

## Asynchronous carbon sink saturation in African and Amazonian tropical forests

ForestPlots

DOI:

[10.1038/s41586-020-2035-0](https://doi.org/10.1038/s41586-020-2035-0)

License:

None: All rights reserved

Document Version

Peer reviewed version

Citation for published version (Harvard):

ForestPlots 2020, 'Asynchronous carbon sink saturation in African and Amazonian tropical forests', *Nature*, vol. 579, no. 7797, pp. 80-87. <https://doi.org/10.1038/s41586-020-2035-0>

[Link to publication on Research at Birmingham portal](#)

### General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

### Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.

1 **Asynchronous Carbon Sink Saturation in African and Amazonian Tropical Forests**

2

3 **Authors**

4 Wannes Hubau<sup>1,2,3\*</sup>, Simon L. Lewis<sup>1,4\*</sup>, Oliver L. Phillips<sup>1</sup>, Kofi Affum-Baffoe<sup>5</sup>, Hans Beeckman<sup>2</sup>, Aida  
5 Cuní-Sánchez<sup>4,6</sup>, Armandu K. Daniels<sup>7</sup>, Corneille E.N. Ewango<sup>8,9,10</sup>, Sophie Fauset<sup>11,1</sup>, Jacques M. Mukinzi  
6<sup>8,12,13</sup>, Douglas Sheil<sup>14,15,16</sup>, Bonaventure Sonké<sup>17</sup>, Martin J.P. Sullivan<sup>1,18</sup>, Terry C.H. Sunderland<sup>16,19</sup>, Hermann  
7 Taedoumg<sup>17,20</sup>, Sean C. Thomas<sup>21</sup>, Lee J.T. White<sup>22,23,24</sup>, Katharine A. Abernethy<sup>24,23</sup>, Stephen Adu-Bredou<sup>25</sup>,  
8 Christian A. Amani<sup>26,16</sup>, Timothy R. Baker<sup>1</sup>, Lindsay F. Banin<sup>27</sup>, Fidèle Baya<sup>28,29</sup>, Serge K. Begne<sup>17,1</sup>, Amy C.  
9 Bennett<sup>1</sup>, Fabrice Benedet<sup>30,31</sup>, Robert Bitariho<sup>15</sup>, Yannick E. Bocko<sup>32</sup>, Pascal Boeckx<sup>33</sup>, Patrick Boundja<sup>34,16,35</sup>,  
10 Roel J.W. Brienen<sup>1</sup>, Terry Brncic<sup>34</sup>, Eric Chezeaux<sup>36</sup>, George B. Chuyong<sup>37</sup>, Connie J. Clark<sup>38</sup>, Murray  
11 Collins<sup>39,40</sup>, James A. Comiskey<sup>41,42</sup>, David A. Coomes<sup>43</sup>, Greta C. Dargie<sup>1</sup>, Thales de Haulleville<sup>2</sup>, Marie Noel  
12 Djuikouo K.<sup>37</sup>, Jean-Louis Doucet<sup>44</sup>, Adriane Esquivel-Muelbert<sup>1,45</sup>, Ted R. Feldpausch<sup>46</sup>, Alusine Fofanah<sup>47</sup>,  
13 Ernest G. Foli<sup>25</sup>, Martin Gilpin<sup>1</sup>, Emanuel Gloor<sup>1</sup>, Christelle Gonmadje<sup>48</sup>, Sylvie Gourlet-Fleury<sup>30,31</sup>, Jefferson  
14 S. Hall<sup>49</sup>, Alan C. Hamilton<sup>50</sup>, David J. Harris<sup>51</sup>, Terese B. Hart<sup>52,53</sup>, Mireille B.N. Hockemba<sup>34</sup>, Annette  
15 Hladik<sup>54</sup>, Suspense A. Ifo<sup>55</sup>, Kathryn J. Jeffery<sup>24</sup>, Tommaso Jucker<sup>56</sup>, Emmanuel Kasongo Yakusu<sup>10,3,2</sup>,  
16 Elizabeth Kearsley<sup>57,2</sup>, David Kenfack<sup>49,58</sup>, Alexander Koch<sup>4,59</sup>, Miguel E. Leal<sup>60</sup>, Aurora Levesley<sup>1</sup>, Jeremy A.  
17 Lindsell<sup>61,62</sup>, Janvier Lisingo<sup>63</sup>, Gabriela Lopez-Gonzalez<sup>1</sup>, Jon C. Lovett<sup>1,64</sup>, Jean-Remy Makana<sup>63</sup>, Yadvinder  
18 Malhi<sup>65</sup>, Andrew R. Marshall<sup>6,66,67</sup>, Jim Martin<sup>68</sup>, Emanuel H. Martin<sup>58,69</sup>, Faustin M. Mbayu<sup>10</sup>, Vincent P.  
19 Medjibe<sup>70,71,38</sup>, Vianet Mihindou<sup>71,22</sup>, Edward T.A. Mitchard<sup>39</sup>, Sam Moore<sup>65</sup>, Pantaleo K.T. Munishi<sup>72</sup>,  
20 Natacha Nssi Bengone<sup>22</sup>, Lucas Ojo<sup>73</sup>, Fidèle Evouna Ondo<sup>71</sup>, Kelvin Peh<sup>74,75</sup>, Georgia C. Pickavance<sup>1</sup>, Axel  
21 D. Poulsen<sup>51</sup>, John R. Poulsen<sup>38</sup>, Lan Qie<sup>1,76</sup>, Jan Reitsma<sup>77</sup>, Francesco Rovero<sup>78,79</sup>, Michael D. Swaine<sup>80</sup>, Joey  
22 Talbot<sup>1</sup>, James Taplin<sup>81</sup>, David M. Taylor<sup>82</sup>, Duncan W. Thomas<sup>83</sup>, Benjamin Toirambe<sup>84,2</sup>, John Tshibamba  
23 Mukendi<sup>2,10,85</sup>, Darlington Tuagben<sup>7</sup>, Peter M. Umunay<sup>86,87</sup>, Geertje M.F. Van Der Heijden<sup>88</sup>, Hans  
24 Verbeeck<sup>57</sup>, Jason Vleminckx<sup>89,90</sup>, Simon Willcock<sup>91</sup>, Hannsjoerg Woell<sup>92</sup>, John T. Woods<sup>93</sup>, Lise Zemagho<sup>17</sup>

25

26 \*Contributed equally

27

## 28 Author affiliations

1. University of Leeds, School of Geography, Leeds, UK

2. Royal Museum for Central Africa, Service of Wood Biology, Tervuren, Belgium

3. Ghent University, Department of Environment, Laboratory of Wood Technology (Woodlab), Ghent, Belgium

4. University College London, Department of Geography, London, UK

5. Forestry Commission of Ghana, Mensuration Unit, Kumasi, Ghana

6. University of York, Department of Environment and Geography, York, UK

7. Forestry Development Authority of the Government of Liberia (FDA), Monrovia, Liberia

8. Wildlife Conservation Society, DR Congo Programme, Kinshasa, Democratic Republic of Congo

9. Centre de Formation et de Recherche en Conservation Forestiere (CEFRECOF), Epubu, Democratic Republic of Congo

10. Université de Kisangani, Faculté de Gestion de Ressources Naturelles Renouvelables, Kisangani, Democratic Republic of Congo

11. University of Plymouth, School of Geography, Earth and Environmental Sciences, Plymouth, UK

12. Salonga National Park, Kinshasa, Democratic Republic of Congo

13. World Wide Fund for Nature, Gland, Switzerland

14. Norwegian University of Life Sciences, Faculty of Environmental Sciences and Natural Resource Management, Ås, Norway

15. Mbarara University of Science and Technology (MUST), The Institute of Tropical Forest Conservation (ITFC) , Mbarara, Uganda

16. Center for International Forestry Research (CIFOR), Bogor, Indonesia

52 17. University of Yaounde I, Plant Systematic and Ecology Laboratory, Higher Teachers' Training College, Yaounde, Cameroon

53 18. Manchester Metropolitan University, Department of Natural Sciences, Manchester, UK

54 19. University of British Columbia, Faculty of Forestry, Vancouver, Canada

55 20. Biodiversity International, Yaounde, Cameroon

56 21. University of Toronto, Faculty of Forestry, Toronto, Canada

57 22. Ministry of Forests, Seas, Environment and Climate, Libreville, Gabon

58 23. Institut de Recherche en Ecologie Tropicale, Libreville, Gabon

59 24. University of Stirling, Biological and Environmental Sciences, Stirling, UK

60 25. Forestry Research Institute of Ghana (FORIG), Kumasi, Ghana

61 26. Université Officielle de Bukavu, Bukavu, Democratic Republic of Congo

62 27. Centre for Ecology and Hydrology, Penicuik, UK

63 28. Ministère des Eaux, Forêts, Chasse et Pêche (MEFCP), Bangui, Central African Republic

64 29. Institut Centrafricain de Recherche Agronomique (ICRA), Bangui, Central African Republic

65 30. Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), Forêts et Sociétés (F&S), Montpellier, France

66 31. Université de Montpellier, Forêts et Sociétés (F&S), Montpellier, France

67 32. Université Marien Ngouabi, Faculté des Sciences et Techniques, Laboratoire de Botanique et Ecologie, Brazzaville, Republic of Congo

68 33. Ghent University, Isotope Bioscience Laboratory-ISOFYS, Gent, Belgium

69 34. Wildlife Conservation Society, Congo Programme, Brazzaville, Republic of Congo

70 35. Resources and Synergies Development (R&SD), Singapore, Singapore

71 36. Rougier-Gabon, Libreville, Gabon

72 37. University of Buea, Faculty of Science, Department of Botany and Plant Physiology, Buea, Cameroon

77 38. Duke University, Nicholas School of the Environment, Durham, NC, USA

78 39. University of Edinburgh, School of GeoSciences, Edinburgh, UK

79 40. Grantham Research Institute on Climate Change and the Environment, London, UK, London,

80 UK

81 41. National Park Service, Inventory & Monitoring Program, Fredericksburg, VA, USA

