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Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa

Land-use vs. rainfall effects on tree cover

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### Abstract

Global change will likely affect savanna and forest structure and distributions, with implications for diversity within both biomes. Few studies have examined the impacts of both expected precipitation and land-use changes on vegetation structure in the future, despite their likely severity. Here we modeled tree cover in Sub-Saharan Africa, as a proxy for vegetation structure and land cover change, using climatic, edaphic and anthropic data ( $R^2 = 0.97$ ).

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Projected tree cover for the year 2070, simulated using scenarios that include climate and land-use projections, generally decreased, both in forest and savanna, although the directionality of changes varied locally. The main driver of tree cover changes was land-use change; the effects of precipitation change were minor by comparison. Interestingly, carbon emissions mitigation via increasing biofuels production resulted in decreases in tree cover, more severe than scenarios with more intense precipitation change, especially within savannas.

Evaluation of tree cover change against protected area extent at the WWF Ecoregion scale suggested areas of high biodiversity and ecosystem services concern. Those forests most vulnerable to large decreases in tree cover were also highly protected, potentially buffering the effects of global change. Meanwhile, savannas, especially where they immediately bordered forests (*e.g.* West and Central Africa), were characterized by a dearth of protected areas, making them highly vulnerable. Savanna must become an explicit policy priority in the face of climate and land use change if conservation and livelihoods are to remain viable into the next century.

## **Introduction**

The tropical biosphere will potentially respond substantially to both climate and land use change. Existing predictions have focused mostly on the impacts of changing climate ([Higgins & Scheiter, 2012](#), [Midgley & Bond, 2015](#), [Zeng \*et al.\*, 2014](#), [Zeng \*et al.\*, 2013](#)). Direct impacts of land use change have received less predictive attention ([Asner \*et al.\*, 2010](#), [Davies - Barnard \*et al.\*, 2015](#), [Heubes \*et al.\*, 2011](#)) despite the expectation that rapid population growth in tropical Africa (United Nations, 2013), agricultural expansion and intensification (Tilman *et al.*, 2001), and bioenergy production (Alexandratos & Bruinsma, 2012, [Laurance \*et al.\*, 2014](#)) constitute a direct threat both to the biodiversity and the

sustainability of services provisioning of savanna and forest ecosystems in the tropics ([Gardner et al., 2010](#), [Geist & Lambin, 2002](#), [Sala et al., 2000](#)). Even fewer studies have examined climate change and land-use change together ([Davies - Barnard et al., 2015](#), [Heubes et al., 2011](#)), and so their relative effects on tropical vegetation remain largely unknown.

In Sub-Saharan Africa, two biomes dominate: tree-dominated forests and grass-dominated savannas. Tree cover effectively differentiates the two: forest ecosystems are characterized by a closed tree canopy and a shade-tolerant understory ([Ratnam et al., 2011](#)), while savannas are defined by the coexistence of a continuous grass layer with a discontinuous tree layer ([Parr et al., 2014](#), [Ratnam et al., 2011](#)). Tree cover therefore differentiates forests from savannas at large scale ([Hirota et al., 2011](#), [Staver et al., 2011b](#)).

Savanna and forest distributions and structure result from interactions between climate, soils and disturbance regimes, especially fire and herbivory ([Sankaran et al., 2005](#)). Rainfall is a primary although not singular driver of biome distributions globally ([Hirota et al., 2011](#), [Staver et al., 2011b](#)); rainfall constrains maximum tree cover ([Sankaran et al., 2005](#)), but tree cover varies substantially below this maximum due to edaphic and top-down processes, including fire and herbivory ([Bond, 2008](#), [Bucini & Hanan, 2007](#), [Sankaran et al., 2008](#)). Fire and herbivory themselves represent complex ecological processes: feedbacks with vegetation can strongly influence both fire regimes and herbivore population dynamics ([Bond, 2008](#)); abundant grassy fuels make fires vastly more likely in savannas than in forests ([Hoffmann et al., 2003](#)), while the accessibility of forage in savannas directly elevates herbivore densities ([Riginos & Grace, 2008](#)).

Climate and land use change will potentially affect each of these processes. In the tropics, climate change is expected to lead to increasing temperature and, more importantly, to changing precipitation patterns (IPCC, 2014). Although fire and herbivory pre-date humans in savannas ([Bird & Cali, 1998](#), [Keeley & Rundel, 2005](#)), human activities have substantial impacts on both fire and herbivory regimes globally (Van Langevelde *et al.*, 2003). Land use, especially agriculture, can also have significant direct effects on ecosystem structure and on tree cover ([Laurance \*et al.\*, 2014](#)). Changes in rainfall, fire and herbivory regimes, and land use will thus likely have major impacts on tree cover, of interest in and of themselves from an ecosystems perspective.

However, tree cover change is also tightly linked to habitat loss in both savanna and forest systems, especially when it results from land-use change. A degraded forest is not a savanna, nor is an encroached savanna a forest ([Mitchard & Flintrop, 2013](#), [Veldman \*et al.\*, 2015a](#), [Veldman & Putz, 2011](#)). Indeed, tree cover and biodiversity usually decrease in tropical forests that are logged or subject to intensive agriculture ([Barlow \*et al.\*, 2007](#), [Gardner \*et al.\*, 2009](#), [Gibson \*et al.\*, 2011](#), [Laurance \*et al.\*, 2007](#)). Moreover, degraded forests, where the canopy has been opened resulting in grass invasion, are very different in terms of biodiversity and ecosystem services from old-growth savannas ([Veldman \*et al.\*, 2015a](#), [Veldman & Putz, 2011](#)). Savanna structure is also related to habitat and diversity, both faunal and floral ([Du Toit, 1996](#), [Du Toit & Cumming, 1999](#), [Price & Morgan, 2008](#), [Zaloumis & Bond, 2011](#)), and agricultural conversion to intensive cropping and ranching is responsible for tree cover modification and associated biodiversity. However, protected areas have the potential to mitigate against the effects of climate and land-use change on species distributions ([Loarie \*et al.\*, 2009](#), [Ordonez \*et al.\*, 2014](#)), such that the net effect of tree cover loss on natural and managed systems depends on their conservation context.

