6), e0125814.

Holmgren, M., & Scheffer, M. (2010). Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology, 98*(6), 1269-1275.

Huffman, G. J., Bolvin, D. T., Nelkin, E. J., Wolff, D. B., Adler, R. F., Gu, G., . . . Stocker, E. F. (2007). The TRMM multisatellite precipitation analysis (TMPA): Quasi-global, multiyear, combined-sensor precipitation estimates at fine scales. *Journal of Hydrometeorology, 8*(1), 38-55.

Karlson, M., Reese, H., & Ostwald, M. (2014). Tree crown mapping in managed woodlands (parklands) of semi-arid West Africa using Worldview-2 imagery and geographic object based image analysis. *Sensors, 14*(12), 22643-22669.

Lane, D. R., Coffin, D. P., & Lauenroth, W. K. (1998). Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States. *Journal of Vegetation Science, 9*(2), 239-250.

Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S., Hoffmann, W. A., . . . Bond, W. J. (2014). Savanna Vegetation-Fire-Climate Relationships Differ Among Continents. *Science, 343*(6170), 548-552. doi: 10.1126/science.1247355

Leprun, J. C. (1999). The influences of ecological factors on tiger bush and dotted bush patterns along a gradient from Mali to northern Burkina Faso. *Catena, 37*(1), 25-44.

Ludwig, J. A., Wilcox, B. P., Breshears, D. D., Tongway, D. J., & Imeson, A. C. (2005). Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology, 86*(2), 288-297.

McDonald, A. K., Kinucan, R. J., & Loomis, L. E. (2009). Ecohydrological interactions within banded vegetation in the northeastern Chihuahuan Desert, USA. *Ecohydrology, 2*(1), 66-71.

Morrison, T. A., Holdo, R. M., & Anderson, T. M. (2016). Elephant damage, not fire or rainfall, explains mortality of overstorey trees in Serengeti. *Journal of Ecology, 104*(2), 409-418.

Pillay, T., & Ward, D. (2014). Competitive effect and response of savanna tree seedlings: comparison of survival, growth and associated functional traits. *Journal of Vegetation Science, 25*(1), 226-234.

Pouliot, D., & King, D. (2005). Approaches for optimal automated individual tree crown detection in regenerating coniferous forests. *Canadian Journal of Remote Sensing, 31*(3), 255-267.

Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., . . . Liu, Y. Y. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature, 509*(7502), 600-603.

Pueyo, Y., Kefi, S., Alados, C., & Rietkerk, M. (2008). Dispersal strategies and spatial organization of vegetation in arid ecosystems. *Oikos, 117*(10), 1522-1532.

Rasmussen, M. O., Göttsche, F.-M., Diop, D., Mbow, C., Olesen, F.-S., Fensholt, R., & Sandholt, I. (2011). Tree survey and allometric models for tiger bush in northern Senegal and comparison with tree parameters derived from high resolution satellite data. *International Journal of Applied Earth Observation and Geoinformation, 13*(4), 517-527.

Rietkerk, M., & van de Koppel, J. (2008). Regular pattern formation in real ecosystems. *Trends in ecology & evolution, 23*(3), 169-175.

Riginos, C., & Grace, J. B. (2008). Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology, 89*(8), 2228-2238.

Ripley, B. D. (1977). Modelling spatial patterns. *Journal of the Royal Statistical Society. Series B (Methodological)*, 172-212.

Saco, P. M., & Moreno-de las Heras, M. (2013). Ecogeomorphic coevolution of semiarid hillslopes: Emergence of banded and striped vegetation patterns through interaction of biotic and abiotic processes. *Water Resources Research*.

Sankaran, M., Augustine, D. J., & Ratnam, J. (2013). Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology, 101*(6), 1389-1399.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., . . . Ludwig, F. (2005). Determinants of woody cover in African savannas. *Nature*, *438*(7069), 846-849.

Sankaran, M., Ratnam, J., & Hanan, N. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography, 17*(2), 236-245.

Scanlon, T. M., Caylor, K. K., Levin, S. A., & Rodriguez-Iturbe, I. (2007). Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature, 449*(7159), 209-212.

Scholes, R., & Archer, S. (1997). Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 517-544.

Shackleton, C., & Scholes, R. (2011). Above ground woody community attributes, biomass and carbon stocks along a rainfall gradient in the savannas of the central lowveld, South Africa. *South African Journal of Botany, 77*(1), 184-192.