82 42. Smithsonian Institution, Washington, DC, USA

83 43. University of Cambridge, Department of Plant Sciences, Cambridge, UK

84 44. University of Liège, Forest Resources Management, Gembloux Agro-Bio Tech, Liège,

85 Belgium

86 45. University of Birmingham, School of Geography, Earth and Environmental Sciences,

87 Birmingham, UK

88 46. University of Exeter, Geography, College of Life and Environmental Sciences, Exeter, UK

89 47. The Gola Rainforest National Park, Kenema, Sierra Leone

90 48. National Herbarium, Yaounde, Cameroon

91 49. Smithsonian Tropical Research Institute, Forest Global Earth Observatory (ForestGEO),

92 Washington, DC, USA

93 50. Kunming Institute of Botany, Kunming, China

94 51. Royal Botanic Garden Edinburgh, Edinburgh, UK

95 52. Lukuru Wildlife Research Foundation, Kinshasa, Democratic Republic of Congo

96 53. Yale Peabody Museum of Natural History, Division of Vertebrate Zoology, New Haven, CT,

97 USA

98 54. Muséum National d'Histoire Naturel, Département Hommes, natures, sociétés, Paris, France

99 55. Université Marien Ngouabi, École Normale Supérieure (ENS), Département des Sciences et

100 Vie de la Terre, Laboratoire de Géomatique et d'Ecologie Tropicale Appliquée, Brazzaville,

101 Republic of Congo

102 56. University of Bristol, School of Biological Sciences, Bristol, UK

103 57. Ghent University, Department of Environment, Computational & Applied Vegetation

104 Ecology (Cavelab), Ghent, Belgium

105 58. Tropical Ecology, Assessment and Monitoring (TEAM) Network, Arlington, VA, USA

106 59. University of Hong Kong, Department of Earth Sciences, Hong Kong, Hong Kong SAR

107 60. Wildlife Conservation Society, Uganda Programme, Kampala, Uganda

108 61. A Rocha International, Cambridge, UK

109 62. The Royal Society for the Protection of Birds, Centre of Conservation Science, Sandy, UK

110 63. Université de Kisangani, Faculté des Sciences, Laboratoire d'écologie et aménagement

111 forestier, Kisangani, Democratic Republic of Congo

112 64. Royal Botanic Gardens, Kew, UK

113 65. University of Oxford, Environmental Change Institute, School of Geography and the

114 Environment, Oxford, UK

115 66. University of the Sunshine Coast, Tropical Forests and People Research Centre, Sippy

116 Downs, Australia

117 67. Flamingo Land Ltd, Kirby Misperton, UK

118 68. Fleming College, Peterborough, Canada

119 69. Udzungwa Ecological Monitoring Centre, Mang'ula, Tanzania

120 70. Commission of Central African Forests (COMIFAC), Yaounde, Cameroon

121 71. Agence Nationale des Parcs Nationaux, Libreville, Gabon

122 72. Sokoine University of Agriculture, Morogoro, Tanzania

123 73. University of Abeokuta, Abeokuta, Nigeria

124 74. University of Southampton, School of Biological Sciences, Southampton, UK

125 75. University of Cambridge, Department of Zoology, Conservation Science Group, Cambridge,

126 UK

127 76. University of Lincoln, School of Life Sciences, Lincoln, UK

128 77. Bureau Waardenburg, Culemborg, The Netherlands

129 78. University of Florence, Department of Biology, Florence, Italy

130 79. MUSE - Museo delle Scienze, Tropical Biodiversity Section , Trento, Italy

131 80. University of Aberdeen, Department of Plant & Soil Science, School of Biological Sciences,

132 Aberdeen, UK

133 81. UK Research & Innovation, Innovate UK, London, UK

134 82. National University of Singapore, Department of Geography, Singapore, Singapore

135 83. Washington State University, Biology Department, Vancouver, WA, USA

136 84. Ministère de l'Environnement et Développement Durable, Kinshasa, Democratic Republic of

137 Congo

138 85. Université de Mbujimayi, Faculté des Sciences Appliquées, Mbujimayi, Democratic Republic

139 of Congo

140 86. Yale University, Yale School of Forestry & Environmental Studies, New Haven, CT, USA

141 87. Wildlife Conservation Society, New York, NY, USA

142 88. University of Nottingham, School of Geography, Nottingham, UK

143 89. Florida International University, International Center for Tropical Botany, Department of

144 Biological Sciences, Florida, FL, USA

145 90. Université Libre de Bruxelles, Faculté des Sciences, Service d'Évolution Biologique et

146 écologie, Brussels, Belgium

147 91. University of Bangor, School of Natural Sciences, Bangor, UK

148 92. Sommersbergseestrasse, Bad Aussee, Austria

149 93. University of Liberia, W.R.T College of Agriculture and Forestry, Monrovia, Liberia

150

151

152      **Summary**

153

154      Structurally intact tropical forests sequestered ~50% of global terrestrial carbon uptake over  
155      the 1990s and early 2000s, removing ~15% of anthropogenic CO<sub>2</sub> emissions<sup>1-3</sup>. Climate-driven  
156      vegetation models typically predict that this tropical forest ‘carbon sink’ will continue for  
157      decades<sup>4,5</sup>. Here, we assess trends in the carbon sink using 244 structurally intact African  
158      tropical forests spanning 11 countries, we compare them with 321 published plots from  
159      Amazonia and investigate the underlying drivers of the trends. The carbon sink in live  
160      aboveground biomass in intact African tropical forests has been stable for the three decades to  
161      2015, at 0.66 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (95% CI:0.53-0.79), in contrast to the long-term decline in  
162      Amazonian forests<sup>6</sup>. Thus, the carbon sink responses of Earth’s two largest expanses of  
163      tropical forest have diverged. The difference is largely driven by carbon losses from tree  
164      mortality, with no detectable multi-decadal trend in Africa and a long-term increase in  
165      Amazonia. Both continents show increasing tree growth, consistent with the expected net effect  
166      of rising atmospheric CO<sub>2</sub> and air temperature<sup>7-9</sup>. Despite the past stability of the African  
167      carbon sink, our data suggest a post-2010 increase in carbon losses, delayed compared to  
168      Amazonia, indicating asynchronous carbon sink saturation on the two continents. A statistical  
169      model including CO<sub>2</sub>, temperature, drought and forest dynamics accounts for the observed  
170      trends and indicates a long-term future decline in the African sink, while the Amazonian sink  
171      continues to rapidly weaken. Overall, the uptake of carbon into Earth’s intact tropical forests  
172      peaked in the 1990s. Given that the global terrestrial carbon sink is increasing in size,  
173      observations indicating greater recent carbon uptake into the Northern hemisphere landmass<sup>10</sup>  
174      reinforce our conclusion that the intact tropical forest carbon sink has already saturated. This  
175      tropical forest sink saturation and ongoing decline has consequences for policies to stabilise  
176      Earth’s climate.

177 **Main text**

178

179 Tropical forests account for approximately one-third of Earth's terrestrial Gross Primary Productivity  
180 and one-half of Earth's carbon stored in terrestrial vegetation<sup>11</sup>. Thus, small biome-wide changes in  
181 tree growth and mortality can have global impacts, either buffering or exacerbating the increase in  
182 atmospheric CO<sub>2</sub>. Models<sup>2,4,5,7,12</sup>, ground-based observations<sup>13-15</sup>, airborne atmospheric CO<sub>2</sub>  
183 measurements<sup>3,16</sup>, inferences from remotely sensed data<sup>17</sup>, and synthetic approaches<sup>3,8,18</sup> each suggest  
184 that, after accounting for land-use change, remaining structurally intact tropical forests (i.e. not  
185 impacted by direct anthropogenic impacts such as logging) are increasing in carbon stocks. This  
186 structurally intact tropical forest carbon sink is estimated at ~1.2 Pg C yr<sup>-1</sup> over 1990-2007 using  
187 scaled inventory plot measurements<sup>1</sup>. Yet, despite its policy relevance, changes in this key carbon  
188 sink remain highly uncertain<sup>19,20</sup>.

189

190 Globally the terrestrial carbon sink is increasing<sup>2,7,8,21</sup>. Between 1990 and 2017 the land surface  
191 sequestered ~30% of all anthropogenic carbon dioxide emissions<sup>1,21</sup>. Rising CO<sub>2</sub> concentrations are  
192 thought to have boosted photosynthesis more than rising air temperatures have enhanced respiration,  
193 resulting in an increasing global terrestrial carbon sink<sup>2,4,7,8,21</sup>. Yet, for Amazonia, recent results from  
194 repeated censuses of intact forest inventory plots show a progressive two-decade decline in sink  
195 strength primarily due to an increase of carbon losses from tree mortality<sup>6</sup>. It is unclear if this simply  
196 reflects region-specific drought impacts<sup>22,23</sup>, or potentially chronic pan-tropical impacts of either  
197 heat-related tree mortality<sup>24,25</sup>, or internal forest dynamics resulting from past increases in carbon  
198 gains leaving the system<sup>26</sup>. A more recent deceleration of the rate of increase in carbon gains from  
199 tree growth is also contributing to the declining Amazon sink<sup>6</sup>. Again, it is not known if this is a  
200 result of either pan-tropical CO<sub>2</sub> 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

202 inventory dataset from Africa, (ii) pool the new African and existing Amazonian records to  
203 investigate the putative environmental drivers of changes in the tropical forest carbon sink, and (iii)  
204 project its likely future evolution.

205

206 We collected, compiled and analysed data from structurally intact old-growth forests from the  
207 African Tropical Rainforest Observation Network<sup>27</sup> (217 plots) and other sources (27 plots) spanning  
208 the period 1968 to 2015 (Extended Data Figure 1; Supplementary Table 1). In each plot (mean size,  
209 1.1 ha), all trees  $\geq$ 100 mm in stem diameter were identified, mapped and measured at least twice  
210 using standardised methods (135,625 trees monitored). Live biomass carbon stocks were estimated  
211 for each census date, with carbon gains and losses calculated for each interval (Extended Data Figure  
212 2).

