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Asynchronous carbon sink saturation in African and Amazonian tropical forests

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1 Asynchronous Carbon Sink Saturation in African and Amazonian Tropical Forests

2

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154 Structurally intact tropical forests sequestered ~50% of global terrestrial carbon uptake over the 1990s and early 2000s, removing ~15% of anthropogenic CO₂ emissions¹⁻³. Climate-driven 155 vegetation models typically predict that this tropical forest 'carbon sink' will continue for 156 decades^{4,5}. Here, we assess trends in the carbon sink using 244 structurally intact African 157 158 tropical forests spanning 11 countries, we compare them with 321 published plots from Amazonia and investigate the underlying drivers of the trends. The carbon sink in live 159 160 aboveground biomass in intact African tropical forests has been stable for the three decades to 2015, at 0.66 Mg C ha⁻¹ vr⁻¹ (95% CI:0.53-0.79), in contrast to the long-term decline in 161 Amazonian forests⁶. Thus, the carbon sink responses of Earth's two largest expanses of 162 163 tropical forest have diverged. The difference is largely driven by carbon losses from tree mortality, with no detectable multi-decadal trend in Africa and a long-term increase in 164 Amazonia. Both continents show increasing tree growth, consistent with the expected net effect 165 of rising atmospheric CO_2 and air temperature⁷⁻⁹. Despite the past stability of the African 166 carbon sink, our data suggest a post-2010 increase in carbon losses, delayed compared to 167 168 Amazonia, indicating asynchronous carbon sink saturation on the two continents. A statistical model including CO₂, temperature, drought and forest dynamics accounts for the observed 169 trends and indicates a long-term future decline in the African sink, while the Amazonian sink 170 171 continues to rapidly weaken. Overall, the uptake of carbon into Earth's intact tropical forests peaked in the 1990s. Given that the global terrestrial carbon sink is increasing in size, 172 observations indicating greater recent carbon uptake into the Northern hemisphere landmass¹⁰ 173 174 reinforce our conclusion that the intact tropical forest carbon sink has already saturated. This tropical forest sink saturation and ongoing decline has consequences for policies to stabilise 175 Earth's climate. 176

177 Main text

178

Tropical forests account for approximately one-third of Earth's terrestrial Gross Primary Productivity 179 and one-half of Earth's carbon stored in terrestrial vegetation¹¹. Thus, small biome-wide changes in 180 tree growth and mortality can have global impacts, either buffering or exacerbating the increase in 181 atmospheric CO_2 . Models^{2,4,5,7,12}, ground-based observations¹³⁻¹⁵, airborne atmospheric CO_2 182 measurements^{3,16}, inferences from remotely sensed data¹⁷, and synthetic approaches^{3,8,18} each suggest 183 that, after accounting for land-use change, remaining structurally intact tropical forests (i.e. not 184 impacted by direct anthropogenic impacts such as logging) are increasing in carbon stocks. This 185 structurally intact tropical forest carbon sink is estimated at ~1.2 Pg C yr⁻¹ over 1990-2007 using 186 187 scaled inventory plot measurements¹. Yet, despite its policy relevance, changes in this key carbon sink remain highly uncertain^{19,20}. 188

189

Globally the terrestrial carbon sink is increasing^{2,7,8,21}. Between 1990 and 2017 the land surface 190 sequestered ~30% of all anthropogenic carbon dioxide emissions^{1,21}. Rising CO₂ concentrations are 191 thought to have boosted photosynthesis more than rising air temperatures have enhanced respiration, 192 resulting in an increasing global terrestrial carbon sink^{2,4,7,8,21}. Yet, for Amazonia, recent results from 193 194 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 195 reflects region-specific drought impacts^{22,23}, or potentially chronic pan-tropical impacts of either 196 197 heat-related tree mortality^{24,25}, or internal forest dynamics resulting from past increases in carbon gains leaving the system²⁶. A more recent deceleration of the rate of increase in carbon gains from 198 tree growth is also contributing to the declining Amazon sink⁶. Again, it is not known if this is a 199 200 result of either pan-tropical CO₂ fertilisation saturation, or rising air temperatures, or is merely a 201 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 to
investigate the putative environmental drivers of changes in the tropical forest carbon sink, and (iii)
project its likely future evolution.

205

We collected, compiled and analysed data from structurally intact old-growth forests from the African Tropical Rainforest Observation Network²⁷ (217 plots) and other sources (27 plots) spanning the period 1968 to 2015 (Extended Data Figure 1; Supplementary Table 1). In each plot (mean size, 1.1 ha), all trees \geq 100 mm in stem diameter were identified, mapped and measured at least twice using standardised methods (135,625 trees monitored). Live biomass carbon stocks were estimated for each census date, with carbon gains and losses calculated for each interval (Extended Data Figure 2).

213

214 Continental Carbon Sink Trends

We detect no long-term trend in the per unit area African tropical forest carbon sink over three 215 decades to 2015 (Figure 1). The aboveground live biomass sink averaged 0.66 Mg C ha⁻¹ yr⁻¹ (95% 216 CI: 0.53-0.79; n=244) and was significantly greater than zero for every year since 1990 (Figure 1). 217 While very similar to past reports $(0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1})^{13}$, this first estimate of the temporal trend in 218 Africa contrasts with the declining Amazonian trend⁶ (Figure 1). A linear mixed effect model shows 219 220 a significant difference in the slopes of the sink trends for the two continents over the common time 221 window (pooled data from both continents, 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 diverged in the 222 1990s and 2000s. 223

224

The proximal cause of the divergent sink patterns is a significant increase in carbon losses (from tree mortality, i.e. the loss of carbon from the live biomass pool) in Amazonian forests, with no

227 detectable trend over three decades in African forests (Figure 1). A linear mixed effects model using pooled data shows a significant difference in slopes of carbon losses between the two continents over 228 229 the common 1983-2011.5 time window (p=0.027). Long-term trends in carbon gains (from tree 230 growth and newly recruited trees) on both continents show significant increases (Figure 1), and we 231 could detect no difference in slopes between the continents (p=0.348; carbon gains from tree growth alone also show no continental difference in long-term trends, p=0.322). However, an assessment of 232 233 how underlying environmental drivers affect carbon gains and losses is needed to understand the ultimate causes of the divergent sink patterns. 234

235

236 Understanding the Carbon Sink Trends

We first investigate environmental drivers exhibiting long-term change that impact theory-driven 237 238 models of photosynthesis and respiration: atmospheric CO₂ concentration, surface air temperature, 239 and water availability. 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 240 relationship with CO₂, and significant negative relationships with mean annual temperature (MAT) 241 and drought (measured as the Maximum Climatological Water Deficit, MCWD¹⁴; Figure 2; 242 Extended Data Table 1). These results are consistent with a positive CO₂ fertilisation effect, and 243 244 negative effects of higher temperatures and drought on tree growth, consistent with temperature-245 dependent increases in autotrophic respiration, and temperature- and drought-dependent reductions 246 in carbon assimilation. By contrast, the equivalent model for carbon losses (i.e. tree mortality) shows no significant relationships with CO₂, MAT or MCWD (Figure 2; Extended Data Table 1). 247

248

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 additionally include the change in environmental conditions (CO₂-change, MAT-change, MCWD-change, see Extended Data Figure 3 for calculation details), and two attributes of forests that may influence their response to the same environmental change: plot mean wood density (which in old-growth forests correlates with below-ground resource availability^{28,29}), 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 losses³⁰).

257

258 The minimum adequate carbon gain model using our expanded explanatory variables (best ranked model using multimodel inference) has a positive relationship with CO₂-change, and negative 259 260 relationships with MAT, MAT-change, MCWD, and wood density (Table 2; model-average results are similar, see Methods and Supplementary Tables 2-4). The retention of both MAT and MAT-261 change suggests that higher temperatures correspond to lower tree growth, and that trees only 262 263 partially acclimate to recently rising temperatures, which further reduces growth, consistent with warming experiments³¹ and observations⁹. The inclusion of higher wood density, and it being related 264 to lower carbon gains (Extended Data Figure 4), alongside no temporal trends in wood density 265 (Extended Data Figure 5), suggests that old-growth forests with denser-wooded tree communities 266 267 typically have fewer available below-ground resources, or such patterns may also emerge from disturbance regimes lacking large-scale exogenous events, consistent with prior studies^{26,28,32}. 268

269

The minimum adequate carbon gain model using our expanded explanatory variables also highlights continental differences. Between 2000 and 2015 African forest carbon gains increased by 3.1%compared with a 0.1% decline in Amazonia over the same interval (Table 2). In Africa, from 2000 to 2015, the increase was composed of a 3.7% increase from CO₂-change, partially offset by increasing droughts depleting gains by 0.5%, and only a slight decline in gains of 0.1% resulting from temperature increases (Table 2), because the rate of temperature change (MAT-change) decelerated over this time window (Extended Data Figure 5). For Amazonia, the same 3.7% increase due to CO₂- 277 change was seen, while increasing droughts-and these forests' greater sensitivity to drought-278 reduced gains by 2.7% (five times the impact in Africa), and temperature increases at the same rate as in the past (i.e. MAT-change is zero) further reduced gains by 1.1% (ten times the impact in 279 280 Africa), leaving a net change in gains slightly below zero (Table 2). Thus, the recent stalling of carbon gain increases in Amazonia⁶ is a response to drought and temperature and not due to an 281 unexpected saturation of CO₂ fertilisation. Overall, the larger modelled increase in gains in Africa 282 283 relative to Amazonia appear to be driven by slower warming, fewer or less extreme droughts, lower forest sensitivity to droughts, and overall lower temperatures (African forests are on average ~1.1°C 284 285 cooler than Amazonian forests, as they typically grow at ~200 m higher elevation). Other continental differences may also be influencing the results, including higher nitrogen deposition in African 286 tropical forests due to the seasonal burning of nearby savannas³³ and biogeographic history resulting 287 in differing contemporary species pools and resulting functional attributes^{34,35}. 288

289

The minimum adequate carbon loss model using our expanded explanatory variables shows higher 290 losses with CO2-change and MAT-change, and lower losses with MCWD and the carbon residence 291 292 time (CRT; Table 2). Thus, changes in carbon losses appear to be largely a function of carbon gains. 293 First, the greater losses in forests with shorter CRT conform to a 'high-gain high-loss' forest dynamics pattern²⁶. Second, wetter plots have a longer growing season and so have higher gains and 294 295 correspondingly higher losses, explaining the negative relationship with MCWD. Third, as 296 increasing CO₂ levels result in additional carbon gains, after some time these additional past gains leave the system resulting in greater carbon losses, explaining the positive relationship with CO₂-297 change. Finally, in addition to these relationships with carbon gains, the inclusion of MAT-change 298 (p<0.001) indicates heat- or vapour pressure deficit-induced tree mortality²⁴. Overall, our results 299 imply that chronic long-term environmental change factors, temperature and CO₂, rather than simply 300

the direct effects of drought, underlie longer-term trends in tropical forest tree mortality, although
 other changes such as rising liana infestation rates seen in Amazonia^{36,37} cannot be excluded.

303

304 The minimum adequate carbon loss model using our expanded explanatory variables replicates the 305 continental trends (Figure 3). The overall lower loss rates in Africa reflect their longer CRT (69 yrs, 95% CI, 66-72), compared with Amazonian forests (56 yrs, 95% CI, 54-59) while over the 2000-306 307 2015 window the much smaller increase in loss rates in Africa compared to Amazonia results from a slower increase in warming and a stable CRT in Africa compared to continued warming at previous 308 309 rates and a shortening CRT in Amazonian forests (Extended Data Figure 5). Furthermore, given that 310 losses appear to lag behind gains they should relate to the long-term CRT of plots. This is what we 311 find: the longer the CRT the smaller the increase in carbon losses, with no increase in losses for plots 312 with CRT \geq 77 years (Extended Data Figure 6). Consequently, due to the typically longer residence 313 times of African forests, increasing losses in Africa ought to appear 10-15 years after the increase in 314 Amazon losses began (c.1995). Strikingly, in Africa the most intensely monitored plots suggest that 315 losses began increasing from c.2010 (Extended Data Figure 7), and plots with shorter CRT are driving the increase (Extended Data Figure 8). Thus, a mortality-dominated African carbon sink 316 decline appears to have begun very recently. 317

318

319 Future of the Tropical Forest Carbon Sink

Our carbon gain and loss models (Table 2) can be used to make a tentative estimate of the future size of the per unit area intact forest carbon sink (Figure 3). 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 (Figure 3). By 2030 the carbon sink in aboveground live biomass in intact African tropical forest is predicted to decline by 14% from the measured 2010-15 mean, to 0.57 Mg C ha⁻¹ yr⁻ 1 (2 σ range, 0.16-0.96; Figure 3). The Amazon sink continues to decline, reaching zero in 2035 (2 σ range, 2011-2089; Figure 3). Our estimated sink strength on both continents in the 2020s and 2030s is sensitive to future CO₂ emissions pathways (CO₂-change)³⁸, resulting temperature increase (MAT, MAT-change) and hydrological changes (MCWD), plus changes in forest dynamics (CRT), but the sink is always lower than levels seen in the 2000s (see Methods and Supplementary Table 5). Thus, the carbon sink strength of the world's two most extensive tropical forests have now saturated, albeit asynchronously.

