

Asynchronous Saturation of the Carbon Sink in African and Amazonian tropical forests

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Abstract

Structurally intact tropical forests sequestered ~50% of global terrestrial carbon uptake over the 1990s and early 2000s, offsetting ~15% of anthropogenic CO₂ emissions¹⁻³. Climate-driven vegetation models typically predict that this tropical forest ‘carbon sink’ will continue for decades^{4,5}. However, recent inventories of intact Amazonian forests show declining carbon sequestration⁶. Here, we assess the trends in African forests and compare with Amazonia. Records from 244 multi-census plots spanning 11 countries reveal that the carbon sink in aboveground live biomass in intact African tropical forests has been stable for the three decades to 2015, at 0.66 Mg C ha⁻¹ yr⁻¹ (95% CI: 0.53-0.79). Thus, the carbon sink responses of Earth’s two largest expanses of tropical forest have diverged. As both continents show increasing tree growth (consistent with the expected net effect of rising atmospheric CO₂ and air temperature on photosynthesis and respiration⁷), the divergence arises from differences in carbon losses from tree mortality (no detectable multi-decadal trend in Africa; monotonic increase in Amazonia). Despite the past stability of the African carbon sink, our data suggest a very recent (*c.* 2010) increase in carbon losses, delayed compared to Amazonia, indicating asynchronous carbon sink saturation on the two continents. A statistical model including CO₂, temperature, drought, and forest dynamics can account for the observed trends. Extrapolating these predictor variables indicates a long-term decline in the African sink, being 18% smaller in 2030, while the Amazonian sink continues to rapidly weaken, reaching zero in the 2030s. Overall, the uptake of carbon into Earth’s intact tropical forests peaked in the 1990s. Furthermore, this tropical sink is set to end decades sooner than even the most pessimistic vegetation models predict^{4,5}. Observations indicating greater recent carbon uptake into the Northern hemisphere landmass⁸ reinforce our conclusion that the intact tropical forest carbon sink has already saturated.

Main text

Tropical forests account for one-third of Earth's terrestrial Gross Primary Productivity and half of Earth's carbon stored in terrestrial vegetation⁹. Thus, small biome-wide changes in tree growth and mortality can have global impacts, either buffering or exacerbating the increase in atmospheric CO₂. Models^{2,7,10}, ground-based observations¹¹⁻¹³, airborne atmospheric CO₂ measurements^{3,14}, inferences from remotely sensed data¹⁵, and synthetic approaches^{3,16,17} each suggest that, after accounting for land-use change, remaining structurally intact tropical forests (i.e. not impacted by logging or fire) are increasing in carbon stocks. This structurally intact tropical forest 'carbon sink' is estimated at 1.2 Pg C yr⁻¹ over 1990-2007 using inventory plot measurements¹. Yet, despite its policy relevance, changes in this key carbon sink remain highly uncertain^{18,19}.

Rising CO₂ concentrations are thought to have boosted photosynthesis more than rising air temperatures have enhanced respiration, resulting in an increasing global terrestrial carbon sink^{2,7,16,20}. Yet, for Amazonia, recent results from repeated censuses of intact forest inventory plots show a progressive two-decade decline in sink strength primarily due to an increase of carbon losses from tree mortality⁶. It is unclear if this simply reflects region-specific drought impacts^{21,22}, or potentially chronic pan-tropical impacts of either heat-related tree mortality²³ or internal forest dynamics resulting from past increases in carbon gains leaving the system²⁴. A more recent deceleration of the rate of increase in carbon gains from tree growth is also contributing to the declining sink⁶. Again, it is not known if this is a result of either pan-tropical CO₂ fertilisation saturation or rising air temperatures, or is merely a regional drought impact. To address these uncertainties, we (i) analyze an unprecedented long-term inventory dataset from Africa, (ii) pool the new African and existing Amazonian records together to investigate the putative environmental drivers of changes in the tropical forest carbon sink, and (iii) project its likely future evolution.

We collected, compiled and analysed data from structurally intact old-growth forests from the African Tropical Rainforest Observation Network²⁵ (217 plots) and other sources (27 plots) spanning the period 1968 to 2015 (Extended Data Figure 1). In each plot (mean size, 1.1 ha), all trees ≥ 100 mm in stem diameter were identified, mapped and measured on at least two occasions using standardized methods (135,625 trees monitored) and live biomass carbon stocks were estimated for each census date, with carbon gains and losses calculated for each interval (Extended Data Figure 2).

We detect no long-term trend in the per unit area African tropical forest carbon sink over three decades to 2015 (Figure 1). The aboveground live biomass sink averaged $0.66 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (95% CI: 0.53-0.79; $n=244$) and was significantly greater than zero for every year since 1990 (Figure 1). While very similar to past reports¹¹ ($0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), this first estimate of the temporal trend in Africa contrasts with the Amazonian trend⁶ (Figure 1). A linear mixed effect model shows a significant difference in the slopes of the sink trends for the two continents over the common time window (1983-2011.5; $p=0.017$). Thus, the per unit area sink strength of the two largest expanses of tropical forest on Earth have diverged.

The proximal cause of the divergent sink patterns is a significant increase in carbon losses (from tree mortality) in Amazonian forests, with no detectable trend over three decades in African forests (Figure 1). A linear mixed effects model shows a significant difference in slopes of carbon losses between the two continents over the common time window ($p=0.027$). Long-term trends in carbon gains (tree growth and newly recruited trees) are similar: we could detect no difference between the continents (Figure 1b; $p=0.348$). However, an assessment of how underlying environmental drivers affect carbon gains and losses is needed to understand the ultimate causes of the divergent sink patterns.

A linear mixed effects model of carbon gains, with censuses nested within plots, and pooling the new African and published Amazonian data, shows a significant positive relationship with CO₂, and significant negative relationships with mean annual temperature (MAT) and drought (measured as the Maximum Climatological Water Deficit, MCWD¹²; Figure 2; Extended Data Table 1). These results are consistent with a positive CO₂ fertilization effect, and negative effects of higher temperatures and drought on tree growth, consistent with temperature-dependent increases in autotrophic respiration, and temperature- and drought-dependent reductions in carbon assimilation. By contrast the equivalent model for carbon losses shows no significant relationships with CO₂, MAT or MCWD.

We further investigate the responses of carbon gains and losses (for which the above analysis has no explanatory power) by expanding our potential explanatory variables to include the environmental conditions during the census interval (CO₂, MAT and MCWD), the change in these conditions (CO₂-change, MAT-change, MCWD-change, see Extended Data Figure 3 for calculation details), and two forest attributes that may influence their response to the same environmental change: plot mean wood density (which in old-growth forests correlates with resource availability^{26,27}), and the plot carbon residence time (which measures how long fixed carbon remains in the system, hence dictates when past increases in carbon gains leave the system as elevated carbon losses²⁸).

The minimum adequate carbon gain model has a positive relationship with CO₂-change, and negative relationships with MAT, MAT-change, MCWD, and wood density (Table 2). The retention of both MAT and MAT-change suggests that higher temperatures correspond to lower tree growth, and that trees only partially acclimate to recently rising temperatures, which further reduces growth, consistent with warming experiments²⁹ and observations³⁰. Given that lower carbon gains are related to higher wood density (Extended Data Figure 4) which shows no temporal trend (Extended Data Figure 5)

together suggests that old-growth forests with denser-wooded tree communities typically have fewer available resources, consistent with expectations^{24,26}.

The minimum adequate carbon gain model using our expanded explanatory variables also highlights continental differences. In Africa, from 2000 to 2015, carbon gains increased by 3.64% from CO₂-change, but temperature rises led to a decline in gains of 0.24% (MAT and MAT-change together), and increasing droughts further depleted gains by 0.51% (Table 2). For Amazonia, from 2000 to 2015, gains increased by 3.68% due to CO₂-change (as in Africa), but temperature increases reduced gains by 1.44% (six times the impact in Africa) while increasing droughts—and these forests' greater sensitivity to drought—further reduced gains by 2.47% (five times the impact in Africa; Table 2). Thus, the recent deceleration of carbon gains increase in Amazonia⁶ is a response to drought and temperature and not due to unexpected saturation of CO₂ fertilisation. Overall, the larger increase in gains in Africa relative to Amazonia appear to be driven by slower warming, fewer droughts, lower forest sensitivity to droughts, and overall lower temperatures (African forests are on average 1.1°C cooler than Amazonian forests, as they typically grow at ~200 m higher elevation).

The minimum adequate carbon loss model using our expanded explanatory variables shows higher losses with CO₂-change and MAT-change, and lower losses with MCWD and the carbon residence time (CRT; Table 2). Changes in carbon losses appear to be largely a function of carbon gains. Firstly, the greater losses in forests with shorter CRT conform to a 'high-gain high-loss' forest dynamics pattern²⁴. Secondly, wetter plots have a longer growing season and so have higher gains and correspondingly higher losses, explaining the negative relationship with MCWD. Finally, as CO₂ results in additional carbon gains, after some time these additional past gains leave the system resulting in greater carbon losses, explaining the positive relationship with CO₂-change. In addition to these relationships with carbon gains, the inclusion of MAT-change ($p < 0.001$) indicates heat- or Vapour

Pressure Deficit-induced tree mortality²³. Overall, our results imply that chronic long-term environmental change factors, temperature and CO₂, rather than simply the direct effects of drought, underlie longer-term trends in tropical forest tree mortality.

The minimum adequate carbon loss model using our expanded explanatory variables replicates the divergent continental trends (Figure 3). The higher loss rates in Amazonia reflect the shorter CRT of Amazonian (56 yrs, 95% CI, 54-59) compared to African forests (69 yrs, 95% CI, 66-72), while the greater increase in loss rates in Amazonia results from faster warming and a shortening of CRT, which has been stable in African forests (Extended Data Figure 5). Furthermore, given that losses appear to lag behind gains they should relate to CRT. This is what we find: the longer the CRT the smaller the increase in carbon losses, with no increase in losses for plots with CRT ≥ 77 years (Extended Data Figure 6). Consequently, due to the typically longer residence times of African forests, increasing losses in Africa ought to appear 10-15 years after the increase in Amazon losses began (*c.*1995). Strikingly, in Africa the most recently monitored plots suggest that losses began increasing from *c.*2010 (Extended Data Figure 7), and plots with shorter CRT are driving the increase (Extended Data Figure 8).

Finally, our carbon gain and loss models can be used to estimate the future size of the per unit area intact forest carbon sink. Extrapolations of the changes in the predictor variables from 1983-2015 forward to 2040 (Extended Data Figure 5) show declines in the sink on both continents. By 2030 the carbon sink in aboveground live biomass in intact African tropical forest is predicted to decline from its 2010-15 mean by 18% (1 σ range, 6-39%), to 0.54 Mg C ha⁻¹ yr⁻¹ (1 σ range, 0.39-0.65). The Amazon sink is predicted to reach zero in 2034 (1 σ range, 2023-2055; Figure 3). Thus, the carbon sink strength of the world's two most extensive tropical forests have now saturated, albeit asynchronously.

Together, our measurements and analyses signify that Earth recently passed the point of peak carbon sequestration into intact tropical forests (Table 1). The continental sink in Amazonia peaked in the 1990s and has declined since, driven by both reduced sink strength and forest area (Table 1; see Extended Data Table 2 for forest area). The African sink also peaked in the 1990s. In the 2000-10 decade the per ha sink peaked but was more than countered by continued forest area decline (Table 1). Including the modest uptake in the much smaller area of Asian tropical forest indicates that total pan-tropical carbon uptake peaked in the 1990s (Table 1). Given that the global terrestrial carbon sink has continued to increase, our results strongly imply that the extra-tropical terrestrial carbon sink has increased over the past two decades. Independent inter-hemispheric analyses of atmospheric CO₂ show Northern hemisphere forests have increased uptake over this time period⁸.

In summary, while intact tropical forests remain key centres of biodiversity and major stores of carbon, our results show that their ability to sequester additional carbon is waning. Although tropical forests are more immediately threatened by deforestation and degradation, our analyses show that they are impacted by climate change. Given that no climate-driven vegetation model shows that peak net carbon uptake into intact tropical forests has already been passed^{4,5}, our analyses suggest that climate change impacts in the tropics may become more severe than predicted. Our findings also have political implications: as tropical forests are likely to sequester less carbon in the future than Earth System Models predict, an earlier date to reach net zero anthropogenic greenhouse gas emissions will be required to meet any given commitment to limit the global heating of Earth.

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Author Contributions

S.L.L. conceived the study and the AfriTRON forest plot re-census program. W.H., S.L.L., and O.L.P. developed the study. All authors, except M.S., R.B., E.G., A.L., G.L.-G., A.E.-M., A.K. and G.P., contributed data. W.H., M.S., S.L.L., O.L.P., R.B., A.L. G.L.-G., A.E.-M., A.K. and G.P. contributed analysis tools. W.H. and S.L.L. analysed the data. S.L.L. and W.H. wrote the paper, with all co-authors contributing to the manuscript.