213

#### 214 **Continental Carbon Sink Trends**

215 We detect no long-term trend in the per unit area African tropical forest carbon sink over three  
216 decades to 2015 (Figure 1). The aboveground live biomass sink averaged  $0.66 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  (95%  
217 CI: 0.53-0.79; n=244) and was significantly greater than zero for every year since 1990 (Figure 1).  
218 While very similar to past reports ( $0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ )<sup>13</sup>, this first estimate of the temporal trend in  
219 Africa contrasts with the declining Amazonian trend<sup>6</sup> (Figure 1). A linear mixed effect model shows  
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  
222 per unit area sink strength of the two largest expanses of tropical forest on Earth diverged in the  
223 1990s and 2000s.

224

225 The proximal cause of the divergent sink patterns is a significant increase in carbon losses (from tree  
226 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  
228 pooled data shows a significant difference in slopes of carbon losses between the two continents over  
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  
232 alone also show no continental difference in long-term trends,  $p=0.322$ ). However, an assessment of  
233 how underlying environmental drivers affect carbon gains and losses is needed to understand the  
234 ultimate causes of the divergent sink patterns.

235

### 236 **Understanding the Carbon Sink Trends**

237 We first investigate environmental drivers exhibiting long-term change that impact theory-driven  
238 models of photosynthesis and respiration: atmospheric CO<sub>2</sub> concentration, surface air temperature,  
239 and water availability. A linear mixed effects model of carbon gains, with censuses nested within  
240 plots, and pooling the new African and published Amazonian data, shows a significant positive  
241 relationship with CO<sub>2</sub>, and significant negative relationships with mean annual temperature (MAT)  
242 and drought (measured as the Maximum Climatological Water Deficit, MCWD<sup>14</sup>; Figure 2;  
243 Extended Data Table 1). These results are consistent with a positive CO<sub>2</sub> fertilisation effect, and  
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  
247 no significant relationships with CO<sub>2</sub>, MAT or MCWD (Figure 2; Extended Data Table 1).

248

249 We further investigate the responses of carbon gains and losses (for which the above analysis has no  
250 explanatory power) by expanding our potential explanatory variables to additionally include the  
251 change in environmental conditions (CO<sub>2</sub>-change, MAT-change, MCWD-change, see Extended Data

252 Figure 3 for calculation details), and two attributes of forests that may influence their response to the  
253 same environmental change: plot mean wood density (which in old-growth forests correlates with  
254 below-ground resource availability<sup>28,29</sup>), and the plot carbon residence time (which measures how  
255 long fixed carbon remains in the system, hence dictates when past increases in carbon gains leave the  
256 system as elevated carbon losses<sup>30</sup>).

257

258 The minimum adequate carbon gain model using our expanded explanatory variables (best ranked  
259 model using multimodel inference) has a positive relationship with CO<sub>2</sub>-change, and negative  
260 relationships with MAT, MAT-change, MCWD, and wood density (Table 2; model-average results  
261 are similar, see Methods and Supplementary Tables 2-4). The retention of both MAT and MAT-  
262 change suggests that higher temperatures correspond to lower tree growth, and that trees only  
263 partially acclimate to recently rising temperatures, which further reduces growth, consistent with  
264 warming experiments<sup>31</sup> and observations<sup>9</sup>. The inclusion of higher wood density, and it being related  
265 to lower carbon gains (Extended Data Figure 4), alongside no temporal trends in wood density  
266 (Extended Data Figure 5), suggests that old-growth forests with denser-wooded tree communities  
267 typically have fewer available below-ground resources, or such patterns may also emerge from  
268 disturbance regimes lacking large-scale exogenous events, consistent with prior studies<sup>26,28,32</sup>.

269

270 The minimum adequate carbon gain model using our expanded explanatory variables also highlights  
271 continental differences. Between 2000 and 2015 African forest carbon gains increased by 3.1%  
272 compared with a 0.1% decline in Amazonia over the same interval (Table 2). In Africa, from 2000 to  
273 2015, the increase was composed of a 3.7% increase from CO<sub>2</sub>-change, partially offset by increasing  
274 droughts depleting gains by 0.5%, and only a slight decline in gains of 0.1% resulting from  
275 temperature increases (Table 2), because the rate of temperature change (MAT-change) decelerated  
276 over this time window (Extended Data Figure 5). For Amazonia, the same 3.7% increase due to CO<sub>2</sub>-

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  
279 as in the past (i.e. MAT-change is zero) further reduced gains by 1.1% (ten times the impact in  
280 Africa), leaving a net change in gains slightly below zero (Table 2). Thus, the recent stalling of  
281 carbon gain increases in Amazonia<sup>6</sup> is a response to drought and temperature and not due to an  
282 unexpected saturation of CO<sub>2</sub> fertilisation. Overall, the larger modelled increase in gains in Africa  
283 relative to Amazonia appear to be driven by slower warming, fewer or less extreme droughts, lower  
284 forest sensitivity to droughts, and overall lower temperatures (African forests are on average ~1.1°C  
285 cooler than Amazonian forests, as they typically grow at ~200 m higher elevation). Other continental  
286 differences may also be influencing the results, including higher nitrogen deposition in African  
287 tropical forests due to the seasonal burning of nearby savannas<sup>33</sup> and biogeographic history resulting  
288 in differing contemporary species pools and resulting functional attributes<sup>34,35</sup>.

289

290 The minimum adequate carbon loss model using our expanded explanatory variables shows higher  
291 losses with CO<sub>2</sub>-change and MAT-change, and lower losses with MCWD and the carbon residence  
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  
294 dynamics pattern<sup>26</sup>. Second, wetter plots have a longer growing season and so have higher gains and  
295 correspondingly higher losses, explaining the negative relationship with MCWD. Third, as  
296 increasing CO<sub>2</sub> levels result in additional carbon gains, after some time these additional past gains  
297 leave the system resulting in greater carbon losses, explaining the positive relationship with CO<sub>2</sub>-  
298 change. Finally, in addition to these relationships with carbon gains, the inclusion of MAT-change  
299 ( $p<0.001$ ) indicates heat- or vapour pressure deficit-induced tree mortality<sup>24</sup>. Overall, our results  
300 imply that chronic long-term environmental change factors, temperature and CO<sub>2</sub>, rather than simply

301 the direct effects of drought, underlie longer-term trends in tropical forest tree mortality, although  
302 other changes such as rising liana infestation rates seen in Amazonia<sup>36,37</sup> 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,  
306 95% CI, 66-72), compared with Amazonian forests (56 yrs, 95% CI, 54-59) while over the 2000-  
307 2015 window the much smaller increase in loss rates in Africa compared to Amazonia results from a  
308 slower increase in warming and a stable CRT in Africa compared to continued warming at previous  
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  
316 driving the increase (Extended Data Figure 8). Thus, a mortality-dominated African carbon sink  
317 decline appears to have begun very recently.

318

### 319 **Future of the Tropical Forest Carbon Sink**

320 Our carbon gain and loss models (Table 2) can be used to make a tentative estimate of the future size  
321 of the per unit area intact forest carbon sink (Figure 3). Extrapolations of the changes in the predictor  
322 variables from 1983-2015 forward to 2040 (Extended Data Figure 5) show declines in the sink on  
323 both continents (Figure 3). By 2030 the carbon sink in aboveground live biomass in intact African  
324 tropical forest is predicted to decline by 14% from the measured 2010-15 mean, to  $0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$   
325 <sup>1</sup> ( $2\sigma$  range, 0.16-0.96; Figure 3). The Amazon sink continues to decline, reaching zero in 2035 ( $2\sigma$

326 range, 2011-2089; Figure 3). Our estimated sink strength on both continents in the 2020s and 2030s  
327 is sensitive to future CO<sub>2</sub> emissions pathways (CO<sub>2</sub>-change)<sup>38</sup>, resulting temperature increase (MAT,  
328 MAT-change) and hydrological changes (MCWD), plus changes in forest dynamics (CRT), but the  
329 sink is always lower than levels seen in the 2000s (see Methods and Supplementary Table 5). Thus,  
330 the carbon sink strength of the world's two most extensive tropical forests have now saturated, albeit  
331 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  
336 continental sink in Amazonia peaked in the 1990s, followed by a decline, driven by sink strength  
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,  
339 due to the decline in forest area in the 2000s outpacing the small per unit area increase in sink  
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  
342 intact forest uptake of 1.26 Pg C yr<sup>-1</sup> in the 1990s, we project a continued decline reaching just 0.29  
343 Pg C yr<sup>-1</sup> in the 2030s (multi-decade decline of ~0.24 Pg C yr<sup>-1</sup> decade<sup>-1</sup>), driven by (i) reduced mean  
344 pan-tropical sink strength decline of 0.1 Mg C ha<sup>-1</sup> yr<sup>-1</sup> decade<sup>-1</sup> and (ii) ongoing forest area losses of  
345 ~13.5 million ha yr<sup>-1</sup> (see Extended Data Table 2 for forest area details). Critically, climate-driven  
346 vegetation model simulations have not predicted that peak net carbon uptake into intact tropical  
347 forests has already been passed<sup>2,4,5</sup>.

