LETTERS

Increasing carbon storage in intact African tropical forests

Simon L. Lewis[1], Gabriela Lopez-Gonzalez[1], Bonaventure Sonké[2], Kofi Affum-Baffoe[3], Timothy R. Baker[1], Lucas O. Ojo[4], Oliver L. Phillips[1], Jan M. Reitsma[5], Lee White[6], James A. Comiskey[7]†, Marie-Noël Djuikouo K.[2], Corneille E. N. Ewango[8], Ted R. Feldpausch[1], Alan C. Hamilton[9], Manuel Gloor[1], Terese Hart[10], Annette Hladik[11], Jon Lloyd[1], Jon C. Lovett[12], Jean-Remy Makana[10], Yadvinder Malhi[13], Frank M. Mbago[14], Henry J. Ndangalasi[14], Julie Peacock[1], Kelvin S.-H. Peh[1], Douglas Sheil[15]†, Terry Sunderland[7]†, Michael D. Swaine[16], James Taplin[12], David Taylor[17], Sean C. Thomas[18], Raymond Votere[3] & Hannsjörg Wöll[19]

The response of terrestrial vegetation to a globally changing environment is central to predictions of future levels of atmospheric carbon dioxide[1,2]. The role of tropical forests is critical because they are carbon-dense and highly productive[3,4]. Inventory plots across Amazonia show that old-growth forests have increased in carbon storage over recent decades[5–7], but the response of one-third of the world's tropical forests in Africa[8] is largely unknown owing to an absence of spatially extensive observation networks[9,10]. Here we report data from a ten-country network of long-term monitoring plots in African tropical forests. We find that across 79 plots (163 ha) above-ground carbon storage in live trees increased by 0.63 Mg C ha^{-1} yr^{-1} between 1968 and 2007 (95% confidence interval (CI), 0.22–0.94; mean interval, 1987–96). Extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C yr^{-1} (CI, 0.15–0.43). These reported changes in carbon storage are similar to those reported for Amazonian forests per unit area[6,7], providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon. Indeed, combining all standardized inventory data from this study and from tropical America and Asia[5,6,11] together yields a comparable figure of 0.49 Mg C ha^{-1} yr^{-1} ($n = 156$; 562 ha; CI, 0.29–0.66; mean interval, 1987–97). This indicates a carbon sink of 1.3 Pg C yr^{-1} (CI, 0.8–1.6) across all tropical forests during recent decades. Taxon-specific analyses of African inventory and other data[12] suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks[13], as some theory[14] and models[2,10,15] predict.

Tropical forests cover 7–10% of the global land area, store 40–50% of carbon in terrestrial vegetation and annually process approximately six times as much carbon via photosynthesis and respiration as humans emit from fossil fuel use[3,4]. Tropical forests are therefore a critical, yet very poorly quantified, component of the global carbon cycle. Although atmospheric CO_2 concentration data, combined with estimates of fossil fuel emissions, ocean carbon fluxes and carbon released from land-use change, indicate a global land carbon sink averaging 2.2 Pg C annually from 1980 to 2000, the location(s) of the sink has remained elusive[1]. Attempts to refine our understanding of these land sinks have predominantly focused on the interpretation of patterns of atmospheric CO_2 data using atmospheric transport models. However, studies remain poorly constrained and contradictory, largely because of a lack of atmospheric observations in the tropics[15–17]. A complementary approach towards solving the global carbon budget is to directly monitor specific land carbon pools. Over recent decades, long-term monitoring plots across Amazonia show that remaining old-growth forest trees are a sink of 0.62 ± 0.23 Mg C ha^{-1} yr^{-1} (0.5–0.8 Pg C yr^{-1} for all Amazonia[6,7]). However, it is not known if this is a regional or pan-tropical phenomenon because data from the largest tropical continent, Africa, have been almost completely absent[9,10].

To assess whether similar changes are currently occurring in African tropical forest, we assembled existing long-term monitoring data and complementary field campaigns to create a ten-country network of monitoring plots called Afritron (African Tropical Rainforest Observation Network, www.afritron.org). Here we report data from 79 permanent sample plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central and Eastern Africa (Supplementary Fig. 1, Supplementary Table 1). Our approach is to measure the diameter of all trees that are ≥100 mm in diameter in a given area (mean 2.1 ha) at least twice (mean interval 9.4 years), and apply allometric equations to convert tree-diameter measurements to carbon content, using standardized procedures (Methods). Following an empirical method to weight plot results relative to sampling effort (Methods, Supplementary Figs 4–10), we estimate that above-ground carbon stored in live trees averages 202 Mg ha^{-1} ($n = 79$; bootstrapped

