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

5 **Authors:**

6 **Martin Brandt**, Department of Geosciences and Natural Resource Management, University of Copenhagen,
7 1350 Copenhagen, Denmark, mabr@ign.ku.dk.

8 **Kjeld Rasmussen**, Department of Geosciences and Natural Resource Management, University of Copenhagen,
9 1350 Copenhagen, Denmark, kr@ign.ku.dk.

10 **Josep Peñuelas**, CSIC, Global Ecology Unit CREAM-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain and
11 CREAM, Cerdanyola del Vallès, 08193 Catalonia, Spain, josep.penuelas@uab.cat.

12 **Feng Tian**, Department of Geosciences and Natural Resource Management, University of Copenhagen, 1350
13 Copenhagen, Denmark, feng.tian@ign.ku.dk.

14 **Guy Schurgers**, Department of Geosciences and Natural Resource Management, University of Copenhagen,
15 1350 Copenhagen, Denmark, gusc@ign.ku.dk.

16 **Alexandre Verger**, CSIC, Global Ecology Unit CREAM-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain and
17 CREAM, Cerdanyola del Vallès, 08193 Catalonia, Spain, verger@creaf.uab.cat.

18 **Ole Mertz**, Department of Geosciences and Natural Resource Management, University of Copenhagen, 1350
19 Copenhagen, Denmark, om@ign.ku.dk.

20 **John R.B. Palmer**, Interdisciplinary Research Group on Immigration, Pompeu Fabra University, Barcelona,
21 Spain, john.palmer@upf.edu.

22 **Rasmus Fensholt**, Department of Geosciences and Natural Resource Management, University of Copenhagen,

23 1350 Copenhagen, Denmark, rf@ign.ku.dk.

24

25

26 **Abstract**

27 The rapidly growing human population in sub-Saharan Africa generates increasing demand for agricultural land
28 and forest products which presumably leads to deforestation. Conversely, a greening of African drylands has
29 been reported, but this has been difficult to associate with changes in woody vegetation. There is thus an incom-
30 plete understanding of how woody vegetation responds to socio-economic and environmental change. Here we
31 used a passive microwave Earth Observation data set to document two different trends in woody cover land area
32 for 1992-2011: an 36% increase (6,870,000 km²), largely in drylands, and an 11% decrease (2,150,000 km²),
33 mostly in humid zones. Increases in woody cover were associated with low population growth and driven by
34 increases in CO₂ in the humid zones and by increases in precipitation in drylands, whereas decreases in woody
35 cover were associated with high population growth. The spatially distinct pattern of these opposing trends re-
36 flects (1) the natural response of vegetation to precipitation and atmospheric CO₂ and (2) deforestation in humid
37 areas, minor in size but important for ecosystem services, such as biodiversity and carbon stocks. This nuanced
38 picture of changes in woody cover challenges widely held views of a general and ongoing reduction of the
39 woody vegetation in Africa.

40 **Introduction**

41 Africa's human population has increased from about 230 million in 1950 to over 1000 million in 2010 and is
42 expected to grow to as high as 5700 million by the end of the 21st century¹. This growth has led to the expansion
43 of agricultural land and the reduction of natural forests and other woody vegetation^{2,3,4}, affecting biodiversity and
44 carbon storage³. Severe droughts in recent decades have also had an adverse impact on humid and sub-humid
45 forested areas⁵. In contrast, studies of drylands have shown an increase in vegetation productivity over the last
46 30 years^{6,7,8}, also highlighting the importance of drylands for global carbon variability and as land CO₂ sink⁹.
47 Whether this increase in vegetation productivity is driven by the growth of woody vegetation and/or by an in-
48 crease in productivity of herbaceous vegetation is not clear^{6,7,8}. This is because the scattered nature of woody
49 plants in drylands is very different from forests with closed canopies and challenging to detect with optical satel-
50 lite imagery at regional to continental scales^{10,11}. Previous studies have used vegetation indices as proxies for net
51 primary productivity, but these indices measure the photosynthetically active part of the vegetation and most
52 studies do not distinguish between woody and herbaceous vegetation^{12,13}. Furthermore, studies of deforestation
53 in humid areas traditionally report the presence or absence of forests³ and do not assess gradual changes in forest
54 biomass within existing forests (e.g., forest degradation). They are also based on temporal snapshots of satellite
55 imagery at a higher spatial resolution and only capture forests based on given definitions, e.g. tree height and
56 canopy cover percentage^{3,14}, which substantially underestimate shrubs and scattered trees in drylands¹⁰. Conse-
57 quently, little quantitative information is available about the state, rate, and drivers of change in the cover of
58 woody vegetation at the scale of the African continent. This information is crucial for ensuring that the design of
59 natural resource management in relation to deforestation and desertification is based on observations rather than
60 those based on narratives.