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Competing interests

The authors declare no competing financial interests.

Data and code availability

Source data and R-code to generate figures and tables are available from: <https://figshare.com/s/60f48673202283421f43>.

Figures and Tables

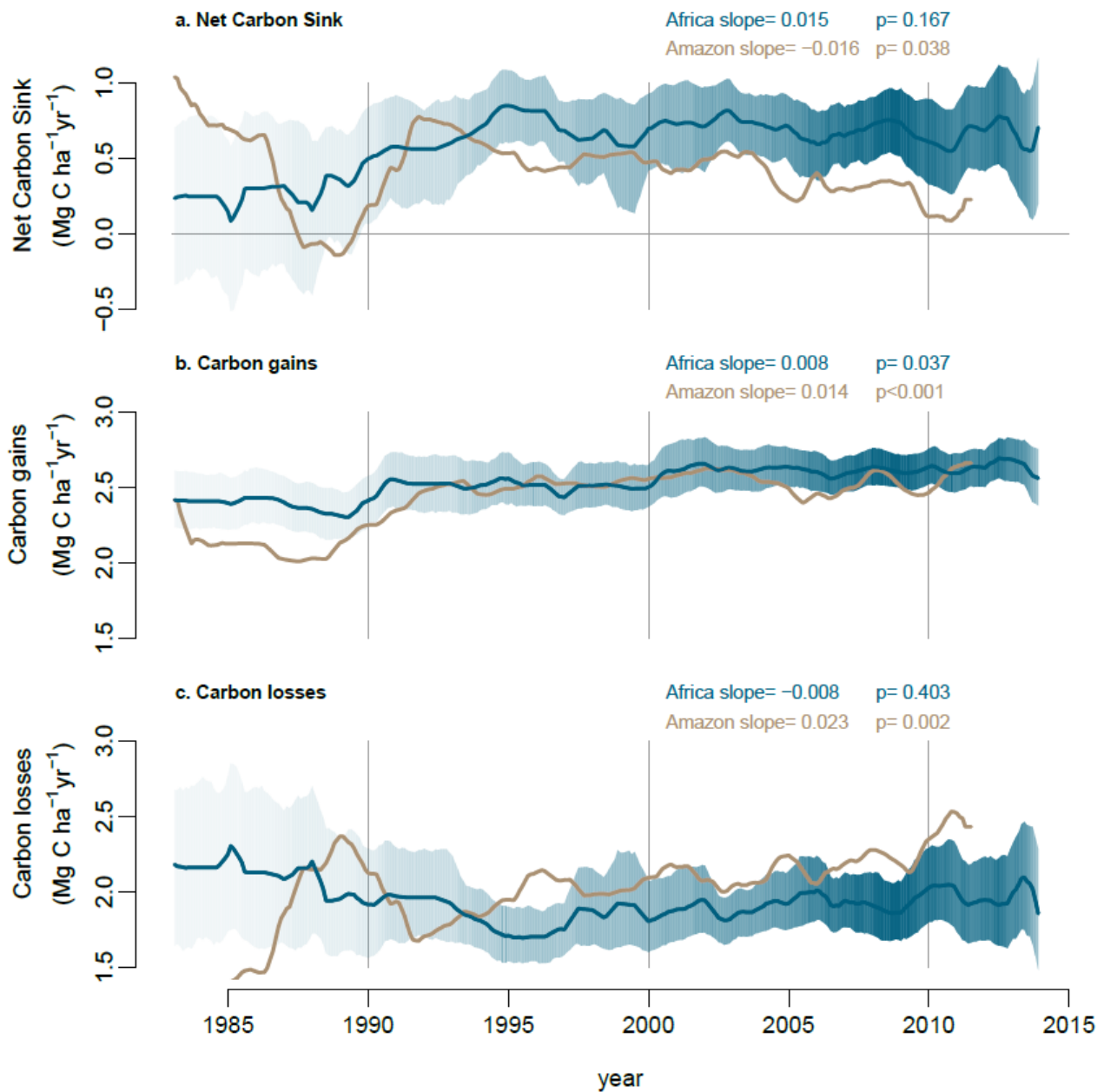


Figure 1. Long-term carbon dynamics of structurally intact tropical forests in Africa (blue) and Amazonia (brown). Trends in net aboveground live biomass carbon sink (a), carbon gains to the system from wood production (b), and carbon losses from the system from tree mortality (c), measured in 244 African inventory plots (blue lines) and contrasting published⁶ Amazonian inventory data (brown lines; 321 plots). Shading corresponds to the 95% CI, with less transparent shading indicating a greater number of plots monitored in that year (most transparent: minimum 25 plots monitored). Printed slopes and p-values are from linear mixed effects models.

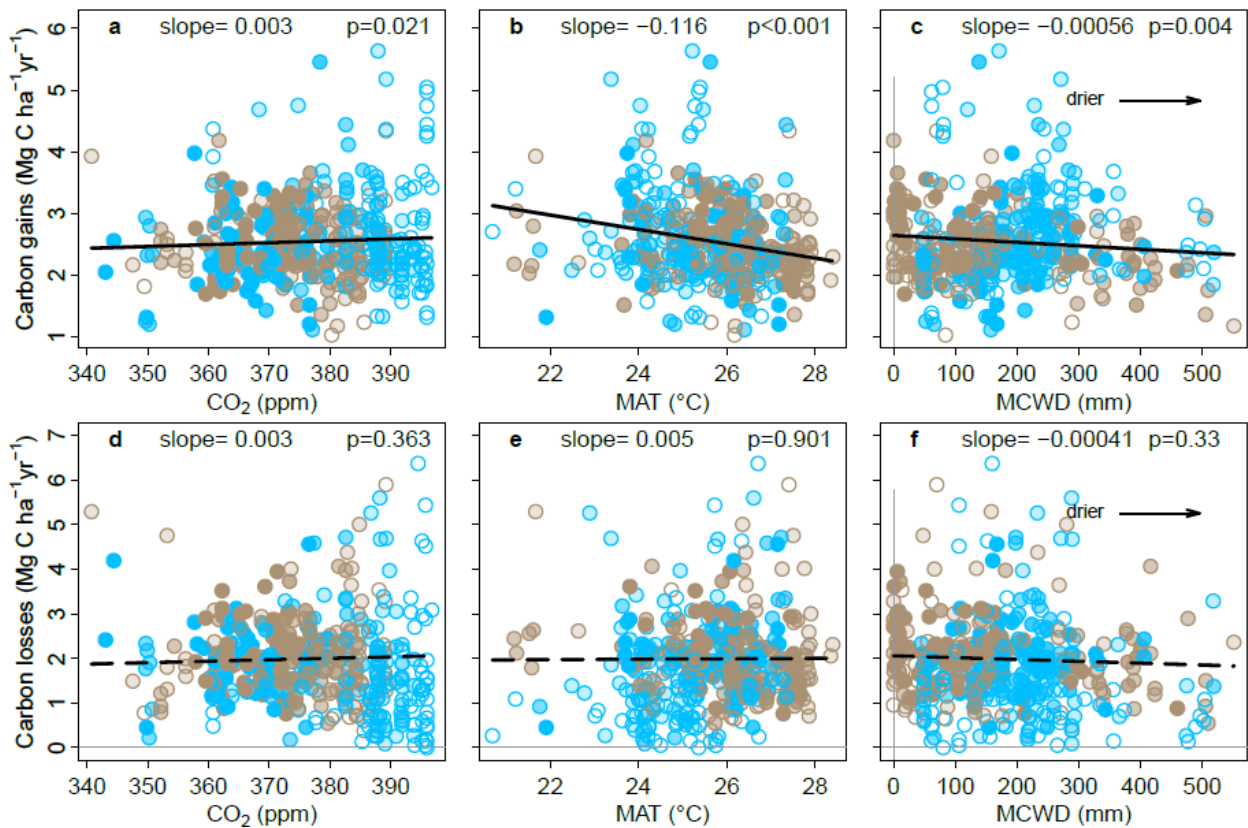


Figure 2. Potential environmental drivers of carbon gains and losses in structurally intact old-growth African and Amazonian tropical forests. The aboveground carbon gains, from woody productivity (a-c), and aboveground carbon losses, from mortality (d-f), are plotted as time-weighted plot-level mean values against the corresponding values of atmospheric carbon dioxide concentration (CO₂), mean annual air temperature (MAT) and drought (as Maximum Climatological Water Deficit, MCWD), for African (blue) and Amazonian (brown) inventory plots. Linear mixed effect models were performed with census intervals (n=1566) nested within plots (n=565), using an empirically derived weighting based on interval length and plot area (see methods); solid lines show significant regression lines for the complete dataset and non-significant regressions are shown as dashed lines. Transparency of the inner part of each data point represents total monitoring length, with empty circles corresponding to plots monitored for ≤ 5 years and solid dots for plots monitored for >20 years. Carbon loss data are presented untransformed for clarity; linear mixed effects models on data transformed to fit normality assumptions do not change the significance of the results (see Extended Data Table 1).

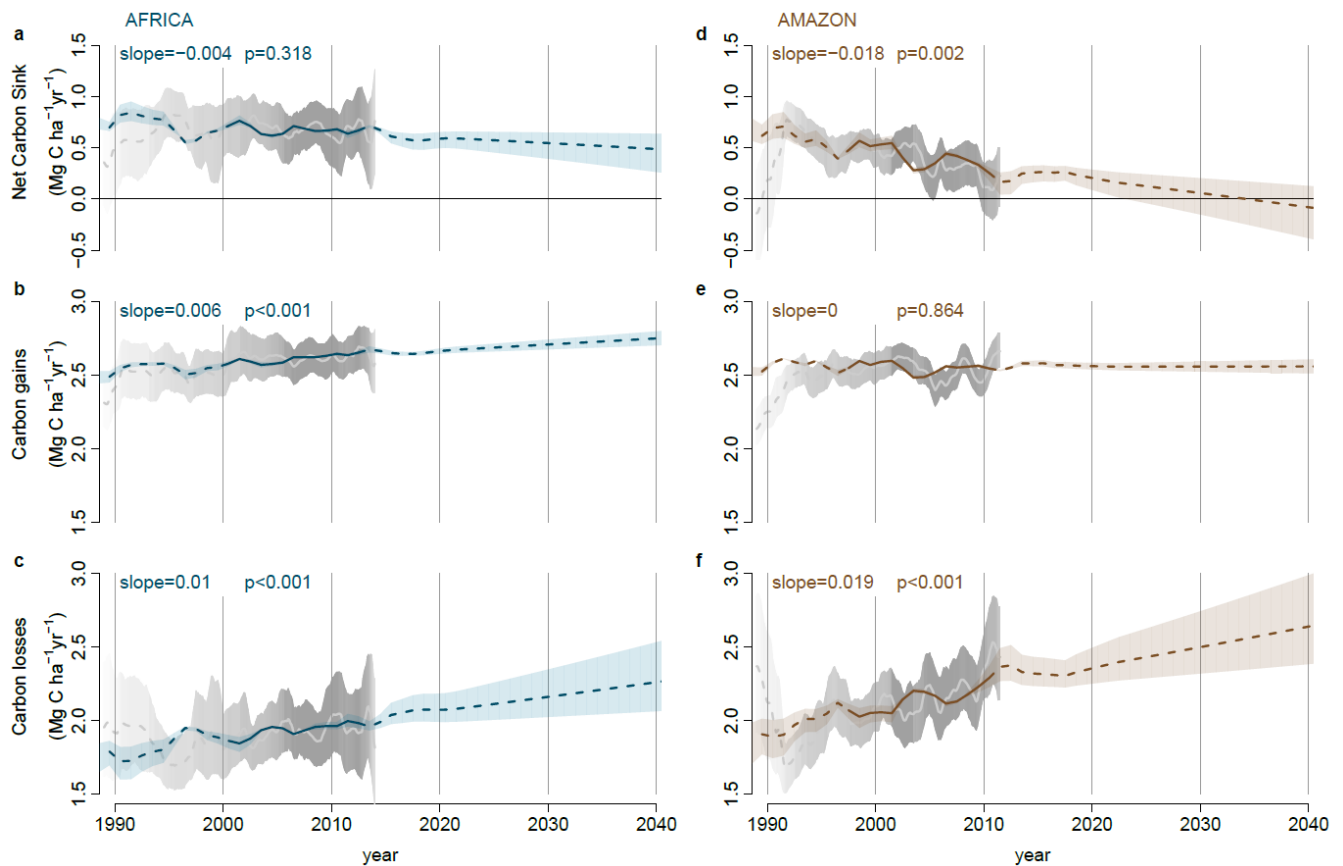


Figure 3. Modelled past and future carbon dynamics of structurally intact tropical forests in Africa and Amazonia. Predictions of net aboveground live biomass carbon sink (a,d), carbon gains (b,e), and carbon losses (c,f), for African (left panels) and Amazonian (right panels) plot inventory networks, based on CO₂-change, Mean Annual Temperature, Mean Annual Temperature-change, drought (as Maximum Climatological Water Deficit), plot wood density and plot carbon residence time. Model predictions are in blue (Africa) and brown (Amazon), with solid lines spanning the window when $\geq 75\%$ of plots were monitored to show model consistency with the observed trends, and shading showing $\pm 1\sigma$ uncertainty. Light grey lines and grey shading are from Fig.1, the mean observed and 95% CI of the observed trends.