[1]Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds LS2 9JT, UK. [2]Plant Systematic and Ecology Laboratory, University of Yaounde I, PO Box 047, Yaounde, Cameroon. [3]Resource Management Support Centre, Forestry Commission of Ghana, PO Box 1457, Kumasi, Ghana. [4]Department of Environmental Management and Toxicology, University of Agriculture, PMB 2240, Abeokuta, Ogun State, Nigeria. [5]Bureau Waardenburg bv, PO Box 365, 4100 AJ Culemborg, The Netherlands. [6]Institut de Recherche en Ecologie Tropicale (IRET), BP 7847, Libreville, Gabon. [7]SI/MAB Biodiversity Program, Smithsonian Institution, Suite 3123, 1100 Jefferson Drive SW, Washington DC 20560, USA. [8]Forest Ecology & Management Group, Department of Environmental Sciences, Wageningen University, PO Box 342, NL-6700, The Netherlands. [9]Plantlife International, 14 Rollestone Street, Salisbury, Wiltshire SP1 1DX, UK. [10]Wildlife Conservation Society–DRC, 1725 Avenue Monjiba, Chanic Building 2nd floor, Ngalinema, BP 240, Kinshasa I, Democratic Republic of Congo. [11]Eco-anthropologie et ethnobiologie, Département Hommes, Natures, Sociétés, MNHN, 4 av. du Petit Château, 91 800 Brunoy, France. [12]Centre for Ecology, Law and Policy, Environment Department, University of York, York YO10 5DD, UK. [13]Environmental Change Institute, School of Geography and the Environment, Oxford University, Oxford OX1 3QY, UK. [14]Department of Botany, University of Dar es Salaam, PO Box 35060, Dar es Salaam, Tanzania. [15]Centre for International Forestry Research, PO Box 0113 BOCBD, Bogor 16000, Indonesia. [16]Department of Plant & Soil Science, Cruickshank Building, School of Biological Sciences, University of Aberdeen, St Machar Drive, Aberdeen AB24 3UU, UK. [17]Department of Geography, Museum Building, School of Natural Sciences, Trinity College, University of Dublin, Dublin 2, Republic of Ireland. [18]Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, Ontario M5S 3B3, Canada. [19]Sommersbergseestr. 291, A-8990 Bad Aussee, Austria. †Present addresses: Inventory & Monitoring Program, National Park Service, 120 Chatham Lane, Fredericksburg, Virginia 22405, USA (J.A.C.); Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, PO Box 44, Kabale, Uganda (D.S.); Centre for International Forestry Research, PO Box 6596 JKPWB, Jakata 10065, Indonesia (T.S.).

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95% CI, 174–244; Supplementary Table 2). Carbon storage increased by 0.63 Mg ha^{-1} yr^{-1}, with 73% of plots showing increased storage ($n = 79$; bootstrapped 95% CI, 0.22–0.94; Fig. 1; 0.29% increase, CI, 0.05–0.50; Supplementary Table 2, see Supplementary Fig. 2 and Supplementary Table 2 for unweighted data). The distribution is non-normal, being a left-skewed leptokurtic distribution, because occasional disturbance events may sharply reduce carbon stocks in relatively small plots monitored over relatively short time periods (Fig. 1). Grouping plots into spatial clusters (Supplementary Fig. 1, Supplementary Table 2) gives similar results (Supplementary Information).

We monitored 163 ha for a combined census length of 744 years, but a simple scaling of the weighted mean increase in carbon stocks by total forest area may overestimate the actual carbon sink, because tree growth is relatively constant, yet mortality is highly variable and large mortality events are rare. Specifically, if there was no carbon sink and we sampled all African forest over a long enough period, the mean and median change in carbon storage would, by definition, be zero. However, when sampling over shorter time periods, most forest plots will be increasing in carbon storage (approximately constant growth), offset by occasional larger losses (stochastic mortality), thus we are sampling from a left-skewed long-tail distribution[18]. If the disturbance regimes in tropical forests are dominated by large and rare events then the tail of the distribution of change in carbon stocks would be very heavy, leading to likely positive biases in estimating changes in carbon stocks unless sample sizes are very large[19]. The only data on very large-scale mortality events come from a survey of Brazilian Amazonia (3.9×10^6 km^2), which found only 19 large (>0.3 km^2) natural canopy gaps <2 years old, totalling 0.0001% of the area surveyed, suggesting that large disturbances are very rare[20]. Furthermore, quantitative analyses of the statistical distributions of the large-scale Amazon data, less spatially extensive African data and carbon losses from mortality from this study are all consistent: mortality events in non-cyclone-affected tropical forests are dominated by small and frequent events (Supplementary Information and Supplementary Table 4). Forest simulations using these new analyses show that our estimates of changes in above-ground carbon stocks are unlikely to be biased[19].