Here, we evaluate the potential influences of climate and land-use change on tree cover in tropical Africa. We begin by examining climate, disturbance, and land use effects on current tree cover, and this relationship to predict the future of tree cover under a variety of different climate and land-use change scenarios. By comparing these expected changes against baseline biome distributions ([White, 1983](#)) and protected area distributions from the World Database on Protected Areas, we then evaluate which areas of tropical Africa are potentially most vulnerable to global change.

### **Material and Methods**

We use tree cover as a proxy for vegetation structure and land cover ([Mayaux \*et al.\*, 2004](#)) and build a statistical model linking tree cover data in Sub-Saharan Africa with climatic, edaphic and anthropogenic data, from global and remote sensing databases. We use climate and land-use projections from the Representative Concentration Pathways scenarios ([Van Vuuren \*et al.\*, 2011](#)) to simulate tree cover changes in the year 2070. We compare tree cover changes against historical biome distributions ([White, 1983](#)) and protected area extent, by WWF Ecoregion (defined as areas sharing homogeneous biophysical features ([Olson \*et al.\*, 2001](#))), in order to identify areas of high biodiversity and ecosystem services concern.

#### *Data*

Percent tree cover data for the year 2000 were derived from the 250m MOD44B Collection 5 product from the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor ([DiMiceli \*et al.\*, 2011](#)). This product gives percent canopy cover and was calibrated only against trees > 5m tall ([Hansen \*et al.\*, 2003](#)), thus potentially underestimating shrub cover. Rainfall and seasonality are expected to have a greater influence on vegetation structure than temperature in the tropics ([Sankaran \*et al.\*, 2005](#)). Mean annual rainfall (mm

year<sup>-1</sup>) and seasonality were derived from the 30-arcsec WorldClim Version 1.4 datasets (data averaged from 1950 to 2000, Table S1, Hijmans *et al.*, 2005). The seasonality index used here represents a measure of the variation in monthly rainfall totals over the course of the year and is computed as the ratio of the standard deviation of the monthly total rainfall to the mean monthly total rainfall, expressed as a percentage (Hijmans *et al.*, 2005). The soil map of Africa at 1km resolution was obtained from the ISRIC World Soil Information team in collaboration with the African Soil Information System project ([www.isric.org](http://www.isric.org)) and was used to extract soil properties estimates for six soil characteristics that can be potential determinants of savanna structure (Bucini & Hanan, 2007, Sankaran *et al.*, 2005, Sankaran *et al.*, 2008): percent sand, clay and silt, organic carbon content ( $\text{g kg}^{-1}$ ), pH (~ phosphorus availability) and the cation exchange capacity (~ fertility, in  $\text{cmol kg}^{-1}$ ) average for the top 100 cm of soil (Table S1). We used the monthly L3JRC burnt area product to derive an estimate of fire frequency (Giglio *et al.*, 2010). For this analysis, monthly data layers from 2000 to 2007 were combined to calculate the total number of times individual pixels burned over the time period (Table S1). We used population density data for the year 2000 (Bengtsson *et al.*, 2006). Finally, land-use data (here, the proportion of cropland and pasture per pixel; Table S1), were extracted and computed for the year 2000 from the Harmonized Global Land Use database version 1 (Chini *et al.*, 2014), available for the entire globe at 0.5-degree spatial resolution.

Our analysis was restricted to low elevation and tropical and sub-tropical climates. Pixels with elevation greater than 1500m or less than 0m were excluded using the elevation layer from the Food and Agriculture Organization Harmonized World Soils Database. We also excluded sites with winter rainfall, which are characterized by vegetation other than savanna and forest (Staver *et al.*, 2011b). Finally, we compiled the World Wildlife Fund (WWF)

Terrestrial Ecoregions (Olson *et al.*, 2001) and protected areas from the World Database on protected Areas (WDPA) Annual Release 2014 (web download version – February 2015; <http://www.protectedplanet.net>) for Sub-Saharan Africa.

All data were re-projected in WGS-84 at a resolution of  $0.08333^{\circ}$  (~10km) using a nearest neighbor procedure. We extracted percent tree cover, fire frequency, climate, soil and land-use data on a regular grid of 215,160 points for statistical analysis. We computed Pearson correlation coefficients among all predictor variables, and chose only one variable for inclusion in analysis when variables covaried by  $r > 0.7$ . We calibrated the model with 70% of the dataset and used the remaining 30% for validation.

#### *Modeling framework*

Random forest models use a classification and regression tree approach that recursively partitions predictor variables. The algorithm creates multiple bootstrapped regression trees without pruning and averages the outputs; each tree is grown using a randomized subset of predictors (Breiman, 2001). These models are very effective in reducing variance and error in high dimensional data sets by taking an ensemble of unpruned trees. Moreover, growing large numbers of trees reduces overfitting, and random predictor selection keeps bias low, providing models appropriate for use in prediction (Prasad *et al.*, 2006). Several metrics are available to help interpreting these models. Variable importance can be evaluated based on how much predictions deteriorated when values for the predictors were randomly permuted (Breiman, 2001); we used this approach to compare relative importance among predictors variables. All data were extracted and analyzed in R (R Core Team, 2015), using the “raster” and “randomForest” packages.

### *Future projections*

The emissions scenarios that provide inputs to climate models are produced by Integrated Assessment Models (IAMs), driven by assumptions about socioeconomic forces (e.g. demography, economy, land-use..., Moss *et al.*, 2010). Over time, these scenarios have provided more complex and comprehensive information about air pollutant emissions and land-use (Moss *et al.*, 2010). The latest set of scenarios is contained in four Representative Concentration Pathways (RCPs) which correspond to different radiative forcing trajectories. Each scenario is 'representative' as it provides only one possible trajectory for greenhouse gas and radiative forcing reached by the year 2100 (IPCC, 2014). The term 'pathway' emphasizes that the scenarios represent trajectories over time. RCPs are thus sets of scenarios with independent and clear narratives of emission, socioeconomic and policy trajectories produced by four individual IAMs (Moss *et al.*, 2010).