Staver, A. C., Archibald, S., & Levin, S. (2011). Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. *Ecology, 92*(5), 1063-1072.

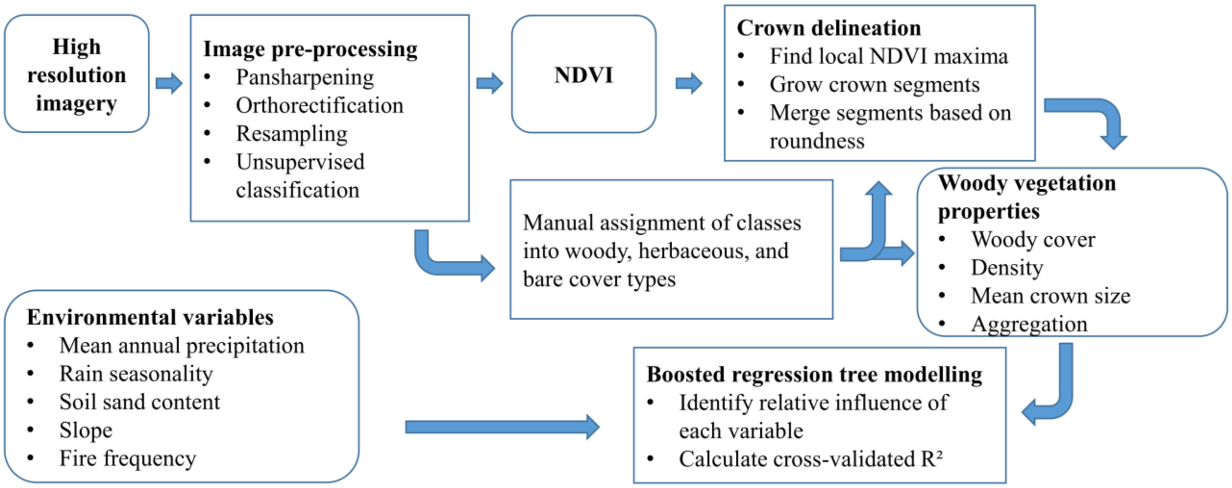
Valentin, C., d'Herbès, J.-M., & Poesen, J. (1999). Soil and water components of banded vegetation patterns. *Catena, 37*(1), 1-24.

Veldhuis, M. P., Hulshof, A., Fokkema, W., Berg, M. P., & Olff, H. (2016). Understanding nutrient dynamics in an African savanna: local biotic interactions outweigh a major regional rainfall gradient. *Journal of Ecology*.

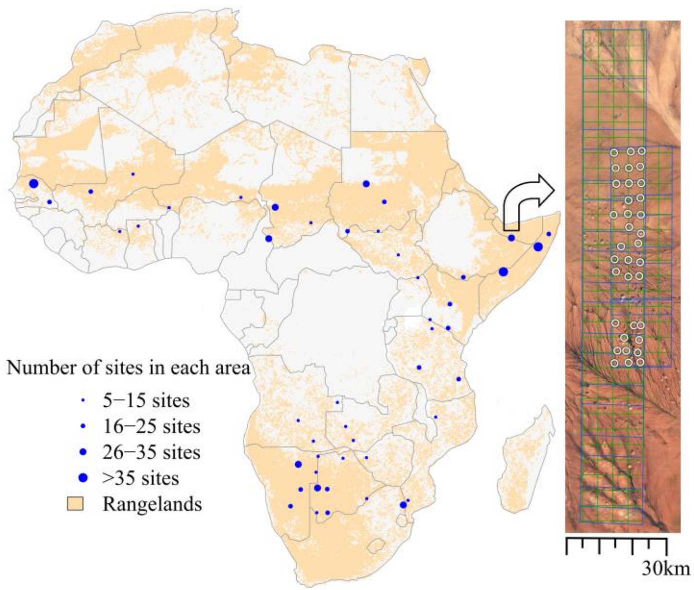
Veldhuis, M. P., Rozen-Rechels, D., Roux, E., Cromsigt, J. P., Berg, M. P., & Olff, H. (2016). Determinants of patchiness of woody vegetation in an African savanna. *Journal of Vegetation Science*.

Williams, R., Duff, G., Bowman, D., & Cook, G. (1996). Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography*, *23*(6), 747-756.