332

333 Scaling Results to the Pan-tropics

334 Scaling our estimated mean sink strength by forest area for each continent signifies that Earth 335 recently passed the point of peak carbon sequestration into intact tropical forests (Table 1). The continental sink in Amazonia peaked in the 1990s, followed by a decline, driven by sink strength 336 337 peaking in the 1990s and a continued decline in forest area (Table 1). In Africa the per unit area sink 338 strength peaked later in the 2000-2010 period, but the continental African sink peaked in the 1990s, due to the decline in forest area in the 2000s outpacing the small per unit area increase in sink 339 340 strength. Including the modest uptake in the much smaller area of intact Asian tropical forest 341 indicates that total pan-tropical carbon uptake peaked in the 1990s (Table 1). From peak pan-tropical intact forest uptake of 1.26 Pg C yr⁻¹ in the 1990s, we project a continued decline reaching just 0.29 342 Pg C yr⁻¹ in the 2030s (multi-decade decline of ~0.24 Pg C yr⁻¹ decade⁻¹), driven by (i) reduced mean 343 pan-tropical sink strength decline of 0.1 Mg C ha⁻¹ yr⁻¹ decade⁻¹ and (ii) ongoing forest area losses of 344 345 ~13.5 million ha yr⁻¹ (see Extended Data Table 2 for forest area details). Critically, climate-driven vegetation model simulations have not predicted that peak net carbon uptake into intact tropical 346 forests has already been passed 2,4,5 . 347

349 **Discussion**

350 Our method of scaling to arrive at a pan-tropical sink estimate – in common with other studies using similar datasets^{1,6,13} – is limited. Yet, pervasive net carbon uptake is expected given that we find a 351 352 strong and ongoing CO₂ fertilisation effect. Using our CO₂ response in Table 2, we find an increase in aboveground carbon stocks of 10.8±3.7 Mg C ha⁻¹ 100 ppm⁻¹ CO₂, or 6.5±2.2% (±SE; using an 353 area-weighted pan-tropical mean aboveground C stock of 165 Mg C ha⁻¹), comparable to the 354 5.0±1.2% increase in tropical forest C stocks 100 ppm⁻¹ CO₂ derived from a recent synthesis of CO₂ 355 fertilisation experiments, despite a lack of data from mature tropical forests³⁹. Our result is within the 356 range of climate-driven vegetation models^{2,7}, although it is greater than a number of recently-357 published models that include potential nutrient constraints, reported as 5.9±4.7 Mg C ha⁻¹ 100 ppm⁻¹ 358 359 CO_2 (Ref.⁴⁰). We find that the CO_2 fertilisation uptake is currently only partially offset by the negative impacts of similarly widespread rising air temperatures (-2.0±0.4 Mg C ha⁻¹ °C⁻¹, from 360 Table 2), consistent with models⁷, limited experiments³¹ and independent observations⁹, plus 361 negative responses to drought^{41,42}. Long-term and extensive increases in satellite-derived greenness 362 in tropical regions not experiencing major changes in land-use management^{17,43}, particularly in 363 central Africa in the past decade⁴⁴, indicate increases in tropical forest net primary productivity, 364 providing further evidence that the sink is a widespread phenomenon⁴⁴. 365

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Nonetheless, our analyses show that this pervasive tropical forest sink in live biomass is in long-term decline, first saturating in Amazonia, and more recently followed by African forests, explaining the prior Africa-Amazon carbon sink divergence as part of a longer-term pattern of asynchronous saturation and decline. From an atmospheric perspective the full impacts of the contribution to the saturation of the sink from slowing carbon gains are experienced immediately, but the contribution from rising carbon losses is delayed because dead trees do not decompose instantaneously. Decomposition of this dead tree mass is ~50% in 4 yrs, and ~85% in 10 yrs, thus rising carbon losses result in delayed carbon additions to the atmosphere⁴⁵. Hence, from an atmospheric perspective the intact tropical forest biomass carbon sink likely peaked a few years later than our plot data indicate and the full impacts are not yet realised. The pan-tropical carbon sink in live biomass reduced by $0.27 \text{ Pg C yr}^{-1}$ between the 1990s and 2000s (Table 1), but accounting for dead wood decomposition⁴⁵ shows a smaller 0.17 Pg C yr⁻¹ reduction from an atmospheric perspective (see Methods).

380

Given that the global terrestrial carbon sink is increasing, a weakening intact tropical forest sink 381 382 implies that the extra-tropical carbon sink has increased over the past two decades. Independent 383 observations of inter-hemispheric atmospheric CO₂ concentration indicates that carbon uptake into the Northern hemisphere landmass has increased at a greater rate than the global terrestrial carbon 384 sink since the 1990s, with a further disproportionate increase in the 2000s¹⁰. The inter-hemispheric 385 analysis suggests a weakening of the tropical forest sink by ~0.2 Pg C yr⁻¹ between the 1990s and 386 2000s¹⁰, which is similar to the 0.17 Pg C yr⁻¹ weakening over the same time period that we find. 387 388 This reinforces our conclusion that the intact tropical forest carbon sink has already saturated.

389

390 In summary, our results indicate that while intact tropical forests remain major stores of carbon and are key centres of biodiversity¹¹, their ability to sequester additional carbon is waning. In the 1990s 391 392 intact forests removed 17% of anthropogenic CO₂ emissions. This has declined to 6% in the 2010s, 393 because the pan-tropical weighted average per unit area sink strength declined by 33%, forest area decreased by 19%, and CO₂ emissions increased by 46%. Although tropical forests are more 394 immediately threatened by deforestation⁴⁶ and degradation⁴⁷, and the future carbon balance will also 395 depend on secondary forest dynamics⁴⁸ and forest restoration plans⁴⁹, our analyses show that they are 396 also impacted by atmospheric chemistry and climatic changes. Given that the intact tropical forest 397 398 carbon sink is set to end sooner than even the most pessimistic climate-driven vegetation models predict^{4,5}, our analyses suggest that climate change impacts in the tropics may become more severe than predicted. Furthermore, the carbon balance of intact tropical forests will only stabilise once CO_2 concentrations and the climate stabilises.

402

403 Continued on-the-ground monitoring of the world's remaining intact tropical forests will be required 404 to test our prediction that the intact tropical forest carbon sink will continue to decline. Such direct 405 ground-based measurements also provide a constraint on estimating the size and location of the terrestrial carbon sink. In addition, our conclusion that tree mortality and internal forest dynamics are 406 407 important controls on the future of the tropical forest carbon sink, may assist in improving the vegetation components of future Earth System Models⁵⁰ and contribute to reducing terrestrial carbon 408 409 cycle feedback uncertainty^{19,20}. Our findings also have policy implications. At the country-level: 410 given intact tropical forests are a carbon sink, but the size is changing, national greenhouse gas 411 reporting will require careful forest monitoring. At the international-level: given tropical forests are likely to sequester less carbon in the future than Earth System Models predict, an earlier date to reach 412 413 net zero anthropogenic greenhouse gas emissions will be required to meet any given commitment to 414 limit the global heating of Earth.

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416 **References**

- 418 1 Pan, Y. et al. A Large and Persistent Carbon Sink in the World's Forests. Science 333, 988419 993, doi:10.1126/science.1201609 (2011).
- 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).
- 422 3 Gaubert, B. et al. Global atmospheric CO₂ inverse models converging on neutral tropical land 423 exchange, but disagreeing on fossil fuel and atmospheric growth rate. Biogeosciences **16**,
- 424 117-134, doi:10.5194/bg-16-117-2019 (2019).

- 4 Huntingford, C. et al. Simulated resilience of tropical rainforests to CO₂-induced climate
 426 change. Nature Geoscience 6, 268-273, doi:10.1038/ngeo1741 (2013).
- 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).
- Brienen, R. J. W. et al. Long-term decline of the Amazon carbon sink. Nature 519, 344-348,
 doi:10.1038/nature14283 (2015).
- 432 7 Piao, S. et al. Evaluation of terrestrial carbon cycle models for their response to climate
 433 variability and to CO₂ trends. Global Change Biology 19, 2117-2132, doi:10.1111/gcb.12187
 434 (2013).
- Schimel, D., Stephens, B. B. & Fisher, J. B. Effect of increasing CO₂ on the terrestrial carbon 435 8 436 cycle. Proceedings of the National Academy of Sciences 112, 436-441, doi:10.1073/pnas.1407302112 (2015). 437
- Anderegg, W. R. L. et al. Tropical nighttime warming as a dominant driver of variability in
 the terrestrial carbon sink. Proceedings of the National Academy of Sciences 112, 1559115596, doi:10.1073/pnas.1521479112 (2015).
- 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).
- Lewis, S. L., Edwards, D. P. & Galbraith, D. Increasing human dominance of tropical forests.
 Science 349, 827-832, doi:10.1126/science.aaa9932 (2015).
- 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).
- Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. Nature 457,
 1003-1006, doi:10.1038/nature07771 (2009).

- 449 14 Phillips, O. L. et al. Drought sensitivity of the Amazon rainforest. Science 323, 1344-1347,
 450 doi:10.1126/science.1164033 (2009).
- 451 15 Qie, L. et al. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to 452 edge effects. Nature Communications **8**, 1966, doi:10.1038/s41467-017-01997-0 (2017).
- 453 16 Gatti, L. V. et al. Drought sensitivity of Amazonian carbon balance revealed by atmospheric
 454 measurements. Nature 506, 76-80, doi:10.1038/nature12957 (2014).
- Nemani, R. R. et al. Climate-driven increases in global terrestrial net primary production
 from 1982 to 1999. Science **300**, 1560-1563 (2003).
- 457 18 Keenan, T. F. et al. Recent pause in the growth rate of atmospheric CO₂ due to enhanced
 458 terrestrial carbon uptake. Nature Communications 7, 13428, doi:10.1038/ncomms13428
 459 (2016).
- Booth, B. B. B. et al. High sensitivity of future global warming to land carbon cycle
 processes. Environmental Research Letters 7, 024002 (2012).
- Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S. & Fisher, R. A. Temperature
 acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate
 feedback. Geophysical Research Letters 42, 8624-8631, doi:doi:10.1002/2015GL065934
 (2015).
- 466 21 Le Quéré, C. et al. Global Carbon Budget 2018. Earth Syst. Sci. Data 10, 2141-2194,
 467 doi:10.5194/essd-10-2141-2018 (2018).
- Lewis, S. L., Brando, P. M., Phillips, O. L., van der Heijden, G. M. F. & Nepstad, D. The
 2010 Amazon Drought. Science 331, 554 (2011).
- 470 23 Feldpausch, T. R. et al. Amazon forest response to repeated droughts. Global
 471 Biogeochemical Cycles 30, 964-982, doi:doi:10.1002/2015GB005133 (2016).
- 472 24 McDowell, N. et al. Drivers and mechanisms of tree mortality in moist tropical forests. New
 473 Phytologist 219, 851-869, doi:doi:10.1111/nph.15027 (2018).

- Aleixo, I. et al. Amazonian rainforest tree mortality driven by climate and functional traits.
 Nature Climate Change 9, 384-388, doi:10.1038/s41558-019-0458-0 (2019).
- 476 26 Lewis, S. L. et al. Concerted changes in tropical forest structure and dynamics: evidence from
- 477 50 South American long-term plots. Philosophical Transactions of the Royal Society of
 478 London Series B-Biological Sciences 359, 421-436 (2004).
- 479 27 Lewis, S. L. et al. Above-ground biomass and structure of 260 African tropical forests.
 480 Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120295481 20120295, doi:10.1098/rstb.2012.0295 (2013).
- 482 28 Quesada, C. A. et al. Basin-wide variations in Amazon forest structure and function are
 483 mediated by both soils and climate. Biogeosciences 9, 2203-2246, doi:10.5194/bg-9-2203484 2012 (2012).
- 485 29 Malhi, Y. et al. The above-ground coarse wood productivity of 104 Neotropical forest plots.
 486 Global Change Biology 10, 563-591 (2004).
- 487 30 Galbraith, D. et al. Residence times of woody biomass in tropical forests. Plant Ecology &
 488 Diversity 6, 139-157, doi:10.1080/17550874.2013.770578 (2013).
- 489 31 Reich, P. B. et al. Boreal and temperate trees show strong acclimation of respiration to
 490 warming. Nature 531, 633-636, doi:10.1038/nature17142 (2016).
- 491 32 ter Steege, H. et al. Continental-scale patterns of canopy tree composition and function across
 492 Amazonia. Nature 443, 444-447 (2006).
- Bauters, M. et al. High fire-derived nitrogen deposition on central African forests.
 Proceedings Of The National Academy Of Sciences Of The United States Of America 115,
 549-554, doi:10.1073/pnas.1714597115 (2018).
- 496 34 Parmentier, I. et al. The odd man out? Might climate explain the lower tree alpha-diversity of
 497 African rain forests relative to Amazonian rain forests? Journal of Ecology **95**, 1058-1071
 498 (2007).