Yet, is our data set significantly different from that expected from a domain that is not increasing in carbon stocks? The ultimate cause of most large mortality events is the climate system producing extreme windstorms, rainfall events and droughts, often modelled using one of a family of long-tail generalized extreme value (GEV) distributions[18]. GEV theory[18] indicates that our data fit a Weibull distribution (Fig. 1, Methods). Shifting this distribution left to fix the mean change in carbon storage to zero provides a parsimonious 'null model' with which to compare the actual data (Supplementary Fig. 3, Methods). Re-sampling from this zero-mean distribution shows that it is highly unlikely that our data derive from a domain that was not increasing in carbon storage ($P < 0.001$).

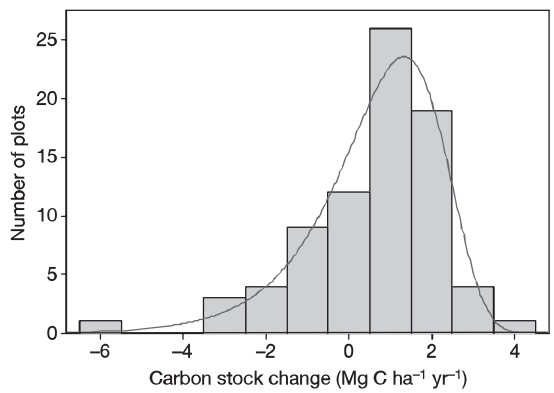


Figure 1 | Histogram of annualized change in carbon stocks from 79 long-term monitoring plots across 10 countries in Africa. Results presented are weighted by sampling effort (plot size and census-interval length), and fitted three-parameter Weibull distribution.

As the term 'tropical forest' does not have a universally agreed definition, because there are continua to sub-tropical, drier and open forest systems which are open to interpretation[4], we estimate the total African closed-canopy forest sink using four widely used estimates of the extent of similar forest categories, giving an increase in above-ground live tree carbon stocks of 0.24 Pg yr^{-1} (CI, 0.08–0.35; Table 1). Assuming proportionate increases in (1) unmeasured below-ground live tree carbon stocks (because a larger mass of roots is required to support a larger mass of trees), (2) coarse woody inputs (necromass; because the mass of recently dead trees will be larger if the mass of live trees, of which a fraction die, is larger) and (3) stems smaller than our 100 mm diameter threshold, we estimate total tree carbon (live, dead, above- and below-ground) in African tropical forests to be increasing at a rate of 0.34 Pg C yr^{-1} (CI, 0.15–0.43, Table 1). Of course, the limited number of sampling locations, absence of plots in some areas (notably central Democratic Republic of Congo, Supplementary Fig. 1) and differences in forest-area assessments all indicate that these first-estimate figures will require refinement in the future.

What are the implications of these findings for the carbon balance of Africa and the global carbon cycle more generally? The sink is of similar size to the estimated carbon flux from deforestation in tropical Africa[21,22] (0.1–0.3 Pg yr^{-1} over 1980–2000) and exceeds the flux from fossil fuel use in tropical Africa (0.04 Pg yr^{-1} in 2000); also, it is consistent with a recent model prediction of a 0.3 Pg C yr^{-1} sink in African forest vegetation[10], and a recent African carbon cycle synthesis implying a terrestrial sink of 0.4 Pg C yr^{-1} (ref. 9). More generally, combining all standardized inventory data from tropical Africa, America and Asia[5,6,11] (Methods) gives 156 inventory plots (562 ha monitored for a combined census length of 1,649 years), and a mean sampling effort-weighted increase in above-ground carbon stocks in live trees ≥100 mm of 0.49 Mg C ha^{-1} yr^{-1} (95% CI, 0.29–0.66). This suggests a carbon sink over recent decades across all tropical forests of 0.9 Pg C yr^{-1} (CI, 0.5–1.2), for above-ground live tree carbon, or 1.3 Pg C yr^{-1} (CI, 0.8–1.6), for total tree carbon (Table 2, Supplementary Table 5). These estimates are consistent with a recent analysis of atmospheric CO_2 concentration data and atmospheric transport models that indicates a terrestrial tropical sink of ~1.5 Pg C yr^{-1} (ref. 15). Accounting for these results while balancing the global carbon cycle implies that the carbon source from land-use change, mostly tropical deforestation and degradation, is larger, and/or the carbon sink at temperate latitudes is smaller, than current central estimates suggest[1].