348

349 **Discussion**

350 Our method of scaling to arrive at a pan-tropical sink estimate – in common with other studies using  
351 similar datasets<sup>1,6,13</sup> – is limited. Yet, pervasive net carbon uptake is expected given that we find a  
352 strong and ongoing CO<sub>2</sub> fertilisation effect. Using our CO<sub>2</sub> response in Table 2, we find an increase  
353 in aboveground carbon stocks of 10.8±3.7 Mg C ha<sup>-1</sup> 100 ppm<sup>-1</sup> CO<sub>2</sub>, or 6.5±2.2% (±SE; using an  
354 area-weighted pan-tropical mean aboveground C stock of 165 Mg C ha<sup>-1</sup>), comparable to the  
355 5.0±1.2% increase in tropical forest C stocks 100 ppm<sup>-1</sup> CO<sub>2</sub> derived from a recent synthesis of CO<sub>2</sub>  
356 fertilisation experiments, despite a lack of data from mature tropical forests<sup>39</sup>. Our result is within the  
357 range of climate-driven vegetation models<sup>2,7</sup>, although it is greater than a number of recently-  
358 published models that include potential nutrient constraints, reported as 5.9±4.7 Mg C ha<sup>-1</sup> 100 ppm<sup>-1</sup>  
359 CO<sub>2</sub> (Ref.<sup>40</sup>). We find that the CO<sub>2</sub> fertilisation uptake is currently only partially offset by the  
360 negative impacts of similarly widespread rising air temperatures (-2.0±0.4 Mg C ha<sup>-1</sup> °C<sup>-1</sup>, from  
361 Table 2), consistent with models<sup>7</sup>, limited experiments<sup>31</sup> and independent observations<sup>9</sup>, plus  
362 negative responses to drought<sup>41,42</sup>. Long-term and extensive increases in satellite-derived greenness  
363 in tropical regions not experiencing major changes in land-use management<sup>17,43</sup>, particularly in  
364 central Africa in the past decade<sup>44</sup>, indicate increases in tropical forest net primary productivity,  
365 providing further evidence that the sink is a widespread phenomenon<sup>44</sup>.

366

367 Nonetheless, our analyses show that this pervasive tropical forest sink in live biomass is in long-term  
368 decline, first saturating in Amazonia, and more recently followed by African forests, explaining the  
369 prior Africa-Amazon carbon sink divergence as part of a longer-term pattern of asynchronous  
370 saturation and decline. From an atmospheric perspective the full impacts of the contribution to the  
371 saturation of the sink from slowing carbon gains are experienced immediately, but the contribution  
372 from rising carbon losses is delayed because dead trees do not decompose instantaneously.  
373 Decomposition of this dead tree mass is ~50% in 4 yrs, and ~85% in 10 yrs, thus rising carbon losses

374 result in delayed carbon additions to the atmosphere<sup>45</sup>. Hence, from an atmospheric perspective the  
375 intact tropical forest biomass carbon sink likely peaked a few years later than our plot data indicate  
376 and the full impacts are not yet realised. The pan-tropical carbon sink in live biomass reduced by  
377 0.27 Pg C yr<sup>-1</sup> between the 1990s and 2000s (Table 1), but accounting for dead wood  
378 decomposition<sup>45</sup> shows a smaller 0.17 Pg C yr<sup>-1</sup> reduction from an atmospheric perspective (see  
379 Methods).

380

381 Given that the global terrestrial carbon sink is increasing, a weakening intact tropical forest sink  
382 implies that the extra-tropical carbon sink has increased over the past two decades. Independent  
383 observations of inter-hemispheric atmospheric CO<sub>2</sub> concentration indicates that carbon uptake into  
384 the Northern hemisphere landmass has increased at a greater rate than the global terrestrial carbon  
385 sink since the 1990s, with a further disproportionate increase in the 2000s<sup>10</sup>. The inter-hemispheric  
386 analysis suggests a weakening of the tropical forest sink by ~0.2 Pg C yr<sup>-1</sup> between the 1990s and  
387 2000s<sup>10</sup>, which is similar to the 0.17 Pg C yr<sup>-1</sup> weakening over the same time period that we find.  
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  
391 are key centres of biodiversity<sup>11</sup>, their ability to sequester additional carbon is waning. In the 1990s  
392 intact forests removed 17% of anthropogenic CO<sub>2</sub> 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  
394 decreased by 19%, and CO<sub>2</sub> emissions increased by 46%. Although tropical forests are more  
395 immediately threatened by deforestation<sup>46</sup> and degradation<sup>47</sup>, and the future carbon balance will also  
396 depend on secondary forest dynamics<sup>48</sup> and forest restoration plans<sup>49</sup>, our analyses show that they are  
397 also impacted by atmospheric chemistry and climatic changes. Given that the intact tropical forest  
398 carbon sink is set to end sooner than even the most pessimistic climate-driven vegetation models

399 predict<sup>4,5</sup>, our analyses suggest that climate change impacts in the tropics may become more severe  
400 than predicted. Furthermore, the carbon balance of intact tropical forests will only stabilise once CO<sub>2</sub>  
401 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  
406 terrestrial carbon sink. In addition, our conclusion that tree mortality and internal forest dynamics are  
407 important controls on the future of the tropical forest carbon sink, may assist in improving the  
408 vegetation components of future Earth System Models<sup>50</sup> and contribute to reducing terrestrial carbon  
409 cycle feedback uncertainty<sup>19,20</sup>. 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  
412 likely to sequester less carbon in the future than Earth System Models predict, an earlier date to reach  
413 net zero anthropogenic greenhouse gas emissions will be required to meet any given commitment to  
414 limit the global heating of Earth.

415

## 416 **References**

417

418 1 Pan, Y. et al. A Large and Persistent Carbon Sink in the World's Forests. *Science* **333**, 988-  
419 993, doi:10.1126/science.1201609 (2011).

420 2 Sitch, S. et al. Recent trends and drivers of regional sources and sinks of carbon dioxide.  
421 *Biogeosciences* **12**, 653-679, doi:10.5194/bg-12-653-2015 (2015).

422 3 Gaubert, B. et al. Global atmospheric CO<sub>2</sub> 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).

425 4 Huntingford, C. et al. Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate  
426 change. *Nature Geoscience* **6**, 268-273, doi:10.1038/ngeo1741 (2013).

427 5 Mercado, L. M. et al. Large sensitivity in land carbon storage due to geographical and  
428 temporal variation in the thermal response of photosynthetic capacity. *New Phytologist* **218**,  
429 1462-1477, doi:doi:10.1111/nph.15100 (2018).

430 6 Brienen, R. J. W. et al. Long-term decline of the Amazon carbon sink. *Nature* **519**, 344-348,  
431 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 CO<sub>2</sub> trends. *Global Change Biology* **19**, 2117-2132, doi:10.1111/gcb.12187  
434 (2013).

435 8 Schimel, D., Stephens, B. B. & Fisher, J. B. Effect of increasing CO<sub>2</sub> on the terrestrial carbon  
436 cycle. *Proceedings of the National Academy of Sciences* **112**, 436-441,  
437 doi:10.1073/pnas.1407302112 (2015).

438 9 Anderegg, W. R. L. et al. Tropical nighttime warming as a dominant driver of variability in  
439 the terrestrial carbon sink. *Proceedings of the National Academy of Sciences* **112**, 15591-  
440 15596, doi:10.1073/pnas.1521479112 (2015).

441 10 Ciais, P. et al. Five decades of northern land carbon uptake revealed by the interhemispheric  
442 CO<sub>2</sub> gradient. *Nature*, doi:10.1038/s41586-019-1078-6 (2019).

443 11 Lewis, S. L., Edwards, D. P. & Galbraith, D. Increasing human dominance of tropical forests.  
444 *Science* **349**, 827-832, doi:10.1126/science.aaa9932 (2015).

445 12 Pugh, T. A. M. et al. Role of forest regrowth in global carbon sink dynamics. *Proceedings of  
446 the National Academy of Sciences* **116**, 4382-4387, doi:10.1073/pnas.1810512116 (2019).

447 13 Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. *Nature* **457**,  
448 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).

455 17 Nemani, R. R. et al. Climate-driven increases in global terrestrial net primary production  
456 from 1982 to 1999. *Science* **300**, 1560-1563 (2003).

457 18 Keenan, T. F. et al. Recent pause in the growth rate of atmospheric CO<sub>2</sub> due to enhanced  
458 terrestrial carbon uptake. *Nature Communications* **7**, 13428, doi:10.1038/ncomms13428  
459 (2016).

460 19 Booth, B. B. B. et al. High sensitivity of future global warming to land carbon cycle  
461 processes. *Environmental Research Letters* **7**, 024002 (2012).

462 20 Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S. & Fisher, R. A. Temperature  
463 acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate  
464 feedback. *Geophysical Research Letters* **42**, 8624-8631, doi:doi:10.1002/2015GL065934  
465 (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).

468 22 Lewis, S. L., Brando, P. M., Phillips, O. L., van der Heijden, G. M. F. & Nepstad, D. The  
469 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).

474 25 Aleixo, I. et al. Amazonian rainforest tree mortality driven by climate and functional traits.

475 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**, 20120295-

481 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-9-2203-

484 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).

493 33 Bauters, M. et al. High fire-derived nitrogen deposition on central African forests.

494 Proceedings Of The National Academy Of Sciences Of The United States Of America **115**,

495 549-554, 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).

499 35 Slik, J. W. F. et al. Phylogenetic classification of the world's tropical forests. *Proceedings of*  
500 *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).

503 37 Schnitzer, S. A. & Bongers, F. Increasing liana abundance and biomass in tropical forests:  
504 emerging patterns and putative mechanisms. *Ecology Letters* **14**, 397-406,  
505 doi:10.1111/j.1461-0248.2011.01590.x (2011).

506 38 Meinshausen, M. et al. The RCP greenhouse gas concentrations and their extensions from  
507 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 CO<sub>2</sub> 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 CO<sub>2</sub> fertilization dependent on plant  
511 phosphorus acquisition. *Nature Geoscience* **12**, 736-741, doi:10.1038/s41561-019-0404-9  
512 (2019).

513 41 Jiang, Y. et al. Widespread increase of boreal summer dry season length over the Congo  
514 rainforest. *Nature Climate Change* **9**, 617-622, doi:10.1038/s41558-019-0512-y (2019).

515 42 Gloor, M. et al. Recent Amazon climate as background for possible ongoing and future  
516 changes of Amazon humid forests. *Global Biogeochemical Cycles* **29**, 1384-1399,  
517 doi:10.1002/2014gb005080 (2015).

518 43 Kolby Smith, W. et al. Large divergence of satellite and Earth system model estimates of  
519 global terrestrial CO<sub>2</sub> fertilization. *Nature Climate Change* **6**, 306, doi:10.1038/nclimate2879  
520 (2015).

521 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).

526 46 Hansen, M. C. et al. High-Resolution Global Maps of 21<sup>st</sup>-Century Forest Cover Change.  
527 *Science* **342**, 850-853, doi:10.1126/science.1244693 (2013).

528 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).