Table 1. Carbon sink in intact forests in Africa, Amazonia and the pan-tropics: 1980-2015 and predictions to 2040 (in italics). Mean values in bold; in brackets 95% bootstrapped confidence intervals for the monitored period (1980-2015), and 2σ for the predictions (2010-2040).

Period	<i>n</i>		Per unit area aboveground C sink		Total Continental C sink *		
	(plots)		(Mg C ha ⁻¹ yr ⁻¹)		(Pg C yr ⁻¹)		
	Af.	Am.	Africa	Amazon	Africa	Amazon	Pan-tropics †
1980-1990	45	73	0.33 (0.06-0.63)	0.35 (0.06-0.59)	0.28 (0.05-0.53)	0.49 (0.08-0.82)	0.87 (0.17-1.53)
1990-2000	96	172	0.67 (0.43-0.89)	0.53 (0.42-0.65)	0.50 (0.32-0.66)	0.68 (0.54-0.83)	1.26 (0.88-1.64)
2000-2010	194	291	0.70 (0.55-0.84)	0.38 (0.26-0.48)	0.46 (0.37-0.56)	0.45 (0.31-0.57)	0.99 (0.70-1.25)
2010-2015	184	172	0.66 (0.40-0.91)	0.24 (0.00-0.47)	0.40 (0.24-0.56)	0.27 (0.00-0.52)	0.73 (0.26-1.18)
2010-2020 ‡	-	-	0.63 (0.49-0.69)	0.23 (0.13-0.30)	0.37 (0.29-0.41)	0.25 (0.14-0.33)	0.68 (0.45-0.83)
2020-2030 ‡	-	-	0.57 (0.28-0.70)	0.12 (-0.05-0.24)	0.30 (0.15-0.37)	0.12 (-0.05-0.24)	0.46 (0.11-0.68)
2030-2040 ‡	-	-	0.51 (0.06-0.72)	-0.02 (-0.28-0.16)	0.24 (0.03-0.34)	-0.02 (-0.26-0.15)	0.25 (-0.22-0.53)

* Total Continental C sink is the per unit area aboveground C sink multiplied by intact forest area. Forest area is from ref.¹ for 1990, 2000 and 2010 (i.e. the total forest area minus forest regrowth); to estimate intact forest area for 1980, 2015, 2020, 2030 and 2040 we fitted exponential models for each continent using the 1990-2010 data. Total Continental C sink includes estimates of trees <100 mm DBH, lianas and roots, following ref.¹¹ for Africa and ref.⁶ for Amazonia.

† Pan-tropical total carbon sink is the sum of African, Amazonian and Southeast Asian total continental carbon sink values. Southeast Asian values were estimated from forest area from ref.¹ and published per unit area carbon sink data¹³ (n=49 plots) for 1990-2015, with 1980-1990 assumed to be the same as 1990-2000 due very low sample sizes. The sink in Southeast Asia has been a modest and declining contribution to the pan-tropical sink, at 0.12, 0.09 and 0.08 Pg C yr⁻¹ in the 1980s, 1990s, and 2000s.

‡ Per unit area total C sink for 2010-2020, 2020-2030 and 2030-2040 was predicted using parameters from Table 2, except for the sink in Asia we assumed the parameters as for Africa, as Asian forest median CRT is 61 years, close to African median, 63 years.

Table 2. Minimum adequate models to predict carbon gains and losses in African and Amazonian tropical forests. Where continental values differ, those for Africa are reported first, followed by Amazonian values.

Carbon gains, Mg C ha ⁻¹ yr ⁻¹					
Predictor variable	Parameter value	Standard Error	t-value	p-value	2000-2015 change in gains (%) *
(Intercept)	5.400 5.530	0.592 0.599	9.121 9.236	<0.001 <0.001	-
CO ₂ -change (ppm yr ⁻¹)	0.234	0.096	2.429	0.015	3.64% 3.68%
MAT (°C)	-0.087	0.025	-3.463	0.001	-0.76% -1.14%
MAT-change (°C yr ⁻¹)	-0.766	0.189	-4.051	<0.001	0.52% -0.3%
MCWD (mm x1000)	-0.411 -1.381	0.376 0.239	-1.091 -5.787	0.275 <0.001	-0.51% -2.47%
Wood Density (g cm ⁻³)	-1.350	0.527	-2.561	0.011	0.05% 0.00%
Carbon losses, Mg C ha ⁻¹ yr ⁻¹ †					
Predictor variable	Parameter value	Standard Error	t-value	p-value	2000-2015 change in losses (%) *
(Intercept)	1.213	0.087	13.931	<0.001	-
CO ₂ -change (ppm yr ⁻¹)	0.125	0.059	2.135	0.033	13.29% 11.95%
MAT-change (°C yr ⁻¹)	0.478	0.130	3.673	<0.001	-1.73% 0.89%
MCWD (mm x1000)	-0.218	0.107	-2.042	0.041	-1.33% -1.74%
CRT (yr)	-0.003	0.001	-5.913	<0.001	-0.68% 1.14%

* The 2000-2015 change in gains/losses for each predictor variable was estimated allowing only the focal predictor to vary; this change was then expressed as a percentage of the annual gains/losses in the year 2000 allowing all predictors to vary.

† carbon loss values were normalized via power-law transformation, $\lambda = 0.361$.

References

- 1 Pan, Y. *et al.* A Large and Persistent Carbon Sink in the World's Forests. *Science* **333**, 988-993, doi:10.1126/science.1201609 (2011).
- 2 Sitch, S. *et al.* Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* **12**, 653-679, doi:10.5194/bg-12-653-2015 (2015).
- 3 Gaubert, B. *et al.* Global atmospheric CO₂ inverse models converging on neutral tropical land exchange, but disagreeing on fossil fuel and atmospheric growth rate. *Biogeosciences* **16**, 117-134, doi:10.5194/bg-16-117-2019 (2019).
- 4 Huntingford, C. *et al.* Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nature Geoscience* **6**, 268-273, doi:10.1038/ngeo1741 (2013).
- 5 Mercado, L. M. *et al.* Large sensitivity in land carbon storage due to geographical and temporal variation in the thermal response of photosynthetic capacity. *New Phytologist* **218**, 1462-1477, doi:doi:10.1111/nph.15100 (2018).
- 6 Brienen, R. J. W. *et al.* Long-term decline of the Amazon carbon sink. *Nature* **519**, 344-348, doi:10.1038/nature14283 (2015).
- 7 Piao, S. *et al.* Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO₂ trends. *Global Change Biology* **19**, 2117-2132, doi:10.1111/gcb.12187 (2013).
- 8 Ciais, P. *et al.* Five decades of northern land carbon uptake revealed by the interhemispheric CO₂ gradient. *Nature*, doi:10.1038/s41586-019-1078-6 (2019).
- 9 Lewis, S. L., Edwards, D. P. & Galbraith, D. Increasing human dominance of tropical forests. *Science* **349**, 827-832, doi:10.1126/science.aaa9932 (2015).
- 10 Pugh, T. A. M. *et al.* Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences* **116**, 4382-4387, doi:10.1073/pnas.1810512116 (2019).

- 489 11 Lewis, S. L. *et al.* Increasing carbon storage in intact African tropical forests. *Nature* **457**,
490 1003-1006, doi:10.1038/nature07771 (2009).
- 491 12 Phillips, O. L. *et al.* Drought sensitivity of the Amazon rainforest. *Science* **323**, 1344-1347,
492 doi:10.1126/science.1164033 (2009).
- 493 13 Qie, L. *et al.* Long-term carbon sink in Borneo's forests halted by drought and vulnerable to
494 edge effects. *Nature Communications* **8**, 1966, doi:10.1038/s41467-017-01997-0 (2017).
- 495 14 Gatti, L. V. *et al.* Drought sensitivity of Amazonian carbon balance revealed by atmospheric
496 measurements. *Nature* **506**, 76-80, doi:10.1038/nature12957 (2014).
- 497 15 Baccini, A. *et al.* Tropical forests are a net carbon source based on aboveground measurements
498 of gain and loss. *Science* **358**, 230-234, doi:10.1126/science.aam5962 (2017).
- 499 16 Schimel, D., Stephens, B. B. & Fisher, J. B. Effect of increasing CO₂ on the terrestrial carbon
500 cycle. *Proceedings of the National Academy of Sciences* **112**, 436-441,
501 doi:10.1073/pnas.1407302112 (2015).
- 502 17 Keenan, T. F. *et al.* Recent pause in the growth rate of atmospheric CO₂ due to enhanced
503 terrestrial carbon uptake. *Nature Communications* **7**, 13428, doi:10.1038/ncomms13428
504 (2016).
- 505 18 Booth, B. B. B. *et al.* High sensitivity of future global warming to land carbon cycle processes.
506 *Environmental Research Letters* **7**, 024002 (2012).
- 507 19 Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S. & Fisher, R. A. Temperature
508 acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate
509 feedback. *Geophysical Research Letters* **42**, 8624-8631, doi:doi:10.1002/2015GL065934
510 (2015).
- 511 20 Le Quéré, C. *et al.* Global Carbon Budget 2018. *Earth Syst. Sci. Data* **10**, 2141-2194,
512 doi:10.5194/essd-10-2141-2018 (2018).

- 513 21 Lewis, S. L., Brando, P. M., Phillips, O. L., van der Heijden, G. M. F. & Nepstad, D. The 2010
514 Amazon drought. *Science* **331**, 554 (2011).
- 515 22 Feldpausch, T. R. *et al.* Amazon forest response to repeated droughts. *Global Biogeochemical*
516 *Cycles* **30**, 964-982, doi:doi:10.1002/2015GB005133 (2016).
- 517 23 Lewis, S. L. *et al.* Concerted changes in tropical forest structure and dynamics: evidence from
518 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London*
519 *Series B-Biological Sciences* **359**, 421-436 (2004).
- 520 24 McDowell, N. *et al.* Drivers and mechanisms of tree mortality in moist tropical forests. *New*
521 *Phytologist* **219**, 851-869, doi:doi:10.1111/nph.15027 (2018).
- 522 25 Lewis, S. L. *et al.* Above-ground biomass and structure of 260 African tropical forests.
523 *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120295-
524 20120295, doi:10.1098/rstb.2012.0295 (2013).
- 525 26 Quesada, C. A. *et al.* Basin-wide variations in Amazon forest structure and function are
526 mediated by both soils and climate. *Biogeosciences* **9**, 2203-2246, doi:10.5194/bg-9-2203-
527 2012 (2012).
- 528 27 Malhi, Y. *et al.* The above-ground coarse wood productivity of 104 Neotropical forest plots.
529 *Global Change Biology* **10**, 563-591 (2004).
- 530 28 Galbraith, D. *et al.* Residence times of woody biomass in tropical forests. *Plant Ecology &*
531 *Diversity* **6**, 139-157, doi:10.1080/17550874.2013.770578 (2013).
- 532 29 Reich, P. B. *et al.* Boreal and temperate trees show strong acclimation of respiration to
533 warming. *Nature* **531**, 633-636, doi:10.1038/nature17142 (2016).
- 534 30 Anderegg, W. R. L. *et al.* Tropical nighttime warming as a dominant driver of variability in the
535 terrestrial carbon sink. *Proceedings of the National Academy of Sciences* **112**, 15591-15596,
536 doi:10.1073/pnas.1521479112 (2015).