61

62 **Results**

63 **Africa's changing woody cover**

64 We used a new passive microwave Earth Observation (EO) data set (Vegetation Optical Depth, VOD) that cap-

65 tures continuous changes in the coverage of canopies of all woody phanerophytes, regardless of size, in both
66 drylands and humid areas¹⁵⁻¹⁷. We applied VOD as a proxy for annual woody cover and documented changes in
67 Africa's woody vegetation between 1992 and 2011, with a special focus on the changes in drylands and humid
68 areas (defined by the ratio between annual precipitation and potential evapotranspiration, Supplementary Fig.
69 1a). Woody vegetation changed significantly (linear regression, $p < 0.05$, $n = 20$) during 1992–2011 in approxi-
70 mately half of sub-Saharan Africa (47% of land areas). A majority (77%) of the significant trends were positive,
71 covering 36% of sub-Saharan Africa and representing an overall increase of 2.1 woody cover (%) (Fig. 1a). Most
72 (70%) of the significant positive changes were in drylands covering approximately 4 900 000 km² (overall
73 change +2.9 woody cover (%)), mainly in the Sahel and southern Africa¹⁸⁻²⁰ (Fig. 2a). Positive trends are also
74 observed in the humid zones to a much smaller extent (2 100 000 km²), with an overall change of +0.8 woody
75 cover (%). Negative changes affected 11% of sub-Saharan Africa, of which 75% were in humid areas (approx-
76 imately 1 600 000 km² in humid zones and 530 000 km² in drylands). The decline in woody cover primarily af-
77 fected areas that are also characterized by high carbon stocks (Supplementary Figs 2a, 2b), suggesting that areas
78 with the largest carbon sinks have been disturbed at the fastest rate. The classification of woody cover change
79 into bioclimate zones²¹ confirms the overall tendency with larger increases in drier zones (except extremely hot
80 xeric) and lower increases and decreases in moister zones (Fig. 2d).

81

82 **Drivers of woody cover changes**

83 The positive changes in woody cover in Africa's drylands are significantly related to precipitation (Fig. 1a). In
84 contrast to herbaceous vegetation, woody plants can benefit from a higher variability and intensity of precipita-
85 tion²², as in southern Africa and the Sahel (Supplementary Fig. 1c). The dependence on precipitation was cor-
86 roborated with simulations of the vegetation using the dynamic vegetation model LPJ-GUESS²³, which simulat-
87 ed an increase in woody biomass for 1992-2011, consistent with the satellite estimates of woody cover (Fig. 3).
88 The relative increase of both woody cover and biomass was largest in drylands, and factorial simulations of the
89 individual driving variables indicated that precipitation accounted for most of the simulated increase in woody
90 biomass in drylands such as the Sahel and southern Africa (Fig. 3, Supplementary Fig. 3). Increasing concentra-

91 tions of atmospheric CO₂ was a minor contributor to these dryland trends yet was the main variable driving the
92 growth of woody vegetation in humid areas, enhancing primary production²⁴ (Fig. 3, Supplementary Figs. 2, 3).
93 The absolute increase in woody biomass was largest in humid areas (mean increase of 0.04 kg C m⁻² y⁻¹ near the
94 equator, Supplementary Fig. 2), coinciding with overall large stocks of woody biomass. Solar radiation, nitrogen
95 deposition and temperature had minor impacts on the changes in woody biomass (Supplementary Fig. 2).