- Slik, J. W. F. et al. Phylogenetic classification of the world's tropical forests. Proceedings of
 the National Academy of Sciences 115, 1837-1842, doi:10.1073/pnas.1714977115 (2018).
- 501 36 Phillips, O. L. et al. Increasing dominance of large lianas in Amazonian forests. Nature 418,
 502 770-774 (2002).
- Schnitzer, S. A. & Bongers, F. Increasing liana abundance and biomass in tropical forests:
 emerging patterns and putative mechanisms. Ecology Letters 14, 397-406,
 doi:10.1111/j.1461-0248.2011.01590.x (2011).
- Meinshausen, M. et al. The RCP greenhouse gas concentrations and their extensions from
 1765 to 2300. Climatic Change 109, 213-241, doi:10.1007/s10584-011-0156-z (2011).
- 508 39 Terrer, C. et al. Nitrogen and phosphorus constrain the CO₂ fertilization of global plant 509 biomass. Nature Climate Change, doi:10.1038/s41558-019-0545-2 (2019).
- 510 40 Fleischer, K. et al. Amazon forest response to CO₂ fertilization dependent on plant 511 phosphorus acquisition. Nature Geoscience **12**, 736-741, doi:10.1038/s41561-019-0404-9 512 (2019).
- Jiang, Y. et al. Widespread increase of boreal summer dry season length over the Congo
 rainforest. Nature Climate Change 9, 617-622, doi:10.1038/s41558-019-0512-y (2019).
- Gloor, M. et al. Recent Amazon climate as background for possible ongoing and future
 changes of Amazon humid forests. Global Biogeochemical Cycles 29, 1384-1399,
 doi:10.1002/2014gb005080 (2015).
- Kolby Smith, W. et al. Large divergence of satellite and Earth system model estimates of
 global terrestrial CO₂ fertilization. Nature Climate Change 6, 306, doi:10.1038/nclimate2879
 (2015).
- 44 Chen, C. et al. China and India lead in greening of the world through land-use management.
 522 Nature Sustainability 2, 122-129, doi:10.1038/s41893-019-0220-7 (2019).

- 523 45 Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V. & Melack, J. M. Decomposition
 524 and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122,
 525 380-388 (2000).
- 46 Hansen, M. C. et al. High-Resolution Global Maps of 21st-Century Forest Cover Change.
 527 Science 342, 850-853, doi:10.1126/science.1244693 (2013).
- 47 Pearson, T. R. H., Brown, S., Murray, L. & Sidman, G. Greenhouse gas emissions from
 529 tropical forest degradation: an underestimated source. Carbon Balance and Management 12,
 530 3, doi:10.1186/s13021-017-0072-2 (2017).
- Schwartz, N. B., Uriarte, M., DeFries, R., Gutierrez-Velez, V. H. & Pinedo-Vasquez, M. A.
 Land-use dynamics influence estimates of carbon sequestration potential in tropical secondgrowth forest. Environmental Research Letters 12, 074023, doi:10.1088/1748-9326/aa708b
 (2017).
- Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A. & Koch, A. Regenerate natural forests to
 store carbon. Nature 568, 25-28 (2019).
- 537 50 Yu, K. et al. Pervasive decreases in living vegetation carbon turnover time across forest 538 climate zones. Proceedings of the National Academy of Sciences, 201821387, 539 doi:10.1073/pnas.1821387116 (2019).
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- 669 R.J.W.B., T.R.F. and M.J.P.S. developed it. W.H., M.J.P.S., S.L.L., O.L.P., R.J.W.B., A.L., G.L.-G.,
- 670 A.E.-M., A.K., E.G., T.R.B., A.C.B. and G.C.P. contributed analysis tools. W.H. and S.L.L. analysed
- 671 the data (with important contributions from M.J.P.S.). S.L.L. and W.H. wrote the paper. All co-

authors read and approved the manuscript (with important insights provided by O.L.P., S.F.,
R.J.W.B., E.G., H.B., D.S., M.J.P.S., S.G.-F., P.B., H.V. and S.C.T).

- 674
- 675 Main Figures

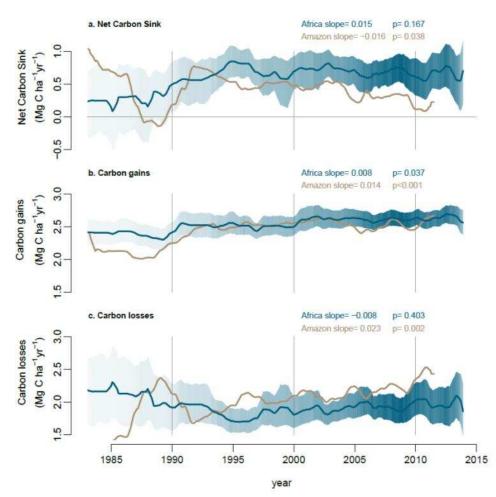


Figure 1. Long-term carbon dynamics of structurally intact tropical forests in Africa (blue) 677 678 and Amazonia (brown). Trends in net aboveground live biomass carbon sink (a), carbon gains to the system from wood production (**b**), and carbon losses from the system from tree mortality (**c**), 679 measured in 244 African inventory plots (blue lines) and contrasting published⁶ Amazonian 680 681 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 25 682 683 plots monitored). The CI for the Amazonian dataset is omitted for clarity, but can be seen in Figure 3. Slopes and p-values are from linear mixed effects models (see Methods). 684

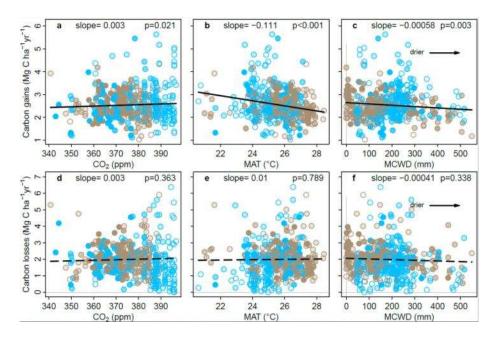
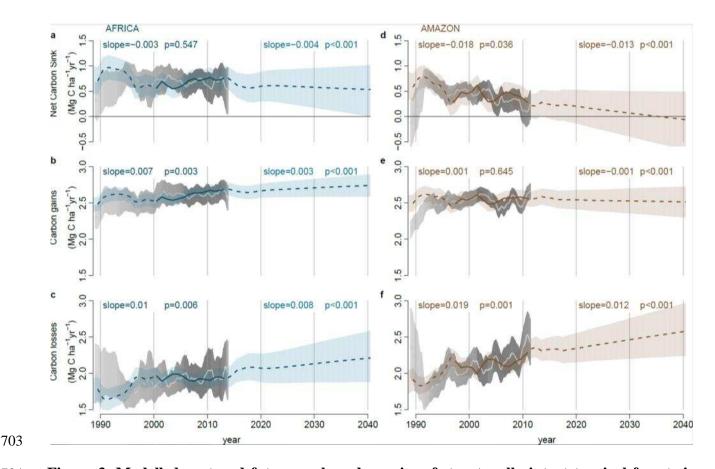


Figure 2. Potential environmental drivers of carbon gains and losses in structurally intact old-686 687 growth African and Amazonian tropical forests. Aboveground carbon gains, from woody production (a-c), and aboveground carbon losses, from tree mortality (d-f), presented as time-688 weighted mean values for each plot, i.e. each census within a plot is weighted by its length, against 689 690 the corresponding values of atmospheric carbon dioxide concentration (CO₂), mean annual air temperature (MAT) and drought (as Maximum Climatological Water Deficit, MCWD), for African 691 (blue) and Amazonian (brown) inventory plots. Each data point therefore represents an inventory 692 plot, for visual clarity, and the level of transparency represents the total monitoring length, with 693 empty circles corresponding to plots monitored for ≤ 5 years and solid circles for plots monitored for 694 695 >20 years. Solid lines show significant trends, dashed lines non-significant trends calculated using 696 linear mixed effect models with census intervals (n=1566) nested within plots (n=565), using an empirically derived weighting based on interval length and plot area, on the untransformed pooled 697 698 Africa and Amazon dataset (see Methods). Slopes and p-values are from the same linear mixed effects models. Carbon loss data and models are presented untransformed for comparison with 699 700 carbon gains, but transformation is needed to fit normality assumptions; linear mixed effects models 701 on transformed carbon loss data does not change the significance of the results, nor does including 702 all three parameters and transformed data in a model (see Extended Data Table 1).



704 Figure 3. Modelled past and future carbon dynamics of structurally intact tropical forests in 705 Africa and Amazonia. Predictions of net aboveground live biomass carbon sink (a,d), carbon gains 706 (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, 707 708 drought (as Maximum Climatological Water Deficit), plot wood density, and plot carbon residence 709 time, using observations in Africa until 2014 and Amazonia until 2011.5, and extrapolations of prior 710 trends to 2040. 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 711 712 observed trends, and shading showing upper and lower confidence intervals accounting for uncertainties in the model (both fixed and random effects) and uncertainties in the predictor 713 714 variables. Light grey lines and grey shading are the mean and 95% CI of the observations from the African and Amazonian plot networks. 715

716 Main Tables

717

718 Table 1. Carbon sink in intact forests in Africa, Amazonia and the pan-tropics: 1980-2015 and

719 predictions to 2040. Mean values in bold, future predictions in italics, uncertainty in parentheses,

720 95% bootstrapped confidence intervals for 1980-2015, and 2σ for the predictions (2010-2040).

Period	No.		Per unit area a	boveground live	biomass C sink	Total C sink *			
	plots			(Mg C ha ⁻¹ yr ⁻¹)			(Pg C yr ⁻¹)		
	Af.	Am.	Africa	Amazon	Pan-tropics†	Africa	Amazon	Pan-tropics [†]	
1980-1990	45	73	0.33 (0.06-0.63)	0.35 (0.06-0.59)	0.35 (0.07-0.62)	0.28 (0.05-0.53)	0.49 (0.08-0.82)	0.87 (0.16-1.52)	
1990-2000	96	172	0.67 (0.43-0.89)	0.53 (0.42-0.65)	0.57 (0.39-0.74)	0.50 (0.32-0.66)	0.68 (0.54-0.83)	1.26 (0.88-1.63)	
2000-2010	194	291	0.70 (0.55-0.84)	0.38 (0.26-0.48)	0.50 (0.35-0.64)	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 (0.15-0.65)	0.40 (0.24-0.56)	0.27 (0.00-0.52)	0.73 (0.25-1.18)	
2010-2020 ‡	-	-	0.63 (0.36-0.89)	0.23 (-0.05-0.50)	0.38 (0.11-0.65)	0.37 (0.21-0.53)	0.25 (-0.05-0.54)	0.68 (0.17-1.16)	
2020-2030 :	: -	-	0.59 (0.24-0.93)	0.12 (-0.29-0.51)	0.30 (-0.08-0.67)	0.31 (0.13-0.49)	0.12 (-0.29-0.52)	0.47 (-0.15-1.07)	
2030-2040 :	: -	-	0.55 (0.08-0.99)	0.00 (-0.54-0.49)	0.21 (-0.29-0.67)	0.26 (0.04-0.47)	0.00 (-0.50-0.46)	0.29 (-0.46-0.97)	

* Total Continental C sink is the per unit area aboveground C sink multiplied by intact forest area for
1990-2010 (from ref.¹, see Extended Data Table 2) and continent specific extrapolations to 2040.
Total Continental C sink includes continent-specific estimates of trees <100 mm DBH, lianas and
roots (see Methods).

725 [†] Pan-tropical aboveground live biomass C sink is the area-weighted mean of African, Amazonian and Southeast Asian sink values. Southeast Asian values were from published per unit area carbon 726 sink data¹⁵ (n=49 plots) for 1990-2015, with 1980-1990 assumed to be the same as 1990-2000 due 727 728 very low sample sizes. Pan-tropical total C sink is the sum of African, Amazonian and Southeast 729 Asian total continental carbon sink values. The continental sink in Southeast Asia is a modest and 730 declining contribution to the pan-tropical sink, due to the very small area of intact forest remaining, at 0.11, 0.08, 0.07 and 0.06 Pg C yr⁻¹ in the 1980s, 1990s, 2000s and 2010s, hence uncertainty in the 731 Southeast Asian sink cannot reverse the pan-tropical declining sink trend. 732

⁷³³ ‡ Per unit area total C sink for 2010-2020, 2020-2030 and 2030-2040 was predicted using parameters
⁷³⁴ from Table 2, except for the 2010-2020 sink in Africa which is the mean of the measured sink from
⁷³⁵ 2010-2015 and the modelled sink from 2015-2020. For the Asian sink we assumed the parameters as
⁷³⁶ for Africa, as Asian forest median CRT is 61 years, close to African median, 63 years.