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Methods

Plot selection

Closed canopy (i.e. not woody savanna) old-growth mixed-age forest inventory plots were selected using commonly used criteria^{6,11,25}: free of fire and industrial logging; all trees with diameter at reference height ≥ 100 mm measured at least twice; ≥ 0.2 ha area; < 1500 m.a.s.l. altitude; MAT $\geq 20.0^{\circ}\text{C}$ ³¹; annual precipitation ≥ 1000 mm³¹; located ≥ 50 m from anthropogenic forest edges. Of the 244 plots included in the study, 217 contribute to the African Tropical Rainforest Observatory Network (AfriTRON; www.afritron.org), with data curated at www.ForestPlots.net. These include plots from Sierra Leone, Liberia, Ghana, Nigeria, Cameroon, Gabon, Republic of Congo, Democratic Republic of Congo (DRC), Uganda and Tanzania³² (Extended Data Figure 1). Fifteen plots are part of the TEAM network, from Cameroon, Republic of Congo, Tanzania, and Uganda³³⁻³⁶. Nine plots contribute to the ForestGEO network, from Cameroon and DRC³⁷ (9 plots from DRC, codes SNG, contribute to both AfriTRON and ForestGEO networks, included above in the AfriTRON total). Finally, three plots from Central African Republic are part of the CIRAD network³⁸. The large majority of plots are sited in terra firme forests and have mixed species composition, although four are in seasonally flooded forest and 14 plots are in *Gilbertiodendron dewevrei* monodominant forest, a locally common forest type in Africa (Supplementary Table 1). The 244 plots have a mean size of 1.1 ha (median, 1 ha), with a total plot area of 277.9 ha. The dataset comprises 391,968 diameter measurements on 135,625 stems, of which 89.9% were identified to species, 97.5% to genus and 97.8% to family. Mean total monitoring period is 11.8 years, mean census length 5.7 years, with a total of 3,214 ha years of monitoring. The 321 Amazon plots are published and were selected using the same criteria⁶, except in the African selection criteria we specified a minimum anthropogenic edge distance and added a minimum temperature threshold.

Plot inventory and Tree Biomass Carbon Estimation

Tree-level aboveground biomass carbon is estimated using an allometric equation with parameters for tree diameter, tree height and wood mass density. The estimated aboveground biomass of a plot is the sum of the estimated biomass of all live trees at that census date.

Tree Diameter: In all plots, all woody stems with ≥ 100 mm diameter at 1.3 m from the base of the stem ('diameter at breast height', DBH), or 0.5 m above deformities or buttresses, were measured, mapped and identified using standard forest inventory methods³⁹. The height of the point of measurement (POM) was marked on the trees and recorded, so that the same POM is used at the subsequent forest census. For stems developing deformities or buttresses over time that could potentially disturb the initial POM, the POM was raised approximately 500 mm above the deformity. Estimates of the diameter growth of trees with changed POM used the ratio of new and old POMs, to create a single trajectory of growth from the series of diameters at two POM heights^{6,11,40}. We used standardized protocols to assess typographical errors and potentially erroneous diameter values (e.g. trees shrinking by >5 mm), missing values, failures to find the original POM, and other issues. Where necessary we estimated the likely value via interpolation or extrapolation from other measurements of that tree, or when this was not possible we used the median growth rate of trees in the same plot, census and size-class, defined as DBH = 100-199 mm, or 200-399 mm, or >400 mm^{32,41}. We interpolate measurements for 1.3% of diameters, extrapolate 0.9%, and use median growth rates for 1.5%.

Tree height: Height of individuals from ground to the top leaf, hereafter H_t , was measured in 204 plots, using a laser hypsometer (Nikon forestry Pro) from directly below the crown (most plots), a laser or ultrasonic distance device with an electronic tilt sensor, a manual clinometer, or by direct measurement, i.e. tree climbing. Only trees where the top was visible were selected⁴². In most plots, tree selection was similar: the 10 largest trees were measured, together with 10 randomly selected trees

per diameter from five classes: 100-199 mm, 200-299 mm, 300-399 mm, 400-499 mm, and 500+ mm trees, following standard protocols⁴². We use these data and the local.heights function in R package BiomasaFP⁴³ to fit 3-parameter Weibull relationships:

$$H_t = a \times \left(1 - e^{\left(-b \times \left(\frac{DBH}{10}\right)^c\right)}\right) \text{ (equation 1).}$$

We chose the Weibull model as it is known to be robust when a large number of measurements are available^{42,44}. We parameterize this H_t -DBH relationship for terra firme forest in three biogeographical regions, parameters in parentheses: (i) West Africa ($a=56.0$; $b=0.0401$; $c=0.744$); (ii) Lower Guinea and Western Congo Basin ($a=47.6$; $b=0.0536$; $c=0.755$); (iii) Eastern Congo Basin and East Africa ($a=50.8$; $b=0.0499$; $c=0.706$); and finally (iv) for seasonally flooded forest from Lower Guinea and Western Congo Basin ($a=38.2$; $b=0.0605$; $c=0.760$; there were no seasonally flooded forest plots in the other regions). The parameters were used to estimate H_t from DBH for all tree DBH measurements for input into the allometric equation.

Wood Density: Dry wood density (ρ) measurements were compiled for 730 African species from published sources and stored in www.ForestPlots.net; most were sourced from the Global Wood Density Database on the Dryad digital repository (www.datadryad.org)^{45,46}. Each individual in the tree inventory database was matched to a species-specific mean wood density value. Species in both the tree inventory and wood density databases were standardized for orthography and synonymy using the African Flowering Plants Database (www.ville-ge.ch/cjb/bd/africa/) to maximize matches¹¹. For incompletely identified individuals or for individuals belonging to species not in the ρ database, we used the mean ρ value for the next higher known taxonomic category (genus or family, as appropriate). For unidentified individuals, we used the mean wood density value of all individual trees in the plot^{11,32}.

612 *Allometric equation:* For each tree we use a published allometric equation⁴⁷ to estimate aboveground
 613 biomass. We then convert this to carbon, assuming that aboveground carbon (AGC) is 45.6% of
 614 aboveground biomass⁴⁸. Thus: $AGC = 0.456 \times ((0.0673 \times (\rho \times (\frac{DBH}{10})^2 \times H_t)^{0.976})/1000)$
 615 (equation 2), with DBH in mm, dry wood density, ρ , in g cm⁻³, and total tree height, H_t , in m (ref.⁴⁷).

617 **Aboveground biomass carbon, carbon gains and carbon losses**

618 *Aboveground Carbon* (AGC, in Mg C ha⁻¹) in living biomass for each plot at each census date was
 619 estimated as the sum of the AGC of each living stem, then divided by plot area (in hectares).

621 *Carbon Gain* is the sum of the aboveground live biomass carbon additions from the growth of
 622 surviving stems and the addition of newly recruited stems, using standard methods⁶. For each stem
 623 that survived a census interval, carbon additions from its growth (Mg C ha⁻¹ yr⁻¹) were calculated as
 624 the difference between its AGC at the end census of the interval and its AGC at the beginning census
 625 of the interval. For each stem that recruited during the census interval (i.e. reaching DBH \geq 100 mm),
 626 carbon additions were calculated in the same way, assuming DBH=0 mm at the start of the interval⁴⁰.
 627 The carbon additions in an interval, from surviving and newly recruited stems, were summed, then
 628 divided by the census interval length (in years), and scaled by plot area (in hectares)⁴⁰. As carbon gains
 629 are affected by a census interval bias, with the underestimate increasing with census length, we
 630 corrected this bias by accounting for (i) the carbon additions from trees that recruited and then died
 631 within the same interval (unobserved recruitment), and (ii) the carbon additions from trees that grew
 632 before they died within an interval (unobserved growth)⁴⁰. These typically add <3% to plot-level
 633 carbon gains.

635 *Carbon Loss* (in Mg C ha⁻¹ yr⁻¹) is estimated, using standard methods⁶, as the sum of aboveground
 636 biomass carbon from all stems that died during a census interval, divided by the census length (in

years) and scaled by plot area (in hectares). Carbon loss is also affected by the same census interval bias, hence we corrected this bias by accounting for (i) the additional carbon losses from the trees that were recruited and then died within the same interval, and (ii) the additional carbon losses resulting from the growth of the trees that died in the interval^{6,13,43}.

Net Carbon Sink (in Mg C ha⁻¹ yr⁻¹) is estimated as carbon gains minus carbon losses. All calculations were performed using the R statistical platform, version 3.2.1⁴⁹ using the BiomasaFP R package v0.2.1⁴³.

Long-term gain, loss and net carbon sink trends estimation

The estimated mean carbon gains, carbon losses and the net carbon sink of the African plots from 1983-2014, the solid lines in Figure 1, were calculated following ref.⁶ to allow direct comparison with published Amazonian results. First, each census interval value was interpolated for each 0.1-yr period within the census interval. Then, for each 0.1-yr period between 1983 and 2014, we calculate a weighted mean of all plots monitored at that time, using the square root of plot area as a weighting factor⁶. Finally, confidence intervals for each 0.1-yr period are bootstrapped. The means and confidence intervals shown in Extended Data Figure 7 and Extended Data Figure 8 were also calculated using this method.

Trends in carbon gains, losses and the net carbon sink over time were assessed using linear mixed effects models (lmer function in R, lme4 package⁵⁰), providing the linear slopes reported in Figure 1. These models regress the mid-point of each census interval against the value of the response variable for that census interval. Plot identity was included as a random effect, i.e. assuming that the intercept can vary randomly among plots. Observations were weighted by plot size and census interval length. Weightings were derived empirically, by assuming *a priori* that there is no significant relation between

the net carbon sink and census interval length or plot size¹¹. The following weighting removes all pattern in the residuals:

$$Weight = \sqrt[3]{length_{int}} + \sqrt[4]{plotsize} - 1 \text{ (equation 3),}$$

where $length_{int}$ is the length of the census interval, in years. Significance was assessed by regressing the residuals of the net carbon sink model against the weights ($p=0.702$).

Differences in long-term slopes between the two continents for carbon gains, carbon losses and net carbon sink were assessed using linear mixed effects models, as described above, but performed on the combined African and Amazonian datasets and limited to their common time window, 1983 to 2011.5. These models had an interaction term between census interval date and continent, where a significant interaction would indicate that the slopes differ between continents. The statistical significance of continental differences in slope were assessed using the F-statistic (Anova function in R, car package⁵¹).

Continental and pan-tropical carbon sink estimates

For Africa, Amazonia and Southeast Asia, we calculate the continental-scale total carbon sink ($Pg\ C\ yr^{-1}$) for each decade between 1980 and 2010 and for 2010-2015 (Table 1). We do this by multiplying the per unit area total net carbon sink (in $Mg\ C\ ha^{-1}\ yr^{-1}$; using all plots monitored in each of the time intervals), by the area of intact forest on each continent at that time interval (in ha).

For each time period we calculate the per unit area *aboveground* net carbon sink in living trees with $DBH \geq 100\ mm$ (expressed in $Mg\ C\ ha^{-1}\ yr^{-1}$) as the mean of all plot-level values, using plots for which census dates overlap the time window, with plots weighted by the square root of plot area (as for the solid lines in Figure 1). For plots with more than one census interval within the target time window, the time-weighted average of the intervals was used. For Africa we use the per unit area net carbon

sink values presented in this paper. For Amazonia, we use data presented in this paper and previously published in ref.⁶. For Southeast Asia, we use inventory data collected using similar standardized methods, for 49 plots in ref.¹³. However there is a lack of Asian data covering 1980-1990, so we assume that the per unit area net carbon sink for this decade is the same as for 1990-2000. We then calculate the per unit area *total* carbon sink (in Mg C ha⁻¹ yr⁻¹) for each period, as the sum of (i) the per unit area *aboveground* carbon sink from large living trees and lianas with DBH \geq 100 mm; (ii) the per unit area *aboveground* carbon sink from living trees and lianas with DBH<100 mm (5.19%, 9.40% and 5.46% of carbon of large living trees in Africa, Amazonia and Southeast Asia respectively⁵²); and (iii) the per unit area *belowground* carbon sink in live biomass, i.e. roots (assuming belowground carbon is 25%, 37% and 17% of aboveground carbon of large living trees in Africa¹¹, Amazonia⁶ and Southeast Asia⁵³ respectively).

For comparability with previous continental-sink results, we used continental values of intact forest area for 1990, 2000 and 2010 as published in ref.¹, *i.e.* total forest area minus forest regrowth. We used the 1990-2010 data to fit an exponential model for each continent and used this model to estimate intact forest area for 1980 and 2015 (Extended Data Table 2). The continent-level total carbon sink (Pg C ha⁻¹ yr⁻¹) for each period is the total per unit area total carbon sink (in Mg C ha⁻¹ yr⁻¹) scaled by the area of remaining intact tropical forest (in ha).