96 This overall increase in woody vegetation driven by climate and CO₂, however, was offset by anthropogenic
97 impacts, especially in humid areas. The increase in woody cover in the VOD analysis was thus most pronounced
98 in areas of low human population density and change (Fig. 4). Areas and countries with a higher population den-
99 sity and growth (Fig. 1b, Supplementary Fig. 1d) had decreases in VOD-based woody cover (Figs. 1a, 4, Sup-
100 plementary Fig. 4), offsetting the climate-driven increases in other parts of the humid zones (Figs. 2c, 3). This
101 separation in areas of high and low human pressure applied to both drylands and humid tropics. The average
102 trend, however, remained positive in drylands, even in areas with strong population growth, but was negative in
103 humid areas with strong population growth, regardless of the trends in precipitation and CO₂ (Fig. 2b, c). Popu-
104 lations increased by an average of 40 persons km² over 20 years in areas where woody cover decreased suppos-
105 edly due to agricultural expansion, logging, and other uses of woody products. In contrast, populations increased
106 by an average of only 6 persons km² in areas where woody cover increased. Human population increase was
107 highest in moist and mesic bioclimate zones and woody cover changes were accordingly negative or low, where-
108 as population growth was lower in xeric areas and woody cover increases were higher (Fig. 2d). At the continen-
109 tal scale, a simultaneous autoregressive model (SAR) explained nearly half of the spatial pattern of changes in
110 woody cover in terms of changes in population and precipitation ($r^2=0.46$), with population being more im-
111 portant than precipitation (standardized slopes of -0.27 and 0.08, respectively) (Supplementary Table 1).

112

113 **Discussion**

114 The opposing trends in dry and humid zones have implications for our understanding of environmental change in
115 sub-Saharan Africa. While areas of high population growth, mostly in humid zones, on average experience a

116 decrease in woody vegetation, areas with low population growth on average experience an increase in woody
117 vegetation, mainly driven by changes in precipitation and CO₂ concentrations. This latter increase is not captured
118 in official forest statistics, since much of it takes place outside of humid forests.

119 This implies that the ‘problem’ of woody cover loss - and thus carbon stocks decreases - in the humid forest
120 zones is at least partly balanced by an increase in drylands. ‘Bush encroachment’ in savannas of southern Africa,
121 however, has traditionally been considered an undesired effect^{14,25}. Since the VOD data used to estimate woody
122 cover does not allow a direct estimation of carbon stocks, the exact balance between gains and losses in carbon
123 cannot be directly assessed in this study. Further work combining field measurements, ecosystem modelling and
124 new satellite-based passive microwave sensors is required to further understand these linkages. In humid areas,
125 woody biomass may actually increase without any change in woody cover.

126 The close relationship between population growth and decreased woody cover suggests that agricultural expan-
127 sion, urbanization and wood fuel harvest were the main causes of the decrease in woody cover, as also found in
128 studies of tropical deforestation^{3,26}. The reduction in woody cover tends to primarily affect areas with high car-
129 bon stocks and other studies suggest that these are also areas characterized by the highest biological diversity²⁷.
130 There is, however, no simple relation between losses and gains in woody cover and biodiversity. While diversity
131 and productivity of natural vegetation are generally positively correlated²⁸, this does not exclude the possibility
132 that great losses may be experienced in areas of deforestation, while only smaller gains are seen in drylands with
133 increasing woody cover.