531 48 Schwartz, N. B., Uriarte, M., DeFries, R., Gutierrez-Velez, V. H. & Pinedo-Vasquez, M. A.  
532 Land-use dynamics influence estimates of carbon sequestration potential in tropical second-  
533 growth forest. *Environmental Research Letters* **12**, 074023, doi:10.1088/1748-9326/aa708b  
534 (2017).

535 49 Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A. & Koch, A. Regenerate natural forests to  
536 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).

540

541 **Acknowledgements**

542 This paper is a product of the African Tropical Rainforest Observatory Network (AfriTRON),  
543 curated at ForestPlots.net. AfriTRON has been supported by numerous people and grants since its  
544 inception. We sincerely thank the people of the many villages and local communities who welcomed  
545 our field teams and without whose support this work would not have been possible: Sierra Leone  
546 (Barrie, Gaura, Koya, Makpele, Malema, Nomo, Tunkia, Gola Rainforest National Park), Liberia  
547 (Garley town, River Gbeh, Glaro Freetown), Ghana (Nkwanta, Asenanyo, Bonsa, Agona, Boekrom,

548 Dadieso, Enchi, Dabiasem, Mangowase, Draw, Fure, Esuboni, Okumaninin, Kadeand Asamankese,  
549 Tinte Bepo, Tonton), Nigeria (Oban), Gabon (Ekobakoba, Mikongo, Babilone, Makokou,  
550 Leke/Moyabi Rougier Forestry Concession, Ivindo National Park, Lope National Park, Ipassa  
551 station, Kingele station, Tchimbele, Mondah, Ivindo, Ebe, Ekouk, Oveng, Sette Cama, Waka  
552 National Park), Cameroon (Campo, Nazareth, Lomié, Djomédjo, Alat-Makay, Somolomo, Deng  
553 Deng, Ejagham forest reserve, Eyumojok, Mbakaou, Myere, Nguti, Bejange, Kekpane, Basho,  
554 Mendhi, Matene, Mboh, Takamanda, Obonyi, Ngoïla), Democratic Republic of Congo (Yoko,  
555 Yangambi, Epulu, Monkoto), Republic of Congo (Bomassa, Ekolongouma, Bolembé, Makao, Mbeli,  
556 Kabo, Niangui, Ngubu, Goualaki, Essimbi), and many others.

557

558 We thank the hundreds of field assistants whose expertise and enthusiasm is indispensable to  
559 successful fieldwork: Menge Elvis Abang, Usaw Philip Achui, Francis Addai, Eyelechon Julius  
560 Agbachon, Jess Agnaka , Archaley John Akaza, Gabarie Alaman, Gregoire Alaman, Abor Enow  
561 Alexander, Kate Allen, Mobembe Amalphi, Danny Amandus, Jean Andju, Lazare Angassike  
562 Limbanga, Samuel Asamoah, Takem Martin Ashu, Moses Ashu, Joel Asse, Bangubaare Augustine,  
563 Henry Badjoko, Mayanga Balimu, Juste Baviogui-Baviogui, Solomon Benteh, Akuemo Bertrand,  
564 Akwo Bettus, Albert Bias, Andre Bikoula, Alain Bimba, Prince Bissiemou, Mensah Boateng, Etshu  
565 Bonyenga, Mopero Bosiko Ekaya, Gael Bouka, Juvenal Boussengui, Didier Bowaka Ngomo,  
566 Charles Chalange, Sylvester Chenikan, Jonathan Dabo, Emmanuel Dadize, Takyi Degrift, Joachim  
567 Dibakou, Jean-Thoussaint Dikangadissi, Pacôme Dimbonda, Edmond Dimoto, Carl Ditougou,  
568 Daniel Dorbor, Morris Dorbor, Vincent Droissart, Kwaku Duah, Edward Ebe, Osong Jerome Eji,  
569 Ekama Bertrand Ekamam, Jean-Robert Ekomindong, Essa Joseph Enow, Hiboux Entombo, Ebai  
570 Mengue Ernest, Courageux Esola, Jules Essouma, Alaman Gabriel, Nteh Genesis, Bilfanim Gideon,  
571 Afedo Godwin, Eric Grear, D. John Grear, Mokondo Ismael, Michel Iwango, Mongali Iyafo,  
572 Narcisse Kamdem, Bondele Kibinda, Alidé Kidimbu, Exaldi Kimumbu, John Kintsieri, Cisquet

573 Kiebou Opepa, Amani Kitegile, Thérence Komo, Pokou Koué, Augustin Kouanga, Jean Jules  
574 Koumikaka, Innocent Liengola, Elias Litonga, Lisa Louvouando, Ondo Luis, Noé Madingou Mady,  
575 Felicien Mahoula, Amani Mahundu, Chris Axel Mandebet, Poungue Maurice, Karl Yannick  
576 Mayossa, Robert Mba Nkogue, Isa David Mbe, Christian Mbina, Herve Mbona, Alain Mboni, Alain  
577 Mbouni, Paulin Menzo, Michael Menge, Andah Michael, Alain Mindoumou, Joseph Minpsa, Jean  
578 Paul Mondjo, E. Mounoumoulossi, Serge Mpouam, Tofile Msigala, John Msirikale, Samuel Mtoka,  
579 Ruben Mwakisoma, Daniel Ndong-Nguema, Gilbert Ndoyame, Guy Ngongbo, Francois Ngowa, D.  
580 Nguema, Luwi Nguye, Raoul Niangadouma, Yaw Nkrumah, Seya Nshimba, Marcel Nziengui  
581 Mboumba, Francis Nzogo Obiang, Lucas Obi, Roland Obi, Eyong Louis Oджong, Félix Okon,  
582 Fabiane Olivieira, Alina Lawrence Owemicho, Leandre Oyen-Amoni, Abia Platini, Pierre Ploton,  
583 Simon Quausah, Elasi Ramazani, Boscu Saïdou Jean, Lebienfalteur Sagang, Rosalind Salter,  
584 Adenani Seki, Deo Shirima, Murielle Simo, Igor Singono, Agboloh Eugene Tabi, Tako Gilbert Tako,  
585 Nteh Gambsi Tambe, Toha Tcho, Andrew Teah, Victor Tehtoe, Bright Joe Telephas, Marie Lesly  
586 Tonda, Angoni Tresor, Hamid Umenendo, Raymond Votere, Cyrus K. Weah, Slonean Weah, Bart  
587 Wursten, Emmanuel Valley, Donatien Zebaze, Laurent Cerbonney, Emilien Dubiez, Hervé  
588 Moinecourt, François Lanckriet, Evina, Monazang, Engonga, Soso Samai, Mohamed Swaray,  
589 Patrick Lamboi, Mohamed Sullay, Dennis Bannah, Ibrahim Kanneh, Michael Kannah, Alhassan  
590 Kemokai, Joseph Kenneh, Morrison Lukulay.

591

592 For logistical and administrative support, we are indebted to international, national and local  
593 institutions: the Forestry Department of the Government of Sierra Leone, the Conservation Society  
594 of Sierra Leone, the Royal Society for the Protection of Birds (RSPB), The Gola Rainforest National  
595 Park, the Forestry Development Authority of the Government of Liberia (FDA), the University of  
596 Liberia, the Forestry Commission of Ghana (FC), the Forestry Research Institute of Ghana (FORIG),  
597 University of Ibadan (Nigeria), the University of Abeokuta (Nigeria), the Ministère des Eaux, Forêts,

598 Chasse et Pêche (MEFCP, Bangui, République Centrafricaine), the Institut Centrafricain de  
599 Recherche Agronomique (ICRA), The Service de Coopération et d'Actions Culturelles  
600 (SCAC/MAE), The University of Bangui, the Société Centrafricaine de Déroulage (SCAD), the  
601 University of Yaounde I, the National Herbarium of Yaounde, the University of Buea, Biodiversity  
602 International (Cameroon), the Ministry of Forests, Seas, Environment and Climate (Gabon), the  
603 Agence Nationale des Parcs Nationaux de Gabon (ANPN), Institut de Recherche en Ecologie  
604 Tropicale du Gabon, Rougier-Gabon, the Marien Ngouabi University of Brazzaville, the Ministère  
605 des Eaux et Forêts (République du Congo), the Ministère de la Recherche Scientifique et de  
606 l'Innovation Technologique (République du Congo), the Nouabalé-Ndoki Foundation, WCS-Congo,  
607 Salonga National Park, The Centre de Formation et de Recherche en Conservation Forestière  
608 (CEFRECOF, Epulu, D.R.Congo), the Institut National pour l'Etude et la Recherche Agronomiques  
609 en R.D.Congo (INERA), the École Régionale Postuniversitaire d'Aménagement et de Gestion  
610 intégrés des Forêts et Territoires tropicaux (ERAIFT Kinshasa), WWF-D.R.Congo, WCS-  
611 D.R.Congo, the Université de Kisangani, Université Officielle de Bukavu, Université de Mbuji-Mayi,  
612 le Ministère de l'Environnement et Développement Durable de la R.D.C., the Lukuru Wildlife  
613 Research Foundation, Mbarara University of Science and Technology (MUST), WCS-Uganda, the  
614 Uganda Forest Department, the Commission of Central African Forests (COMIFAC), the Udzungwa  
615 Ecological Monitoring Centre (Tanzania) and the Sokoine University of Agriculture (Tanzania).

616  
617 Grants that have funded the AfriTRON network including data in this paper are: a NERC grant to  
618 O.L.P., Y.M., and S.L.L. (NER/A/S/2000/01002), a Royal Society University Research Fellowship  
619 to S.L.L., a NERC New Investigators Grant to S.L.L., a Philip Leverhulme Award to S.L.L., a  
620 European Union FP7 grant to E.G. and S.L.L. (GEOCARBON; 283080), Valuing the Arc  
621 Leverhulme Program Grant to Andrew Balmford and S.L.L., a European Research Council  
622 Advanced Grant to O.L.P. and S.L.L. (T-FORCES; 291585; Tropical Forests in the Changing Earth

623 System), a Natural Environment Research Council (NERC) Consortium Grant to Jon Lloyd and  
624 S.L.L. (TROBIT; NE/D005590/), the Gordon and Betty Moore Foundation to L.J.T.W and S.L.L.,  
625 the David and Lucile Packard Foundation to L.J.T.W. and S.L.L., the Centre for International  
626 Forestry Research to T.S. and S.L.L. (CIFOR), and Gabon's National Parks Agency (ANPN) to  
627 S.L.L. W.H. was funded by T-FORCES and the Brain program of the Belgian Federal Government  
628 (BR/132/A1/AFRIFORD and BR/143/A3/HERBAXYLAREDD grants to H.B.). O.L.P., S.L.L.,  
629 M.J.P.S, A.E.-M., A.L., G.L.-G., G.P, and L.Q were supported by T-FORCES.