The RCP 8.5, developed by the MESSAGE modeling team (Riahi *et al.*, 2007), is characterized by increasing greenhouse gas emissions with radiative forcing exceeds  $8.5 \text{ W m}^{-2}$  by 2100 and continues to rise afterward. Within this scenario, a global population increase drives a strong increase in croplands and pasture lands, especially in developing countries (Hurtt *et al.*, 2011). The RCP 6.0 and 4.5, developed respectively by the AIM and the GCAM modeling teams (Van Vuuren *et al.*, 2011), correspond to stabilization scenarios wherein radiative forcing stabilizes at  $\sim 6 \text{ W m}^{-2}$  and  $4.5 \text{ W m}^{-2}$  after 2100 due to mitigation actions. In RCP 6.0, croplands are expected to increase due to increasing food demand, but pasture areas somewhat decrease due to a shift from extensive to more intensive husbandry. The RCP 4.5 predicts a radical change in global land-use because carbon from vegetation will be valued as part of global climate policy (Van Vuuren *et al.*, 2011); cropland and pasture thus decrease as a combined result of reforestation programs, yield improvement and dietary changes. Finally,

the RCP 2.6, developed by the IMAGE modeling team (Van Vuuren *et al.*, 2011), corresponds to a pathway where radiative forcing peaks at  $2.6 \text{ W m}^{-2}$  before 2100 and then declines. A crucial feature of the RCP 2.6 is the use of bio-energy and carbon capture and storage technologies, which results in negative emissions (Van Vuuren *et al.*, 2011); however, this scenario achieves decreases in radiative forcing via a large increase in croplands dedicated to biofuel production, and pasture also increases as animal production does (Hurtt *et al.*, 2011). In summary, each RCP achieves its radiative forcing trajectories by simulating diverse land-use, socio-economic and policy scenarios, such that the intensity of land-use change does not monotonically increase with RCP radiative forcing (Van Vuuren *et al.*, 2011).

The Global Circulation Models (GCM) within the CMIP5 framework (Taylor *et al.*, 2012) used the latest release of RCPs as inputs. We thus used an ensemble of all GCM outputs, available downscaled and calibrated against Worldclim 1.4 as baseline climate (Hijmans *et al.*, 2005), for the four RCPs as future precipitation and seasonality projections in 2070 (average 2061-2080). Future land use projections were derived from the IAM outputs and harmonized against historical and future data (Hurtt *et al.*, 2011). We downloaded cropland and pasture data from Chini *et al.* (2014) and averaged the variables from 2061 to 2080 for the four RCPs for consistency with the climate data. Human population density data were derived from IPPC SRES projections A1B for the year 2100 (SI).

To discriminate between climate vs. land-use change, we calculated future tree cover with the Random Forest model we calibrated and using projected (1) climate change, (2) land-use change, and (3) both. As an approximation, we only changed climate, land use and population variables, keeping fire and soil constant. Indeed, standard future fire projections are not yet

available, and changing soil variables would require building a more complex model taking into account feedbacks between soil and vegetation, which is not possible with a statistical model. Moreover, while our future projections do not explicitly consider the alternative stable state dynamic thought to characterize savanna and forest distributions ([Hirota \*et al.\*, 2011](#), [Staver \*et al.\*, 2011b](#)), preserving present fire patterns across Africa, except where land use and climate explicitly change tree cover, implies that initial conditions largely determine the extent to which fire feedbacks contribute to determining the distribution of tree cover in tropical biomes ([Staver \*et al.\* 2011b](#)).

We present results for RCP 2.6 and RCP 4.5 in the main body, because they highlight a strong contrast; RCP 2.6 assumes decreasing CO<sub>2</sub> emissions ultimately, but drastic cropland extent increase in response to biofuel demand, while RCP 4.5 assumes increasing emissions but decreasing cropland and pasture extent through agricultural intensification ([Van Vuuren \*et al.\*, 2011](#)). We include results from the two remaining scenarios (RCP 6.0 and 8.5) in the Supplementary Information. All the model outputs are available to download as raster files at <http://www.juliealeman.com/GCB-15-1799/>.

#### *Risk assessment*

Tree cover is higher in forest than in savanna, therefore the tree cover threshold necessary for vegetation structure to have negative effects on biodiversity and other ecosystem functions, and thus on habitat in general, is thus lower in savanna than in forest. For our analyses, we thus assumed that forest would experience habitat loss when tree cover change decreased by 20% or more, and that savanna, and grassy biomes in general, would experience habitat loss when tree cover changed (either increased or decreased) by more than 10%. Indeed, both decreases in woody cover ([Veldman & Putz, 2011](#)) and woody

encroachment (Bassett *et al.*, 2000, [Mitchard \*et al.\*, 2009](#), [Mitchard & Flintrop, 2013](#), [Wigley \*et al.\*, 2009](#)) can have negative impacts on habitat in grassy biomes.

We assessed global change vulnerability by comparing absolute tree cover changes with the abundance of protected areas. The rationale behind this idea is that large tree cover changes, and thus habitat loss, can potentially be buffered by a large network of protected areas ([Loarie \*et al.\*, 2009](#), [Ordonez \*et al.\*, 2014](#)) in some ecoregions. Protected areas have the potential to mitigate against the effects of climate and land-use change on species distributions ([Ordonez \*et al.\*, 2014](#)), such that the net effect of tree cover loss on natural and managed systems depends on their conservation context.

To maintain a focus on biodiversity responses, we analyzed patterns at the scale of the WWF Terrestrial Ecoregion (Fig. S3), defined as areas with similar floral and faunal communities (Olson *et al.*, 2001). For each future scenario, we plotted the percentage of protected area against the absolute change in tree cover for each ecoregion. For each ecoregion, we computed and plotted the median of the percentage of protected area and the median of absolute tree cover change; ecoregion risk was defined by the quarters of the protected area vs. tree cover change graph, where quarters were demarcated by the median of each variable.

Thus, if an ecoregion had a percentage of protected area below the median and an absolute tree cover change greater than the median, this ecoregion was estimated as ‘at risk’ (red ecoregion quarter, Fig. 3-4). Conversely, if an ecoregion had a percentage of protected area above the median and an absolute tree cover change greater than the median, this ecoregion was estimated as at ‘mild risk’ (pink ecoregion quarter). Thirdly, if an ecoregion had a percentage of protected area above the median but an absolute tree cover change

superior to the median, this ecoregion was estimated as at ‘no risk’ (blue ecoregion quarter). Finally, if an ecoregion had a percentage of protected area below the median and an absolute tree cover change inferior to the median, this ecoregion was estimated as at ‘no risk but to be monitored’ (light blue ecoregion quarter).

