Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa

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The rapidly growing human population in sub-Saharan Africa generates increasing demand for agricultural land and forest products, which presumably leads to deforestation. Conversely, a greening of African drylands has been reported, but this has been difficult to associate with changes in woody vegetation. There is thus an incomplete understanding of how woody vegetation responds to socio-economic and environmental change. Here we used a passive microwave Earth observation data set to document two different trends in land area with woody cover for 1992–2011: 36% of the land area (6,870,000 km2) had an increase in woody cover largely in drylands, and 11% had a decrease (2,150,000 km2), mostly in humid zones. Increases in woody cover were associated with low population growth, and were driven by increases in CO2 in the humid zones and by increases in precipitation in drylands, whereas decreases in woody cover were associated with high population growth. The spatially distinct pattern of these opposing trends reflects, first, the natural response of vegetation to precipitation and atmospheric CO2, and second, deforestation in humid areas, minor in size but important for ecosystem services, such as biodiversity and carbon stocks. This nuanced picture of changes in woody cover challenges widely held views of a general and ongoing reduction of the woody vegetation in Africa.

Africa’s human population has increased from about 230 million in 1950 to over 1,000 million in 2010 and is expected to grow to as high as 5,700 million by the end of the twenty-first century1. This growth has led to the expansion of agricultural land and the reduction of natural forests and other woody vegetation2–4, affecting biodiversity and carbon storage1. Severe droughts in recent decades have also had an adverse impact on humid and sub-humid forested areas1. In contrast, studies of drylands have shown an increase in vegetation productivity over the past 30 years5–8, also highlighting the importance of drylands for global carbon variability and as a land CO2 sink9. Whether this increase in vegetation productivity is driven by the growth of woody vegetation and/or by an increase in productivity of herbaceous vegetation is not clear6–8. This is because the scattered nature of woody plants in drylands is very different from forests with closed canopies and is challenging to detect with optical satellite imagery at regional to continental scales10,11. Previous studies have used vegetation indices as proxies for net primary productivity, but these indices measure the photosynthetically active part of the vegetation, and most studies do not distinguish between woody and herbaceous vegetation12,13. Furthermore, studies of deforestation in humid areas traditionally report the presence or absence of forests1 and do not assess gradual changes in forest biomass within existing forests (for example forest degradation). They are also based on temporal snapshots of satellite imagery at a higher spatial resolution and only capture forests based on given definitions, such as tree height and canopy cover percentage14, which substantially underestimate shrubs and scattered trees in drylands15. Consequently, little quantitative information is available about the state, rate and drivers of change in the cover of woody vegetation at the scale of the African continent. This information is crucial for ensuring that the design of natural resource management in relation to deforestation and desertification is based on observations rather than based on narratives.

Results

Africa’s changing woody cover. We used a new passive microwave Earth observation (EO) data set (vegetation optical depth, VOD) that captures continuous changes in the coverage of canopies of all woodyphanerophytes, regardless of size, in both drylands and humid areas16–17. We applied VOD as a proxy for annual woody cover, and we documented changes in Africa’s woody vegetation between 1992 and 2011, with a special focus on the changes in drylands and humid areas (defined by the ratio between annual precipitation and potential evapotranspiration, Supplementary Fig. 1a). Woody vegetation changed significantly (linear regression, P<0.05, n=20) during 1992–2011 in approximately half of sub-Saharan Africa (47% of land areas). Most (77%) of the significant trends were positive, covering 36% of sub-Saharan Africa and representing an overall increase of 2.1 woody cover (%) (Fig. 1a). Most (70%) of the significant positive changes were in drylands covering about 4,900,000 km2 (overall change +2.9 woody cover (%)), mainly in the Sahel and southern Africa18–20 (Fig. 2a). Positive trends were also observed in the humid zones to a much smaller extent (2,100,000 km2), with an overall change of +0.8 woody cover (%). Negative changes affected 11% of sub-Saharan Africa, of which 75% were in humid areas (approximately 1,600,000 km2 in humid zones and 530,000 km2 in drylands). The decline in woody cover primarily affected areas that are also characterized by high carbon

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stocks (Supplementary Fig. 2a,b), suggesting that areas with the largest carbon sinks have been disturbed at the fastest rate. The classification of woody cover change into bioclimate zones\(^2\) confirms the overall tendency, with larger increases in drier zones (except for extremely hot xeric), and lower increases and decreases in moister zones (Fig. 2d).