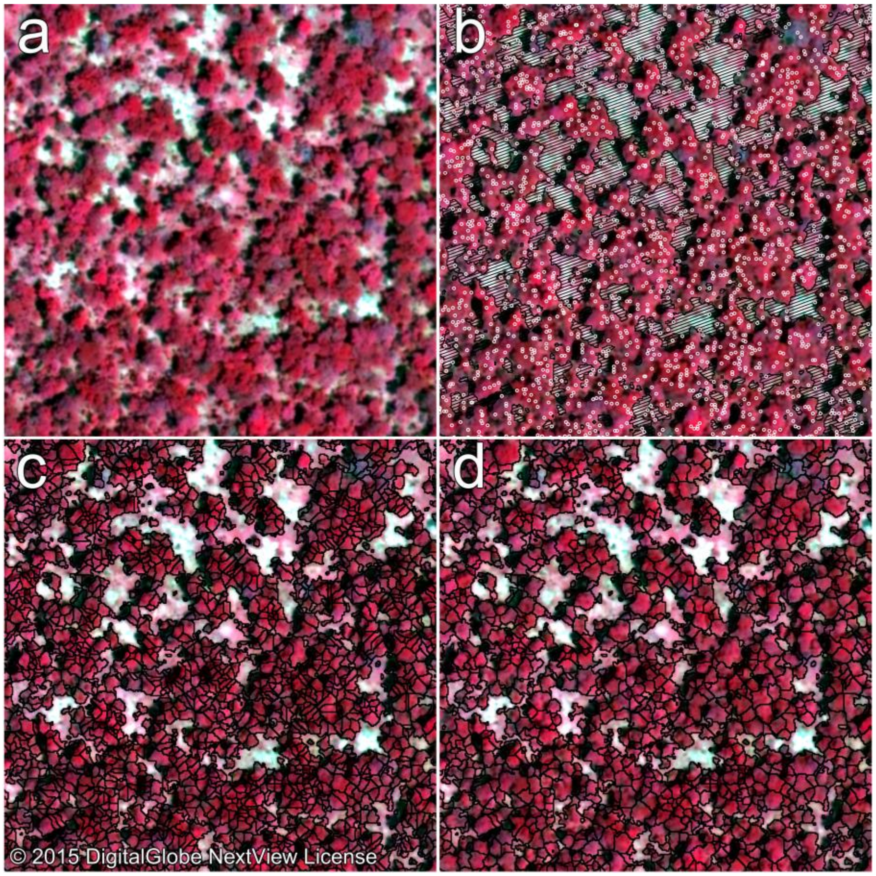
Xu, C., Holmgren, M., Van Nes, E. H., Maestre, F. T., Soliveres, S., Berdugo, M., . . . Scheffer, M. (2015). Can we infer plant facilitation from remote sensing? a test across global drylands. *Ecological Applications, 25*(6), 1456-1462.



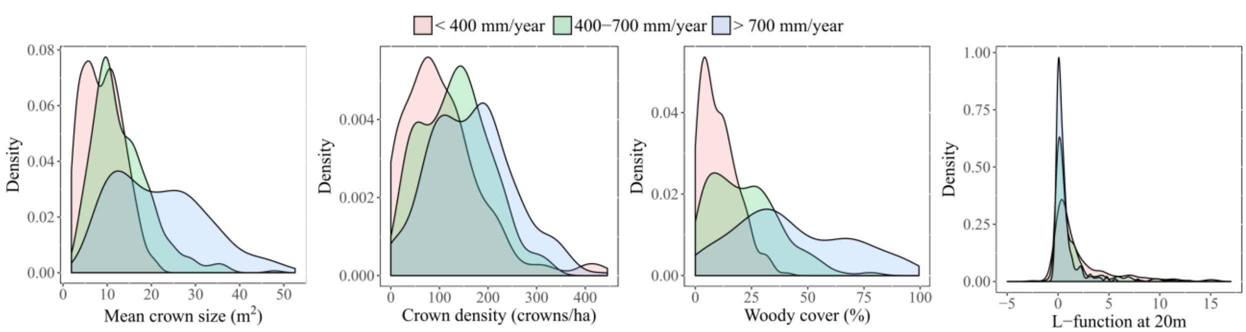
~~**Figure 1. Methodological workflow showing datasets (rounded boxes) and methods (square boxes) used to measure woody vegetation structure and analyze relationships with environmental variables.**~~