The proximate cause of an Africa-wide increase in above-ground carbon storage could be a decrease in mortality rates, an increase in growth rates, or a combination of the two[12]. Long-term monitoring of sufficient plots will help distinguish amongst possibilities. The ultimate cause may be an increase in resource availability or, because trees are long-lived, these systems may still be changing *en masse* from past anthropogenic or natural impacts, or responding to a recent reduction in such disturbances[23,24]. Recent changes in resource availability include fertilization by anthropogenic additions of CO_2 to the atmosphere, changes in solar radiation at the Earth's surface, increases in nutrient deposition rates and changes in rainfall[13,25]. Continental-scale disturbance-recovery cycles are less likely, because if Africa and Amazonia both experienced synchronous past disturbance events causing a carbon sink decades later, there would be indicative evidence, such as a large atmospheric CO_2 signal, of a past large-scale perturbation.

Nevertheless, anthropogenic pressures on African forests may have altered over time. For example, populations of large animals that disturb forests, such as elephants, have decreased, and increasing areas of forest have become protected, possibly also reducing disturbance levels. In addition, most African forest occurs close to the hydrological limits of closed-canopy forest, meaning that they are tightly coupled with climatic variability and change via hydrological

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Table 1 | Estimated carbon stocks and their annual increase for African tropical forest

Study	Category	Area (106 ha)	ALTC§ (Pg)	TTC§ (Pg)	ΔALTC ≥100 mm (Pg yr^{-1})	ΔALTC ≥10 mm (Pg yr^{-1})	ΔATC (Pg yr^{-1})	ΔTTC (Pg yr^{-1})
GLC2000	Humid tropical forest*	232.7	46.9 (40.5–56.8)	69.5 (60.9–80.7)	0.15 (0.05–0.22)	0.15 (0.06–0.23)	0.17 (0.08–0.25)	0.21 (0.09–0.27)
FRA CS	Closed forest†	352.7	71.1 (61.4–86.1)	105.3 (92.3–122.3)	0.22 (0.08–0.33)	0.23 (0.09–0.34)	0.26 (0.12–0.37)	0.32 (0.14–0.41)
FRA RS	Tropical forest	518.5	104.5 (90.2–126.5)	154.8 (135.6–179.8)	0.33 (0.11–0.49)	0.34 (0.13–0.50)	0.39 (0.17–0.55)	0.47 (0.21–0.60)
WCMC	Tropical forest‡	401.0	80.8 (69.8–97.8)	119.7 (104.9–139.1)	0.25 (0.08–0.38)	0.27 (0.10–0.39)	0.30 (0.13–0.42)	0.36 (0.16–0.46)
Mean		376.2	75.8 (65.5–91.8)	112.3 (98.4–130.5)	0.24 (0.08–0.35)	0.25 (0.09–0.37)	0.28 (0.12–0.40)	0.34 (0.15–0.43)

Estimates and 95% confidence intervals in parentheses are based on a measured stock of above-ground carbon in live trees ≥100 mm diameter of 202 Mg C ha^{-1} (CI, 174–244; for ALTC, TTC) and an increase of 0.63 Mg C ha^{-1} yr^{-1} (CI, 0.22–0.94; for ΔALTC, ΔTTC), and under the assumption that unmeasured minor vegetation components (small trees, shrubs, lianas), necromass and below-ground carbon in live trees increase proportionately (that is, are consistently assumed to be at equilibrium with the live trees ≥100 mm). Uncertainties are propagated as: $\sqrt{(\text{error}_1)^2 + \cdots + (\text{error}_n)^2}$. GLC2000 (Global Land Cover Map 2000), FRA CS (Food and Agriculture Organisation Forest Resources Assessment 2000, Country Statistics), FRA RS (Food and Agriculture Organisation Forest Resources Assessment 2000, Remote Sensing statistics), all from ref. 8. WCMC, World Conservation Monitoring Centre (from www.unep-wcmc.org). ALTC, above-ground live tree carbon storage. ATC, above-ground tree carbon storage, including coarse necromass. TTC, total tree carbon storage, including below-ground carbon from tree roots. Trees ≤100 mm are 0.0519% (95% CI, 0.0166) of ALTC, from two African inventory plots[11]; coarse necromass is 0.127% (95% CI, 0.0319) of ALTC, from pan-Amazon forest average[7]; roots are 0.25% (95% CI, 0.10) of ALTC, from an African literature estimate[30].