**Drivers of woody cover changes.** The positive changes in woody cover in Africa’s drylands are significantly correlated with precipitation (Fig. 1a). In contrast to herbaceous vegetation, woody plants can benefit from a higher variability and intensity of precipitation\(^2\), as in southern Africa and the Sahel (Supplementary Fig. 1c). The dependence on precipitation was corroborated with simulations of the vegetation using the dynamic vegetation model LPJ-GUESS\(^3\), which simulated an increase in woody biomass for 1992–2011, consistent with the satellite estimates of woody cover (Fig. 3). The relative increase of both woody cover and biomass was largest in drylands, and factorial simulations of the individual driving variables indicated that precipitation accounted for most of the simulated increase in woody biomass in drylands such as the Sahel and southern Africa (Fig. 3, Supplementary Fig. 3). Increasing concentration of atmospheric CO\(_2\) was a minor contributor to these dryland trends, yet was the main variable driving the growth of woody vegetation in humid areas, enhancing primary production\(^4\) (Fig. 3, Supplementary Figs 2,3). The absolute increase in woody biomass was largest in humid areas (mean increase of 0.04 kg C m\(^{-2}\) yr\(^{-1}\) near the Equator, Supplementary Fig. 2), coinciding with overall large stocks of woody biomass. Solar radiation, nitrogen deposition and temperature had minor impacts on the changes in woody biomass (Supplementary Fig. 2).

This overall increase in woody vegetation driven by climate and CO\(_2\), however, was offset by anthropogenic impacts, especially in humid areas. The increase in woody cover in the VOD analysis was thus most pronounced in areas of low human population density and change (Fig. 4). Areas and countries with a higher population density and growth (Fig. 1b, Supplementary Fig. 1d) had decreases in VOD-based woody cover (Figs 1a, 4, Supplementary Fig. 4), offsetting the climate-driven increases in other parts of the humid zones (Figs 2c, 3). This separation in areas of high and low human pressure applied to both drylands and humid tropics. The average trend, however, remained positive in drylands, even in areas with strong population growth, but was negative in humid areas with strong population growth, regardless of the trends in precipitation and CO\(_2\) (Fig. 2b,c). Populations increased by an average of 40 persons km\(^{-2}\) over 20 years in areas where woody cover decreased presumably because of agricultural expansion, logging and other uses of woody products. In contrast, populations increased by an average of only 6 persons km\(^{-2}\) in areas where woody cover increased. Human population increase was highest in moist and mesic bioclimate zones, and woody cover changes were accordingly negative or low, whereas population growth was lower in xeric areas and woody cover increases were higher (Fig. 2d). At the continental scale, a simultaneous autoregressive model explained nearly half of the spatial pattern of changes in woody cover in terms of changes in population and precipitation (\(r^2 = 0.46\), with population being more important than precipitation (standardized slopes of \(-0.27\) and 0.08, respectively) (Supplementary Table 1).

**Discussion**

The opposing trends in dry and humid zones have implications for our understanding of environmental change in sub-Saharan Africa. Whereas areas of high population growth, mostly in humid zones, on average experience a decrease in woody vegetation, areas with low population growth on average experience an increase in woody vegetation, mainly driven by changes in precipitation and CO\(_2\) concentrations. This latter increase is not captured in official forest statistics, since much of it takes place outside humid forests.