Predictor variables

We examined potential predictor variables for each census interval of each plot that may explain the long-term trends in carbon gains and carbon losses. First, the environmental conditions during the census interval; second the rate of change of these parameters; and third forest attributes that may affect how different forests respond to the same environmental change. The predictor variable estimates for each census need to avoid bias due to seasonal variation, for example the intra-annual

variability in atmospheric CO₂ concentration. We therefore applied the following procedure to avoid seasonal variability impacts on long-term trends: (i) the length of each focal census interval was rounded to the nearest complete year (e.g. a 1.1 year interval became a 1 year interval); (ii) we computed dates that minimised the difference between actual fieldwork dates and complete-year census dates, while ensuring that subsequent census intervals of a plot do not overlap. The resulting sequence of non-overlapping census intervals was used to calculate interval-specific means for each environmental predictor variable to remove seasonal effects. The average difference between the actual fieldwork dates and the complete-year census dates is 0.01 decimal years (i.e. less than one week).

The first group of potential predictor variables, estimated for each census interval of each plot, are theory-driven choices: atmospheric CO₂ concentration (CO₂), mean annual temperature (MAT), and drought intensity, which we quantified as maximum climatological water deficit (MCWD)⁵⁴. *Atmospheric CO₂ concentration* (CO₂, in ppm) is estimated as the mean of the monthly mean values from the Mauna Loa record⁵⁵ over the census interval (corrected to avoid seasonality effects). While atmospheric CO₂ concentration is highly correlated with time ($R^2=0.98$), carbon gains are slightly better correlated with CO₂, as expected.

Mean Annual Temperature (MAT, in °C) was derived from a combination of the fine-scale (~1 km² resolution) static WorldClim dataset³¹ and the coarser scale (~3025 km² resolution) temporally resolved Climatic Research Unit dataset (CRU TS 3.23)⁵⁶. For each plot, we first extracted the monthly mean temperature record covering 1901-2015 from the CRU dataset and calculated mean annual temperature (MAT) over that period. Then we multiplied each value in the monthly CRU record by the ratio of the WorldClim-MAT and the CRU-MAT. We then calculated MAT for each census interval of each plot using the adjusted monthly CRU record.

737 *Maximum Climatological Water Deficit* (MCWD, in mm) was derived from a combination of the fine-
738 scale (~1 km² resolution) static WorldClim precipitation dataset³¹ and the coarser scale (~3025 km²
739 resolution) temporally resolved Global Precipitation Climatology Centre dataset (GPCC) that includes
740 many more gauges than CRU in tropical Africa^{57,58} following a similar approach as to MAT. However,
741 as GPCC ends in 2013 we combined it with satellite-based Tropical Rainfall Measurement Mission
742 data (TRMM 3B43 V7 product, 0.25° resolution)⁵⁹. The fit for the overlapping time period (1998-
743 2013) was used to correct the systematic difference between GPCC and TRMM: $GPCC' = a + b * GPCC$,
744 with GPCC' the adjusted GPCC record and a and b different parameters for each month of the year
745 and for each continent. For each plot, we first extracted the monthly precipitation record covering
746 1901-2015 from the adjusted GPCC dataset and calculated mean monthly precipitation over that
747 period. Then we multiplied each value in the monthly GPCC record by the ratio of the WorldClim
748 mean monthly precipitation to the GPCC mean monthly precipitation. Then for each census interval
749 we extract monthly precipitation values and calculate monthly Climatological Water Deficit (CWD),
750 which is a commonly used metric of dry season intensity for tropical moist forests^{12,20,54}. To avoid
751 intra-annual variability, monthly CWD values are calculated for each subsequent series of 12 months
752 (complete years), using a recursive procedure⁵⁴. Monthly CWD estimation begins with the wettest
753 month of the first year in the interval, and is calculated as 100 mm per month evapotranspiration (ET)
754 minus monthly precipitation (P). Then, CWD values for the subsequent 11 months were calculated
755 recursively as: $CWD_i = ET - P_i + CWD_{i-1}$ (equation 4), where negative CWD_i values were set to
756 zero⁵⁴ (no drought conditions). This procedure was repeated for each subsequent complete 12 months.
757 Then, we calculate the annual MCWD as the largest monthly CWD value for every subsequent
758 complete year within the census interval. Finally the MCWD of a census interval is calculated as the
759 mean of the annual MCWD values within the census interval. MCWD is an easily interpretable drought
760 metric: larger values indicate more severe water deficits.

761

762 To calculate the environmental change of potential predictor variables, CO₂-change, MAT-change and
 763 MCWD-change, we selected an optimum period over which to calculate the change. We derived this
 764 optimum period empirically by assessing the correlation of carbon gains (all plots, all censuses) with
 765 the change in each environmental variable, using linear mixed effects models (lmer function in R, lme4
 766 package⁵⁰). The annualised change in the environmental variable was calculated as the change between
 767 the focal interval and a prior interval (termed the baseline period) with a lengthening time window
 768 ranging from 1 year through to 80 years prior to the focal interval (i.e. 80 linear mixed effects models
 769 per variable). We calculated AIC for each model and selected the interval length with the lowest AIC.
 770 Thus, MAT-change (in °C yr⁻¹) = $\frac{(MAT_i - MAT_b)}{(date_i - date_b)}$ (equation 5), where MAT_i is the MAT over the focal
 771 census interval calculated using the procedure described above, MAT_b is the MAT over a baseline
 772 period prior to the focal interval, date_i is the mid-date of the focal census interval and date_b is the mid-
 773 date of the baseline period. The lmer results show that MAT-change (in °C yr⁻¹) is the difference
 774 between the focal interval and the mean MAT over the prior 5 years; CO₂-change is the difference
 775 between the focal interval and the mean CO₂ over the prior 56 years. MCWD showed no clear trend,
 776 so MCWD-change was not included in the models. All three results conform to *a priori* theoretical
 777 expectations: see Extended Data Figure 3.

778

779 We calculated two forest attributes that may alter responses to environmental change as potential
 780 predictor variables: Wood Density (WD) and Carbon Residence Time (CRT). In intact old-growth
 781 forests, mean WD (in g cm⁻³) is inversely related to resource availability^{26,60,61}, as is seen in our dataset
 782 (carbon gains and plot-level mean WD are negatively correlated, Extended Data Figure 4). WD is
 783 calculated for each census in the dataset, as the mean WD of all trees alive at the end of the census.
 784 Carbon residence time (CRT, in yrs) is a measure of the time that fixed carbon stays in the system.
 785 CRT is a potential correlate of the impact of past carbon gains on later carbon losses²⁸. To avoid
 786 circularity in the models, the equation used to calculate CRT differed depending on the response

variable. If the response variable is carbon loss, the CRT equation is based on gains: $CRT = \frac{AGC}{gains}$ (equation 6), with AGC for each interval based on AGC at the end of the interval, and the gains for each interval calculated as the mean of the gains in the interval and the previous intervals (i.e. long-term gains). If the response variable is carbon gain, the CRT equation is based on losses: $CRT = \frac{AGC}{losses}$ (equation 7). The equation employed for use in the carbon loss model (equation 6) is the standard formula used to calculate CRT and is retained in the minimum adequate model (see below and Table 2). The non-standard CRT equation (equation 7) used in the carbon gain model is not retained in the minimum adequate model (see below).

Modelling census-level carbon gains and losses

We first construct two models including only the environmental variables: atmospheric carbon dioxide (CO_2), mean annual temperature (MAT), and drought as maximum climatological water deficit (MCWD). One model has carbon gains as the response variable, the other has carbon losses as the response variable (both in $Mg\ C\ ha^{-1}\ yr^{-1}$). Models were fitted using the lme function in R, with maximum likelihood (NLME package⁶²). All census intervals within all plots were used, weighted by plot size and census length (using equation 3). Plot identity was included as a random effect, i.e. assuming that the intercept can vary randomly among plots. All predictor variables in the models were scaled without centering (scale function in R, RASTER package⁴⁹). Carbon gain values were normally distributed but carbon loss values required a power-law transformation ($\lambda = 0.361$) to meet normality criteria. Multi-parameter models are:

$$carbon\ gains = intcp + a * CO_2 + b * MAT + c * MCWD \text{ (model 1);}$$

$$carbon\ losses = intcp + a * CO_2 + b * MAT + c * MCWD \text{ (model 2);}$$

where *intcp* is the estimated model intercept, and *a*, *b*, and *c* are model parameters giving the slope of relationships with environmental predictor variables. Multi-parameter model outputs for carbon gain and carbon loss are given in Extended Data Table 1. Single-parameter relations are shown in Figure 2.

812

813 The carbon gains model shows significant trends consistent with *a priori* expectations. However, the
 814 carbon loss model has no explanatory power (all parameters non-significant, see Figure 2 and Extended
 815 Data Table 1), so we further investigated what is driving the trends by constructing two more complex
 816 models, including the same environmental predictors (CO₂, MAT, MCWD), plus their rate of change
 817 (CO₂-change, MAT-change, MCWD-change), and forest attributes that may alter how forests respond
 818 (WD, CRT), as described above. We evaluated the possible inclusion of a differential continent effect
 819 of each variable in the full model. We first construct models with only a single predictor variable, and
 820 allow different slopes in each continent. Next, if removal of the continent-specific slope (using
 821 stepAIC function in R, MASS package⁶³) decreased model Akaike Information Criterion (AIC) then
 822 the continent-specific slope was not included in the full model for that variable. Only MCWD showed
 823 a significant differential continent-specific slope. This implies that forests on both continents have
 824 common responses to CO₂-change, MAT, MAT-change, WD and CRT, but respond differently to
 825 differences in MCWD. This is most likely because wet-adapted species are much rarer in Africa than
 826 in Amazonia as a result of large differences in past climate variation⁶⁴. Lastly, we allowed different
 827 intercepts for the two continents, to potentially account for differing biogeographical or other
 828 continent-specific factors. For the carbon loss model, we applied the same continent-specific effects
 829 for slope as for the carbon gain model, and carbon loss values were transformed using a power-law
 830 transformation ($\lambda = 0.361$) to meet normality criteria.

831

832 For both carbon gains and losses we parameterized full models including the significant continent-
 833 specific effect of MCWD and simplified models using the stepAIC function in R, which sequentially
 834 removes terms until there are no terms that reduce model AIC after removal. As such, the minimum
 835 adequate models are:

836 $carbon\ gains = intcp * continent + a * CO_2\text{-}change + b * MAT + c * MAT\text{-}change + d * MCWD * continent + e * WD$
 837 (model 3);

838 $carbon\ losses = intcp + a * CO_2\text{-}change + b * MAT\text{-}change + c * MCWD + d * CRT$ (model 4).

839 Parameters of these minimum adequate models for carbon gain and carbon loss are given in Table 2.

840 CRT was retained in the carbon loss model, and WD was retained in the carbon gain model. These

841 results are expected *a priori* because growth is likely primarily impacted by resource availability, while

842 losses are likely primarily impacted by how long fixed carbon is retained in the system.

843

844 **Predicting the future carbon gain, loss and the net carbon sink**

845 We used estimates of the predictor variables and the parameters of the minimum adequate gain and

846 loss models (Table 2) to estimate the mean gains and losses for the plot networks in Africa and

847 Amazonia from 1983 through to 2040, with the net carbon sink per unit area obtained by subtracting

848 the losses from the gains (seen in Figure 3). For predictor variables in the past, we calculated annual

849 records for $CO_2\text{-}change$, MAT, MAT-change, MCWD, WD and CRT for each plot location from 1983

850 to 2015, as described above (mean trends shown in Extended Data Figure 5). For predictor variables

851 in the future, we used the annual records from 1983 to 2015 to parameterize a continent-specific linear

852 regression for $CO_2\text{-}change$, MAT, MAT-change, MCWD, WD, and CRT, which is used to estimate

853 predictor variables for each plot location from 2015 to 2040 (mean trends shown in Extended Data

854 Figure 5). Predicted mean annual gains and losses for 1983 to 2040 are calculated by multiplying

855 model parameters by annual values of the corresponding predictor variables. Model prediction

856 uncertainty is derived from model parameters multiplied by each predictor variable value $\pm 1\sigma$. To

857 obtain total continental sink values in the future (Table 1), per unit area sink estimates were multiplied

858 by future forest area, using the area in each continent from 1990-2010 and an exponential model for

859 each continent to estimate each continents' forest area in 2020, 2030 and 2040 (see Continental and

860 pan-tropical carbon sink estimates, above).

Extended Data

Extended Data Table 1. Models based on environmental variables alone to predict carbon gains and losses in African and Amazonian tropical forests. Where continental values differ, those for Africa are reported first, followed by Amazon values. Significant values in **bold**.