738 Table 2. Minimum adequate models to predict carbon gains and losses in African and

739 Amazonian tropical forests. These are the best ranked gains and loss models. Where continental

Carbon going Mg C ha⁻¹ un⁻¹

	(Carbon gains,	, Mg C ha	'yr'		
Predictor variable	Parameter	Standard	t-value	p-value	2000-2015 change in gains	
	value	Error			(%) *	
(Intercept)	5.255 5.395	0.603 0.614	4 8.7 8.8	< 0.001	-	
CO ₂ -change (ppm yr ⁻¹) †	0.238	0.096	2.5	0.013	3.69% 3.71%	
MAT (°C)	-0.083	0.025	-3.3	0.001	-0.67% -1.07%	
MAT-change (°C yr ⁻¹) ‡	-1.243	0.233	-5.3	< 0.001	0.58% 0.00% §	
MCWD (mm x1000)	-0.405 -1.39	1 0.381 0.24	-1.1 -5.8	8 0.289 <0.001	-0.52% -2.73%	
WD (g cm ⁻³)	-1.295	0.530	-2.4	0.015	$0.05\% \mid 0.00\%$	
	C	arbon losses,	Mg C ha ⁻¹	yr-1		
Predictor variable	Parameter	Standard	t-value	p-value	2000-2015 change in losses	
	value	Error			(%) *	
(Intercept)	1.216	0.086	14.1	< 0.001	-	
CO ₂ -change (ppm yr ⁻¹) †	0.130	0.059	2.2	0.026	11.38% 14.81%	
MAT-change (°C yr ⁻¹)	0.766	0.162	4.7	< 0.001	-1.56% 0.00%	
MCWD (mm x10000) ‡	-0.232	0.107	-2.2	0.030	-1.21% -2.42%	
CRT (yr)	-0.003	0.001	-6.1	< 0.001	-0.57% 1.39%	

values differ, those for Africa are reported first, followed by Amazonian values.

* 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.

744 † Change over the past 56 years.

745 ‡ Change over the past 5 years.

⁷⁴⁶ § A positive value for Africa indicates that MAT increased more slowly over 2000-2015 compared

to the mean increase over 1983-2015, therefore contributing to an increase in gains; a zero value fpr

748 Amazonia indicates that the rate of MAT increase was the same over 2000-2015 as the mean

749 increase over 1983-2015.

750 || Carbon loss values were normalized via power-law transformation, $\lambda = 0.361$.

752 **Online Methods**

753

754 **Plot Selection**

755 Closed canopy (i.e. not woody savanna) old-growth mixed-age forest inventory plots were selected using commonly used criteria^{6,13,27}: free of fire and industrial logging; all trees with diameter at 756 757 reference height ≥100 mm measured at least twice; ≥0.2 ha area; <1500 m.a.s.l. altitude; MAT \geq 20.0°C⁵¹; annual precipitation \geq 1000 mm⁵¹; located \geq 50 m from anthropogenic forest edges. Of the 758 244 plots included in the study, 217 contribute to the African Tropical Rainforest Observatory 759 Network (AfriTRON; www.afritron.org), with data curated at www.ForestPlots.net^{52,53}. These 760 include plots from Sierra Leone, Liberia, Ghana, Nigeria, Cameroon, Gabon, Republic of Congo, 761 Democratic Republic of Congo (DRC), Uganda and Tanzania^{52,53} (Extended Data Figure 1). Fifteen 762 plots are part of the TEAM network, from Cameroon, Republic of Congo, Tanzania, and Uganda⁵⁴⁻ 763 ⁵⁷. Nine plots contribute to the ForestGEO network, from Cameroon and DRC⁵⁸ (9 plots from DRC, 764 codes SNG, contribute to both AfriTRON and ForestGEO networks, included above in the 765 766 AfriTRON total). Finally, three plots from Central African Republic are part of the CIRAD network^{59,60}. The large majority of plots are sited in terra firme forests and have mixed species 767 768 composition, although four are in seasonally flooded forest and 14 plots are in Gilbertiodendron 769 dewevrei monodominant forest, a locally common forest type in Africa (Supplementary Table 1). 770 The 244 plots have a mean size of 1.1 ha (median, 1 ha), with a total plot area of 277.9 ha. The 771 dataset comprises 391,968 diameter measurements on 135,625 stems, of which 89.9% were 772 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 773 plots are published and were selected using the same criteria⁶, except in the African selection criteria 774 we specified a minimum anthropogenic edge distance and added a minimum temperature threshold. 775

777 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 density⁶¹. The calculation of each is discussed in turn. All calculations were performed using the R statistical platform, version 3.2.1 (ref.⁶²) using the BiomasaFP R package, version 0.2.1 (ref.⁶³).

782

783 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, 784 mapped and identified using standard forest inventory methods^{64,65}. The height of the point of 785 786 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 787 788 potentially disturb the initial POM, the POM was raised approximately 500 mm above the deformity. 789 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^{6,13,65}. We used 790 791 standardised 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. 792 793 Where necessary we estimated the likely value via interpolation or extrapolation from other 794 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 mm⁶⁵. 795 796 We interpolated measurements for 1.3% of diameters, extrapolated 0.9%, and used median growth 797 rates for 1.5%.

798

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 selected⁶⁶. In most plots, 802 803 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 804 500+ mm trees, following standard protocols⁶⁶. We measured actual height of 24,270 individual trees 805 from 204 plots. We used these data and the local.heights function in R package BiomasaFP⁶³ to fit 3-806 parameter Weibull relationships: $H_t=a \times (1-e^{((-b \times (DBH/10)^c))})$ (equation 1). We chose the Weibull 807 model as it is known to be robust when a large number of measurements are available^{66,67}. We 808 parameterised separate H_t-DBH relationship for four different combinations of edaphic forest type 809 810 and biogeographical region: (i) terra firme forest in West Africa, (ii) terra firme forest in Lower 811 Guinea and Western Congo Basin, (iii) terra firme forest in Eastern Congo Basin and East Africa, 812 (iv) seasonally flooded forest from Lower Guinea and Western Congo Basin (there were no seasonally flooded forest plots in the other biogeographical regions). The parameters are: (i) terra 813 814 firme forest in West Africa, a=56.0; b=0.0401; c=0.744; (ii) terra firme forest in Lower Guinea and Western Congo Basin, a=47.6; b=0.0536; c=0.755; (iii) terra firme forest in Eastern Congo Basin 815 816 and East Africa, a=50.8; b=0.0499; c=0.706; and finally (iv) seasonally flooded forest from Lower 817 Guinea and Western Congo Basin, a=38.2; b=0.0605; c=0.760. For each of these combinations of forest type and bioregion, the local heights function combines all height measurements from all plots 818 819 belonging to that forest type/bioregion and fits the Weibull model parameters using non-linear least 820 squares (nls function in R with default settings), with starting values of a = 25, b = 0.05 and c = 0.7821 chosen as they led to regular model convergence. We fitted these models either treating each 822 observation equally or with case weights proportional to each trees' basal area. These weights give 823 more importance to large trees during model fitting. We selected the best fitting of these models, 824 determining this as the model that minimised prediction error of stand biomass when calculated with 825 estimated heights or observed heights. The parameters were used to estimate H_t from DBH for all tree DBH measurements for input into the allometric equation. Mean measured individual total tree 826

height is 20.5 m; the height range is 1.5 to 72.5 m. The root mean squared error (RMSE) between the
full dataset of measured heights and the predicted heights, is 5.7 m, which is 8.0% of the total range.
Furthermore, RMSE is 5.3 m in terra firme forest in West Africa (7.5% of the range; n=9771 trees);
RMSE is 6.4 m in terra firme forest in Lower Guinea and Western Congo Basin (8.7% of the range; n=10,838 trees); RMSE is 4.8 m in terra firme forest in Eastern Congo Basin and East Africa (8.8% of the range; n=3269 trees); and RMSE is 4.1 m in seasonally flooded forest from Lower Guinea and Western Congo Basin (12.5% of the range; n=392 trees).

834

835 Wood Density: Dry wood density (p) measurements were compiled for 730 African species from published sources and stored in www.ForestPlots.net; most were sourced from the Global Wood 836 Density Database on the Dryad digital repository (<u>www.datadryad.org</u>)^{68,69}. Each individual in the 837 838 tree inventory database was matched to a species-specific mean wood density value. Species in both 839 the tree inventory and wood density databases were standardized for orthography and synonymy using the African Plants Database (www.ville-ge.ch/cjb/bd/africa/) to maximize matches¹³. For 840 841 incompletely identified individuals or for individuals belonging to species not in the p database, we 842 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 843 trees in the plot 13,52 . 844

845

Allometric equation: For each tree we used a published allometric equation⁶¹ to estimate aboveground biomass. We then converted this to carbon, assuming that aboveground carbon (AGC) is 45.6% of aboveground biomass⁷⁰. Thus: AGC= $0.456 \times (0.0673 \times (\rho \times (DBH/10)^2 \times H_t)^{0.976})/1000$ (equation 2), with DBH in mm, dry wood density, ρ , in g cm⁻³, and total tree height, H_t, in m (ref.⁶¹).

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

853

854 Carbon Gain and Carbon Loss estimation

Net Carbon Sink (in Mg C ha⁻¹ yr⁻¹) is estimated as carbon gains minus carbon losses. Calculation
details are explained below.

857

Carbon Gains (in Mg C ha⁻¹ yr⁻¹) are the sum of the aboveground live biomass carbon additions from 858 859 the growth of surviving stems and the addition of newly recruited stems, divided by the census length (in years) and plot area (in hectares). For each stem that survived a census interval, carbon 860 additions from its growth (Mg C ha⁻¹ yr⁻¹) were calculated as the difference between its AGC at the 861 862 end census of the interval and its AGC at the beginning census of the interval. For each stem that 863 recruited during the census interval (i.e. reaching DBH≥100 mm), carbon additions were calculated in the same way, assuming DBH=0 mm at the start of the interval⁶⁵. Carbon Losses (in Mg C ha⁻¹ yr⁻ 864 865 ¹) are estimated as the sum of aboveground biomass carbon from all stems that died during a census interval, divided by the census length (in years) and plot area (in hectares). Both carbon gains and 866 carbon losses are calculated using standard methods⁶, including a census interval bias correction, 867 using the SummaryAGWP function of R-package BiomasaFP^{63,64,68}. 868

869

As carbon gains are affected by a census interval bias, with the underestimate increasing with census length, we corrected this bias by accounting for (i) the carbon additions from trees that grew before they died within an interval (unobserved growth) and (ii) the carbon additions from trees that recruited and then died within the same interval (unobserved recruitment)^{65,71}.

875 Component (i), the unobserved growth of a stem that died during a census interval, is estimated as the difference between AGC at death and AGC at the start of the census. These are calculated using 876 equation 2, from respectively DBH_{death} and DBH_{start}. The latter is part of the data, the first can be 877 878 estimated as: $DBH_{death} = DBH_{start} \times G \times Y_{mean}$, where G is the plot-level median diameter growth rate (mm yr⁻¹) of the size class the tree was in at the start of the census interval (size classes are defined 879 as D < 200 mm, 400 mm > D \ge 200 mm and D \ge 400 mm) and Y_{mean} is the mean number of years 880 881 trees survived in the census interval before dying. Y_{mean} is calculated from the number of trees that are expected to have died in each year of the census interval, which is derived from the plot-level 882 per-capita mortality rate (m_a ; % dead trees yr⁻¹) calculated following equation 5 in ref.⁷¹. 883

884

Component (ii), growth of recruits that were not observed because they died during the census 885 886 interval, is estimated by calculating the number of unobserved recruits and diameter at death for each unobserved recruit. The number of unobserved recruits (stems ha⁻¹ yr⁻¹) is estimated as: $N_{u,r} = R_a - R_a$ 887 $P_{surv} \times R_a$, where R_a (recruited stems ha⁻¹ yr⁻¹) is the per area annual recruitment calculated following 888 equation 11 in ref.⁷¹ and P_{surv} is the probability of each recruit surviving until the next census: $P_{surv} =$ 889 $(1-m_a)^T$, where T is the number of years remaining in the census interval. Summing N_{u.r} for each year 890 in a census interval gives the total number of unobserved recruits in that census interval. We then 891 estimate diameter at death for each unobserved recruit, which is given in mm by $DBH_{death,u,r} = 100 +$ 892 $(G_s \times Y_{mean-rec})$, where G_s is the plot-level median diameter growth rate (mm yr⁻¹) of the smallest size 893 894 class (i.e. D < 200 mm) and $Y_{mean-rec}$ is the mean life-span of unobserved recruits calculated as the mean life-span of recruits in a given year, weighted by Nur. The mean life-span of recruits in a given 895 year is calculated from the number of recruits that died in that year, which is derived from the plot-896 level per-capita mortality rate (m_a ; % dead trees yr⁻¹). Growth of each unobserved recruit (mm yr⁻¹) is 897 898 then calculated as DBH_{death,u,r} divided by Y_{mean-rec}.