630

631 Additional African data were included from the consortium MEFCP-ICRA-CIRAD (Centre de  
632 Coopération Internationale en Recherche Agronomique pour le Développement), the Tropical  
633 Ecology Assessment and Monitoring Network (TEAM), and the Forest Global Earth Observatory  
634 Network (ForestGEO; formerly the Center for Tropical Forest Science CTFS). The TEAM network  
635 is a collaboration between Conservation International, the Missouri Botanical Garden, the  
636 Smithsonian Institution and the Wildlife Conservation Society, and funded by the Gordon and Betty  
637 Moore Foundation and other donors. The ForestGEO Network is a collaboration between the  
638 Smithsonian Institution, other federal agencies of the United States, the Wildlife Conservation  
639 Society (WCS) and the World Wide Fund for Nature (WWF), and funded by the U.S. National  
640 Science Foundation and other donors.

641

642 The paper was made possible by the RAINFOR network in Amazonia, with multiple funding  
643 agencies and hundreds of investigators working in Amazonia, acknowledged in Ref.<sup>6</sup>, providing  
644 comprehensive published data and code and allowing onward analysis of their data, see Ref.<sup>6</sup>. Data  
645 from AfriTRON and RAINFOR are stored and curated by ForestPlots.net, a long-term cyber-  
646 infrastructure initiative hosted at the University of Leeds that unites permanent plot records and their  
647 contributing scientists from the world's tropical forests. The development of ForestPlots.net and

648 curation of most data analysed here was funded by many sources, including grants to S.L.L. (Royal  
649 Society University Research Fellowship, NERC New Investigators Award, NERC NE/P008755/1),  
650 O.L.P. (principally from NERC NE/B503384/1, ERC AdG 291585 “T-FORCES”, and Gordon and  
651 Betty Moore Foundation #1656, “RAINFOR”) and E.G. (“GEOCARBON”, and NE/F005806/1  
652 “AMAZONICA”). We acknowledge the contributions of the ForestPlots.net steering committee  
653 (T.R.B., A.L., S.L.L., O.L.P., L.Q., Euridice N. Honorio Coronado and Beatriz S. Marimon) to  
654 advising on database development and management.

655

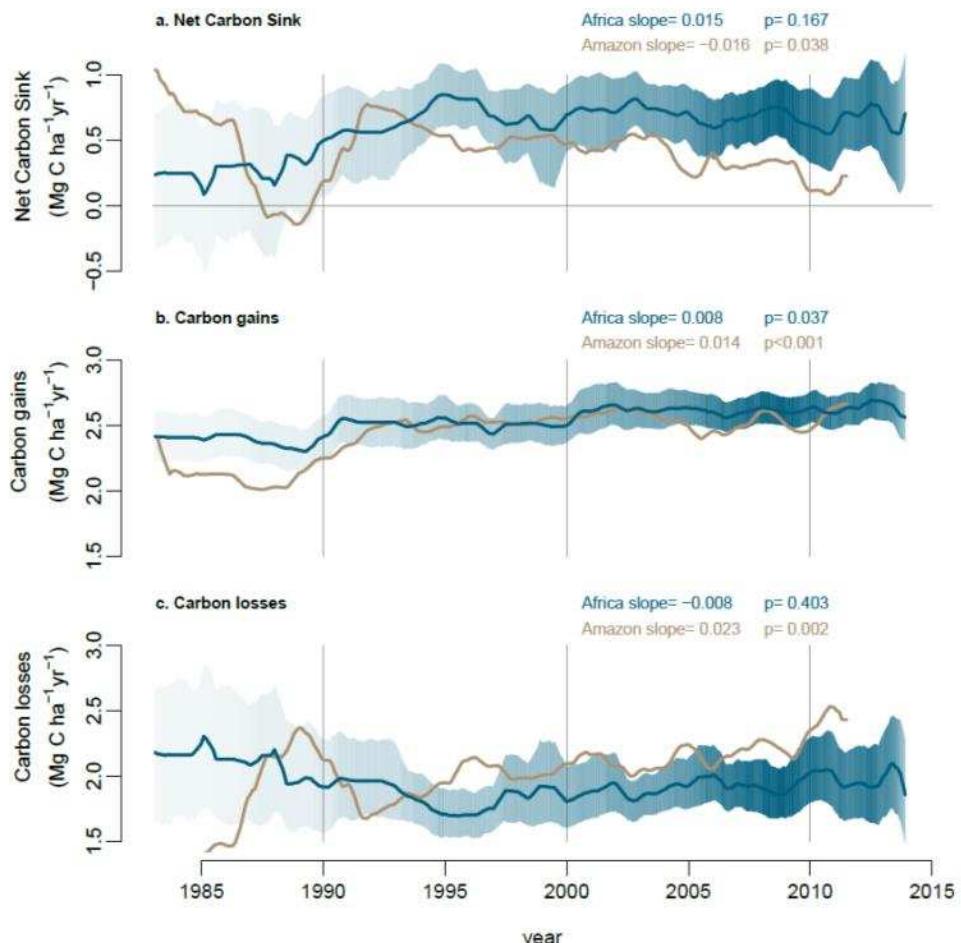
## 656 **Author Contributions**

657 S.L.L. conceived and managed the AfriTRON forest plot recensus programme, O.L.P., T.C.H.S.,  
658 L.J.T.W. and Y.M. contributed to its development. W.H., S.L.L., O.L.P., B.S. & M.J.P.S. developed  
659 the study. W.H., S.L.L., O.L.P., K.A.-B., H.B., A.C.-S., C.E.N.E., S.F., D.S., B.S., T.C.H.S., S.C.T.,  
660 K.A.A., S.A.-B., C.A.A., T.R.B., L.F.B., F.Ba., S.K.B., F.Be., R.B., Y.E.B., P.Boe., P.Bou., T.B.,  
661 E.C., G.B.C., C.J.C., M.C., J.A.C., D.C., A.K.D., G.C.D., T.d.H., M.D.K., J.-L.D., T.R.F., A.F.,  
662 E.G.F., M.G., C.G., S.G.-F., J.S.H., A.C.H., D.J.H., T.B.H., M.B.N.H., A.H., S.A.I., K.J.J., T.J.,  
663 E.K.Y., E.K., D.K., M.E.L., J.A.L., J.L., J.C.L., J.-R.M., Y.M., A.R.M., J.M., E.H.M., F.M.M.,  
664 V.P.M., V.M., E.T.A.M., S.M., J.M.M., P.K.T.M., N.N.B., L.O., F.E., K.P., A.D.P., J.R.P., L.Q.,  
665 J.R., F.R., M.D.S., H.T., J.Tal., J.Tap., D.M.T., D.W.T., B.T., J.T.M., D.T., P.M.U., G.V.D.H., H.V.,  
666 J.V., L.J.T.W., S.W., H.W., J.T.W. and L.Z. contributed data (larger field contributions by S.L.L.,  
667 W.H., A.C.-S., B.S., H.T., A.K.D., C.E.N.E., J.M.M., K.A.-B. and S.F.). O.L.P., T.R.B., S.L.L. and  
668 G.L.-G. conceived and managed forestplots.net; O.L.P., T.R.B., S.L.L., E.G., G.L.-G., G.C.P., A.L.,  
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-

672 authors read and approved the manuscript (with important insights provided by O.L.P., S.F.,  
673 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.).