## Results

### *Tree cover modeling and determinants*

The model predicts tree cover with high accuracy (Fig. 1b,  $R^2 = 0.97$ ,  $N = 20,000$ ,  $P < 0.01$ , t-test), and also captured the spatial pattern of forest and savanna distributions well. Indeed, only 3.7 and 0.7% of forest and savanna pixels, respectively, were misclassified (Fig. 2a-d), and these were generally restricted to locations near savanna-forest boundaries. While our model does not consider the alternative stable state dynamic, thought to characterize savanna and forest distributions ([Hirota \*et al.\*, 2011](#), [Staver \*et al.\*, 2011b](#)), it clearly captures, at least correlatively, the bimodal nature of tree cover in sub-Saharan Africa (Fig. S1).

Climatic variables were strong determinants of tree cover (Fig. 1a), highlighting the importance of annual rainfall and seasonality in determining forest and savanna distributions. Tree cover showed a strong positive dependence on annual rainfall between 0 and 2000 mm and a negative one with seasonality (Fig. S2). Anthropogenic variables also mattered, especially pasture coverage, through pastoralism, which has a very strong negative correlation with tree cover (Fig. 1a, Fig. S2). Cropland intensity in pixels also reduces tree cover and the extent both of forest and savanna (Fig. S2). As expected, fire has major impacts on tree cover, with decreasing tree cover by increasing fire frequency (Fig. S2). Finally, and not surprisingly at this scale, edaphic variables were significant, but less predictive of tree cover; soil organic carbon concentration was the most predictive soil variable (Fig. S2), potentially reflecting vegetation impacts on soil carbon, and not vice versa.

### *Future tree cover and habitat loss projections*

Forests experienced significant tree cover changes in all simulations throughout tropical Africa (Fig. 3 and 4, Fig. S4-5). Under RCP 2.6, tree cover decreased drastically in the forest areas inducing up to ~27% of habitat loss (Fig. 3). Indeed, the Congo forest contracted (especially in Cameroon, Central African Republic, Guinea, Gabon and Uganda) and fragmented (especially in the Democratic Republic of Congo, hereafter DRC, and northern Republic of Congo) (Fig. 3; Table S2). Tree cover decreased provoking the loss of habitat in up to 76.6% of the Guinean forest block (Liberia and Sierra Leone), and to 96.7% of dry forests throughout Africa (in Madagascar, Ethiopia, Angola and Mozambique; RCP 2.6, Table S2). Tree cover in forests also mostly decreased, although somewhat less and with localized increases, under RCP 4.5 (Fig. 4 and Table S2). Interestingly, these widespread changes in tree cover occurred primarily because of changes in pasture and cropland extent (Fig. 3b-c, 4b-c, S8-9); agricultural extensification under RCP 2.6 drove decreases in tree cover, while agricultural intensification (and concomitant contraction) resulted in some tree cover increases in forests under RCP 4.5. Despite a general increase in seasonality with RCPs (Fig. S7), climate did not drive tree cover changes at the continental scale, even under the most extreme climate scenario (RCP 8.5; Fig. S5).

Meanwhile, tree cover was also projected to decrease in savanna throughout tropical Africa (Fig. 3 and 4, Fig. S4-5), but trajectories varied geographically and by scenario. Tree cover in savannas generally decreased under RCP 2.6, especially in savanna areas bordering forests (Fig. 3). Under RCP 4.5, savanna tree cover decreased in southern and some parts of Central Africa (DRC, Cameroon, Angola, Zambia, Mozambique), but increased elsewhere (West and littoral Central Africa and Madagascar; Table S2 and Fig. 4). Comparing projected increases in tree cover with a reclassified map of vegetation types in Africa adapted from

White's (1983) phytogeographic map (Fig. S3C), we identified that 36.8% (and 40.0% for RCP 6.0) of tree cover increases in mesic savannas actually represent regrowth of forests deforested between 1983 and 2000. However, the remainder (43.2% and 60.0% for RCP 4.5 and 6.0 respectively) represents woody encroachment of mesic savanna. Again, tree cover changed mostly as a result of changing cropland and pasture extent (Fig. S8-9), not as a consequence of climate change, despite a predicted increase in seasonality in some areas (Fig. S7).

The forest areas most vulnerable to habitat loss in our predictions were also associated with a large network of protected (Fig. 3-4). However, in savannas, where tree cover also changed substantially, if less consistently, the extent of protected area coverage varied more substantially (Fig. S3B). Under RCP 2.6, tree cover in Zambia, Mozambique and Tanzania (Fig. 3) decreased strongly, but these areas were generally well protected. Tree cover in other savannas (*e.g.* bordering forests and in Angola; Fig. 3) also decreased under RCP 2.6, but protected areas were limited in extent.

## Discussion

### *Vegetation structure and tree cover determinants*

The model we developed here predicts tree cover very well, especially compared to most of other attempts in predicting tree cover at the continental scale ([Bucini & Hanan, 2007](#), [Sankaran \*et al.\*, 2005](#), [Staver \*et al.\*, 2011a](#)), probably because we included land-use variables as predictor. These are known to play an important role in determining vegetation structure currently ([Veldman \*et al.\*, 2015a](#)), especially in savanna ecosystems where land-use has potentially shaped land-cover for millennia ([Kay & Kaplan, 2015](#), [Veldman \*et al.\*, 2015a](#)). Although pastoralism has minimal impact on vegetation cover (*e.g.*, in Central African Republic ([Ankogui-Mpoko, 2003](#))) and can even lead to bush encroachment ([Bassett \*et al.\*,](#)

2000), recent land-use intensification has changed vegetation structure associated with significant biodiversity decrease (Foley *et al.*, 2005). Shifting agriculture in the tropics consists of deforested small patches of forest or savanna for creating cropland, that are then transformed into fallows, obviously decreasing tree cover (Nacoulma *et al.*, 2011). Once again, intensive agriculture increases the rate of tree removal (Laurance *et al.*, 2014).