**Figure 1** | Changes in woody vegetation and human population over two decades. a. Significant trends of woody cover (VOD) for 1992–2011, separated by the presence (**) or absence (x) of a significant \(P < 0.05\), \(n = 12,845\) correlation with cumulative 2-year precipitation during this period. b. Changes in human populations for 1990–2010. The maps in a and b share a clear pattern: in particular, areas with a decrease in woody cover, and no relation to precipitation, coincide with a high population pressure. c. SAR model of the changes in woody cover, precipitation (both 1992–2011) and population (1990–2010). The units are expressed as change in the corresponding unit over the period of analysis.
This implies that the ‘problem’ of woody cover loss — and thus decreases in carbon stocks — in the humid forest zones is at least partly balanced by an increase in drylands. ‘Bush encroachment’ in savannas of southern Africa, however, has traditionally been considered an undesired effect\(^1,2\). Because the VOD data used to estimate woody cover do not allow a direct estimation of carbon stocks, the exact balance between gains and losses in carbon cannot be directly assessed in this study. Further work combining field measurements, ecosystem modelling and new satellite-based passive microwave sensors is required to further understand these linkages. In humid areas, woody biomass may even increase without any change in woody cover.

The close relationship between population growth and decreased woody cover suggests that agricultural expansion, urbanization and wood fuel harvest were the main causes of the decrease in woody cover, as also found in studies of tropical deforestation.\(^3,4\) The reduction in woody cover tends to affect primarily areas with high carbon stocks, and other studies indicate that these are also areas characterized by the highest biological diversity.\(^5\) There is, however, no simple relation between losses and gains in woody cover and biodiversity. Although diversity and productivity of natural vegetation are generally positively correlated,\(^6\), this does not exclude the possibility that great losses may be experienced in areas of deforestation, while only smaller gains are seen in drylands with increasing woody cover.

Owing to the impact on land-surface albedo, woody cover changes in dryland areas may trigger climate feedbacks. Since the hypothesized existence of a ‘biogeophysical feedback’\(^7\), many studies have attempted to model such effects\(^8,9\), with some research claiming that man-made afforestation efforts would give rise to increased precipitation\(^10\). The extent of the observed increase in woody cover in African drylands may affect climate if the increase continues in the coming decades, and this altered feedback should preferably be implemented in regional climate or Earth system models, with the observed increase in woody vegetation providing a test case for these models.

**Methods**

**VOD data and calibration to woody cover.** We define woody cover as the percentage of a given area covered by woody vegetation, including both leaf and woody components of woody plant canopies. The unit is woody cover (%). The VOD data were retrieved from satellite passive microwave observations, quantified as brightness temperature based on the NASA-VU Land Parameter Retrieval Model (LPRM).\(^11\) Three passive microwave sensors — the Special Sensor Microwave Imager, the Advanced Microwave Scanning Radiometer—Earth Observing System, and the radiometer of WindSat — are used to form the merged long-term VOD data set by applying a trend-preserving cumulative distribution function matching without changing the interannual variations and long-term trends of the original retrievals.\(^12\) The merged long-term VOD data set was gridded at a 0.25° spatial resolution and monthly interval from 1992 to 2011, and is consistent between different sensors.\(^13\) VOD is sensitive to the total aboveground water content in both the photosynthetic (foliar) and non-photosynthetic (woody) components of the vegetation stratum.\(^14,15\) Soil moisture conditions are retrieved simultaneously with the VOD information, and the radiometer of WindSat — are used to form the long-term data set by applying a trend-preserving cumulative distribution function matching without changing the interannual variations and long-term trends of the original retrievals.\(^16\) The merged long-term VOD data set was gridded at a 0.25° spatial resolution and monthly interval from 1992 to 2011, and is consistent between different sensors.\(^13\) VOD is sensitive to the total aboveground water content in both the photosynthetic (foliar) and non-photosynthetic (woody) components of the vegetation stratum.\(^14,15\) The VOD signal is separated from soil moisture and is used as a proxy for vegetation biomass globally.\(^16\) The VOD seasonal variation is a combined effect of the seasonal dynamics of both herbaceous (including crops) and woody vegetation.\(^16\) We used the annual minimum VOD values as a proxy for woody