Carbon gains, Mg C ha ⁻¹ yr ⁻¹					
Predictor variable	Parameter value	Standard Error	t-value	p-value	2000-2015 change in gains (%) *
(Intercept)	4.694	0.733	6.402	<0.001	-
CO ₂ (ppm)	0.005	0.001	3.186	0.001	5.78% 5.90%
MAT (°C)	-0.143	0.021	-6.928	<0.001	-1.24% -1.89%
MCWD (mm x1000)	-1.164	0.207	-5.628	<0.001	-1.42% -2.08%
Carbon losses, Mg C ha ⁻¹ yr ⁻¹ †					
Predictor variable	Parameter value	Standard Error	t-value	p-value	2000-2015 change in losses (%) *
(Intercept)	1.033	1.855	0.557	0.578	-
CO ₂ (ppm)	0.004	0.004	0.949	0.343	6.60% 5.83%
MAT (°C)	-0.015	0.044	-0.343	0.732	-0.18% -0.24%
MCWD (mm x1000)	-0.515	0.499	-1.032	0.302	-0.86% -1.09%

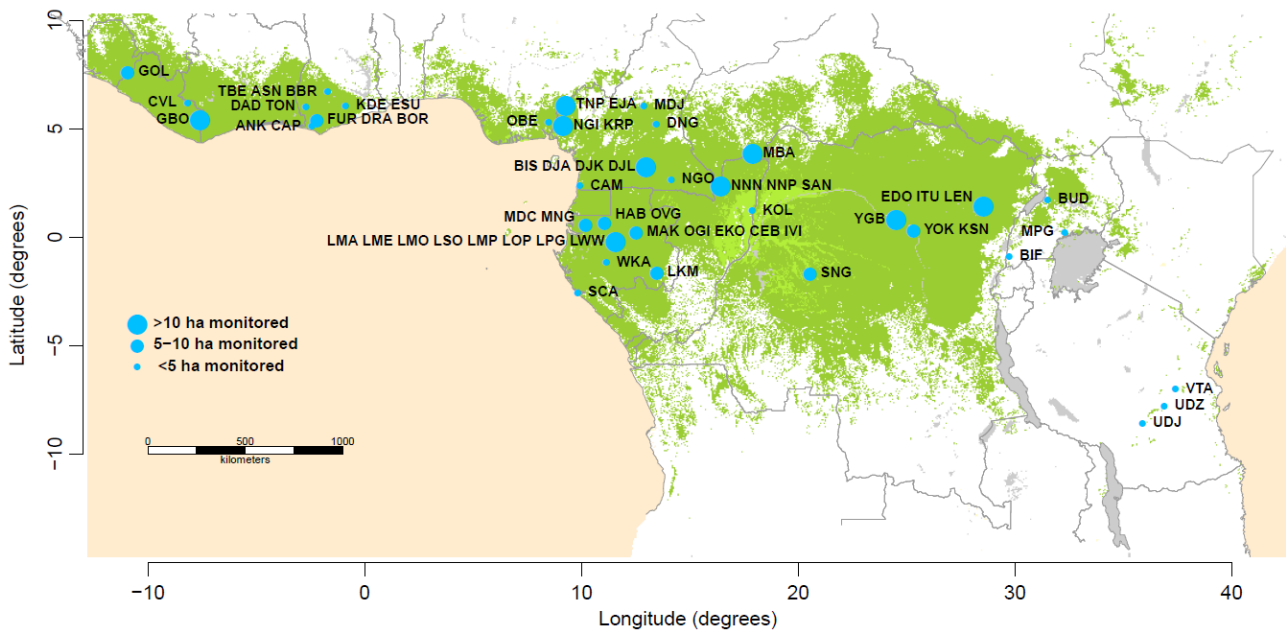
* The 2000-2015 change in gains/losses for each predictor variable was estimated allowing only the focal predictor to vary; this change was then expressed as a percentage of the annual gains/losses in the year 2000 allowing all predictors to vary.

† carbon loss values were normalized via power-law transformation, $\lambda = 0.361$.

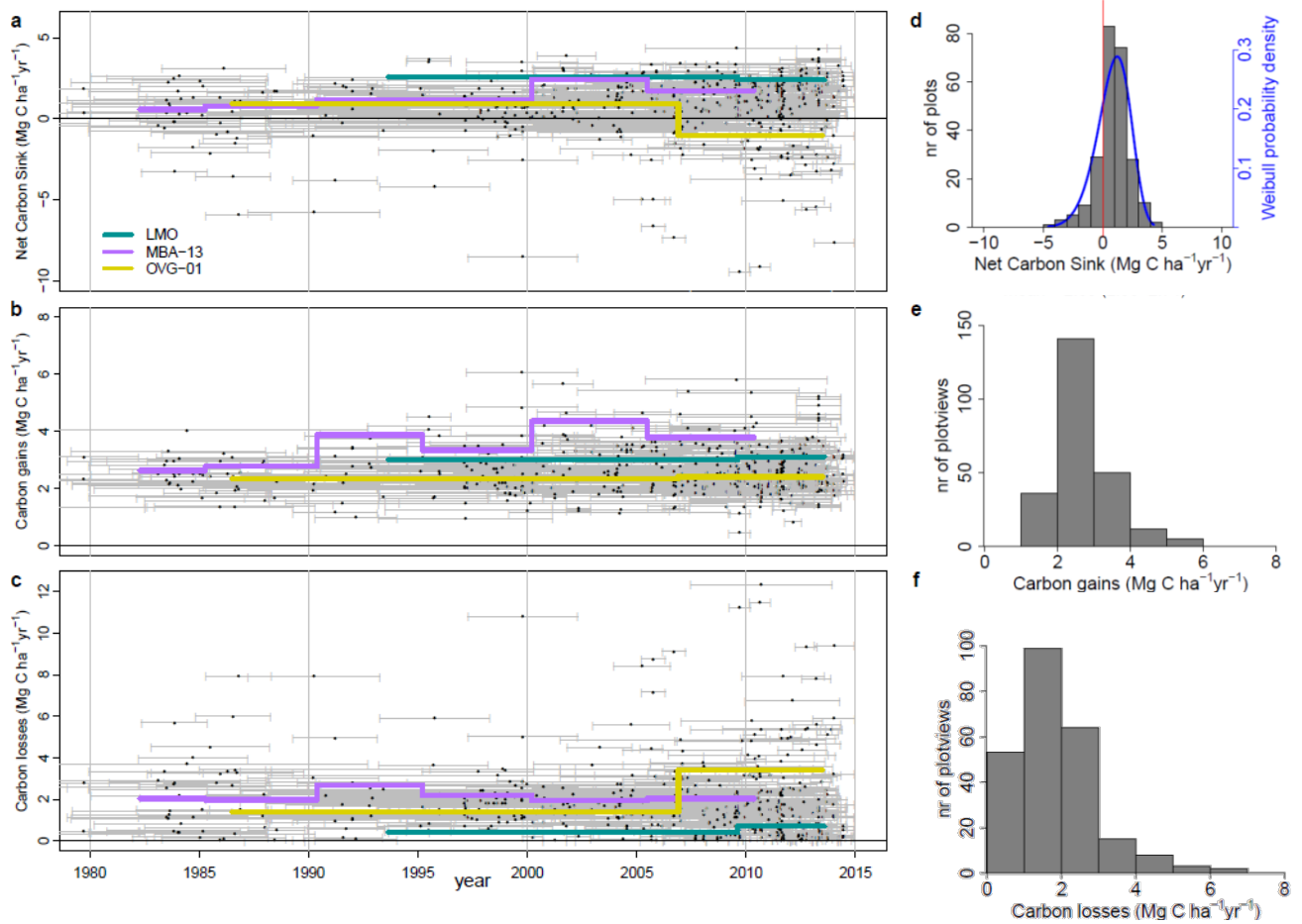
872 **Extended Data Table 2. Forest area estimates used to calculate total continental forest sink.**

Period	intact forest area (Mha) *		
	Africa	Amazon	Southeast Asia
1980	671.5	958.3	233.6
1990	600.2	885.2	190.6
2000	531.8	817.2	136.9
2010	477.8	756.3	118.4
2015	450.5	726.7	101.5
2020	425.5	698.5	90.1
2030	379.7	645.4	71.0
2040	338.8	596.4	56.0

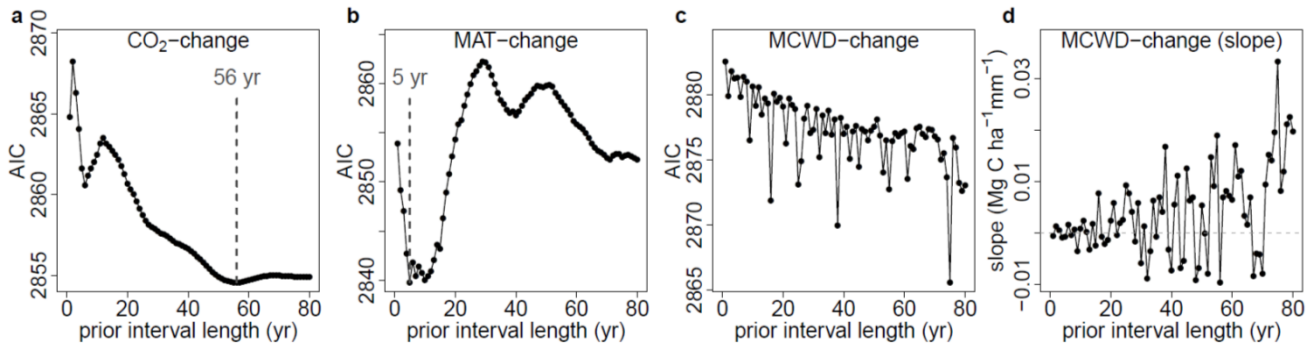
873 * Intact forest area for 1990, 2000 and 2010 is published in ref.¹ (i.e. the total forest area minus forest regrowth);
874 to estimate intact forest area for 1980, 2015, 2020, 2030 and 2040 we fitted exponential models for each
875 continent using the 1990-2010 data.



Extended Data Figure 1. Map showing the locations of the 244 plots included in this study. Dark green represents all lowland closed-canopy forests, submontane forests and forest-agriculture mosaics; light green shows swamp forests and mangroves⁶⁵. The three-letter codes refer to plot-cluster names (see Supplementary Table 1 for the full list of plots). Clusters <50 km apart are shown as one dot for display only. Blue dot size corresponds to sampling effort in terms of hectares monitored.

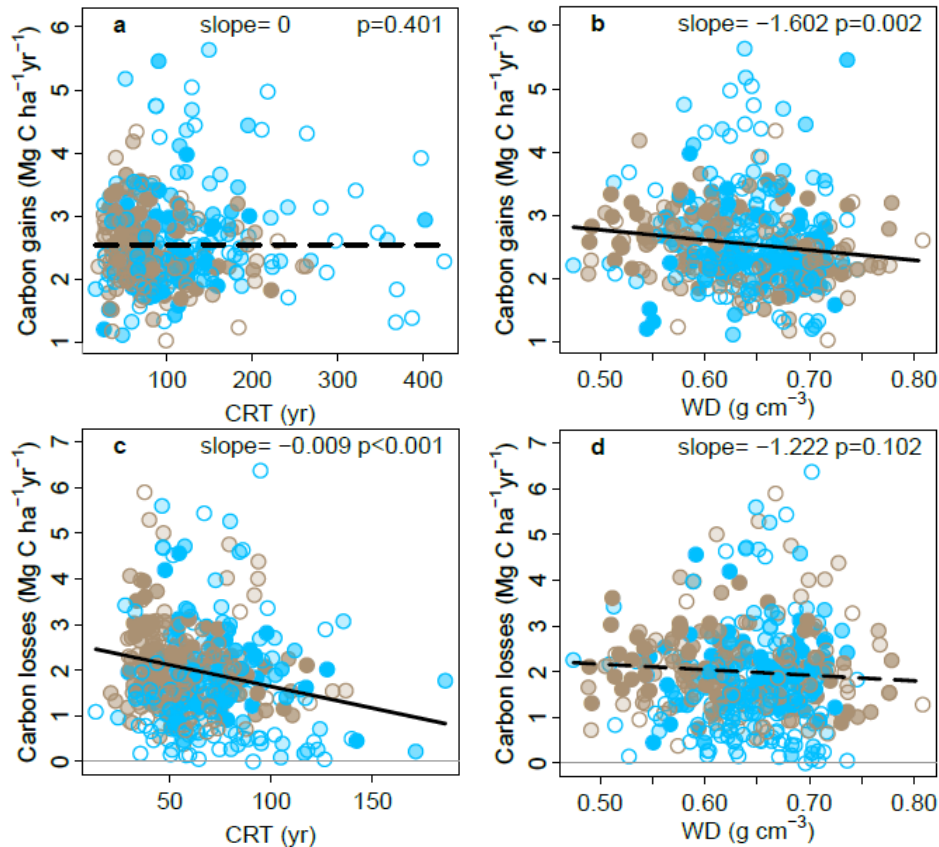


Extended Data Figure 2. Distribution of values of the long-term above-ground carbon dynamics of 244 African intact tropical forest inventory plots. Points in the scatterplots indicate the mid-census interval date, with horizontal bars connecting the start and end date for each census interval for the net carbon sink (a), carbon gains (from woody productivity) (b), and carbon losses (from mortality) (c). Examples of time series for three individual plots are shown in purple, yellow and green. Associated histograms show the distribution of the plot-level net carbon sink (d) (with a three-parameter Weibull probability density distribution fitted in blue, showing the sink is significantly larger than zero; one-tail t-test: $p < 0.001$), carbon gains (e), and carbon losses (f).