The importance of climatic variables in determining tree cover was not surprising, since climate constitutes the primary driver for tree cover in Africa (Bucini & Hanan, 2007, Sankaran *et al.*, 2005, Sankaran *et al.*, 2008). Indeed, annual rainfall determines the climatic envelope where only savanna, savanna and forest, and finally only forest are possible (Staver *et al.*, 2011a). Seasonality and thus water availability is known to be a strong determinant for tree cover in Africa (Bucini & Hanan, 2007, Good & Caylor, 2011, Sankaran *et al.*, 2008), both via direct effects on trees and grasses growth rates (Sankaran *et al.*, 2004) and on the probability of fire spread.

Still, some pixels were misclassified, especially in areas of transitions between the two biomes. This is a well-known issue (Zeng *et al.*, 2014) and probably occurs because forest and savanna are not deterministically related to climate (Staver *et al.*, 2011a). We did not consider the alternative stable state dynamic of savanna and forest distributions (Hirota *et al.*, 2011, Staver *et al.*, 2011b), in part because the model is correlative, linking variables statistically and not dynamically, but also because land-use-driven transitions are not part of the positive feedback that maintains savanna and forest as stable states (Staver *et al.*, 2011a).

## *Projected changes and the vulnerability of tropical ecosystems*

Despite a projected general increase in seasonality, we showed here that climate was not the primary driver of tree cover changes at the continental scale, regardless of scenario and even under the most extreme climate change. This contradicts previous studies that have suggested that changes in vegetation structure would be primarily precipitation-driven ([Good & Caylor, 2011](#), [Scheiter & Higgins, 2009](#), [Zeng \*et al.\*, 2014](#)).

Instead, we showed that land-use change was the main driver of tree cover changes. This should not be wholly surprising, even in savannas, which are often perceived as more anthropogenic than forests ([Parr \*et al.\*, 2014](#)); recent studies have shown that bigger land cover changes originated from land-use than from climate change on shorter time scales ([Arneth, 2015](#), [Davies - Barnard \*et al.\*, 2015](#)), and biodiversity projections have suggested that land-use change can lead to drastic erosion of vegetation structure and biodiversity ([Asner \*et al.\*, 2010](#), [Sala \*et al.\*, 2000](#)).

Tree cover decreases in forest (> 20%) resulting from land-use intensification will be extensive under all scenarios. Under ‘mild’ emissions scenarios (RCP 2.6), agricultural intensification will result from biofuel production while under more severe scenarios (RCP 8.5) it will result from food crops production mostly for feeding increasing human populations. Impacts on plant and animal diversity as well as ecosystem services will then likely be extensive ([Laurance \*et al.\*, 2014](#)). Indeed, “old-growth” forests are irreplaceable ([Barlow \*et al.\*, 2007](#), [Gibson \*et al.\*, 2011](#)) in terms of biodiversity, and studies have shown that forest biodiversity declines along a gradient of land-use ([Schulze \*et al.\* 2004](#); [Harvey \*et al.\* 2006](#); [Basset \*et al.\* 2008](#); [Philpott \*et al.\* 2008](#)), reflecting the decline in floristic and structural diversity. Forest fragmentation is causing high rates of extinction ([Turner, 1996](#)). Moreover, deforestation can cause loss of topsoil and alteration of the water flow, resulting in either flood or drought ([Bradshaw \*et al.\*, 2008](#)). It affects vertebrates’ habitat and so reduces

their diversity (Jetz *et al.*, 2007, [Nichols \*et al.\*, 2007](#), [Slade \*et al.\*, 2011](#)). Finally, secondary forests and plantation are much less diverse than primary forests (Barlow *et al.*, 2007, [Laurance, 2007](#)).

Likewise, the replacement of “old-growth” grassy biome by grass-dominated “secondary” vegetation is often associated with a plant diversity collapse ([Veldman & Putz, 2011](#)). Land-use intensification will have thus equally severe impacts in grass-dominated biomes. The Brazilian *cerrado*, for instance, is highly threatened as a result of large-scale conversion mainly to soybean and cattle ranching, resulting in water pollution, fire regime modifications, and biodiversity loss (Klink & Machado, 2005). The degradation of grassy biomes by agricultural conversion results in the displacement of native species, the alteration of soil chemistry, fire regime and hydrology (Veldman *et al.*, 2015a). Therefore, as in forests, “secondary” grassy ecosystems are less diverse and resilient than the “old-growth” ones (Veldman *et al.*, 2015a, [Zaloumis & Bond, 2011](#)).

In our simulations, humid savannas were highly threatened for RCPs 2.6 and 8.5, in large part because they have been identified as suitable for biofuel production and agriculture intensification (Alexandratos & Bruinsma, 2012, Deininger & Byerlee, 2011). These studies mistakenly (Parr *et al.*, 2014, Veldman *et al.*, 2015a) assume savannas to be less valuable than forests in terms of biodiversity, carbon storage and water quality, and consequently meriting less protection (Searchinger *et al.*, 2015, Veldman *et al.*, 2015b). Converting these savannas to agricultural lands would have catastrophic consequences for numerous endemic species and the high regional bird, mammal and flora richness they sustain (Searchinger *et al.*, 2015). Grass-dominated ecosystems contain numerous hotspots of endemism and the conversion of those to agricultural lands will inevitably lead to irreplaceable species loss (Olson *et al.*, 2001). Once again consider the example of the Brazilian *cerrado*, which is still considered of less conservation value than tropical forest; soybean production and ranching

have reduced native savanna extent by more than 50% (Klink & Machado, 2005). A switch in land-use practices, in African humid savannas, from shifting cultivation to cash crops and biofuel production will increase the pressure of agricultural systems on the vegetation, with potential consequences similar to what is currently happening in the *cerrado*. Moreover, switching from extensive agriculture to a more intensive one, oriented in cash-crops and biofuel production (RCP 2.6), raises food security questions (Escobar *et al.*, 2009)

On the other hand, simulations for RCPs 4.5 and 6.0 project an increase in tree cover in savanna areas; some of this corresponds to forest regrowth after agricultural abandonment, but the majority represents forest encroachment of savanna, with major potential negative consequences. Woody encroachment reduces plant species richness and locally modifies the germinable seed bank (Meik *et al.*, 2002, Price & Morgan, 2008, Sirami *et al.*, 2009). It is also responsible for changes in the composition and spatial distribution of vegetation structures (Skarpe, 1986; Jeltsch *et al.*, 1997), which are accompanied by changes in availability and accessibility of resources (e.g. foraging sites or predation cover), thus affecting rodent communities (Blaum *et al.*, 2007a) and mammalian carnivores (Blaum *et al.*, 2007b).