The census interval bias correction (components i and ii together) typically add <3% to plot-level carbon gains. Carbon Losses are 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^{6,15,63}. These two components are calculated in the same way as for Carbon gains and typically add <3% to plot-level carbon losses.

906

Carbon gains include both gains from the growth of surviving stems and new recruits. Separating 907 908 carbon gains from tree growth of surviving stems and newly recruited stems, shows that carbon gains 909 from recruitment are small overall, and are significantly lower in Africa than in the Amazon, likely 910 due to the lower stem turnover rates and longer carbon residence time (Africa: 0.17 Mg C ha⁻¹ yr⁻¹; CI: 0.16-0.18 versus Amazon: 0.27 Mg C ha⁻¹ yr⁻¹; CI: 0.25-0.28, p<0.001; two-way Wilcoxon test), 911 912 but this is compensated by carbon gains from survivors being significantly larger in Africa (2.33 Mg C ha⁻¹ yr⁻¹; CI: 2.27-2.39) than in the Amazon (2.13 Mg C ha⁻¹ yr⁻¹; CI: 2.09-2.17, p=0.014). 913 914 Therefore, gains overall (sum of gains from surviving stems and newly recruited stems) are indistinguishable between the continents (Africa: 2.57 Mg C ha⁻¹ yr⁻¹; CI: 2.51-2.67 vs Amazon: 2.46 915 Mg C ha⁻¹ yr⁻¹; CI: 2.41-2.50, p=0.460; two-way Wilcoxon test). 916

917

918 Long-term Gain, Loss and Net Carbon Sink Trend Estimation, 1983-2014

The estimated mean and uncertainty in carbon gains, carbon losses and the net carbon sink of the African plots from 1983-2014 (Figure 1, Extended Data Figure 7 and Extended Data Figure 8) 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 calculated a weighted mean of all plots monitored at that time, using the square root of plot area as a weighting factor⁶. Confidence intervals for each 0.1yr period were bootstrapped.

926

927 Trends in carbon gains, losses and the net carbon sink over time were assessed using linear mixed effects models (lmer function in R, lme4 package⁷²), providing the linear slopes reported in Figure 1. 928 These models regress the mid-point of each census interval against the value of the response variable 929 930 for that census interval. Plot identity was included as a random effect, i.e. assuming that the intercept 931 can vary randomly among plots. We did not include slope as a random effect, consistent with previously published Amazon analyses⁶, because models did not converge due to some plots having 932 933 too few census intervals. Observations were weighted by plot size and census interval length. 934 Weightings were derived empirically, by assuming a priori that there is no significant relation 935 between the net carbon sink and census interval length or plot size, following ref.¹³. The following weighting removes all pattern in the residuals: Weight= $\sqrt[3]{length_{int}} + \sqrt[4]{plotsize} -1$ (equation 3), 936 where length_{int} is the length of the census interval, in years. Significance was assessed by regressing 937 938 the residuals of the net carbon sink model against the weights (p=0.702).

939

Differences in long-term slopes between the two continents for carbon gains, carbon losses and net 940 carbon sink, reported in the main text, were also assessed using linear mixed effects models, as 941 942 described above, but performed on the combined African and Amazonian datasets and limited to 943 their common time window, 1983 to 2011.5. For these three tests on the pooled data we included an 944 additional interaction term between census interval date and continent, where a significant interaction would indicate that the slopes differ between continents. The statistical significance of 945 946 continental differences in slope were assessed using the F-statistic (Anova function in R, car package⁷³). Shortening the common time window to the 20 years when the continents are best-947 948 sampled, 1991.5 to 2011.5, gave very similar results, including a divergent continental sink (p=0.04).

950 Continental and Pan-Tropical Carbon Sink Estimates

The per unit area total net carbon sink (in Mg C ha⁻¹ yr⁻¹) for each time period in Table 1 (each 951 decade between 1980 and 2010; and 2010-2015) is the sum of three components. The first 952 953 component is the per unit area aboveground carbon sink from living trees and lianas with DBH > 100 954 mm. For Africa we use the per unit area net carbon sink values presented in this paper. For Amazonia, we use data in ref.⁶. For Southeast Asia, we use inventory data collected using similar 955 standardised methods from 49 plots in ref.¹⁵. For each time window, we use all plots for which 956 957 census dates overlap the period, weighted by the square root of plot area, as for the solid lines in Figure 1. The second component is the per unit area aboveground carbon sink from living trees and 958 959 lianas with DBH<100 mm. This is calculated as 5.19%, 9.40% and 5.46% of the first component (i.e. aboveground carbon of large living trees) in Africa, Amazonia and Southeast Asia respectively^{13,74}. 960 The third component is the per unit area belowground carbon sink in live biomass, i.e. roots. This is 961 962 calculated as 25%, 37% and 17% of the aboveground carbon of living trees with DBH≥100 mm in Africa¹³, Amazonia⁶ and Southeast Asia⁷⁵ respectively. 963

964

For each time period in Table 1 we calculated the continental-scale total carbon sink (Pg C yr⁻¹) by multiplying the per unit area total net carbon sink described above by the area of intact forest on each continent at that time interval (in ha) reported in Extended Data Table 2. Decades are calculated from 1990.01 to 1999.99. 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.

972

973 Finally, in the main text we calculated the proportion of anthropogenic CO₂ emissions removed by Earth's
974 intact tropical forests, as the total pan-tropical carbon sink from Table 1 divided by the total anthropogenic

975 CO_2 emissions. Total anthropogenic CO_2 emissions are calculated as the sum of emissions from fossil fuel and 976 land-use change and are estimated at 7.6 Pg C yr⁻¹ in the 1990s, 9.0 Pg C yr⁻¹ in the 2000s, and 11.1 Pg C yr⁻¹ 977 in the 2010s (ref.²¹, assuming 1.7% growth in fossil fuel emissions in 2018 and 2019, and mean 2010-2017 978 land-use change emissions for 2018 and 2019).

979

980 Carbon Sink from an Atmospheric Perspective

981 To estimate the evolution of the carbon sink from an atmospheric perspective, we assumed that the 982 contribution to the atmosphere from carbon gains are experienced immediately, while the 983 contribution to the atmosphere from carbon losses must take into account the delay in decomposition of dead trees. We did this by calculating total forest carbon loss (Mg C ha⁻¹ yr⁻¹) for each year 984 985 between 1950-2015, using the mean 1983-2015 records from Figure 1 and assuming constant losses prior to 1983 (1.9 and 1.5 Mg C ha⁻¹ yr⁻¹ for Africa and Amazonia respectively). Then, for each focal 986 year between 1950-2015, we calculated how much carbon was released to the atmosphere in the 987 subsequent years as: $y_t = x_0 \times e^{-0.17 \times (t-1)} - x_0 \times e^{-0.17 \times t}$, where x_0 is the total forest carbon loss of the 988 focal year; y_t is the carbon released to the atmosphere at t years from the focal year; and -0.17 yr⁻¹ is 989 a constant decomposition rate calculated for tropical forests in the Amazon⁴⁵. For example, carbon 990 loss was 1.95 Mg C ha⁻¹ in 1990 in African forests (Figure 1), from which 0.31 Mg C ha⁻¹ was 991 released to the atmosphere in 1991; 0.26 Mg C ha⁻¹ in 1992; 0.22 Mg C ha⁻¹ in 1993; 0.07 Mg C ha⁻¹ 992 in 2000 and 0.01 Mg C ha⁻¹ in 2010. Hence, of the full 1.95 Mg C ha⁻¹ dead tree biomass from 1990, 993 ~50% was released to the atmosphere after 4 yrs, ~85% after 10 yrs, and ~97% after 20 years. 994 995 Finally, for each year between 1983 and 2015, the total contribution to the atmosphere from carbon losses was calculated as the sum of all carbon contributions released at that year, from all total yearly 996 997 forest carbon loss pools of the previous years. We then calculated decadal-scale mean contributions 998 to the atmosphere from carbon losses, reported in the main text.

1000 Predictor Variable Estimates, 1983-2014

1001 For each census interval of each plot, we examined potential predictor variables that may explain the long-term trends in carbon gains and carbon losses, reported in Extended Data Table 1 and main text 1002 1003 Table 2. First, the environmental conditions during the census interval; second the rate of change of 1004 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 1005 1006 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: 1007 1008 (i) the length of each focal census interval was rounded to the nearest complete year (e.g. a 1.1 year 1009 interval became a 1 year interval); (ii) we computed dates that minimised the difference between 1010 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 1011 1012 used to calculate interval-specific means for each environmental predictor variable to remove 1013 seasonal effects. The mean difference between the actual fieldwork dates and the complete-year 1014 census dates is 0.01 decimal years.

1015

1016 The first group of potential predictor variables, estimated for each census interval of each plot, are 1017 theory-driven choices: atmospheric CO₂ concentration (CO₂), mean annual temperature (MAT), and 1018 drought intensity, which we quantified as maximum climatological water deficit (MCWD)^{14,20,76,77}.

1019

1020 Atmospheric CO₂ concentration (CO₂, in ppm) is estimated as the mean of the monthly mean values 1021 from the Mauna Loa record⁷⁸ over the census interval. While atmospheric CO₂ concentration is 1022 highly correlated with time (R^2 =0.98), carbon gains are slightly better correlated with CO₂ 1023 (R_{adj}^2 =0.0027) than with time (R_{adj}^2 =0.0025).

Mean Annual Temperature (MAT, in °C) was derived from the temporally resolved (1901-2015) dataset of monthly mean temperature from the Climatic Research Unit (CRU TS version 4.03; ~3025 km^2 resolution; released 15 May 2019; https://crudata.uea.ac.uk/cru/data/hrg/)⁷⁹. We downscaled the data to ~1 km² resolution using the WorldClim dataset^{51,80}, by subtracting the difference in mean monthly temperature, and applying this monthly correction to all months⁸¹. We then calculated MAT for each census interval of each plot using the downscaled monthly CRU record.

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1032 Maximum Climatological Water Deficit (MCWD, in mm) was derived from the ~3025 km² 1033 resolution Global Precipitation Climatology Centre dataset (GPCC version 6.0) that includes many more rain gauges than CRU in tropical Africa^{82,83}. As GPCC ends in 2013 we combined it with 1034 1035 satellite-based Tropical Rainfall Measurement Mission data (TRMM 3B43 V7 product, ~757 km² 1036 resolution)⁸⁴. The fit for the overlapping time period (1998-2013) was used to correct the systematic difference between GPCC and TRMM: GPCC' = a+b*GPCC, with GPCC' the adjusted GPCC 1037 1038 record and a and b different parameters for each month of the year and for each continent. Precipitation was then downscaled to $\sim 1 \text{ km}^2$ resolution using the WorldClim dataset^{51,80}, by dividing 1039 by the ratio in mean monthly rainfall, and applying this monthly correction to all months⁸¹. For each 1040 1041 census interval we extracted monthly precipitation values and estimated evapotranspiration (ET) to calculate monthly Climatological Water Deficit (CWD), a commonly used metric of dry season 1042 intensity for tropical forests^{14,76,77}. Monthly CWD values were calculated for each subsequent series 1043 1044 of 12 months (complete years)⁷⁷. Monthly CWD estimation begins with the wettest month of the first 1045 year in the interval, and is calculated as 100 mm per month evapotranspiration (ET) minus monthly 1046 precipitation (P). Then, CWD values for the subsequent 11 months were calculated recursively as: $CWD_i = ET - P_i + CWD_{i-1}$, where negative CWD_i values were set to zero⁷⁷ (no drought conditions). 1047 This procedure was repeated for each subsequent complete 12 months. We then calculated the annual 1048 1049 MCWD as the largest monthly CWD value for every complete year within the census interval, with the MCWD of a census interval being the mean of the annual MCWD values within the censusinterval. Larger MCWD indicates more severe water deficits.

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We assume ET is 100 mm month⁻¹ on both continents, based on measurements from Amazonia^{76,77}, more limited measurements from West Africa summarized in ref.⁸⁵, predictive skill⁸⁶, and use in past studies on both continents^{14,87}. MCWD therefore represents a precipitation-driven dry season deficit, as ET remains constant. An alternative assessment, using a data-driven ET product^{88,89}, gave a mean ET of 95 and 98 mm month⁻¹ for the African and Amazonian plot networks respectively. Using these values did not affect the results.