134 Due to the impact on land surface albedo, woody cover changes in dryland areas may trigger climate feed-backs.
135 Since the hypothesized existence of a ‘biogeophysical feed-back’²⁹, many studies have attempted to model such
136 effects^{30,31}, with some research claiming that man-made afforestation efforts would give rise to increased precipi-
137 tation³². The extent of the observed increase in woody cover in African drylands may impact climate if the in-
138 crease continues in the coming decades, and this altered feed-back should preferably be implemented in regional
139 climate or Earth system models, with the observed increase in woody vegetation providing a test case for these
140 models.

141

142 **Methods**

143 **VOD data and calibration to woody cover.** We define woody cover as the percentage of a given area covered
144 by woody vegetation, including both leaf and woody components of woody plant canopies. The unit is woody
145 cover (%). The VOD data was retrieved from satellite passive microwave observations quantified as brightness
146 temperature based on the NASA-VU Land Parameter Retrieval Model (LPRM)³³. Three passive microwave
147 sensors, i.e. the Special Sensor Microwave Imager, the Advanced Microwave Scanning Radiometer – Earth Ob-
148 serving System, and the radiometer of WindSat are used to form the long-term data set by applying a trend-
149 preserving cumulative distribution function matching without changing the inter-annual variations and long-term
150 trends of the original retrievals^{34,35}. The merged long-term VOD data set was gridded at a 0.25° spatial resolution
151 and monthly interval from 1992 to 2011 and is consistent between different sensors³⁶. VOD is sensitive to the
152 total aboveground water content in both the photosynthetic (foliar) and non-photosynthetic (woody) components
153 of the vegetation stratum^{15,37}. Soil moisture conditions are retrieved simultaneously with the VOD information in
154 LPRM and large variations in soil moisture can influence the accuracy of VOD, especially for dense rainforest
155 regions³³. Thus VOD values exceeding 1.2 are suggested to be excluded in vegetation studies¹⁶. The VOD signal
156 has been separated from soil moisture and is used as a proxy for vegetation biomass globally³⁴. The VOD sea-
157 sonal variation is a combined effect of the seasonal dynamics of both herbaceous (including crops) and woody
158 vegetation¹⁵. We used the annual minimum VOD values as a proxy for woody vegetation cover to minimize the
159 influence of annual herbaceous vegetation¹⁰ and avoided values exceeding 1.2 (Supplementary Fig. 5). Areas
160 with perennial herbaceous vegetation may lead to an over-estimation of woody cover; however, the woody cover
161 in % is usually higher in these areas concealing the influence from the herbaceous plant understory. Also, VOD
162 data have been used to estimate forest change in South America by limiting the range of VOD values to 0.6-
163 1.2¹⁶. We did not restrict the VOD range to also include young trees and shrubs, which form an important part of
164 the community of woody vegetation. Minimum VOD agrees well with a field data based map of woody cover
165 for Sahel ($r^2=0.80$)¹⁰ (Supplementary Fig. 5). A global map calibrated with optical high spatial resolution images
166 and also assessing smaller trees produced similar results³⁸ and was thus used to transform the annual minimum
167 VOD to the unit woody cover (%) for further analyses ($r^2=0.85$, slope=0.86) (Supplementary Fig. 5). A third-

168 degree polynomial regression was used for the transformation. Woody cover <10% was predicted with an expo-
169 nential regression to avoid underestimation of very low values. The VOD is insensitive to the effects of atmos-
170 pheric and cloud contamination, ensuring reliable retrievals in cloudy regions e.g. central Africa.