#### *Protected areas and buffering habitat loss*

In the face of massive global changes, protected areas are crucial to sustaining biodiversity and natural ecosystem processes. In forests, where our model predicted widespread reductions in tree cover, a large network of protected areas already potentially confers some degree of local resilience to change. However, concern is widespread that protected areas are not effectively enforced, due primarily to conflict and governance issues (Chape *et al.*, 2005), potentially compromising their role in maintaining forest resilience. Indeed, tropical protected areas face growing threats as population grows (Laurance *et al.*,

2014), especially due to limited funding for management (Bruner *et al.*, 2004) and illegal logging, grazing and agricultural lands are common in poorly enforced protected areas (Laurance *et al.*, 2012), especially in West and Central Africa (Tranquilli *et al.*, 2014) compared to East and South Africa (Pfeifer *et al.*, 2012). As a result, agricultural expansion near protected areas tends to erode biodiversity due to edge effects (Laurance *et al.*, 2014, Wittemyer *et al.*, 2008). However, if protected area integrity can be achieved, as for example by involving local population (Vodouhê *et al.*, 2010), African forests may remain relatively resilient in the face of land-use and rainfall change.

By contrast, savannas where tree cover change is likely are relatively unprotected. For example, we projected savannas from Zambia and southern DRC, which currently sustain some of the world's highest terrestrial mammal species relative richness (Olson *et al.*, 2001), to experience drastic tree cover reductions (RCP 2.6). However, while Zambian savannas are extensively protected, savannas in the southern DRC are not, such that the consequences of decreasing tree cover potentially diverge. One possibility solution is an increase in formal conservation activities (parks and otherwise) within savanna ecosystems, especially in West and Central Africa, which may mitigate or even prevent tree cover effects of land-use change in the future (Parr *et al.*, 2014, Veldman *et al.*, 2015b). Grassy biomes may also lend themselves to alternative conservation practices. Protected areas in grassy biomes are often associated with reduced plant diversity compared to communally managed areas (Dahlberg, 2000, Hahn-Hadjali *et al.*, 2006, Nacoulma *et al.*, 2011, Paré *et al.*, 2010, Shackleton, 2000), perhaps because grassy biomes are intrinsically associated with disturbances (Veldman *et al.*, 2015a), such that traditional land management does not lead to degradation of savanna habitats (Augusseau *et al.*, 2006, Nacoulma *et al.*, 2011). Indeed, re-evaluation of systematic land-use change planning for mitigations scenarios may also be warranted, to explicitly include the conservation and agricultural value of savanna ecosystems (Veldman *et al.*,

2015a). Some authors have even argued that effective biodiversity conservation will rely on associating traditional, communally managed areas with reserves (Abel & Blaikie, 1989, [Nacoulma et al., 2011](#), [Yayneshet & Treydte, 2015](#)). The status for grassy biomes conservation in protected areas is currently too linked to management of forest ecosystems. There is thus an urgent need to develop a framework for grass-dominated biomes (Veldman et al., 2015a, Veldman et al., 2015b) and to better estimate the environmental values of such biomes.

Historically, the vast majority of conservation work has focused on forests ([Laurance et al., 2014](#), [Tranquilli et al., 2014](#)), but savannas are at equal if not greater risk of change under plausible land-use change scenarios. Wet savannas and transition zones between forest and savannas in West and Central Africa may be particularly susceptible, because of the few protected areas located there. Sustainable management plans, including a strong monitoring component, serving both biodiversity and development needs, should be a high priority.

#### *Limitations of the approach used*

Here, we explicitly considered neither direct CO<sub>2</sub> nor temperature effects on vegetation, although under RCP 8.5, [CO<sub>2</sub>] more than doubles and temperatures could rise locally by as much as 4°C in tropical Africa. Rising [CO<sub>2</sub>] may promote woody encroachment in increasingly arid environments by increasing growth rates and water use efficiency (Bond & Midgley, 2012), such that increasing CO<sub>2</sub> could result in shifts from savanna towards a woodier plant community, such as thicket or even closed forest ([Higgins & Scheiter, 2012](#)). We were unlikely to detect this possibility in any case, since the MODIS VCF does not record trees with less than 5m height and therefore only poorly captures the conservation and functional costs of woody encroachment, which are ongoing in savannas worldwide. These studies still do not take into account land-use (Midgley & Bond, 2015), however, which may

be at least locally sufficient to counter CO<sub>2</sub>-related changes (Midgley *et al.*, 2010, Sala *et al.*, 2000, Tredennick & Hanan, 2015, Wessels *et al.*, 2013).

The extant range of temperature variability projected for the future exceeds the current one, such that our statistical model is not built to take it into account. Although temperature changes are expected to be less severe than in boreal and temperate ecosystems (IPCC, 2014), rising temperatures could have major negative effects on tropical vegetation, especially forest trees (Allen *et al.*, 2010), and are likely to exacerbate the consequences of land-use change on tree cover. Additionally, another source of discrepancy in our simulations may originate from the high uncertainty in future climate projections that are related to GCM biases (Knutti & Sedláček, 2013) and which are especially noticeable in Africa (Heubes *et al.*, 2011).

However, our conclusions regarding land-use changes being the main driver of vegetation structure modifications in the future remain supported because the scenarios are coherent regarding cropland and pasture projections (Hurt *et al.*, 2011).

Finally, fire has a key role globally in the distribution of savanna and forest by maintaining a feedback on vegetation structure (Staver *et al.*, 2011a) and locally to determine savanna tree cover (Brando *et al.*, 2014, Nepstad *et al.*, 1999, Veldman & Putz, 2011).

Future changes in fire regimes may therefore impact the structure of both forest and savanna (Brando *et al.*, 2014, Nepstad *et al.*, 1999, Veldman & Putz, 2011). Unfortunately, global fire models are still in their nascency, and no standardized projections for future fire regime are currently available. Incorporating fire model projections into biosphere projections for tropical and sub-tropical Africa will be critical, once they are more available.