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1060 To calculate the environmental change of potential predictor variables, CO₂-change (in ppm yr⁻¹), MAT-change (in °C yr⁻¹) and MCWD-change (in mm yr⁻¹), we selected an optimum period over 1061 1062 which to calculate the change, derived empirically by assessing the correlation of carbon gains (all plots, all censuses) with the change in each environmental variable, using linear mixed effects 1063 models (Imer function in R, Ime4 package⁷²). The annualised change in the environmental variable 1064 1065 was calculated as the change between the focal interval and a prior interval (termed the baseline period) with a lengthening time window ranging from 1 year through to 80 years prior to the focal 1066 interval (i.e. 80 linear mixed effects models per variable). We calculated AIC for each model and 1067 selected the interval length with the lowest AIC. Thus, MAT-change (in $^{\circ}C$ yr⁻¹) = (MAT_i-1068 1069 $MAT_b)/(date_i-date_b)$, where MAT_i is the MAT over the focal census interval calculated using the 1070 procedure described above, MAT_b is the MAT over a baseline period prior to the focal interval, date_i 1071 is the mid-date of the focal census interval and date_b is the mid-date of the baseline period. The Imer 1072 results show that the baseline period for MAT-change is 5 years and for CO₂-change it is 56 years, while MCWD showed no clear trend, so MCWD-change was not included in the models (see 1073 1074 Extended Data Figure 3). All three results conform to a priori theoretical expectations. For CO₂ a 1075 maximum response to an integrated 56 years of change is expected because forest stands will 1076 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 1077 residence time of a forest stand^{30,90} (mean of 62 years in this dataset). For MAT, 5 years is consistent 1078 1079 with experiments showing temperature acclimation of leaf- and plant-level photosynthetic and respiration processes over half-decadal timescales^{31,91}. MCWD has no overall trend suggesting that 1080 once a drought ends, its impact on tree growth fades rapidly, as seen in other studies^{14,92}. Also in the 1081 1082 moist tropics wet-season rainfall is expected to re-charge soil water, hence lagged impacts of 1083 droughts are not expected.

1084

1085 We calculated estimates of two forest attributes that may alter responses to environmental change as 1086 potential predictor variables: Wood Density (WD) and Carbon Residence Time (CRT). In intact oldgrowth forests, mean WD (in g cm⁻³) is inversely related to resource availability^{28,93,94}, as is seen in 1087 1088 our dataset (carbon gains and plot-level mean WD are negatively correlated, Extended Data Figure 1089 4). WD is calculated for each census interval in the dataset, as the mean WD of all trees alive at the end of the census interval, to be consistent with the previous Amazon analysis⁶. Carbon residence 1090 1091 time (CRT, in yrs) is a measure of the time that fixed carbon stays in the system. CRT is a potential correlate of the impact of past carbon gains on later carbon losses³⁰. To avoid circularity in the 1092 1093 models, the equation used to calculate CRT differed depending on the response variable. If the 1094 response variable is carbon loss, the CRT equation is based on gains: CRT=AGC/gains, with AGC 1095 for each interval based on AGC at the end of the interval, and the gains for each interval calculated 1096 as the mean of the gains in the interval and the previous intervals (i.e. long-term gains). If the 1097 response variable is carbon gains, the CRT equation is based on losses: CRT=AGC/losses. The equation employed for use in the carbon loss model (based on gains) is the standard formula used to 1098 1099 calculate CRT and is retained in the minimum adequate model (see below and Table 2). The nonstandard CRT equation (based on losses) used in the carbon gain model is not retained in the minimum adequate model (see below).

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1103 Statistical modelling of the Carbon Gain, Loss and Sink Trends

1104 We first constructed two models including those environmental drivers exhibiting long-term change that impact theory-driven models of photosynthesis and respiration as predictor variables: CO₂, 1105 MAT, and MCWD. One model had carbon gains as the response variable, the other had carbon 1106 losses as the response variable (both in Mg C ha⁻¹ yr⁻¹). Models were fitted using the lme function in 1107 R, with maximum likelihood (NLME package⁹⁵). All census intervals within all plots were used, 1108 weighted by plot size and census length (using equation 3 above). Plot identity was included as a 1109 1110 random effect, i.e. assuming that the intercept can vary randomly among plots. All predictor 1111 variables in the models were scaled without centering (scale function in R, RASTER package⁶²). 1112 Carbon gain values were normally distributed but carbon loss values required a power-law 1113 transformation (λ = 0.361) to meet normality criteria. Multi-parameter models are: carbon gains = 1114 $intcp + a \times CO_2 + b \times MAT + c \times MCWD$ (model 1); carbon losses = $intcp + a \times CO_2 + b \times MAT + b \times MAT$ c×MCWD (model 2); where intep is the estimated model intercept, and a, b, and c are model 1115 parameters giving the slope of relationships with environmental predictor variables. For multi-1116 1117 parameter model outputs see Extended Data Table 1, for single-parameter relationships, Figure 2.

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The second pair of models include the same environmental predictors (CO₂, MAT, MCWD), plus their rate of change (CO₂-change, MAT-change, but not MCWD-change as explained above), and forest attributes that may alter how forests respond (WD, CRT), as described above. We also evaluated the possible inclusion of a differential continent effect of each variable in the full model. We first constructed models with only a single predictor variable, and allowed different slopes in each continent. Next, if removal of the continent-specific slope (using stepAIC function in R, MASS

package⁹⁶) decreased model Akaike Information Criterion (AIC) then the continent-specific slope 1125 was not included in the full model for that variable. Only MCWD showed a significant differential 1126 1127 continent-specific slope. This implies that forests on both continents have common responses to CO_2 , CO₂-change, MAT, MAT-change, WD and CRT, but respond differently to differences in MCWD. 1128 1129 This is likely because wet-adapted species are much rarer in Africa than in Amazonia as a result of large differences in past climate variation³⁴. Lastly, we allowed different intercepts for the two 1130 1131 continents to potentially account for differing biogeographical or other continent-specific factors. For the carbon loss model, we applied the same continent-specific effects for slope as for the carbon gain 1132 1133 model. Carbon loss values were transformed using a power-law transformation ($\lambda = 0.361$) to meet 1134 normality criteria.

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1136 For both carbon gains and losses we parameterized a global model including the significant 1137 continent-specific effect of MCWD, selecting the most parsimonious simplified model using allsubsets regression^{97,98}. To do so, we first generated a set of models with all possible combinations 1138 1139 (subsets) of fixed effect terms in the global model using the dredge function of the MuMIn package in R⁹⁹. We then chose the best-ranked simplified model based on the AICc criterion, hereafter called 1140 "minimum adequate carbon gain/loss model", reported in Table 2. The minimum adequate models 1141 are: carbon gains = intcp×continent + a×CO₂-change + b×MAT + c×MAT-change + 1142 1143 $d \times MCWD \times continent + e \times WD \pmod{3}$; carbon losses = intcp + $a \times CO_2$ -change + $b \times MAT$ -change 1144 $+ c \times MCWD + d \times CRT$ (model 4). WD was retained in the carbon gain model, likely because growth 1145 is primarily impacted by resource availability, while CRT was retained in the carbon loss model, 1146 likely because losses are primarily impacted by how long fixed carbon is retained in the system.

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1148 Table 2 presents model coefficients of the best-ranked gain model and best-ranked loss model 1149 selected using all-subsets regression. These best-ranked gain and loss models have weights of 0.310 and 0.132 respectively, which is almost double the weight of the second ranked models (0.152 and 0.075 respectively). In Supplementary Table 2 we also used the model.avg function of the MuMIn package to calculate a weighted mean of the coefficients of the best-ranked models together representing a cumulative weight-sum of 0.95 (i.e. a 95% confidence subset). Supplementary Table 2 (model-averaged) and main text Table 2 (best-ranked) model parameters are very similar. Supplementary Tables 3 and 4 report the complete sets of carbon gains and loss models that contribute to the model average results.

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1158 The model-average results show the same continental differences in sensitivity to environmental 1159 variables as the best-ranked models. From 2000 to 2015, carbon gains increased due to CO₂-change 1160 (+3.7% in both the averaged and the best-ranked models, both continents), while temperature rises 1161 led to a decline in gains, which especially had an effect in the Amazon (-1.14% and -1.07% due to 1162 MAT and MAT-change together in the averaged and best-ranked model respectively). Finally, both models result in similar predictions of the net carbon sink over the 1983-2040 period: the future net 1163 1164 sink trend in Africa is -0.004 and -0.003 in the best-ranked and averaged models respectively; in 1165 Amazonia the future net sink trend is -0.013 and -0.011 in the best-ranked and averaged models respectively. The Amazon sink reaches zero in 2041 using model-averaged parameters compared to 1166 1167 2035 using the best-ranked models.

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1169 Estimating Future Predictor Variables to 2040

To calculate future modelled trends in carbon gains and losses (Figure 3), we first estimated annual records of the predictor variables (CO₂-change, MAT, MAT-change, MCWD, WD and CRT) to 2040 (Extended Data Figure 5).

1174 To do so we first calculated annual records for the period of the observed trends for each plot location (i.e. from 1983-2014 in Africa and 1983-2011.5 in Amazonia). For CO₂-change, MAT, 1175 1176 MAT-change and MCWD we extracted monthly records as described in section Predictor Variable 1177 Estimates (above). For WD and CRT we interpolated to a 0.1-yr period within each census interval 1178 (as in Figure 1). Then, we calculated the mean annual value of each predictor variable from the 244 plot locations in Africa, and separately the mean annual value of each predictor variable from the 1179 1180 321 plot locations in Amazonia (i.e. solid lines in ED Figure 5). For each predictor variable, we calculated annual records of upper and lower confidence intervals by respectively adding and 1181 1182 subtracting 2σ to the mean of each annual value (shaded area in ED Figure 5).

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Secondly, for each predictor variable we parameterised a linear model for each continent using the annual records for the period of the observed trends. Then for each predictor variable, the continentspecific linear regression models were used to estimate predictor variables for each plot location from 2014 to 2040 in Africa and from 2011.5 to 2040 in the Amazon (dotted lines in Extended Data Figure 5). For each predictor variable, we calculated annual records of upper and lower confidence intervals by respectively adding and subtracting 2σ to the slope of each linear model (shaded area around dotted lines in ED Figure 5).

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1192 Estimating Future Carbon Gain, Loss and Net Carbon Sink

We used the minimum adequate models (Table 2) to predict annual records of carbon gain, carbon loss and the carbon sink for the plot networks in Africa and Amazonia over the period 1983 through to 2040 (Figure 3). We extracted fitted carbon gain and loss values using the mean annual records for each predictor variable (predictSE.lme function, AICcmodavg package¹⁰⁰). Upper and lower confidence intervals were calculated accounting for uncertainties in the model (both fixed and random effects) and predictor variables using the 2 σ upper and lower confidence interval for each predictor variable (using predictSE.lme). Finally the net carbon sink was calculated by subtracting the losses from the gains. To obtain sink values in the future in Table 1, annual per unit area sink predictions, from Figure 3, were averaged over each decade and multiplied by the future forest area, as described above.

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To test the sensitivity of the future predictions in Figure 3, we reran the analysis by modifying future 1204 1205 trajectories of predictor variables one at a time, while keeping all others the same, to assess the mean C sink over 2010-15 and 2030 (averaging at 2030 is not necessary as trends in MAT-change and 1206 1207 MCWD, which largely drive modelled inter-annual variability, are estimated as smooth trends in the 1208 future). For each predictor variable, we explored potential impacts of the likely bounds of possibility, 1209 (i) by taking the steepest slope of either continent from the extrapolated trends, doubling this slope 1210 and applying it on both continents; and (ii) by taking the steepest slope of either continent from the 1211 extrapolated trends, taking the opposite of this slope and applying it on both continents. These bounds represent deviations of >2 sigma from observed trends. Change in MAT also alters MAT-1212 change, so we present the sensitivity of both parameters together. 1213

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1215 Additionally, for CO₂-change and MAT, we also calculated future slopes under three future Representative Concentration Pathway (RCP) scenarios³⁸ with different radiative forcing in 2100: 1216 RCP2.6, 4.5, and 8.5. Future RCP CO₂-change slopes (ppm yr⁻¹) were calculated using RCP CO₂ 1217 1218 concentration data for the years between 2015 and 2030 inclusive. Future RCP MAT and MAT-1219 change slopes were obtained from plot-specific MAT values extracted from downscaled 30 seconds resolution data for current⁸⁰ and future⁵¹ climate from WorldClim, and averaged over 19 CMIP5 1220 1221 models. We subtracted the mean 2040-2060 climate MAT (i.e. 2050) from the mean 1970-2000 climate MAT (i.e. 1985), divided by 65 years to give the annual rate of change. We then calculated a 1222 1223 mean slope over all plots per continent. Finally, to avoid mismatches between RCP-derived values of 1224 CO₂ and MAT and the observed records we removed any difference in intercept between the RCP trends and observed trends, so the RCP trends were a continuation of the end-point of the observed 1225 1226 trajectory in 2015. We did not estimate the sensitivity of MCWD under the RCP scenarios, because 1227 the CMIP5 model means do not show drought trends for our forest plot networks, unlike rain gauge 1228 data for the recent past, and thus would show little or no sensitivity to MCWD. For each modified slope, Supplementary Table 5 reports the absolute decline in the sink in each continent in 2030 1229 1230 compared to the 2010-15 mean sink. This shows that the future sink strength is sensitive to future environmental conditions, but within both RCP scenarios and our bounds of possibility we show a 1231 1232 decline in the sink strength in both continents over the 2020s.