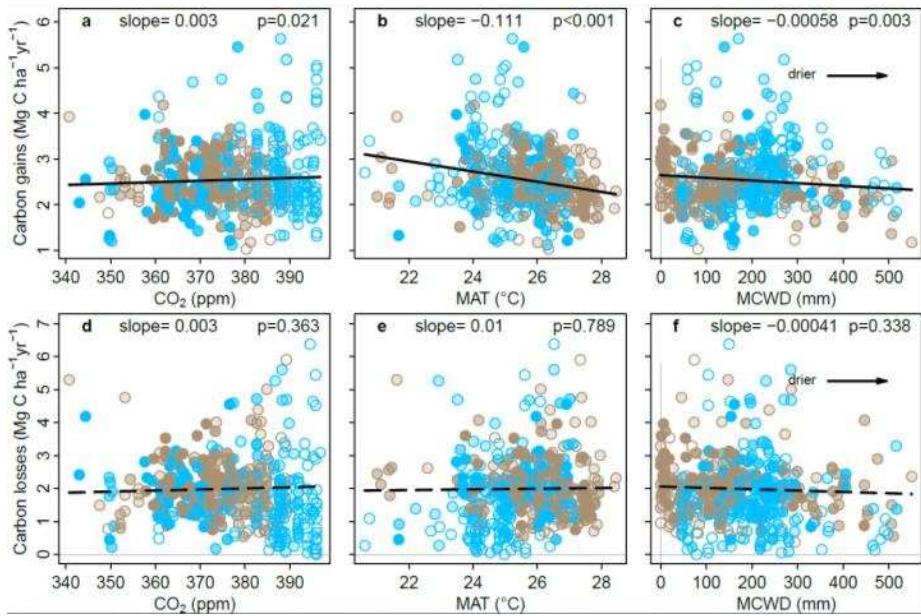
674

675 **Main Figures**



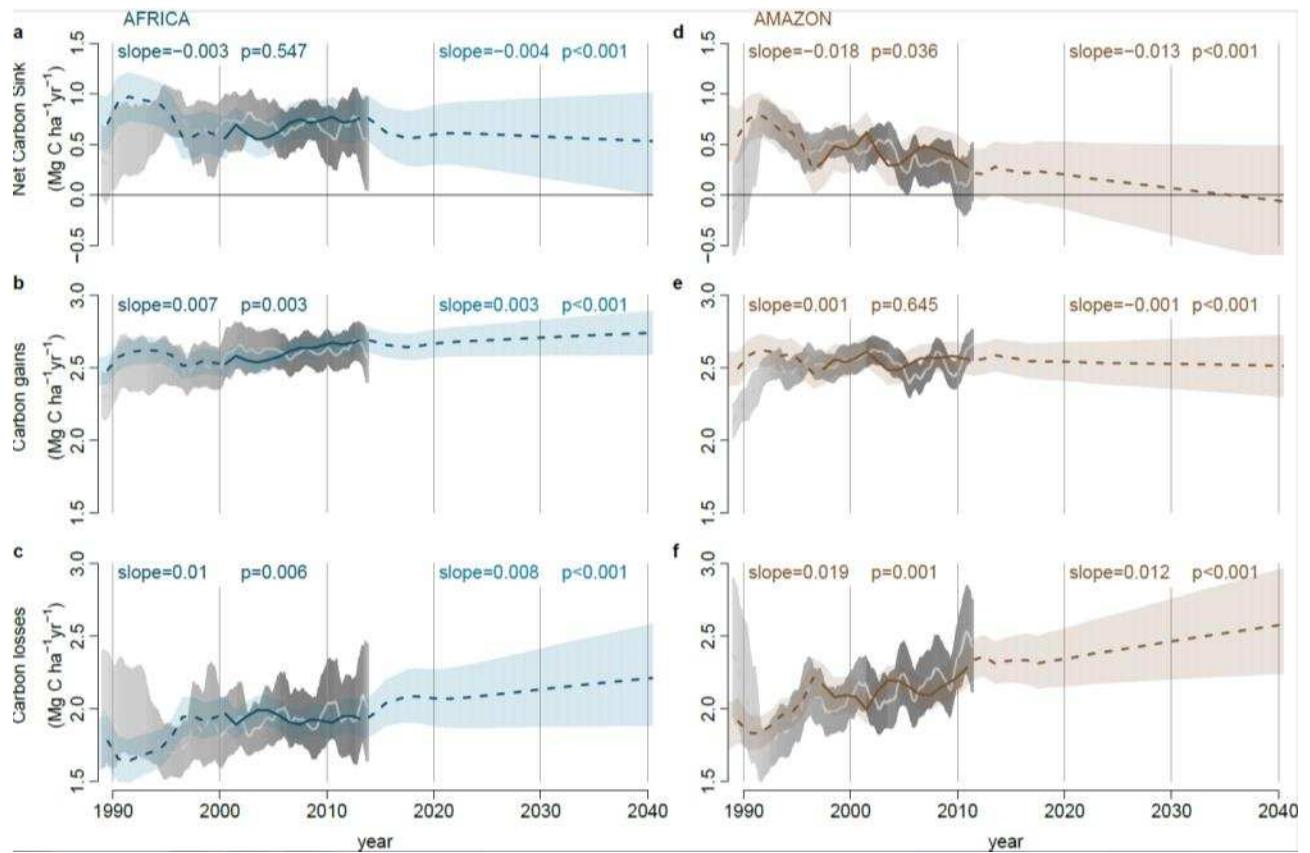
676

677 **Figure 1. Long-term carbon dynamics of structurally intact tropical forests in Africa (blue)**  
678 **and Amazonia (brown).** Trends in net aboveground live biomass carbon sink (a), carbon gains to  
679 the system from wood production (b), and carbon losses from the system from tree mortality (c),  
680 measured in 244 African inventory plots (blue lines) and contrasting published<sup>6</sup> Amazonian  
681 inventory data (brown lines; 321 plots). Shading corresponds to the 95% CI, with less transparent  
682 shading indicating a greater number of plots monitored in that year (most transparent: minimum 25  
683 plots monitored). The CI for the Amazonian dataset is omitted for clarity, but can be seen in Figure  
684 3. Slopes and p-values are from linear mixed effects models (see Methods).



685

686 **Figure 2. Potential environmental drivers of carbon gains and losses in structurally intact old-**  
 687 **growth African and Amazonian tropical forests.** Aboveground carbon gains, from woody  
 688 production (**a-c**), and aboveground carbon losses, from tree mortality (**d-f**), presented as time-  
 689 weighted mean values for each plot, i.e. each census within a plot is weighted by its length, against  
 690 the corresponding values of atmospheric carbon dioxide concentration (CO<sub>2</sub>), mean annual air  
 691 temperature (MAT) and drought (as Maximum Climatological Water Deficit, MCWD), for African  
 692 (blue) and Amazonian (brown) inventory plots. Each data point therefore represents an inventory  
 693 plot, for visual clarity, and the level of transparency represents the total monitoring length, with  
 694 empty circles corresponding to plots monitored for  $\leq 5$  years and solid circles for plots monitored for  
 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  
 697 empirically derived weighting based on interval length and plot area, on the untransformed pooled  
 698 Africa and Amazon dataset (see Methods). Slopes and p-values are from the same linear mixed  
 699 effects models. Carbon loss data and models are presented untransformed for comparison with  
 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).



703

**Figure 3. Modelled past and future carbon dynamics of structurally intact tropical forests in Africa and Amazonia.** Predictions of net aboveground live biomass carbon sink (a,d), carbon gains (b,e), and carbon losses (c,f), for African (left panels) and Amazonian (right panels) plot inventory networks, based on CO<sub>2</sub>-change, Mean Annual Temperature, Mean Annual Temperature-change, drought (as Maximum Climatological Water Deficit), plot wood density, and plot carbon residence time, using observations in Africa until 2014 and Amazonia until 2011.5, and extrapolations of prior 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 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 variables. Light grey lines and grey shading are the mean and 95% CI of the observations from the African and Amazonian plot networks.

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  $2\sigma$  for the predictions (2010-2040).

| Period      | No. plots | Per unit area aboveground live biomass C sink |                          |                          |                         | Total C sink *           |                          |              |
|-------------|-----------|---|--------------------------|--------------------------|-------------------------|--------------------------|--------------------------|--------------|
|             |           | (Mg C ha <sup>-1</sup> yr <sup>-1</sup> )     |                          |                          |                         | (Pg C yr <sup>-1</sup> ) |                          |              |
|             |           | Af. Am.                                       | Africa                   | Amazon                   | Pan-tropics†            | Africa                   | Amazon                   | Pan-tropics† |
| 1980-1990   | 45 73     | <b>0.33</b> (0.06-0.63)                       | <b>0.35</b> (0.06-0.59)  | <b>0.35</b> (0.07-0.62)  | <b>0.28</b> (0.05-0.53) | <b>0.49</b> (0.08-0.82)  | <b>0.87</b> (0.16-1.52)  |              |
| 1990-2000   | 96 172    | <b>0.67</b> (0.43-0.89)                       | <b>0.53</b> (0.42-0.65)  | <b>0.57</b> (0.39-0.74)  | <b>0.50</b> (0.32-0.66) | <b>0.68</b> (0.54-0.83)  | <b>1.26</b> (0.88-1.63)  |              |
| 2000-2010   | 194 291   | <b>0.70</b> (0.55-0.84)                       | <b>0.38</b> (0.26-0.48)  | <b>0.50</b> (0.35-0.64)  | <b>0.46</b> (0.37-0.56) | <b>0.45</b> (0.31-0.57)  | <b>0.99</b> (0.70-1.25)  |              |
| 2010-2015   | 184 172   | <b>0.66</b> (0.40-0.91)                       | <b>0.24</b> (0.00-0.47)  | <b>0.40</b> (0.15-0.65)  | <b>0.40</b> (0.24-0.56) | <b>0.27</b> (0.00-0.52)  | <b>0.73</b> (0.25-1.18)  |              |
| 2010-2020 ‡ | - -       | <b>0.63</b> (0.36-0.89)                       | <b>0.23</b> (-0.05-0.50) | <b>0.38</b> (0.11-0.65)  | <b>0.37</b> (0.21-0.53) | <b>0.25</b> (-0.05-0.54) | <b>0.68</b> (0.17-1.16)  |              |
| 2020-2030 ‡ | - -       | <b>0.59</b> (0.24-0.93)                       | <b>0.12</b> (-0.29-0.51) | <b>0.30</b> (-0.08-0.67) | <b>0.31</b> (0.13-0.49) | <b>0.12</b> (-0.29-0.52) | <b>0.47</b> (-0.15-1.07) |              |
| 2030-2040 ‡ | - -       | <b>0.55</b> (0.08-0.99)                       | <b>0.00</b> (-0.54-0.49) | <b>0.21</b> (-0.29-0.67) | <b>0.26</b> (0.04-0.47) | <b>0.00</b> (-0.50-0.46) | <b>0.29</b> (-0.46-0.97) |              |

721 \* Total Continental C sink is the per unit area aboveground C sink multiplied by intact forest area for  
 722 1990-2010 (from ref.<sup>1</sup>, see Extended Data Table 2) and continent specific extrapolations to 2040.  
 723 Total Continental C sink includes continent-specific estimates of trees <100 mm DBH, lianas and  
 724 roots (see Methods).

725 † Pan-tropical aboveground live biomass C sink is the area-weighted mean of African, Amazonian  
 726 and Southeast Asian sink values. Southeast Asian values were from published per unit area carbon  
 727 sink data<sup>15</sup> (n=49 plots) for 1990-2015, with 1980-1990 assumed to be the same as 1990-2000 due  
 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,  
 731 at 0.11, 0.08, 0.07 and 0.06 Pg C yr<sup>-1</sup> in the 1980s, 1990s, 2000s and 2010s, hence uncertainty in the  
 732 Southeast Asian sink cannot reverse the pan-tropical declining sink trend.

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.