To conclude, we evaluated the potential contributions of climate and land-use changes to changing tree cover in tropical Africa, and the implications for potential habitat loss. Land-use changes were the main driver of tree cover change. Moreover, we show that savannas are

at an equal if not greater risk of change under global change scenarios. Finally, our results also highlight the importance of how global and local policies decide to mitigate climate change. Mitigation scenarios by definition overwhelmingly prioritize a reduction in carbon emissions, but at what cost? Biofuel production and agricultural intensification potentially result in direct negative consequences for forest and especially savanna extent in tropical Africa.

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### **Figures captions**

**Figure 1 | Model predictor importance (a) and model evaluation (b).** MAR = mean annual rainfall; CEC = Cation exchange capacity. Relative importance of model predictors was computed by randomly permuting variables and evaluating model deterioration. Model evaluation was performed on a subset of tree cover pixels in Africa ( $N = 20,000$ ,  $R^2 = 0.97$ ,  $RMSE = 4.47$ ).

**Figure 2 | Tree cover and biome distribution in tropical Africa.** Tree cover for the year 2000 from MODIS data (a), predicted tree cover for the year 2000 using the Random Forest model (b), the difference between real and modeled tree cover (c), and biome classification/misclassification (d). Forest and savanna biomes were defined using a tree cover threshold of 55 (Staver *et al.*, 2011b).

**Figure 3 | Tree cover change projections from 2000-2070 – RCP 2.6 (left maps), biome distribution shifts based on tree cover changes (middle), and WWF Ecoregion conservation risk based on tree cover change and protected area coverage (right).** Projections are based on climate and anthropogenic change together (a), anthropogenic change only (b) and climate change only (c).

**Figure 4 | Tree cover change projections from 2000-2070 – RCP 4.5 (left maps), biome distribution shifts based on tree cover changes (middle), and WWF Ecoregion conservation risk based on tree cover change and protected area coverage (right).** Projections are based on climate and anthropogenic change together (a), anthropogenic change only (b) and climate change only (c).

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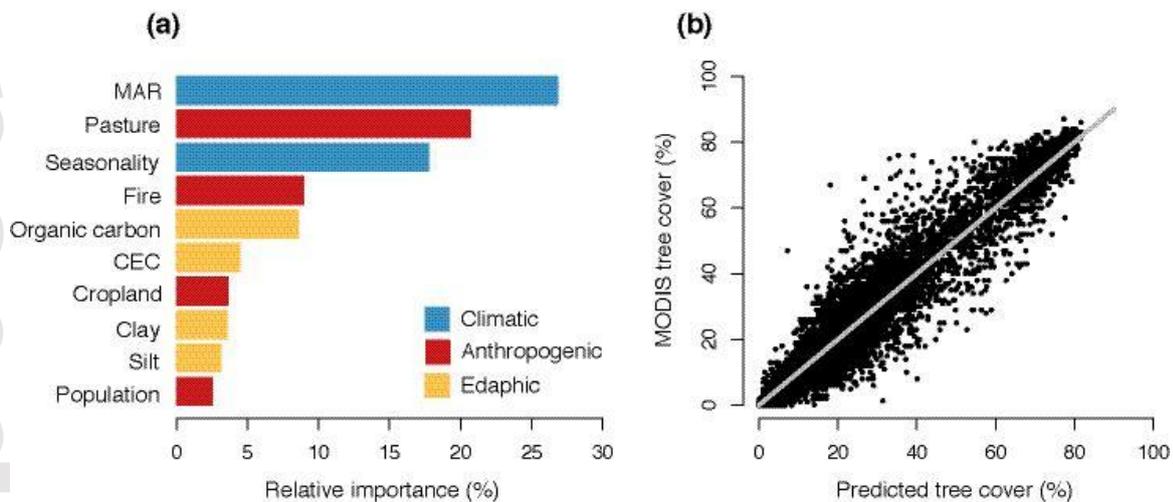
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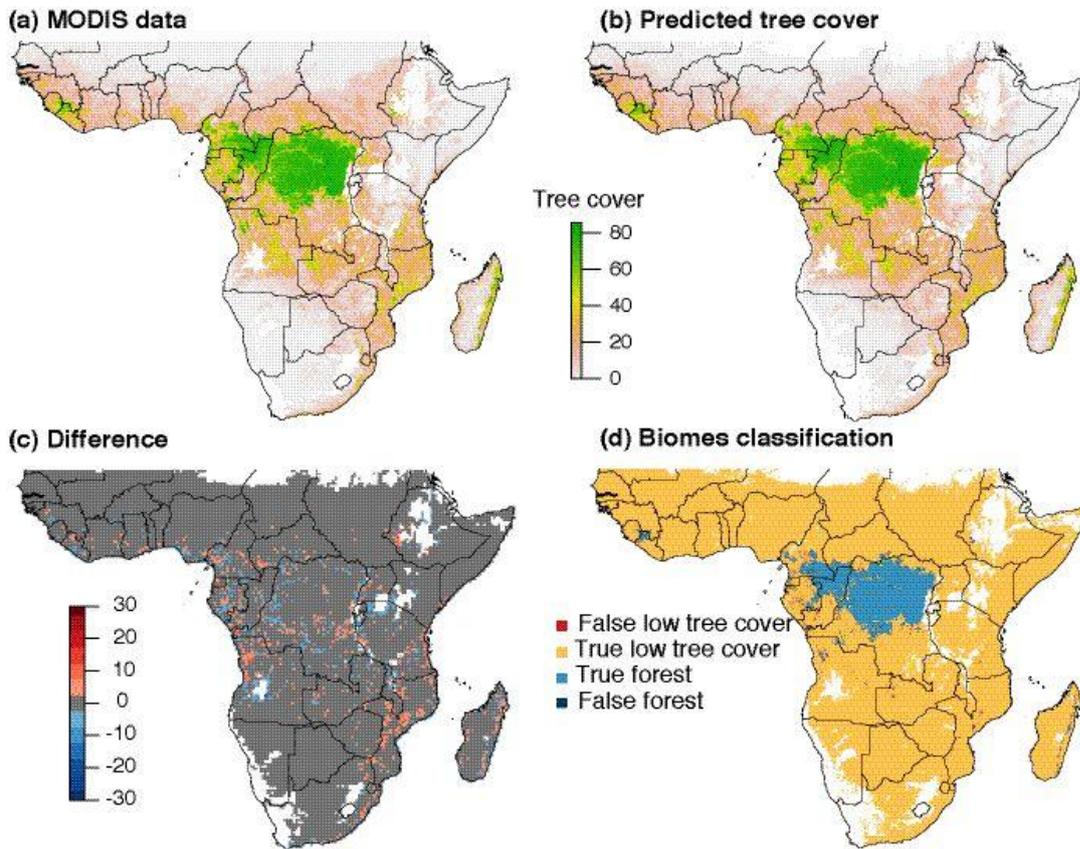
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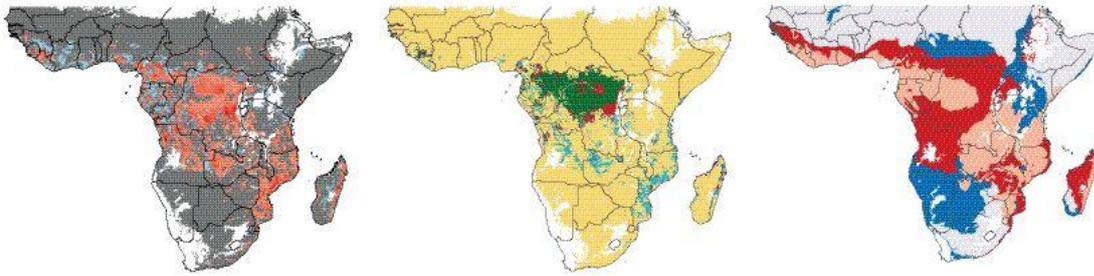
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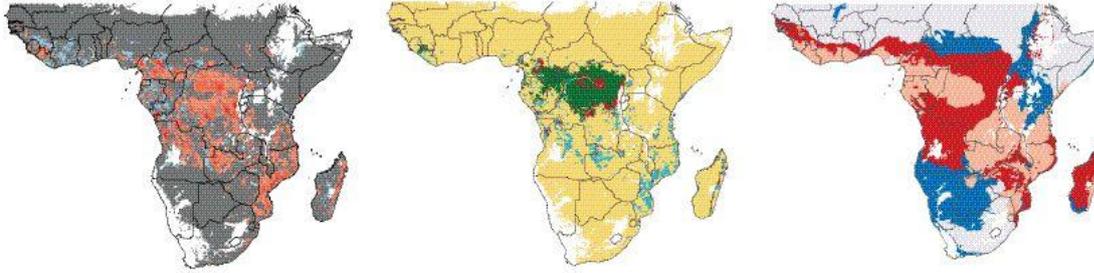