~~**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 0.04° 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.**~~



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

Table 1: Relative influence of each environmental variable and the cross-validated R^2 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 R^2	0.68	0.49	0.73

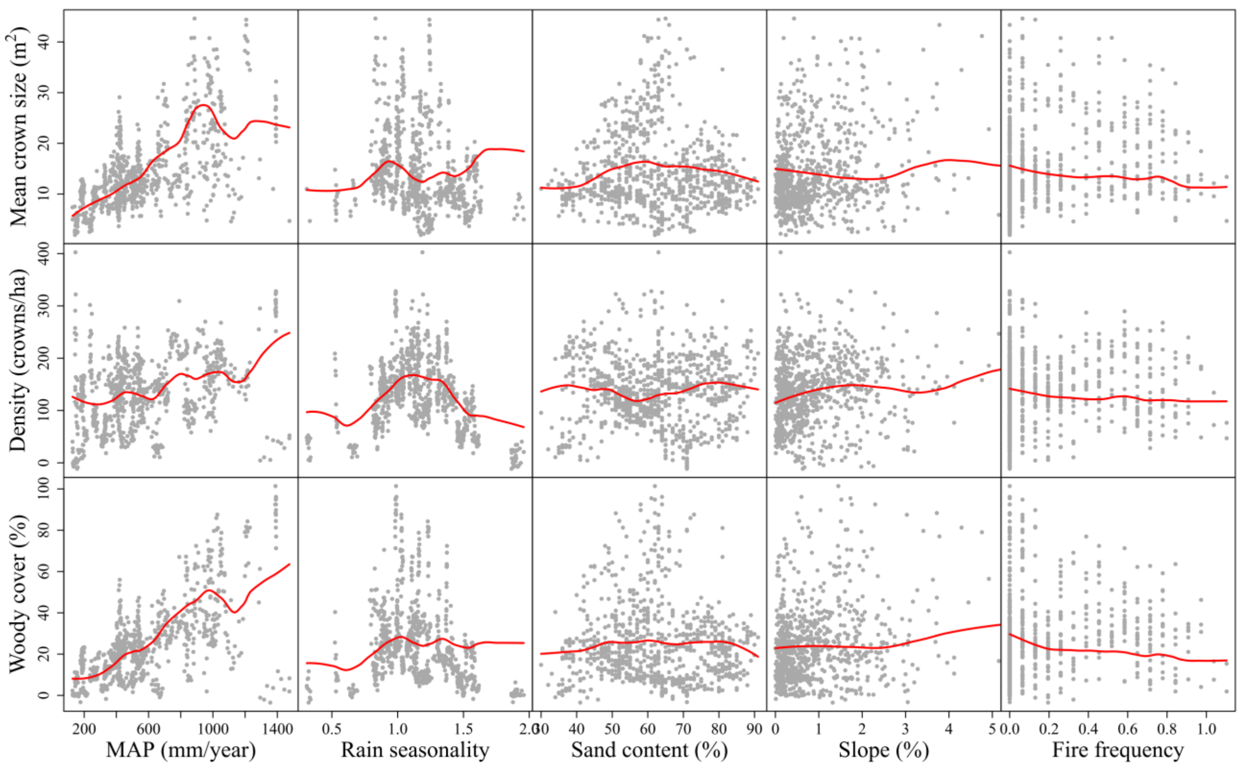
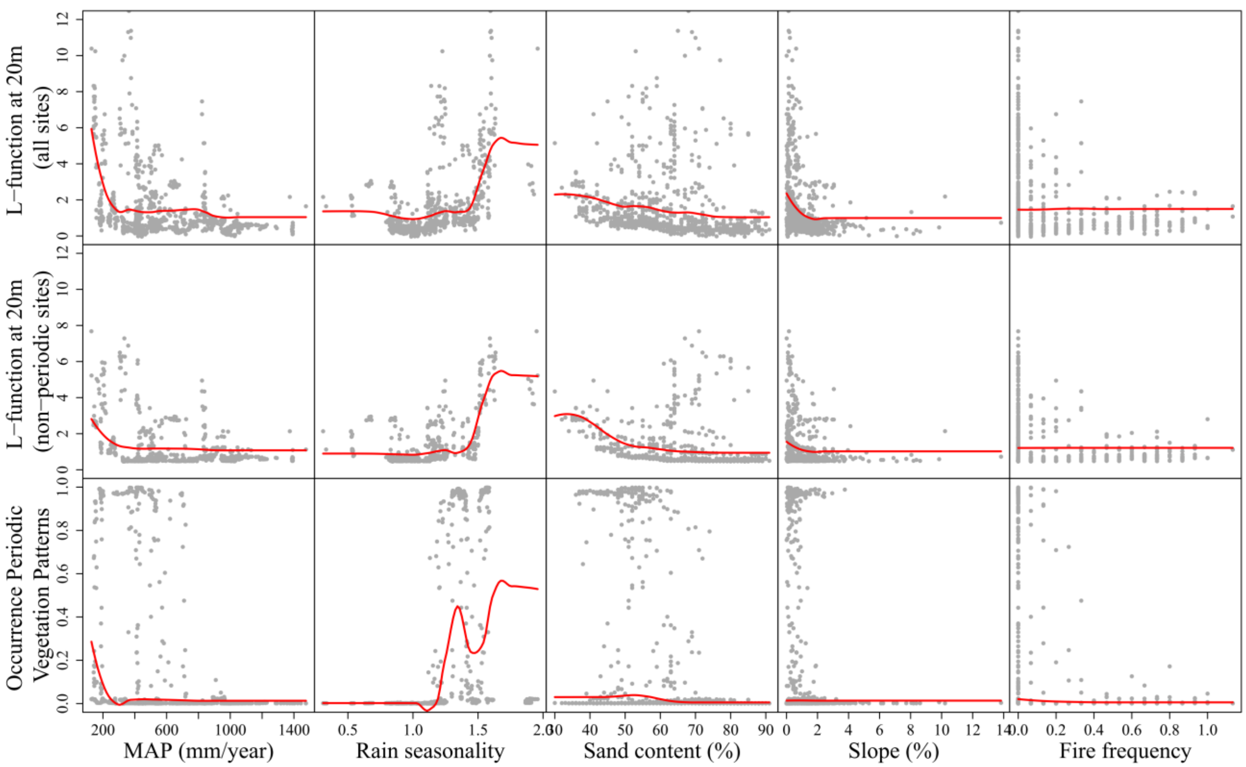