* Also 415.1 × 10^6 ha 'dry forest'.

† Also 288.9 × 10^6 ha 'open forest'.

‡ Lowland evergreen, semi-evergreen, deciduous/semi-evergreen, and lower montane categories combined.

§ Scaled stock estimates from intact forest plots do not account for forest degradation and therefore will be modest overestimates.

changes. Today's African wet tropics have previously been climatically modestly drier at times over the past two to three millennia, which led to significant changes in vegetation, with much more open, disturbed, fire-prone, and less carbon-dense forests then covering many areas that are currently closed-canopy forest[23,24]. African forests are clearly sensitive to climatic changes, and past events may have left their signature on present day forests.

Taxon-level analyses can assist in distinguishing between the resource availability and disturbance-recovery hypotheses. If the increase in carbon stocks was caused by recovery from past disturbance events, then lighter-wooded species (lower wood mass density) would decline as a proportion of the forest stand, and heavier-wooded species increase, as is well known from ecological theory and observational evidence[26]. We would therefore predict a positive relationship between the change in the carbon stocks of a given taxon, relative to the forest stand, and its wood density. Alternatively, if increases in resource levels are the cause of the changes, then we predict either no relationship between the change in the carbon stocks of a taxon relative to the forest stand, and wood density, if all species benefit, or possibly an increase in lighter-wooded species relative to heavier-wooded species, because lighter-wooded species may dominate some types of more resource-rich environments[27]. Figure 2 shows that there is no relationship between the performance of taxa, relative to the stand as a whole, and their wood density; this suggests that the increase in mean carbon stocks across the 79 African plots has been caused, at least in part, by an increase in resource availability favouring species with a wide range of ecological habits, rather than recovery from past disturbance.

African tropical forests are providing important ecosystem services by storing carbon and being a carbon sink, thereby reducing the rate of increase of atmospheric CO_2. With adequate protection these forests are likely to remain large carbon stores in the longer term. Securing this service will probably require formalizing and enforcing land rights for forest dwellers, alongside payments for ecosystem services to those

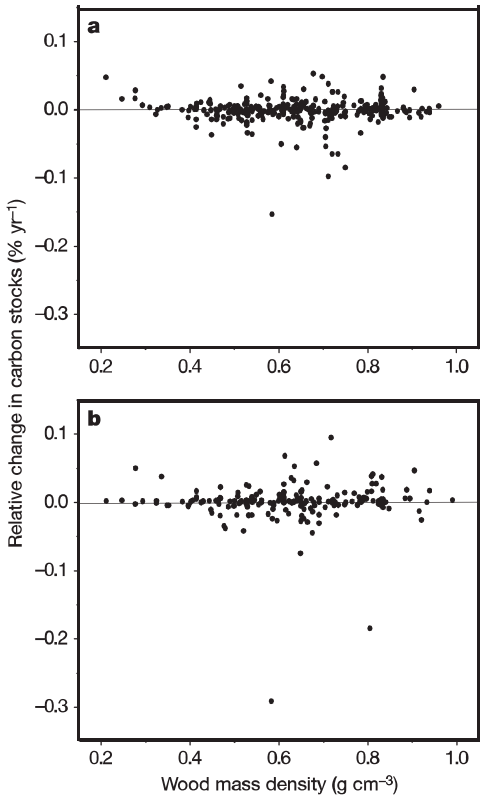


Figure 2 | Relative change in carbon stocks and corresponding wood mass density values. a, All 612 fully identified species occurring in ≥5 plots; **b**, all 200 fully identified genera occurring in ≥5 plots.

Table 2 | Estimated annual increase in tropical forest carbon stocks

Continent	Area (10^6 ha)	ΔALTC ≥100 mm (Pg yr^{-1})	ΔALTC ≥10 mm (Pg yr^{-1})	ΔATC (Pg yr^{-1})	ΔTTC (Pg yr^{-1})
Central and South America	786.8	0.39 (0.23–0.52)	0.42 (0.27–0.56)	0.47 (0.31–0.61)	0.62 (0.39–0.73)
Africa	632.3	0.31 (0.18–0.42)	0.33 (0.20–0.43)	0.37 (0.24–0.48)	0.44 (0.26–0.53)
Asia	358.3	0.18 (0.10–0.24)	0.18 (0.11–0.25)	0.21 (0.13–0.27)	0.25 (0.15–0.30)
Total	1777.3	0.87 (0.52–1.17)	0.93 (0.58–1.24)	1.04 (0.68–1.35)	1.31 (0.79–1.56)

Estimates are based on a measured increase of above-ground carbon in live trees ≥100 mm diameter of 0.49 Mg C ha^{-1} yr^{-1} (CI, 0.29–0.66). Areas are averages of 'tropical forest' (including more open and drier forest types) from four sources (GLC2000, FRA CS, FRA RS, WCMC). Full details of all forest types and sources of forest area data are in Supplementary Table 5. Abbreviations as in Table 1.