171 **Correlation between the trends in woody cover and changes in human population and precipitation.** Pre-
172 cipitation data were derived from the Climate Research Unit (CRU) (data set version 3.23), which is globally
173 available for a 0.5° grid at monthly scale and is based on the upscaling of data from rain gauges³⁹. CRU precipi-
174 tation data intrinsically includes some uncertainty, as the number of stations used for each grid cell varies con-
175 siderably between cells and years. Even though it is the most widely used precipitation data set in dynamic vege-
176 tation modelling⁴⁰ and consistency with other data sets has been shown⁴¹, results have to be considered with cau-
177 tion⁷. We have tested the blended GPCP data set, without significant changes of the results, still it has to be not-
178 ed that a linear trend analysis on annually summed data includes uncertainties and simplification. We summed
179 the monthly observations to obtain annual sums from 1992 to 2011 and resampled the data to 0.25° using a bicu-
180 bic interpolation. Population data were acquired from Gridded Population of the World (GPW) v3⁴², which in-
181 cludes estimates for 1990, 1995, 2000, 2005, and 2010, gridded with an output resolution of 2.5 arc-minutes,
182 resampled for this study to 0.25° (nearest neighbor). GPW population data were acquired from national statisti-
183 cal offices and gridded based on the proportional method, which allocates population counts to grid cells based
184 on the proportion of each administrative areal unit that overlaps the cell. The gridded counts for existing census
185 years are then projected to the set of output years based on a simple model of population growth. The modeling
186 was thus not based on any additional layers of data, such as land cover, avoiding potential problems of endoge-
187 neity between VOD and simulated population grids. A linear trend analysis was conducted for annual woody
188 cover and precipitation data, and the slope multiplied with the number of years to retrieve the absolute change
189 over time in the corresponding unit, facilitating the direct comparison with the human population data. We quan-
190 tified the relationships between the changes in woody cover (estimated by VOD), population increase (GPW),
191 and precipitation (CRU) by applying a simultaneous autoregressive model (SAR) (spatial error type⁴³) to the
192 three gridded data sets. The SAR model accounts for spatial autocorrelation and uses change in woody cover as
193 response and log(change in population) and change in precipitation as explanatory variables. The logarithm of

194 the human population data was applied since the relation between woody cover changes and human population is
195 non-linear at pixel scale, i.e. if a high number of population is reached (mostly in cities), the woody cover stops
196 to decrease further. Standardized variables were used to enable model coefficients inter-comparison (standard-
197 ized variable = (variable - mean) / standard deviation).

198 Fires frequently occur in most African ecosystems. However, at the spatial and temporal scale of our analysis,
199 we do not expect changes in fire regimes as a major cause of changes in woody cover in itself but rather as a
200 consequence of human induced deforestation and land use change⁴⁴.

201 **Dynamic ecosystem model.** The dynamic ecosystem model LPJ-GUESS²³ was applied to simulate changes in
202 woody-biomass carbon in natural vegetation for 1992-2011. LPJ-GUESS simulates the distribution of plant
203 functional types, and each type is represented by four pools of biomass carbon: leaves, roots, sapwood, and
204 heartwood. The latter two were added to represent the amounts of stem (wood) carbon. This variable is closely
205 related to the woody cover estimated by VOD, but especially in tropical forests, differences are expected, as
206 VOD is not able to fully penetrate the tree crowns⁴⁵. Simulations were run for 1992-2011, applying monthly
207 climate data (temperature, precipitation, sunshine duration) from meteorological stations, gridded to 0.5°×0.5°
208 resolution (CRU TS 3.21³⁹), monthly model-derived estimates for nitrogen deposition⁴⁶, and annual mean at-
209 mospheric CO₂ concentrations^{47,48} based on ice-core data and atmospheric observations as forcing. Land use and
210 land use change were not accounted for in the simulations, which were only applied to quantify the changes in
211 natural vegetation. The simulations were preceded by a two-stage spinup: For the first stage, vegetation growth
212 starts from bare-ground conditions, using climatic data for 1901-1930, and CO₂ levels were kept constant at the
213 concentration for 1901. For the second stage, representing 1901-1991, the actual climate data, atmospheric CO₂
214 concentration and N deposition were used.