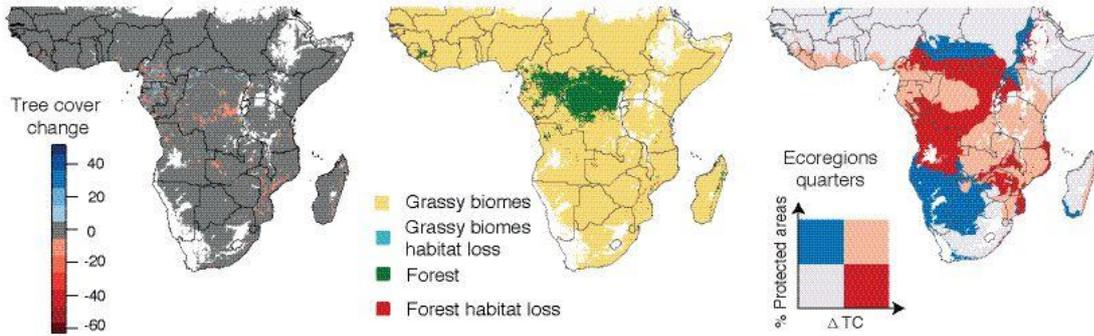
(a) Global change



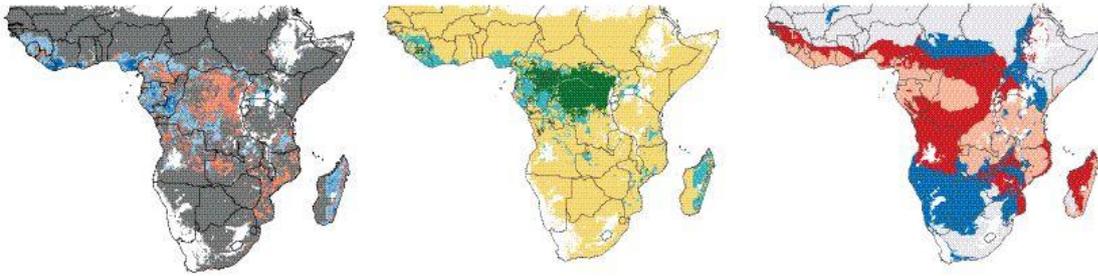
(b) Anthropogenic only



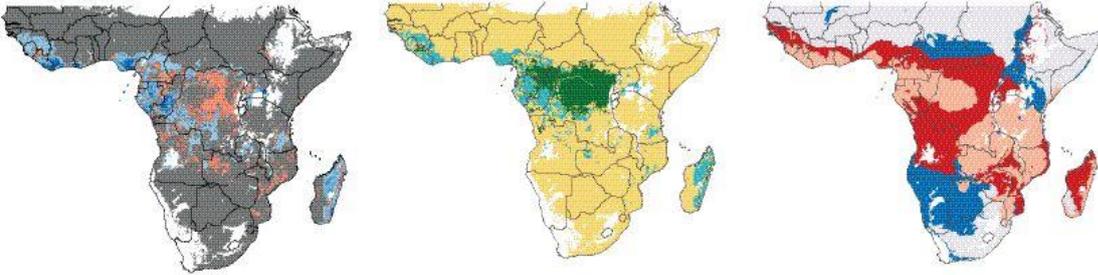
(c) Climate only



(a) Global change



(b) Anthropogenic only



(c) Climate only