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living near forested areas. Whether remaining intact forests will continue to sequester carbon, become neutral, or become a net source of carbon in the future is highly uncertain[2,28]. Improved monitoring and modelling of the tropical environment is required to better understand this trajectory.

METHODS SUMMARY

All plots were selected in apparently mature closed-canopy forest ≥0.2 ha with diameters of all free-standing woody stems ≥100 mm measured using standardized methods within a given area at least twice and at least two years apart[6], with 63 plots located at random within landscapes, and up to 16 plots placed in 'representative' areas of forest (see Supplementary Fig. 1 and Supplementary Table 1 for full details). Trees that increased in diameter >40 mm yr^{-1} or shrunk 0.5 mm, including newly recruited stems >100 mm in the final census, were assessed and errors corrected, as necessary (for example, interpolation between other censuses). For trees with changes in the point of measurement, we standardized growth rates obtained from the two points of measurement to a common line (Methods). We also calculated changes in carbon stocks using seven other methods to process trees with point of measurement changes (Supplementary Information). Diameter measurements were converted to carbon stocks using a published allometric equation for moist forests that includes terms for wood mass density and tree height[29]. We accounted for uncertainty associated with allometry using Monte Carlo techniques (Methods). Biomass was assumed to be 50% carbon[29]. We also calculated changes in carbon stocks using two other allometric equations (Supplementary Information). Seventy-nine random samples were taken from the zero-mean distribution 1,000 times, and the mean of each run calculated to compare with the actual mean from the data. Relative changes in species-level or genus-level C stocks were calculated as: [(taxa_C_stock_final / stand_C_stock_final) − (taxa_C_stock_initial / stand_C_stock_initial)] / census_interval × 100. Only taxa identified with an accepted name in the African Flowering Plants database (www.ville-ge.ch/cjb/bd/africa/) were included in the analyses.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. Denman, K. L. *et al.* in *Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) 663–745 (Cambridge Univ. Press, 2007).
2. Friedlingstein, P. *et al.* Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *J. Clim.* **19,** 3337–3353 (2006).
3. Malhi, Y. & Grace, J. Tropical forests and atmospheric carbon dioxide. *Trends Ecol. Evol.* **15,** 332–337 (2000).
4. Lewis, S. L. Tropical forests and the changing Earth system. *Phil. Trans. R. Soc. Lond. B* **261,** 195–210 (2006).
5. Phillips, O. L. *et al.* Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282,** 439–442 (1998).
6. Baker, T. R. *et al.* Increasing biomass in Amazonian forest plots. *Phil. Trans. R. Soc. Lond. B* **359,** 353–365 (2004).
7. Phillips, O., Lewis, S. L., Baker, T. R., Chao, K.-J. & Higuchi, N. The changing Amazon forest. *Phil. Trans. R. Soc. B* **363,** 1819–1827 (2008).
8. Mayaux, P. *et al.* Tropical forest cover change in the 1990s and options for future monitoring. *Phil. Trans. R. Soc. B* **360,** 373–384 (2005).
9. Williams, C. *et al.* Africa and the global carbon cycle. *Carbon Balance Mgmt* **2,** 3, doi:10.1186/1750-0680-2-3 (2007).
10. Ciais, P., Piao, S.-L., Cadule, P., Friedlingstein, P. & Chedin, A. Variability and recent trends in the African carbon balance. *Biogeosciences* **5,** 3497–3532 (2008).
11. Chave, J. *et al.* Assessing evidence for a pervasive alteration of tropical tree communities. *PLoS Biol.* **6,** e45 (2008).
12. Lewis, S. L. *et al.* Concerted changes in tropical forest structure and dynamics: Evidence from 50 South American long-term plots. *Phil. Trans. R. Soc. Lond. B* **359,** 421–436 (2004).
13. Lewis, S. L., Malhi, Y. & Phillips, O. L. Fingerprinting the impacts of global change on tropical forests. *Phil. Trans. R. Soc. Lond. B* **359,** 437–462 (2004).
14. Lloyd, J. & Farquhar, G. D. The CO_2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO_2 concentrations and their interaction with soil nutrient status. 1. General principles and forest ecosystems. *Funct. Ecol.* **10,** 4–32 (1996).
15. Stephens, B. B. *et al.* Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO_2. *Science* **316,** 1732–1735 (2007).
16. Gurney, K. R. *et al.* Towards robust regional estimates of CO_2 sources and sinks using atmospheric transport models. *Nature* **415,** 626–630 (2002).
17. Rodenbeck, C., Houweling, S., Gloor, M. & Heimann, M. CO_2 flux history 1982–2001 inferred from atmospheric data using a global inversion of atmospheric transport. *Atmos. Chem. Phys.* **3,** 1919–1964 (2003).
18. Katz, R. W., Brush, G. S. & Parlange, M. B. Statistics of extremes: Modeling ecological disturbances. *Ecology* **86,** 1124–1134 (2005).