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1234 Data and Code Availability

1235 Source data and R-code to generate figures and tables are available from: 1236 http://dx.doi.org/10.5521/Forestplots.net/2019_1

1237

1238 **References (Methods only)**

- 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).
- 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).
- 1245 53 Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., T.R., B. & Phillips, O. L. ForestPlots.net
 1246 Database. www.forestplots.net. Date of extraction [10/11/2017]. (2009).
- 1247 54 Sheil, D. & Bitariho, R. Bwindi Impenetrable Forest TEAM Site. Data Set Identifier: TEAM-
- 1248 DataPackage-20151201235855_1254. (2009).

- 1249 55 Kenfack, D. Korup National Park TEAM Site. Data Set Identifier: TEAM-DataPackage1250 20151201235855_1254. (2011).
- 1251 56 Rovero, F., Marshall, A. & Martin, E. Udzungwa TEAM Site. Data Set Identifier: TEAM1252 DataPackage-20151130235007_5069. (2009).
- 1253 57 Hockemba, M. B. N. Nouabalé Ndoki TEAM Site. Data Set Identifier: TEAM-DataPackage1254 20151201235855 1254. (2010).
- 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).
- Gourlet-Fleury, S. et al. Tropical forest recovery from logging: a 24 year silvicultural
 experiment from Central Africa. Philosophical Transactions of the Royal Society BBiological Sciences 368, 20120302, doi:10.1098/rstb.2012.0302 (2013).
- 1260 60 Claeys, F. et al. Climate change would lead to a sharp acceleration of Central African forests 1261 dynamics by the end of the century. Environmental Research Letters **14**, 044002, 1262 doi:10.1088/1748-9326/aafb81 (2019).
- 1263 61 Chave, J. et al. Improved allometric models to estimate the aboveground biomass of tropical 1264 trees. Global Change Biology **20**, 3177-3190, doi:10.1111/gcb.12629 (2014).
- 1265 62 R Development Core Team. R: A Language and Environment for Statistical Computing.
 1266 Available at http://www.R-project.org/. (2015).
- Lopez-Gonzalez, G., Sullivan, M. & Baker, T. BiomasaFP package. Tools for analysing data
 downloaded from ForestPlots.net. R package version 0.2.1. Available at
 <u>http://www.forestplots.net/en/resources/analysis</u>. (2017).
- Phillips, O., Baker, T., Brienen, 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).

- 1274 65 Talbot, J. et al. Methods to estimate aboveground wood productivity from long-term forest 1275 inventory plots. Forest Ecology and Management **320**, 30-38, 1276 doi:10.1016/j.foreco.2014.02.021 (2014).
- Sullivan, M. J. P. et al. Field methods for sampling tree height for tropical forest biomass
 estimation. Methods in Ecology and Evolution 9, 1179-1189, doi:10.1111/2041-210X.12962
 (2018).
- Feldpausch, T. R. et al. Tree height integrated into pantropical forest biomass estimates.
 Biogeosciences 9, 3381-3403, doi:10.5194/bg-9-3381-2012 (2012).
- 1282 68 Chave, J. et al. Towards a worldwide wood economics spectrum. Ecology Letters 12, 3511283 366, doi:10.1111/j.1461-0248.2009.01285.x (2009).
- 1284 69 Zanne, A. E. et al. Data from: Towards a worldwide wood economics spectrum (Dryad
 1285 Digital Repository, 2009).
- Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration
 across the world's trees and forests. Nature Geoscience 11, 915-920, doi:10.1038/s41561018-0246-x (2018).
- Kohyama, T. S., Kohyama, T. I., Sheil, D. & Rees, M. Definition and estimation of vital rates
 from repeated censuses: Choices, comparisons and bias corrections focusing on trees.
 Methods in Ecology and Evolution 9, 809-821, doi:10.1111/2041-210x.12929 (2018).
- 1292 72 Bates, D., Maechler, M., Bolker, B. & Walker, S. Ime4: Linear mixed-effects models using
 1293 Eigen andS4.Rpackage version, 1.0-4. Available at http://www.inside1294 r.org/packages/Ime4/versions/1-0-4. (2013).
- 1295 73 Fox, J. Applied Regression Analysis and Generalized Linear Models. Second edn, (Sage
 1296 Publishing, 2008).
- 1297 74 Chave, J. et al. Assessing evidence for a pervasive alteration in tropical tree communities.
 1298 PLoS Biology 6, 0455-0462, doi:10.1371/journal.pbio.0060045 (2008).

- 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**, 915926, doi:10.1016/j.foreco.2013.09.042 (2013).
- Aragão, L. E. O. C. et al. Spatial patterns and fire response of recent Amazonian droughts.
 Geophysical Research Letters 34, 1-5, doi:10.1029/2006gl028946 (2007).
- 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).
- 1306 78 Tans, P. & Keeling, R. Mauna Loa CO₂ monthly mean data. Available at
 1307 http://www.esrl.noaa.gov/gmd/ccgg/trends/. (2016).
- 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).
- Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for
 global land areas. International Journal of Climatology 37, 4302-4315, doi:10.1002/joc.5086
 (2017).
- 1314 81 Ramirez-Villegas, J. & Jarvis, A. Downscaling Global Circulation Model Outputs: The Delta
 1315 Method. Decision and Policy Analysis Working Paper No. 1., 18 (2010).
- 131682Schneider, U. et al. GPCC Full Data Reanalysis Version 6.0 at 0.5°: Monthly Land-Surface
- 1317 Precipitation from Rain-Gauges built on GTS-based and Historic Data.
 1318 doi:10.5676/DWD_GPCC/FD_M_V6_050 (2011).
- 1319 83 Sun, Q. et al. Review of Global Precipitation Data Sets: Data Sources, Estimation, and
 1320 Intercomparisons. Reviews of geophysics 56, 79-107, doi:10.1002/ (2017).
- Huffman, G. J. et al. The TRMM Multisatellite Precipitation Analysis (TMPA): QuasiGlobal, Multiyear, Combined-Sensor Precipitation Estimates at Fine Scales. Journal of
 Hydrometeorology 8, 38-55, doi:10.1175/jhm560.1 (2007).

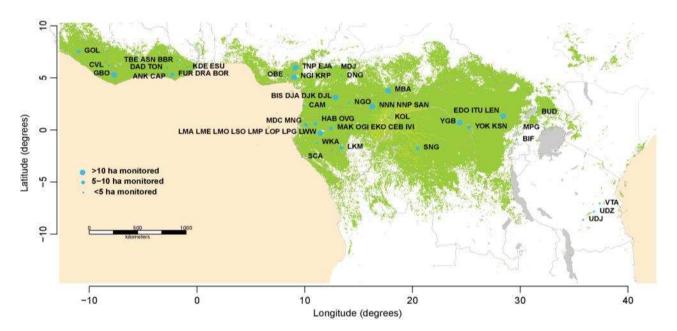
- Kume, T. et al. Ten-year evapotranspiration estimates in a Bornean tropical rainforest.
 Agricultural and Forest Meteorology 151, 1183-1192, doi:10.1016/j.agrformet.2011.04.005
 (2011).
- 1327 86 Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. & Fisher, J. B. Changes in the potential
 1328 distribution of humid tropical forests on a warmer planet. Philosophical Transactions of the
 1329 Royal Society A: Mathematical, Physical and Engineering Sciences 369, 137-160,
 1330 doi:10.1098/rsta.2010.0238 (2011).
- James, R., Washington, R. & Rowell, D. P. Implications of global warming for the climate of
 African rainforests. Philosophical transactions of the Royal Society of London. Series B,
 Biological sciences 368, 20120298, doi:10.1098/rstb.2012.0298 (2013).
- 1334 88 Jung, M. et al. Recent decline in the global land evapotranspiration trend due to limited
 1335 moisture supply. Nature 467, 951-954, doi:10.1038/nature09396 (2010).
- Jung, M. et al. Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and
 sensible heat derived from eddy covariance, satellite, and meteorological observations.
 Journal of Geophysical Research 116, doi:10.1029/2010jg001566 (2011).
- 1339 90 Lloyd, J. & Farquhar, G. D. The CO₂ dependence of photosynthesis, plant growth responses
 1340 to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. I.
 1341 General principles and forest ecosystems. Functional Ecology 10, 4-32, doi:10.2307/2390258
 1342 (1996).
- 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 Phytol 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).

- 1349 93 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).
- 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).
- Pinheiro, J. C. & Bates, D. M. Mixed-Effects Models in S and S-PLUS. First edn, 528
 (Springer, 2000).
- 1356 96 Venables, W. N. & Ripley, B. D. Modern Applied Statistics with S. Fourth edn, 498
 1357 (Springer, 2002).
- Olejnik, S., Mills, J. & Keselman, H. Using Wherry's Adjusted R² and Mallow's Cp for
 Model Selection From All Possible Regressions. The Journal of Experimental Education 68,
 365-380, doi:10.1080/00220970009600643 (2000).
- Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. Why do we still use
 stepwise modelling in ecology and behaviour? Journal of Animal Ecology 75, 1182-1189,
 doi:10.1111/j.1365-2656.2006.01141.x (2006).
- Bartoń, K. MuMIn: Multi-Model Inference. Tools for performing model selection and model
 averaging. R package version 1.43.6. (2019).
- 1366 100 Gelman, A. & Hill, J. Data Analysis Using Regression and Multilevel/Hierarchical Models.
 1367 (Cambridge University Press, New York, 2007).
- 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/S00344257(99)00073-5 (2000).

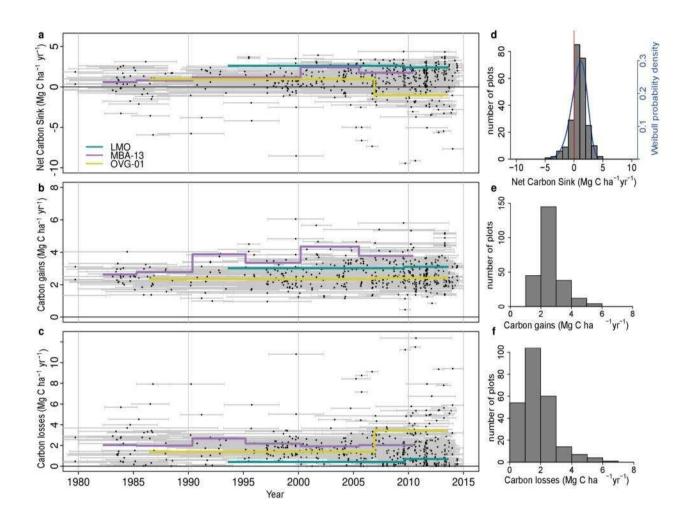
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- 1374 authors declare no competing financial interests. Supplementary Information is available online for
- 1375 this paper.
- 1376
- 1377 Extended Data Figures

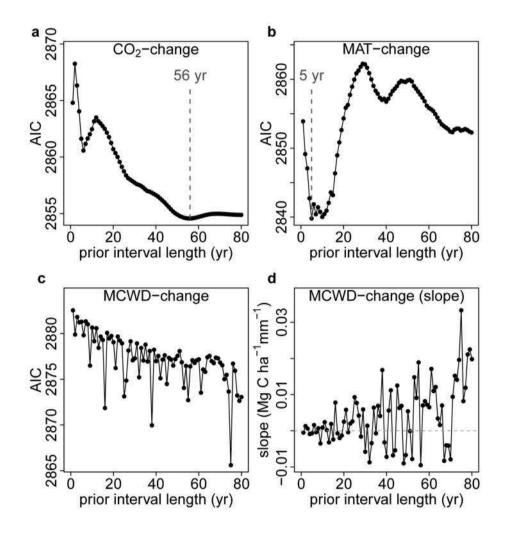


Extended Data Figure 1. Map showing the locations of the 244 plots included in this study. Dark green represents all lowland closed-canopy forests, submontane forests and forest-agriculture mosaics; light green shows swamp forests and mangroves¹⁰¹, blue circles represent plot clusters, referred to by three-letter codes (see Supplementary Table 1 for the full list of plots). Clusters <50 km apart are shown as one point for display only, with the circlesize corresponding to sampling effort in terms of hectares monitored.