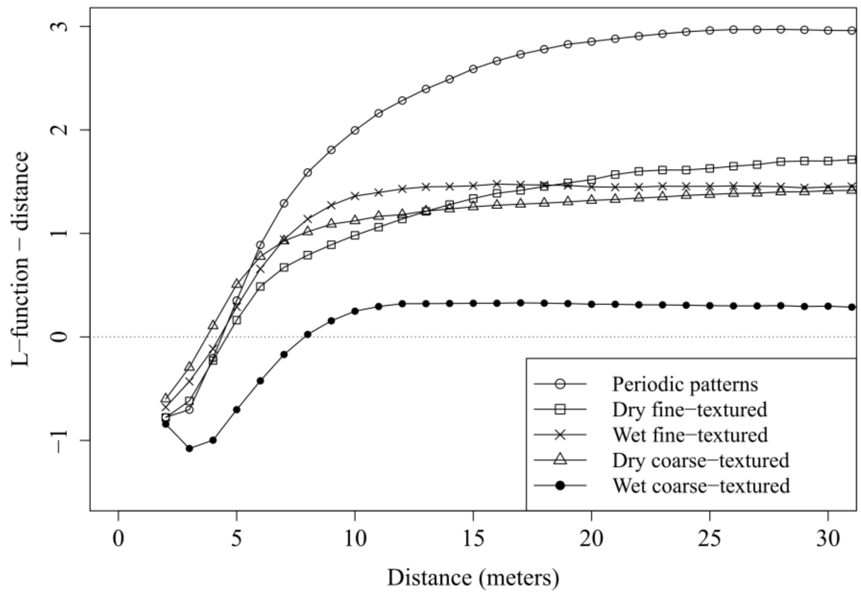
Figure 5: Modeled BRT responses ("partial dependencies") of woody canopy properties to each environmental variable when accounting for the average effect of the other four variables. The red lines are smoothed representations of the fitted functions, with fitted values for each of the 876 sites shown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

~~**Table 2: Relative influence of each environmental variable and the cross-validated R^2 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 R^2~~	~~0.31~~	~~0.29~~	~~0.83~~



~~**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).**~~



~~**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.**~~