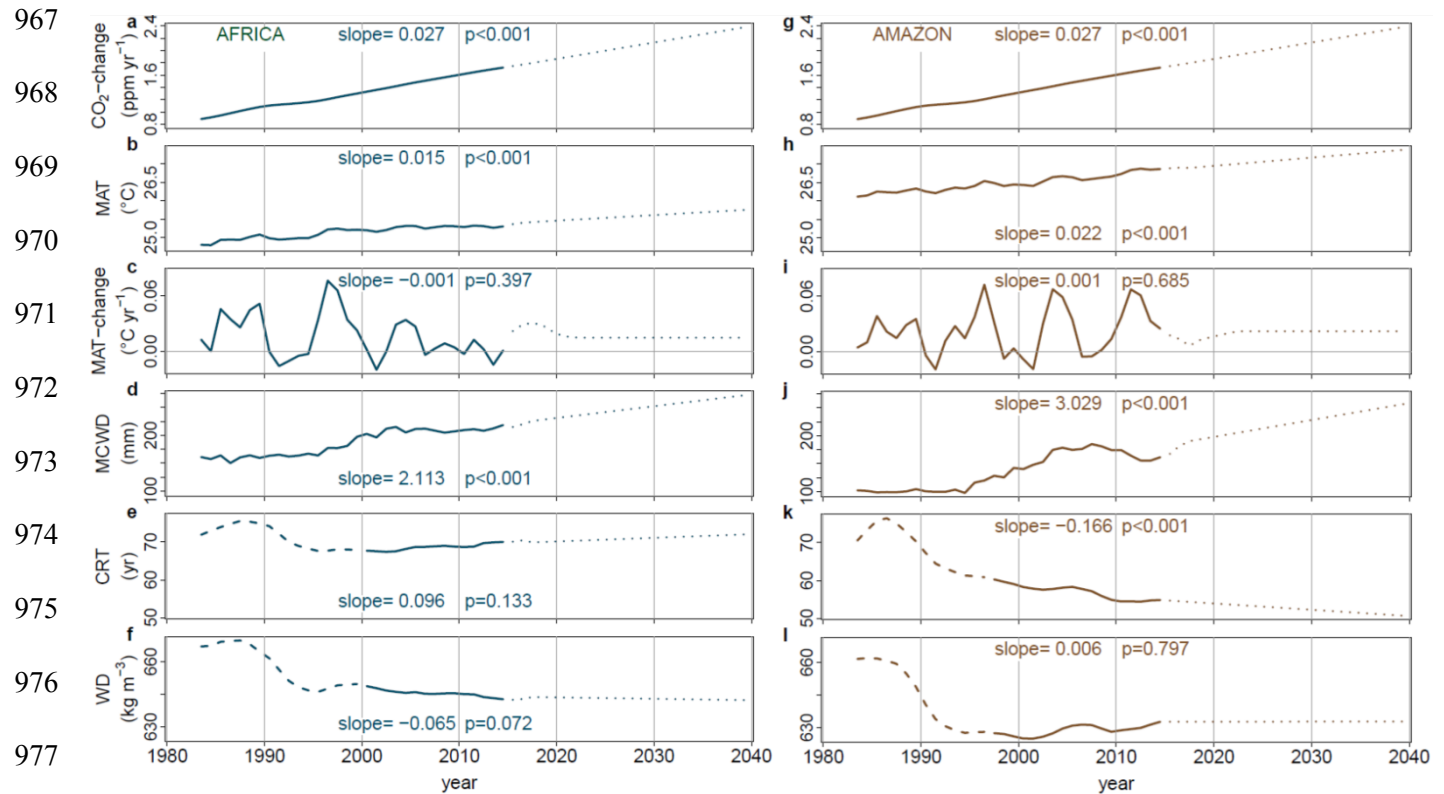


Extended Data Figure 3. Akaike's Information Criterion (AIC) from correlations between the carbon gain in tropical forest inventory plots and changes in either atmospheric CO₂, temperature (as MAT) or drought (as MCWD) each calculated over ever-longer prior intervals.

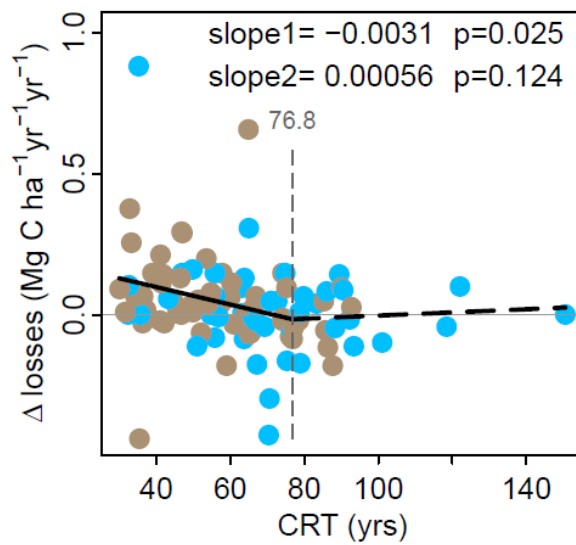
Panels show AIC from linear mixed effects models of carbon gains and, atmospheric CO₂ (CO₂-change) (a), Mean Annual Temperature (MAT-change) (b), and Maximum Climatological Water Deficit (MCWD-change, $n=565$ plots) (c). For CO₂ the AIC minimum was observed when predicting the carbon gain from the change in CO₂ calculated over a 56 year long prior interval length. We use this length of time to calculate our CO₂-change parameter. Such a value is expected *a priori* because forest stands will respond most strongly to CO₂ when most individuals have grown under the new rapidly changing condition, which should be at its maximum at a time approximately equivalent to the carbon residence time of a forest stand^{66,67} (a mean of 62 years in this dataset). For MAT the AIC minimum was 5 years, which we use as the prior interval to calculate our MAT-change parameter. This length is consistent with experiments showing temperature acclimation of leaf-level and plant-level photosynthetic and respiration processes over half-decadal timescales^{29,68}. For MCWD the AIC minimum is not obvious, while the slope of the correlation, shown in panel (d), has no overall trend and oscillates between positive or negative values, meaning there is no obvious relationship between carbon gains and the change in MCWD over intervals longer than 1 year; thus MCWD-change is not included in our models. This result is expected, because once a drought ends, its impact on tree growth fades rapidly^{12,69}, hence lagged impacts of past droughts are not expected.



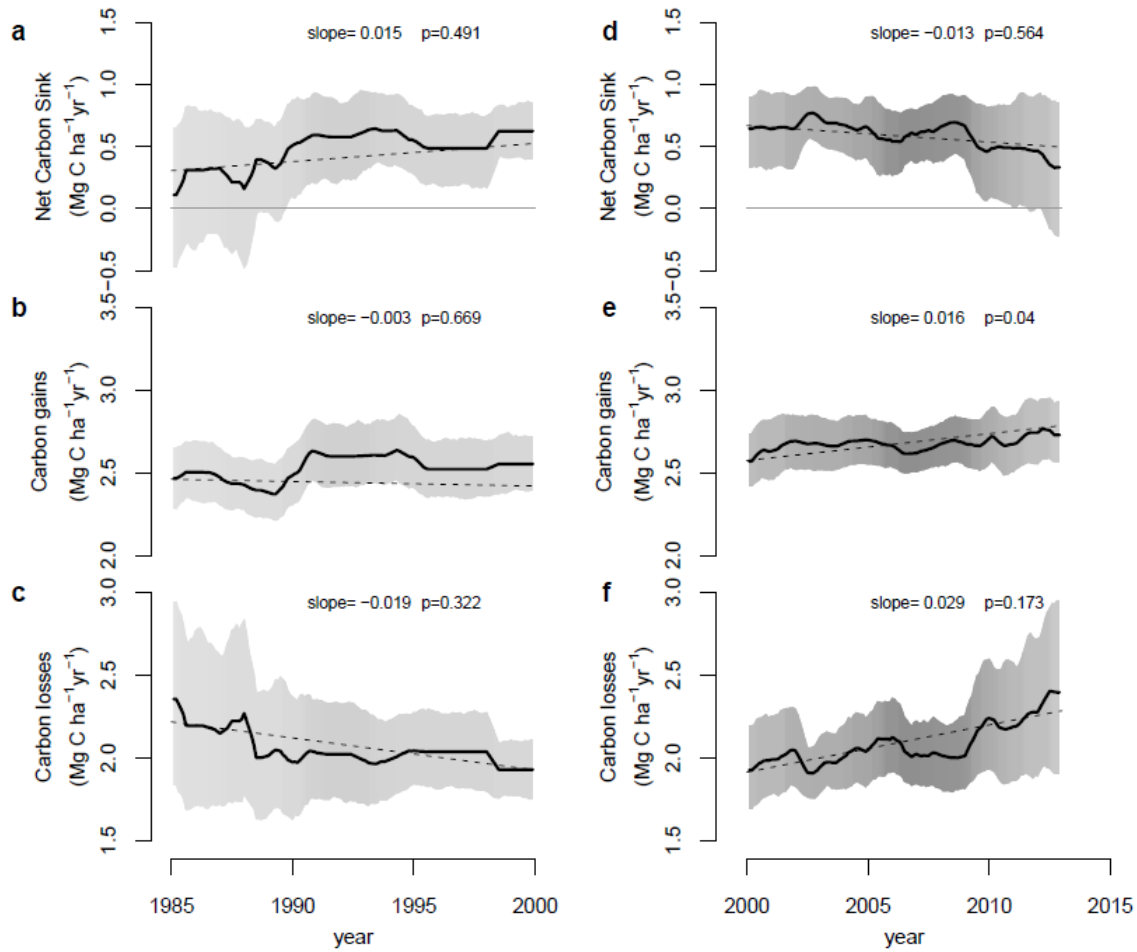
Extended Data Figure 4. Potential forest-dynamics-related drivers of carbon gains and losses in structurally intact old-growth African and Amazonian tropical forests. The aboveground carbon gains, from woody productivity (**a-b**), and aboveground carbon losses, from mortality (**c-d**), are plotted against the carbon residence time (CRT), and wood density (WD), for African (blue) and Amazonian (brown) inventory plots. Linear mixed effect models were performed with census intervals (n=1566) nested within plots (n=565) to avoid pseudo-replication, using an empirically derived weighting based on interval length and plot area (see methods). Significant regression lines for the complete dataset are shown as a solid line; non-significant regressions as a dashed line. Each dot represents a time-weighted average plot-level value; transparency of the inner part of the dot represents total monitoring length, with empty circles corresponding to plots monitored for ≤ 5 years and solid dots for plots monitored for >20 years. Carbon loss data are presented untransformed for clarity; linear mixed effects models on transformed data to fit normality assumptions do not change the results. For the carbon gains and losses models CRT is calculated differently: see methods.