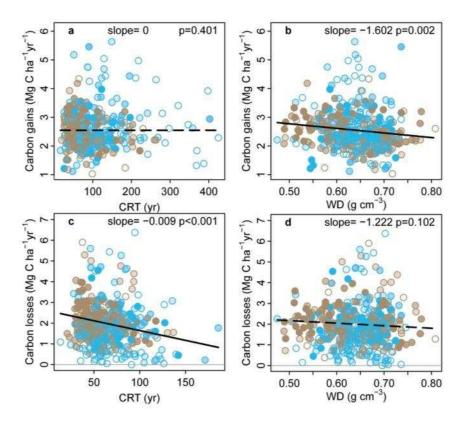
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Extended Data Figure 2. Long-term above-ground carbon dynamics of 244 African intact 1386 1387 tropical forest inventory plots. Points in the scatterplots indicate the mid-census interval date, with 1388 horizontal bars connecting the start and end date for each census interval for net aboveground biomass carbon change (a), carbon gains (from woody production from tree growth and newly 1389 1390 recruited stems) (b), and carbon losses (from tree mortality) (c). Examples of time series for three individual plots are shown in purple, yellow and green. Associated histograms show the distribution 1391 1392 of the plot-level net aboveground biomass carbon (d) (with a three-parameter Weibull probability 1393 density distribution fitted in blue, showing the carbon sink is significantly larger than zero; one-tail ttest: p<0.001), carbon gains (e), and carbon losses (f). 1394

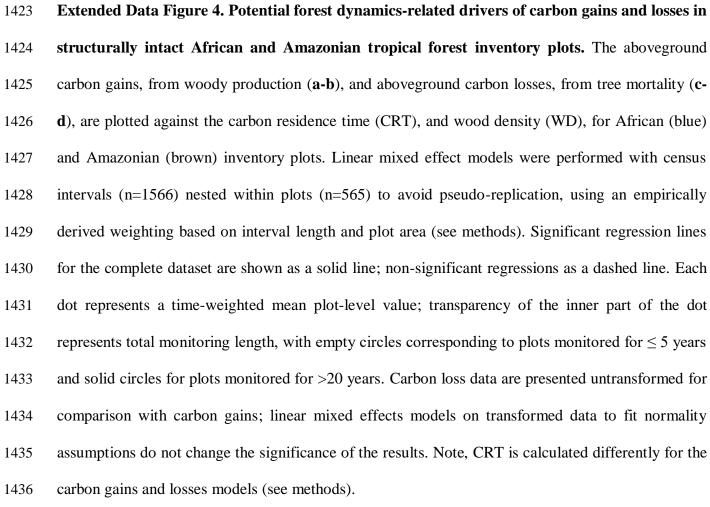


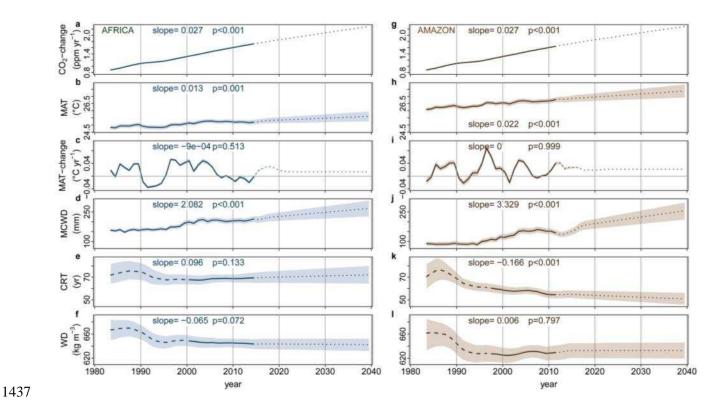
1396 Extended Data Figure 3. Akaike's Information Criterion (AIC) from correlations between the 1397 carbon gain in tropical forest inventory plots and changes in either atmospheric CO₂, 1398 temperature (as MAT) or drought (as MCWD), each calculated over ever-longer prior intervals. Panels show AIC from linear mixed effects models of carbon gains from 565 plots and 1399 1400 corresponding, atmospheric CO_2 (CO_2 -change) (**a**), Mean Annual Temperature (MAT-change) (**b**), and Maximum Climatological Water Deficit (MCWD-change) (c). For CO₂ the AIC minimum was 1401 1402 observed when predicting the carbon gain from the change in CO₂ calculated over a 56 year long 1403 prior interval length. We use this length of time to calculate our CO_2 -change parameter. Such a value 1404 is expected 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 1405 approximately equivalent to the carbon residence time of a forest stand^{30,90} (mean of 62 years in this 1406

pooled African and Amazonian 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- and plant-level photosynthetic and respiration processes over approximately half-decadal timescales^{31,91}. For MCWD the AIC minimum is not obvious, while the slope of the correlation, shown in panel (d), shows no overall trend and oscillates between positive or negative values, meaning there is no 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 suggests that once a drought ends, its impact on tree growth fades rapidly, as seen in other studies^{14,92}. Also in the moist tropics wet-season rainfall is expected to re-charge soil water, hence lagged impacts of droughts are not expected.

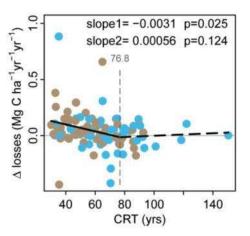




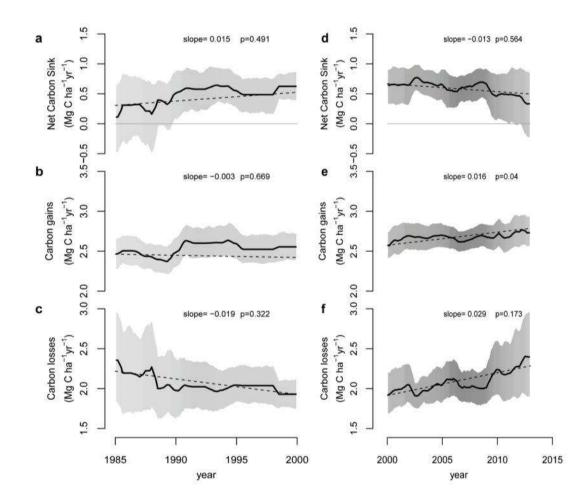




Extended Data Figure 5. Trends in predictor variables used to estimate long-term trends in 1438 above-ground carbon gains, carbon losses and the resulting net carbon sink in African and 1439 Amazonian intact tropical forest plot networks. Mean annual CO₂-change (a), MAT (b), MAT-1440 1441 change (c), MCWD (d), CRT (e), and WD (f) for African plot locations in blue, and corresponding Amazon plots locations in brown (g-l). Solid lines for CO₂-change, MAT, MAT-change, MCWD 1442 represent obervational data, and solid lines for CRT and WD represent plot means and a time 1443 window where >75% of the plots were monitored, long-dashed lines are plot means were <75% of 1444 1445 plots were monitored. Dotted lines are future values estimated from linear trends on the 1983-2014 (Africa) or 1983-2011 (Amazon) data (slope and p-value reported in each panel), see methods for 1446 1447 details. Upper and lower confidence intervals (shaded area) for the past (Africa: 1983-2014; Amazonia: 1983-2011) are calculated by respectively adding and subtracting 2σ to the mean of each 1448 1449 annual value. Upper and lower confidence intervals for the future were estimated by adding and subtracting 2σ from the slope of the regression model. 1450

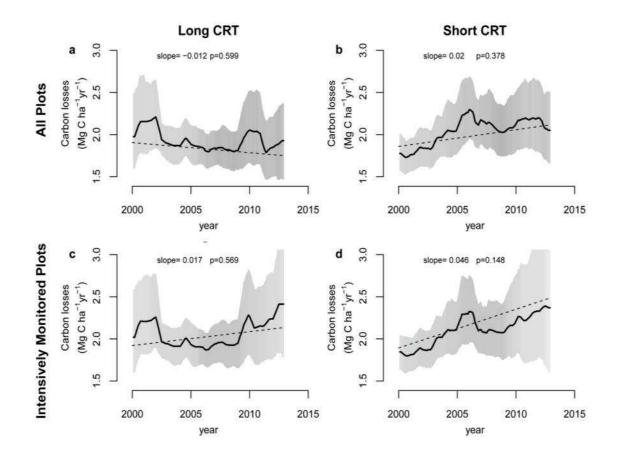


1452 Extended Data Figure 6. The change in carbon losses versus carbon residence time (CRT) of inventory plots in Africa and Amazonia. For plots with two census intervals, we calculated the 1453 change in carbon losses (∆losses, in Mg C ha⁻¹ yr⁻¹ yr⁻¹) as the carbon losses (Mg C ha⁻¹ yr⁻¹) of the 1454 1455 second interval minus the carbon losses of the first interval, divided by the difference in mid-interval dates. For plots with more than two intervals, we calculated the change in carbon losses for each pair 1456 of subsequent intervals, then calculated the plot-level mean over all pairs, weighted by the time 1457 length between mid-interval dates. This analysis includes only plots with at least two census intervals 1458 1459 and monitored for ≥ 20 years (i.e. roughly one-third of the mean CRT of the pooled African and 1460 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 recent long-term increase in 1461 carbon losses, longer CRT plots do not. Blue points are African plots, brown points are Amazonian 1462 1463 plots.



1464

Extended Data Figure 7. Trends in African tropical forest net aboveground live biomass 1465 carbon, carbon gains and carbon losses, calculated for the last 15 years of the twentieth 1466 century (left panels a-c) and the first 15 years of the twenty-first century (right panels d-f). 1467 Plots were selected from the full dataset if their census intervals cover at least 50% of the respective 1468 time windows, i.e. they are intensely monitored (n=56 plots for 1985-2000, and n=134 plots for 1469 2000-2015, respectively). Solid lines show mean values, shading corresponds to the 95% CI, as 1470 calculated in Figure 1. Dashed lines, slopes and p-values are from linear mixed effects models, as in 1471 Figure 1. The data shows a difference compared to Figure 1, notably the sink decline after ~2010 1472 1473 driven by rising carbon losses. This is because in Figure 1 we include all available plots over the 1983-2015 window, which includes clusters of plots monitored only in the 2010s that had low carbon 1474 1475 loss and high carbon sink values.





1477 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) 1478 1479 carbon residence time. Upper panels include all plots, i.e. as in Figure 1, but split into a long-CRT 1480 group (a), and a short-CRT group (b), each containing half the 244 plots. Lower panels restrict plots 1481 to those spanning >50% of the time window, i.e. intensely monitored plots, as in Extended Data Figure 7, but split into a long-CRT group (c), and a short-CRT group (d), each containing half the 1482 1483 134 plots. Solid lines indicate mean values, shading the 95% CI, as for Figure 1. Dashed lines, slopes and p-values are from linear mixed-effects models, as for Figure 1. Carbon losses increase at a higher 1484 1485 rate in the short-CRT than the long-CRT group of plots, in both datasets, although this increase is not 1486 statistically significant.

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1490 Extended Data Tables

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Extended Data Table 1. Models to predict carbon gains and losses in African and Amazonian tropical forests, including only environmental variables, showing long-term trends that impact theory-driven models of photosynthesis and respiration. Significant values in bold.

	Carbon ga	ins, Mg C ha ⁻¹ yr ⁻¹		
Predictor variable	Parameter value	Standard Error	t-value	p-value
(Intercept)	4.694	0.739	6.354	0.000
CO ₂ (ppm)	0.005	0.001	3.196	0.001
MAT (°C)	-0.143	0.021	-6.844	0.000
MCWD (mm x1000)	-1.232	0.210	-5.878	0.000
	Carbon loss	ses, Mg C ha ⁻¹ yr ⁻¹ *		
Predictor variable	Parameter value	Standard Error	t-value	p-value
(Intercept)	0.926	1.854	0.500	0.617
CO ₂ (ppm)	0.004	0.004	0.947	0.344
MAT (°C)	-0.011	0.044	-0.249	0.804
MCWD (mm x1000)	-0.498	0.505	-0.985	0.325

1495

* carbon loss values were normalized via power-law transformation, λ = 0.361.

1496

1497 **Extended Data Table 2.** Forest area estimates used to calculate total continental forest sink.

Period	intact forest area (Mha)*					
	Africa	Amazon	Southeast Asia	Pan-tropics		
1980	671.5	958.3	233.6	1863.4		
1985	634.3	921.1	207.4	1762.8		
1990	600.2	885.2	190.6	1676.0		
1995	565.9	851.1	163.5	1580.5		
2000	531.8	817.2	136.9	1485.9		
2005	504.8	784.5	129.2	1418.5		
2010	477.8	756.3	118.4	1352.5		
2015	450.5	726.7	101.5	1278.7		
2020	425.5	698.5	90.1	1214.2		
2025	402.0	671.5	80.0	1153.4		
2030	379.7	645.4	71.0	1096.1		
2035	358.6	620.4	63.0	1042.1		
2040	338.8	596.4	56.0	991.1		

* Intact forest area for 1990, 2000 and 2007 is published in ref.1 (i.e. the total forest area minus forest regrowth). To estimate intact forest area for the other years in this table, we fitted exponential models for each continent using the published data.