215 In addition to a full simulation with the forcing as described above, five factorial simulations were performed to
216 separate the impact of individual driving variables. Only one of the four parameters (temperature, precipitation,
217 radiation, or CO₂) was applied using the transient data as described above, whereas the other three parameters
218 used a climatology for 1992-2011, applying monthly means over this 20-year period for the climatic parameters
219 and an annual mean for CO₂. In the fifth factorial simulation, similar to the transient CO₂ simulation above, the

220 changing CO₂ concentration was combined with a climatology for N deposition, to separate the impacts of at-
221 mospheric CO₂ and N deposition on the CO₂ fertilization. These simulations were applied to determine the im-
222 pact of the individual driving variables on the simulated trend.

223 **Data availability** CRU precipitation data are available from the University of East Anglia
224 (<http://www.cru.uea.ac.uk/>). The global tree cover map is available from the Geospatial Information Authority of
225 Japan, Chiba University (<http://www.iscgm.org/gm/ptc.html#use>). VOD raster data are developed by Yi Liu,
226 University of New South Wales. Gridded population maps are provided by CIESIN
227 (<http://sedac.ciesin.columbia.edu/>). Humidity zones are available from <http://www.grid.unep.ch/index.php>.
228 DGVM results are available from the corresponding author upon reasonable request.

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230 **References**

1. Gerland, P. et al. World population stabilization unlikely this century. *Science* 346, 234–237 (2014).
2. Lambin, E. F. & Meyfroidt, P. Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci.* 108, 3465–3472 (2011).
3. Hansen, M. C. et al. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342, 850–853 (2013).
4. Mayaux, P. et al. State and evolution of the African rainforests between 1990 and 2010. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20120300 (2013).
5. Zhou, L. et al. Widespread decline of Congo rainforest greenness in the past decade. *Nature* 509, 86–90 (2014).
6. Fensholt, R. et al. Greenness in semi-arid areas across the globe 1981–2007 — an Earth Observing Satellite based analysis of trends and drivers. *Remote Sens. Environ.* 121, 144–158 (2012).
7. Andela, N., Liu, Y. Y., van Dijk, A. I. J. M., de Jeu, R. A. M. & McVicar, T. R. Global changes in dryland

- vegetation dynamics (1988–2008) assessed by satellite remote sensing: comparing a new passive microwave vegetation density record with reflective greenness data. *Biogeosciences* 10, 6657–6676 (2013).
8. Kaptué, A. T., Prihodko, L. & Hanan, N. P. On greening and degradation in Sahelian watersheds. *Proc. Natl. Acad. Sci.* 201509645 (2015). doi:10.1073/pnas.1509645112
 9. Ahlström, A. et al. The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science* 348, 895–899 (2015).
 10. Brandt, M. et al. Woody plant cover estimation in drylands from Earth Observation based seasonal metrics. *Remote Sens. Environ.* 172, 28–38 (2016).
 11. Donohue, R. J., McVicar, T. R. & Roderick, M. L. Climate-related trends in Australian vegetation cover as inferred from satellite observations, 1981–2006. *Global Change Biology* 15, 1025–1039 (2009).
 12. Zhu, Z. et al. Greening of the Earth and its drivers. *Nature Clim. Change* advance online publication, (2016).
 13. Kolby Smith, W. et al. Large divergence of satellite and Earth system model estimates of global terrestrial CO₂ fertilization. *Nature Climate Change* 6, 306–310 (2015).
 14. Shimada, M. et al. New global forest/non-forest maps from ALOS PALSAR data (2007–2010). *Remote Sens. Environ.* 155, 13–31 (2014).
 15. Tian, F., Brandt, M., Liu, Y. Y., Rasmussen, K. & Fensholt, R. Mapping gains and losses in woody vegetation across global tropical drylands. *Global Change Biology* (2016). doi:10.1111/gcb.13464.
 16. van Marle, M. J. E., van der Werf, G. R., de Jeu, R. A. M. & Liu, Y. Y. Annual South American forest loss estimates based on passive microwave remote sensing (1990–2010). *Biogeosciences* 13, 609–624 (2016).
 17. Jones, M. O., Kimball, J. S. & Jones, L. A. Satellite microwave detection of boreal forest recovery from the extreme 2004 wildfires in Alaska and Canada. *Glob. Change Biol.* 19, 3111–3122 (2013).
 18. Brandt, M. et al. Ground- and satellite-based evidence of the biophysical mechanisms behind the greening