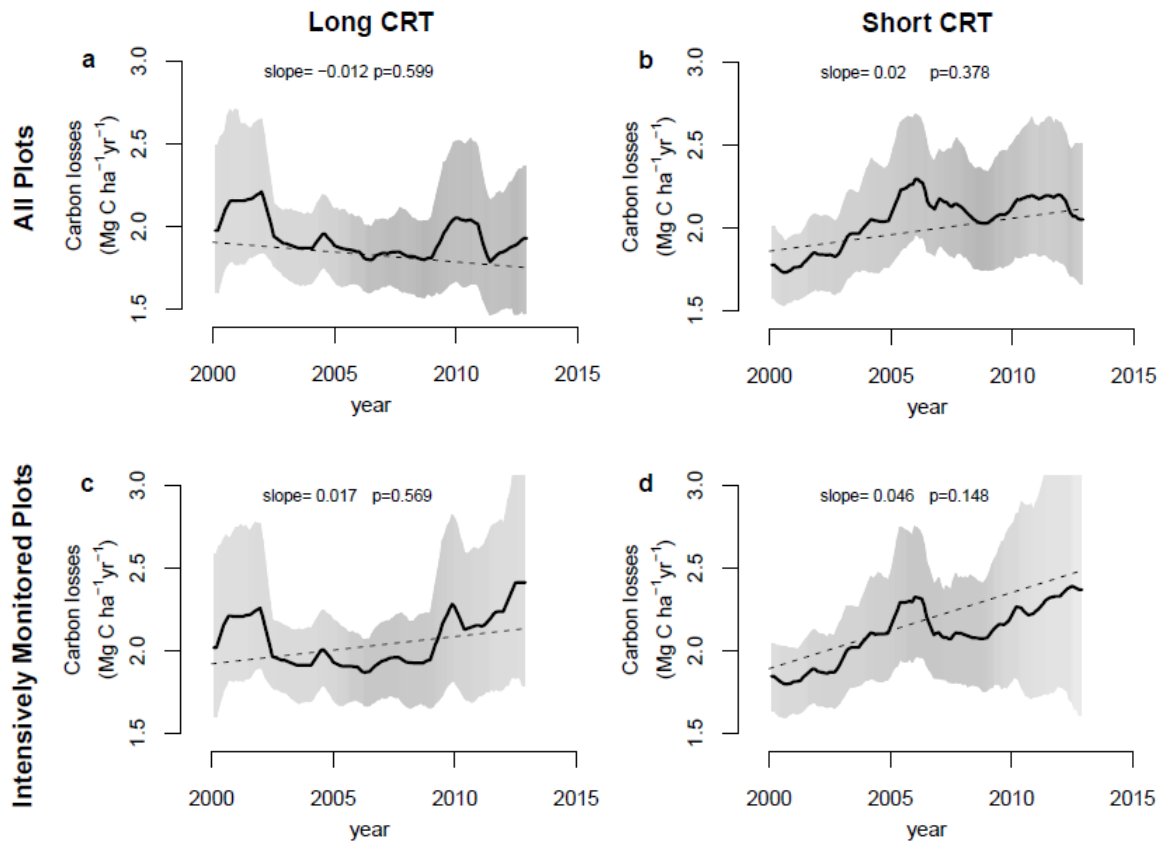
Extended Data Figure 5. Trends in predictor variables used to estimate long-term trends in above-ground carbon gains, carbon losses and the resulting net carbon sink in African and Amazonian tropical forest plot networks. Solid lines, blue for Africa (a-f), brown for Amazonia (g-l), are the mean annual value for all plot locations on each continent, from published datasets (CO_2 -change, MAT, MAT-change, MCWD), or estimated from the plot data (WD, CRT). Dotted lines are future values estimated from linear trends on the 1983-2014 data (slope and p-value reported in each panel). Trends for environmental variables (CO_2 -change, MAT, MAT-change, MCWD) are from simple linear models using the mean annual record. Trends for CRT and WD are from linear mixed effects models using the plot data, i.e. regressing the mid-point of each census interval against the value of the predictor variable for that census interval, using plot identity as a random effect, and weighting observations by plot size and census interval length (as in Figure 1). Dashed lines in panels e-f and k-l represent the time window where <75% of plots were monitored, hence contributing less to the linear mixed effects model.



Extended Data Figure 6. The change in carbon losses versus carbon residence time (CRT) of plots in Africa and Amazonia. The data include only plots monitored for >20 years (i.e. roughly one-third of the mean CRT of the pooled African and Amazon dataset; $n = 116$). Breakpoint regression was used to assess the CRT length below which forest carbon losses begin to increase. Plots with CRT < 77 years show a long-term increase in carbon losses. Blue dots are African plots, brown dots are Amazonian plots.



Extended Data Figure 7. Trends in African forest net aboveground live biomass carbon sink, carbon gains and carbon losses, calculated for the last 15 years of the twentieth century (left panels a-c) and the first 15 years of the twenty-first century (right panels d-f). Plots were selected from the full dataset if their census intervals covered at least 50% of the respective time windows ($n=56$ plots for 1985-2000, and $n=134$ plots for 2000-2015, respectively). Solid lines show mean values calculated as for Figure 1; shading corresponds to the 95% CI. Dashed lines, slopes and p-values are from linear mixed effects models.



Extended Data Figure 8. Twenty-first century trends in aboveground biomass carbon losses from African tropical forest inventory plots with either long (left panels) or short (right panels) carbon residence time. Upper panels include all plots, i.e. as in Figure 1, but split into a long-CRT group (a), and a short-CRT group (b), each containing half the 244 plots. Lower panels restrict plots to those spanning >50% of the time window, i.e. as in Extended Data Figure 7, but split into a long-CRT group (c), and a short-CRT group (d), each containing half the 134 plots. Solid lines indicate mean values, shading the 95% CI. Dashed lines, slopes and p-values are from linear mixed-effects models. Carbon losses increase more through time in the short-CRT than the long-CRT group of plots, in both datasets, although this increase is not statistically significant.

References (Methods only)

- 31 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution
interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**,
1965-1978, doi:10.1002/joc.1276 (2005).
- 32 Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M. & Phillips, O. L. ForestPlots.net: a web
application and research tool to manage and analyse tropical forest plot data. *Journal of*
Vegetation Science **22**, 610–613, doi:10.1111/j.1654-1103.2011.01312.x (2011).
- 33 Sheil, D. & Bitariho, R. Bwindi Impenetrable Forest TEAM Site. Data Set Identifier: TEAM-
DataPackage-20151201235855_1254. (2009).
- 34 Kenfack, D. Korup National Park TEAM Site. Data Set Identifier: TEAM-DataPackage-
20151201235855_1254. (2011).
- 35 Rovero, F., Marshall, A. & Martin, E. Udzungwa TEAM Site. Data Set Identifier: TEAM-
DataPackage-20151130235007_5069. (2009).
- 36 Hockemba, M. B. N. Nouabalé Ndoki TEAM Site. Data Set Identifier: TEAM-DataPackage-
20151201235855_1254. (2010).
- 37 Anderson-Teixeira, K. J. *et al.* CTFS-ForestGEO: a worldwide network monitoring forests in
an era of global change. *Global Change Biology* **21**, 528-549, doi:10.1111/gcb.12712 (2015).
- 38 Gourlet-Fleury, S. *et al.* Tropical forest recovery from logging: a 24 year silvicultural
experiment from Central Africa. *Philosophical Transactions of the Royal Society B-*
Biological Sciences **368**, 20120302, doi:10.1098/rstb.2012.0302 (2013).
- 39 Phillips, O., Baker, T., Brien, R. & Feldpausch, T. RAINFOR field manual for plot
establishment and remeasurement. Available at
http://www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_2016.pdf.
(2016).

- 1081 40 Talbot, J. *et al.* Methods to estimate aboveground wood productivity from long-term forest
1082 inventory plots. *Forest Ecology and Management* **320**, 30-38,
1083 doi:10.1016/j.foreco.2014.02.021 (2014).
- 1084 41 Lopez-Gonzalez, G., Hubau, W., Pickavance, G., Lewis, S. & Phillips, O. Forestplots.net
1085 Manual. Available at
1086 http://www.forestplots.net/upload/ManualsEnglish/ForestPlotsManualApril112016_sm.pdf.
1087 (2016).
- 1088 42 Sullivan, M. J. P. *et al.* Field methods for sampling tree height for tropical forest biomass
1089 estimation. *Methods in Ecology and Evolution* **9**, 1179-1189, doi:10.1111/2041-210X.12962
1090 (2018).
- 1091 43 Lopez-Gonzalez, G., Sullivan, M. & Baker, T. BiomasaFP package. Tools for analysing data
1092 downloaded from ForestPlots.net. R package version 0.2.1. Available at
1093 <http://www.forestplots.net/en/resources/analysis>. (2017).
- 1094 44 Feldpausch, T. R. *et al.* Tree height integrated into pantropical forest biomass estimates.
1095 *Biogeosciences* **9**, 3381-3403, doi:10.5194/bg-9-3381-2012 (2012).
- 1096 45 Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351-
1097 366, doi:10.1111/j.1461-0248.2009.01285.x (2009).
- 1098 46 Zanne, A. E. *et al.* *Data from: Towards a worldwide wood economics spectrum* (Dryad
1099 Digital Repository, 2009).
- 1100 47 Chave, J. *et al.* Improved allometric models to estimate the aboveground biomass of tropical
1101 trees. *Global Change Biology* **20**, 3177-3190, doi:10.1111/gcb.12629 (2014).
- 1102 48 Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration
1103 across the world's trees and forests. *Nature Geoscience* **11**, 915-920, doi:10.1038/s41561-
1104 018-0246-x (2018).

- 49 R Development Core Team. R: A Language and Environment for Statistical Computing.
Available at <http://www.R-project.org/>. (2015).
- 50 Bates, D., Maechler, M., Bolker, B. & Walker, S. lme4: Linear mixed-effects models using
Eigen and S4. R package version, 1.0-4. Available at [http://www.inside-](http://www.inside-r.org/packages/lme4/versions/1-0-4)
r.org/packages/lme4/versions/1-0-4. (2013).
- 51 Fox, J. *Applied Regression Analysis and Generalized Linear Models*. Second edn, (Sage
Publishing, 2008).
- 52 Chave, J. *et al.* Assessing evidence for a pervasive alteration in tropical tree communities.
PLoS Biology **6**, 0455-0462, doi:10.1371/journal.pbio.0060045 (2008).
- 53 Yuen, J. Q., Ziegler, A. D., Webb, E. L. & Ryan, C. M. Uncertainty in below-ground carbon
biomass for major land covers in Southeast Asia. *Forest Ecology and Management* **310**, 915-
926, doi:10.1016/j.foreco.2013.09.042 (2013).
- 54 Aragão, L. E. O. C. *et al.* Environmental change and the carbon balance of Amazonian
forests. *Biological Reviews* **89**, 913-931, doi:10.1111/brv.12088 (2014).
- 55 Tans, P. & Keeling, R. Mauna Loa CO₂ monthly mean data. Available at
<http://www.esrl.noaa.gov/gmd/ccgg/trends/>. (2016).
- 56 Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of
monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of*
Climatology **34**, 623–642 doi:10.1002/joc.3711 (2014).
- 57 Schneider, U. *et al.* GPCC Full Data Reanalysis Version 6.0 at 0.5°: Monthly Land-Surface
Precipitation from Rain-Gauges built on GTS-based and Historic Data.
doi:10.5676/DWD_GPCC/FD_M_V6_050 (2011).
- 58 Sun, Q. *et al.* Review of Global Precipitation Data Sets: Data Sources, Estimation, and
Intercomparisons. *Reviews of geophysics* **56**, 79-107, doi:10.1002/ (2017).

- 59 Huffman, G. J. *et al.* The TRMM Multisatellite Precipitation Analysis (TMPA): Quasi-
Global, Multiyear, Combined-Sensor Precipitation Estimates at Fine Scales. *Journal of*
Hydrometeorology **8**, 38-55, doi:10.1175/jhm560.1 (2007).
- 60 Quesada, C. A. *et al.* Variations in chemical and physical properties of Amazon forest soils in
relation to their genesis. *Biogeosciences* **7**, 1515-1541, doi:10.5194/bg-7-1515-2010 (2010).
- 61 Baker, T. R., Swaine, M.D., Burslem, D.F.R.P. Variation in tropical forest growth rates:
combined effects of functional group composition and resource availability. *Perspectives in*
Plant Ecology, Evolution and Systematics **6**, 21-36, doi:10.1078/1433-8319-00040 (2003).
- 62 Pinheiro, J. C. & Bates, D. M. *Mixed-Effects Models in S and S-PLUS*. First edn, 528
(Springer, 2000).
- 63 Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S*. Fourth edn, 498
(Springer, 2002).
- 64 Parmentier, I. *et al.* The odd man out? Might climate explain the lower tree alpha-diversity of
African rain forests relative to Amazonian rain forests? *Journal of Ecology* **95**, 1058-1071
(2007).
- 65 Mayaux, P., De Grandi, G. & Malingreau, J.-P. Central African Forest Cover Revisited: A
Multisatellite Analysis. *Remote Sensing of Environment* **71**, 183–196, doi:10.1016/S0034-
4257(99)00073-5 (2000).
- 66 Lloyd, J. & Farquhar, G. D. The CO₂ dependence of photosynthesis , plant growth responses
to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status . I .
General principles and forest ecosystems. *Functional Ecology* **10**, 4-32, doi:10.2307/2390258
(1996).
- 67 Galbraith, D. *et al.* Residence times of woody biomass in tropical forests. *Plant Ecology &*
Diversity **6**, 139-157, doi:10.1080/17550874.2013.770578 (2013).

- Aspinwall, M. J. *et al.* Convergent acclimation of leaf photosynthesis and respiration to prevailing ambient temperatures under current and warmer climates in *Eucalyptus tereticornis*. *New Phytologist* **212**, 354-367, doi:10.1111/nph.14035 (2016).
- Bonal, D., Burban, B., Stahl, C., Wagner, F. & Hérault, B. The response of tropical rainforests to drought—lessons from recent research and future prospects. *Annals of Forest Science* **73**, 27-44, doi:10.1007/s13595-015-0522-5 (2016).