19. Fisher, J. I., Hurtt, G. C., Thomas, R. Q. & Chambers, J. Q. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol. Lett.* **11,** 554–563 (2008).
20. Nelson, B. W. *et al.* Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* **75,** 853–858 (1994).
21. Houghton, R. A. & Hackler, J. L. Emissions of carbon from land use change in sub-Saharan Africa. *J. Geophys. Res.* **111,** G02003, doi:10.1029/2005JG000076 (2006).
22. Achard, F., Eva, H. D., Mayaux, P., Stibig, H. J. & Belward, A. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. *Glob. Biogeochem. Cycles* **18,** GB2008, doi:10.1029/2003GB002142 (2004).
23. Brncic, T. M., Willis, K. J., Harris, D. J. & Washington, R. Culture or climate? The relative influences of past processes on the composition of the lowland Congo rainforest. *Phil. Trans. R. Soc. B* **362,** 229–242 (2007).
24. Ngomanda, A. *et al.* Lowland rainforest response to hydrological changes during the last 1500 years in Gabon, Western Equatorial Africa. *Quat. Res.* **67,** 411–425 (2007).
25. Wild, M. *et al.* From dimming to brightening: Decadal changes in solar radiation at Earth's surface. *Science* **308,** 847–850 (2005).
26. Urquiza-Haas, T., Dolman, P. M. & Peres, C. A. Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *For. Ecol. Mgmt* **247,** 80–90 (2007).
27. Malhi, Y. *et al.* The above-ground coarse wood productivity of 104 Neotropical forest plots. *Glob. Change Biol.* **10,** 563–591 (2004).
28. Cramer, W. *et al.* Tropical forests and the global carbon cycle: Impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Phil. Trans. R. Soc. Lond. B* **359,** 331–343 (2004).
29. Chave, J. *et al.* Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145,** 87–99 (2005).
30. Deans, J. D., Moran, J. & Grace, J. Biomass relationships for tree species in regenerating semi-deciduous forest tropical moist forest in Cameroon. *For. Ecol. Mgmt* **88,** 215–225 (1996).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Data collection and filtering. Criteria for plot inclusion: ≥0.2 ha, clearly mixed-age stands (therefore apparently old-growth), ≥50 m from the anthropogenic forest edge, and free from major human impacts (for example, logged forest). Sixty-three plots were located at random with respect to gap-phase dynamics and up to 16 were located in 'representative' forest or avoided large tree-fall gaps (Supplementary Table 1). All free-standing woody stems ≥100 mm were measured, mapped and identified using standard forestry methods[6] for 71 plots. For eight plots published data were used (Supplementary Table 1). We identified 95%, 98% and 99% of stems to species, genus and family respectively. Trees that increased in diameter >40 mm yr^{-1} or shrunk 0.5 mm were assessed to determine if they were inaccurately measured in the field (including new recruits). If judged inaccurate—for example, a slow-growing species growing abnormally fast—the diameter was interpolated or extrapolated using data from the same stem measured over other censuses, or, if only one accurate measurement was available, by substituting the median growth rate for the same diameter size-class from that plot (100–199, 200–399 and 400+ mm diameter). The median was chosen (1) to be conservative with respect to the hypothesis being tested, and (2) because sample sizes can be small for the largest size-class, hence the mean may not be robust. The standard method of tree measurement is 'diameter at breast height' (d.b.h.) defined as 1.3 m from the base of the stem, if approximately cylindrical at this point. If the transverse section of the stem is not cylindrical at 1.3 m height—owing to buttresses or other stem deformities—the measurement location is raised to a point where it is. Thus, as some trees grow, buttresses and other stem deformities may develop, and therefore occasionally the height of the point of measurement (POM) must be raised, so the measurement is consistent with standardized protocols. Tree growth estimates are therefore sometimes complicated by different POMs on the same tree, because changes in a POM can cause large negative growth in individuals that have actually grown (and hence needed a POM change). Our approach to trees with changing POMs was to utilize the greatest amount of information about each stems' growth rate to estimate its size. We harmonize the two disjointed sets of growth measurements (from the original POM, and the new POM) by replacing the measured diameters with the mean of (1) the ratio of the original to the new POM diameter measurements (to standardize each diameter measurement to the height of the original POM), and (2) the ratio of the final to the original POM diameter measurement (to standardize each diameter measurement to the height of the final POM). For comparison, we plot seven other methods of dealing with POM changes, including the commonest method—of substituting mean growth rates from the same diameter size-class trees from the plot—which give almost identical results (Supplementary Information and Supplementary Fig. 12).