**Figure 2 | Changes in woody cover (VOD) in different humidity zones.** a. Areas with changes in woody cover (linear regression for 1992–2011). b, c. Annual profiles are shown for areas of statistically significant changes in woody cover in drylands (b) and the humid areas (c) of sub-Saharan Africa (Supplementary Fig. 1a). Black lines characterize areas of high human population increase (>30 persons km\(^{-2}\)) and grey lines areas of low human population increase (<10 persons km\(^{-2}\)) for 1990 to 2010. d. Woody cover and human population changes are grouped according to bioclimatic zones.

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vegetation cover to minimize the influence of annual herbaceous vegetation and avoided values exceeding 1.2 (Supplementary Fig. 5). Areas with perennial herbaceous vegetation may lead to an over-estimation of woody cover; however, the woody cover (in %) is usually higher in these areas, concealing the influence from the herbaceous plant understory. Also, VOD data have been used to estimate forest change in South America by limiting the range of VOD values to 0.6–1.2. We did not restrict the VOD range, and therefore it also includes young trees and shrubs, which form an important part of the community of woody vegetation. The minimum VOD agrees well with a field-data-based map of woody cover for Sahel ($r^2 = 0.80$) (Supplementary Fig. 5). A global map calibrated with optical high-spatial-resolution images and also assessing smaller trees produced similar results and was thus used to transform the annual minimum VOD to the unit woody cover (%) for further analyses ($r^2 = 0.85$, slope = 0.86) (Supplementary Fig. 5). A third-degree polynomial regression was used for the transformation. Woody cover <10% was predicted with an exponential regression to avoid underestimation of very low values. The VOD is insensitive to the effects of atmospheric and cloud contamination, ensuring reliable retrievals in cloudy regions such as central Africa.

Correlation between the trends in woody cover and changes in human population and precipitation. Precipitation data were derived from the Climate Research Unit (CRU) data set (version 3.23), which is globally available for a 0.5° grid at monthly scale and is based on the upsampling of data from rain gauges. CRU precipitation data intrinsically include some uncertainty, as the number of stations used for each grid cell varies considerably between cells and years. Even though it is the most widely used precipitation data set in dynamic vegetation modelling, and consistency with other data sets has been shown, results have to be considered with caution. We have tested the blended GPCP data set, without significant changes to the results, but it must still be noted that a linear trend analysis on annually summed data includes uncertainties and simplification. We summed the monthly observations to obtain annual sums from 1992 to 2011 and resampled the data to 0.25° using a bicubic interpolation. Population data were acquired from Gridded Population of the World (GPW v3), which includes estimates for 1990, 1995, 2000, 2005 and 2010, gridded with an output resolution of 2.5 arc-minutes, resampled for this study to 0.25° (nearest neighbour). GPW population data were acquired from national statistical offices and gridded based on the proportional number of people, which allocates population counts to grid cells based on the proportion of each administrative areal unit that overlaps the cell. The gridded counts for existing census years are then projected to the set of output years based on a simple model of population growth. The modeling was thus not based on any additional layers of data, such as land cover, avoiding potential problems of endogeneity between VOD and simulated population grids. A linear trend analysis was conducted for annual woody cover and precipitation data, and the slope multiplied by the number of years to retrieve the absolute change over time in the corresponding unit, aiding the direct comparison with the human population data. We quantified the relationships between the changes in woody cover (estimated by VOD), population increase (GPW) and precipitation (CRU) by applying a simultaneous autoregressive model (spatial error type) to the three gridded data sets. This model accounts for spatial autocorrelation and uses change in woody cover as response, and log(change in population) and change in precipitation as explanatory variables. The logarithm of the human population data was applied because the relation between woody cover changes and human population is non-linear at small scale: if a small population number is reached (mostly in cities), the woody cover decreases to cease further. Standardized variables were used to enable intercomparison of model coefficients (standardized variable = (variable – mean)/standard deviation).