- Sahel. *Glob. Change Biol.* 21, 1610–1620 (2015).
19. Wigley, B. J., Bond, W. J. & Hoffman, M. T. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob. Change Biol.* 16, 964–976 (2010).
 20. Mitchard, E. T. A. & Flintrop, C. M. Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982–2006. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20120406 (2013).
 21. Metzger, M. J. et al. A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. *Global Ecology and Biogeography* 22, 630–638 (2013).
 22. Gherardi, L. A. & Sala, O. E. Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proc. Natl. Acad. Sci.* 112, 12735–12740 (2015).
 23. Smith, B. et al. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences* 11, 2027–2054 (2014).
 24. Yang, Y., Donohue, R. J., McVicar, T. R., Roderick, M. L. & Beck, H. E. Long-term CO₂ fertilization increases vegetation productivity and has little effect on hydrological partitioning in tropical rainforests. *J. Geophys. Res. Biogeosci.* 2016JG003475 (2016). doi:10.1002/2016JG003475
 25. Bond, W. J. & Midgley, G. F. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Phil. Trans. R. Soc. B* 367, 601–612 (2012).
 26. Lambin, E. F. & Geist, H. J. *Land-Use and Land-Cover Change: Local Processes and Global Impacts.* (Springer Science & Business Media, 2008).
 27. Cincotta, R. P., Wisniewski, J. & Engelman, R. Human population in the biodiversity hotspots. *Nature* 404, 990–992 (2000).
 28. Willig, M. R. Biodiversity and Productivity. *Science* 333, 1709–1710 (2011).
 29. Charney, J. G., Stone, P. H. & Quirk, W. J. Drought in the Sahara: a biogeophysical feedback mechanism.

Science 187, 434–435 (1975).

30. Taylor, C. M., Lambin, E. F., Stephenne, N., Harding, R. J. & Essery, R. L. H. The Influence of Land Use Change on Climate in the Sahel. *Journal of Climate* 15, 3615–3629 (2002).
31. Wu, M. et al. Vegetation–climate feedbacks modulate rainfall patterns in Africa under future climate change. *Earth System Dynamics* 7, 627–647 (2016).
32. Abiodun, B. J., Adeyewa, Z. D., Oguntunde, P. G., Salami, A. T. & Ajayi, V. O. Modeling the impacts of reforestation on future climate in West Africa. *Theoretical and Applied Climatology* 110, 77–96 (2012).
33. Owe, M., de Jeu, R. & Holmes, T. Multisensor historical climatology of satellite-derived global land surface moisture. *J. Geophys. Res.* 113, F01002 (2008).
34. Liu, Y. Y. et al. Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Change* 5, 470–474 (2015).
35. Liu, Y. Y. et al. Trend-preserving blending of passive and active microwave soil moisture retrievals. *Remote Sens. Environ.* 123, 280–297 (2012).
36. Tian, F. et al. Remote sensing of vegetation dynamics in drylands: Evaluating vegetation optical depth (VOD) using AVHRR NDVI and in situ green biomass data over West African Sahel. *Remote Sensing of Environment* 177, 265–276 (2016).
37. Guglielmetti, M. et al. Measured microwave radiative transfer properties of a deciduous forest canopy. *Remote Sens. Environ.* 109, 523–532 (2007).
38. Kobayashi, T., Tsend-Ayush, J. & Tateishi, R. A New Tree Cover Percentage Map in Eurasia at 500 m Resolution Using MODIS Data. *Remote Sens.* 6, 209–232 (2013).
39. Harris, I., Jones, P. d., Osborn, T. j. & Lister, D. h. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642 (2014).
40. Poulter, B. et al. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle.