Carbon stock estimation. Diameter measurements were converted to carbon stocks using a published allometric equation for moist forests including terms for wood mass density and tree height, with biomass assumed to be 50% carbon[29]. A wood density database was compiled from published sources (737 species; Supplementary Table 3). Species in both the wood density and plot databases were standardized for orthography and synonymy using the African Flowering Plants Database (www.ville-ge.ch/cjb/bd/africa/) to maximize matches between the databases. Stems were matched to species-specific wood density values if possible (62% of stems), or the mean values for the genera (23%), or family (11%), as appropriate. For incompletely identified stems, we used the next higher known taxonomic category or the plot-mean wood density (5% of stems). Tree heights were estimated from a height–diameter relationship derived from the measurements of 1,982 trees in African forests (Supplementary Fig. 14). Uncertainty associated with the allometric equation was propagated using Monte Carlo techniques. We used the residuals from the allometric equation to bootstrap the distribution of errors associated with allometry, and similarly for the height–diameter relationship. We then calculated the carbon in each tree with added random error from the bootstrapped distributions, summed over each plot for each census and the change in carbon stocks ha^{-1} yr^{-1} calculated (using Matlab). We repeated this process of adding random error to each tree and summing over each plot for each census 100 times, from which we calculated a mean change in carbon stocks for each plot from the 100 perturbed samples. Supplementary Table 2 reports initial, final and change in C stocks for the actual data and means of 100 perturbed samples. For five plots we used published data where only basal area was available (Supplementary Tables 1, 2). We converted these to carbon stocks by correlating basal area and carbon stocks for the 71 plots with full tree-by-tree data. For three published plots we used the published carbon stock values (Supplementary Tables 1, 2).

Weighting analysis. Optimum weightings of each replicate corresponding to the sampling effort employed (plot size and length of monitoring period) were derived empirically, assuming a priori that there is no pattern in the change in carbon stocks with monitoring period or plot size, by assessing patterns in the residuals of sampling effort versus carbon storage change, following different weightings. Weighting by the square root of the number of years of monitoring removes any pattern in the residuals. Similarly, weighting by the cube root of plot size removes any pattern in the residuals (Supplementary Figs 4–7). These results suggest that these square root and cube root relationships best describe how census length or plot size are related to sampling error, respectively. These results appear to be robust and general, as they are repeated when the Africa data are combined with other standardized data and re-analysed[6,11] (Supplementary Figs 7, 8). The final weighting of the square root of the number of years of monitoring plus cube root of plot size minus one (to avoid double-accounting) shows no pattern in the residuals (Supplementary Fig. 10). Weighting by sampling effort gives a similar mean but reduces the left-skew, because longer monitoring periods and larger plots dampen the impacts of occasional mortality events on underlying carbon storage trends (compare Fig. 1 with Supplementary Fig. 2).

Generalized extreme value and re-sampling analysis. We fitted a GEV distribution using the ExtRemes package[18] in R. It shows that the shape parameter from the distribution is significantly less than zero, indicating the data best fit a Weibull (stretched exponential) distribution[18] (−0.465; 95% CI, −0.556 to −0.371). We then fitted the three-parameter Weibull probability density function to the data and shifted this distribution to have a mean change in carbon stocks of zero, our 'null distribution'. From this distribution we re-sampled 79 values 1,000 times and calculated the mean change in carbon stocks for each run to compare with the mean from our data. The actual mean from our data was larger than any single value from our 1,000 re-samples from the null distribution.

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