Fires frequently occur in most African ecosystems. However, at the spatial and temporal scale of our analysis, we do not expect a change in fire regime to be a major cause of changes in woody cover in itself but rather to be a consequence of human-induced deforestation and land-use change.

Figure 3 | Climatic drivers of changes in woody cover and biomass in sub-Saharan Africa. Relative trends (% of mean year$^{-1}$) for 1992–2011 in woody cover (estimated with VOD) and woody biomass (simulated with LPJ-GUESS) had similar patterns of change from north to south. The trends in woody biomass were mainly driven by CO$_2$ (humid areas) and precipitation (drylands) (Supplementary Figs 2,3).

Data availability. CRU precipitation data are available from the University of East Anglia (http://www.cru.uea.ac.uk/). The global tree-cover map is available from the Geospatial Information Authority of Japan, Chiba University (http://www.iscgm.org/gm/ptc.html#use). VOD raster data are developed by Y. Liu, University of New South Wales. GPW population data are provided by CIESIN (http://sedac.ciesin.columbia.edu/). Hydration zones are available from http://www.grid.unep.ch/index.php. Dynamic vegetation model results are available from the corresponding author upon reasonable request.

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Dynamic ecosystem model. The dynamic ecosystem model LPJ-GUESS was applied to simulate changes in woody biomass carbon in natural vegetation for 1992–2011. LPJ-GUESS simulates the distribution of plant functional types, and each type is represented by four pools of biomass carbon: leaves, roots, sapwood and heartwood. The latter two were added to represent the amounts of stem (wood) carbon. This variable is closely related to the woody cover estimated by VOD, but differences are expected especially in tropical forests, as VOD cannot fully penetrate the tree crowns. Simulations were run for 1992–2011, applying monthly climate data (temperature, precipitation, sunshine duration) from meteorological stations, gridded to 0.5°×0.5° resolution (CRU TS 3.21), monthly model-derived estimates for nitrogen deposition, and annual mean atmospheric CO$_2$ concentrations based on ice-core data and atmospheric observations as forcing. Land use and land-use change were not accounted for in the simulations, which were only applied to quantify the changes in natural vegetation. The simulations were preceded by a two-stage spin-up. For the first stage, vegetation growth started from bare-ground conditions, using climatic data for 1901–1930, and CO$_2$ levels were kept constant at the concentration for 1901. For the second stage, representing 1901–1991, the actual climate data, atmospheric CO$_2$ concentration and nitrogen deposition were used.

In addition to a full simulation with the forcing as described above, five factorial simulations were performed to separate the impact of individual driving variables. Only one of the four parameters (temperature, precipitation, radiation or CO$_2$) was applied using the transient data as described above, whereas the other three parameters used a climatology for 1992–2011, with monthly means over this 20-year period applied for the climatic parameters and an annual mean for CO$_2$. In the fifth factorial simulation, similar to the transient CO$_2$ simulation above, the changing CO$_2$ concentration was combined with a climatology for nitrogen deposition, to separate the impacts of atmospheric CO$_2$ and nitrogen deposition on the CO$_2$ fertilization. These simulations were applied to determine the impact of the individual driving variables on the simulated trend.
Figure 4 | Links between changes in woody cover and human population. Intervals of mean population density (1990–2010, Supplementary Fig. 1d) were used to group the changes in woody cover (VOD) associated with population increases and the number of pixels showing significant woody cover change. A chi-squared test between woody cover and population change indicated the statistically significant dependency between the two variables.

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Author contributions
M.B., R.F., F.T. and A.V. designed the study. M.B. (VOD) and G.S. (ecosystem model) conducted the analyses with support by F.T., J.P., R.F. and J.B.R.P. The paper was drafted by K.R. and M.B. with contributions by all authors.

Additional information
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Competing interests
The authors declare no competing financial interests.