Nature 509, 600–603 (2014).

41. Dinku, T., Connor, S. J., Ceccato, P. & Ropelewski, C. F. Comparison of global gridded precipitation products over a mountainous region of Africa. *Int. J. Climatol.* 28, 1627–1638 (2008).
42. Doxsey-Whitfield, E. et al. Taking Advantage of the Improved Availability of Census Data: A First Look at the Gridded Population of the World, Version 4. *Pap. Appl. Geogr.* 1, 226–234 (2015).
43. Kissling, W. D. & Carl, G. Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* 17, 59–71 (2008).
44. Andela, N. & van der Werf, G. R. Recent trends in African fires driven by cropland expansion and El Nino to La Nina transition. *Nature Clim. Change* 4, 791–795 (2014).
45. Jones, M. O., Kimball, J. S. & Nemani, R. R. Asynchronous Amazon forest canopy phenology indicates adaptation to both water and light availability. *Environ. Res. Lett.* 9, 124021 (2014).
46. Lamarque, J.-F. et al. Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes. *Atmospheric Chemistry and Physics* 13, 7997–8018 (2013).
47. Etheridge, D. M. et al. Natural and anthropogenic changes in atmospheric CO₂ over the last 1000 years from air in Antarctic ice and firn. *Journal of Geophysical Research: Atmospheres* 101, 4115–4128 (1996).
48. Keeling, C. D., Whorf, T. P., Wahlen, M. & van der Plichtt, J. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375, 666–670 (1995).

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236

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242 spondence and requests for materials should be addressed to M.B. (martin.brandt@mailbox.org). The authors
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244 **Figure legends:**

245 **Figure 1 | Changes in woody vegetation and human population over two decades.** **a**, Significant trends of
246 woody cover (VOD) for 1992-2011, separated by the presence or absence of a significant ($p < 0.05$, $n = 12845$)
247 correlation with cumulative 2-year precipitation during this period. **b**, Changes in human populations for 1990-
248 2010. The maps in **(a)** and **(b)** share a clear pattern, especially areas with a decrease in woody cover, and no
249 relation to precipitation coincide with a high population pressure. **c**, SAR model of the changes between woody
250 cover, precipitation (both 1992-2011), and population (1990-2010). The units are expressed as change in the
251 corresponding unit over the period of analysis.

252 **Figure 2 | Changes in woody cover (VOD) in different humidity zones.** **a**, Areas with changes in woody cov-
253 er (linear regression of change in woody cover for 1992-2011). Annual profiles of woody cover for areas of sta-
254 tistically significant changes in woody cover in **b**, drylands and **c**, the humid areas of sub-Saharan Africa (Sup-
255 plementary Fig. 1a). Black lines characterize areas of high human population increase (> 30 persons km^{-2}) and
256 grey lines areas of low human population increase (< 10 persons km^{-2}) for 1990 to 2010. **d**, Woody cover and
257 human population changes are grouped according to bioclimatic zones²¹.

258 **Figure 3 | Climatic drivers of changes in woody cover and biomass in sub-Saharan Africa.** Relative trends
259 (% of mean year⁻¹) for 1992-2011 in woody cover (estimated with VOD) and woody biomass (simulated with
260 LPJ-GUESS) had similar patterns of change from north to south. The trends of woody biomass were mainly
261 driven by CO₂ (humid areas) and precipitation (drylands) (Supplementary Figs. 2, 3).

262

263 **Figure 4 | Links between changes in woody cover and human population.** Intervals of mean population den-
264 sity (1990-2010, Supplementary Fig. 1d) were used to group the changes in woody cover (VOD) associated with
265 population increases and the number of pixels showing significant woody cover change. A Chi-squared test be-
266 tween woody cover and population change indicated the statistically significant dependency between the two
267 variables.