737

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

| Carbon gains, Mg C ha <sup>-1</sup> yr <sup>-1</sup> |                 |                |             |                |                                 |
|--|-----------------|----------------|-------------|----------------|---------------------------------|
| Predictor variable                                   | Parameter value | Standard Error | t-value     | p-value        | 2000-2015 change in gains (%) * |
| (Intercept)  | 5.255   5.395   | 0.603   0.614  | 8.7   8.8   | <0.001         | -                               |
| CO <sub>2</sub> -change (ppm yr <sup>-1</sup> ) †    | 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 <sup>-1</sup> ) ‡                  | -1.243          | 0.233          | -5.3        | <0.001         | 0.58%   0.00% §                 |
| MCWD (mm x1000)                                      | -0.405   -1.391 | 0.381   0.24   | -1.1   -5.8 | 0.289   <0.001 | -0.52%   -2.73%                 |
| WD (g cm <sup>-3</sup> )                             | -1.295          | 0.530          | -2.4        | 0.015          | 0.05%   0.00%                   |

| Carbon losses, Mg C ha <sup>-1</sup> yr <sup>-1</sup> |                 |                |         |         |                                  |
|---|-----------------|----------------|---------|---------|----------------------------------|
| Predictor variable                                    | Parameter value | Standard Error | t-value | p-value | 2000-2015 change in losses (%) * |
| (Intercept)   | 1.216           | 0.086          | 14.1    | <0.001  | -                                |
| CO <sub>2</sub> -change (ppm yr <sup>-1</sup> ) †     | 0.130           | 0.059          | 2.2     | 0.026   | 11.38%   14.81%                  |
| MAT-change (°C yr <sup>-1</sup> )                     | 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%                   |

741 \* The 2000-2015 change in gains/losses for each predictor variable was estimated allowing only the  
 742 focal predictor to vary; this change was then expressed as a percentage of the annual gains/losses in  
 743 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  
 747 to the mean increase over 1983-2015, therefore contributing to an increase in gains; a zero value for  
 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,  $\lambda = 0.361$ .

751

752 **Online Methods**

753

754 **Plot Selection**

755 Closed canopy (i.e. not woody savanna) old-growth mixed-age forest inventory plots were selected  
756 using commonly used criteria<sup>6,13,27</sup>: free of fire and industrial logging; all trees with diameter at  
757 reference height  $\geq 100$  mm measured at least twice;  $\geq 0.2$  ha area;  $< 1500$  m.a.s.l. altitude; MAT  
758  $\geq 20.0^{\circ}\text{C}^{51}$ ; annual precipitation  $\geq 1000$  mm<sup>51</sup>; located  $\geq 50$  m from anthropogenic forest edges. Of the  
759 244 plots included in the study, 217 contribute to the African Tropical Rainforest Observatory  
760 Network (AfriTRON; [www.afritron.org](http://www.afritron.org)), with data curated at [www.ForestPlots.net](http://www.ForestPlots.net)<sup>52,53</sup>. These  
761 include plots from Sierra Leone, Liberia, Ghana, Nigeria, Cameroon, Gabon, Republic of Congo,  
762 Democratic Republic of Congo (DRC), Uganda and Tanzania<sup>52,53</sup> (Extended Data Figure 1). Fifteen  
763 plots are part of the TEAM network, from Cameroon, Republic of Congo, Tanzania, and Uganda<sup>54-</sup>  
764 <sup>57</sup>. Nine plots contribute to the ForestGEO network, from Cameroon and DRC<sup>58</sup> (9 plots from DRC,  
765 codes SNG, contribute to both AfriTRON and ForestGEO networks, included above in the  
766 AfriTRON total). Finally, three plots from Central African Republic are part of the CIRAD  
767 network<sup>59,60</sup>. The large majority of plots are sited in terra firme forests and have mixed species  
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  
773 years, mean census length 5.7 years, with a total of 3,214 ha years of monitoring. The 321 Amazon  
774 plots are published and were selected using the same criteria<sup>6</sup>, except in the African selection criteria  
775 we specified a minimum anthropogenic edge distance and added a minimum temperature threshold.

776

777 **Plot Inventory and Tree Biomass Carbon Estimation**

778 Tree-level aboveground biomass carbon is estimated using an allometric equation with parameters  
779 for tree diameter, tree height and wood mass density<sup>61</sup>. The calculation of each is discussed in turn.  
780 All calculations were performed using the R statistical platform, version 3.2.1 (ref.<sup>62</sup>) using the  
781 BiomasaFP R package, version 0.2.1 (ref.<sup>63</sup>).

782

783 Tree Diameter: In all plots, all woody stems with  $\geq 100$  mm diameter at 1.3 m from the base of the  
784 stem ('diameter at breast height', DBH), or 0.5 m above deformities or buttresses, were measured,  
785 mapped and identified using standard forest inventory methods<sup>64,65</sup>. The height of the point of  
786 measurement (POM) was marked on the trees and recorded, so that the same POM is used at the  
787 subsequent forest census. For stems developing deformities or buttresses over time that could  
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  
790 create a single trajectory of growth from the series of diameters at two POM heights<sup>6,13,65</sup>. We used  
791 standardised protocols to assess typographical errors and potentially erroneous diameter values (e.g.  
792 trees shrinking by  $>5$  mm), missing values, failures to find the original POM, and other issues.  
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  
795 the same plot, census and size-class, defined as DBH = 100-199 mm, or 200-399 mm, or  $>400$  mm<sup>65</sup>.  
796 We interpolated measurements for 1.3% of diameters, extrapolated 0.9%, and used median growth  
797 rates for 1.5%.

798

799 Tree height: Height of individuals from ground to the top leaf, hereafter  $H_t$ , was measured in 204  
800 plots, using a laser hypsometer (Nikon forestry Pro) from directly below the crown (most plots), a  
801 laser or ultrasonic distance device with an electronic tilt sensor, a manual clinometer, or by direct

802 measurement, i.e. tree climbing. Only trees where the top was visible were selected<sup>66</sup>. In most plots,  
803 tree selection was similar: the 10 largest trees were measured, together with 10 randomly selected  
804 trees per diameter from five classes: 100-199 mm, 200-299 mm, 300-399 mm, 400-499 mm, and  
805 500+ mm trees, following standard protocols<sup>66</sup>. We measured actual height of 24,270 individual trees  
806 from 204 plots. We used these data and the local.heights function in R package BiomasaFP<sup>63</sup> to fit 3-  
807 parameter Weibull relationships:  $H_t = a \times (1 - e^{(-b \times (DBH/10)^c)})$  (equation 1). We chose the Weibull  
808 model as it is known to be robust when a large number of measurements are available<sup>66,67</sup>. We  
809 parameterised separate  $H_t$ -DBH relationship for four different combinations of edaphic forest type  
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  
813 seasonally flooded forest plots in the other biogeographical regions). The parameters are: (i) terra  
814 firme forest in West Africa, a=56.0; b=0.0401; c=0.744; (ii) terra firme forest in Lower Guinea and  
815 Western Congo Basin, a=47.6; b=0.0536; c=0.755; (iii) terra firme forest in Eastern Congo Basin  
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  
818 forest type and bioregion, the local.heights function combines all height measurements from all plots  
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 = 0.7  
821 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  
826 tree DBH measurements for input into the allometric equation. Mean measured individual total tree

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

834

835 Wood Density: Dry wood density ( $\rho$ ) measurements were compiled for 730 African species from  
836 published sources and stored in [www.ForestPlots.net](http://www.ForestPlots.net); most were sourced from the Global Wood  
837 Density Database on the Dryad digital repository ([www.datadryad.org](http://www.datadryad.org))<sup>68,69</sup>. Each individual in the  
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  
840 using the African Plants Database ([www.ville-ge.ch/cjb/bd/africa/](http://www.ville-ge.ch/cjb/bd/africa/)) to maximize matches<sup>13</sup>. For  
841 incompletely identified individuals or for individuals belonging to species not in the  $\rho$  database, we  
842 used the mean  $\rho$  value for the next higher known taxonomic category (genus or family, as  
843 appropriate). For unidentified individuals, we used the mean wood density value of all individual  
844 trees in the plot<sup>13,52</sup>.

845

846 Allometric equation: For each tree we used a published allometric equation<sup>61</sup> to estimate  
847 aboveground biomass. We then converted this to carbon, assuming that aboveground carbon (AGC)  
848 is 45.6% of aboveground biomass<sup>70</sup>. Thus:  $AGC=0.456 \times (0.0673 \times (\rho \times (DBH/10)^2 \times H_t)^{0.976}) / 1000$   
849 (equation 2), with DBH in mm, dry wood density,  $\rho$ , in g cm<sup>-3</sup>, and total tree height,  $H_t$ , in m (ref.<sup>61</sup>).

850

851 Aboveground Carbon (AGC, in Mg C ha<sup>-1</sup>) in living biomass for each plot at each census date was  
852 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**

855 Net Carbon Sink (in Mg C ha<sup>-1</sup> yr<sup>-1</sup>) is estimated as carbon gains minus carbon losses. Calculation  
856 details are explained below.

857

858 Carbon Gains (in Mg C ha<sup>-1</sup> yr<sup>-1</sup>) are the sum of the aboveground live biomass carbon additions from  
859 the growth of surviving stems and the addition of newly recruited stems, divided by the census  
860 length (in years) and plot area (in hectares). For each stem that survived a census interval, carbon  
861 additions from its growth (Mg C ha<sup>-1</sup> yr<sup>-1</sup>) were calculated as the difference between its AGC at the  
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 $\geq$ 100 mm), carbon additions were calculated  
864 in the same way, assuming DBH=0 mm at the start of the interval<sup>65</sup>. Carbon Losses (in Mg C ha<sup>-1</sup> yr<sup>-1</sup>)  
865 are estimated as the sum of aboveground biomass carbon from all stems that died during a census  
866 interval, divided by the census length (in years) and plot area (in hectares). Both carbon gains and  
867 carbon losses are calculated using standard methods<sup>6</sup>, including a census interval bias correction,  
868 using the SummaryAGWP function of R-package BiomasaFP<sup>63,64,68</sup>.

869

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

874

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

884

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

899

900 The census interval bias correction (components i and ii together) typically add <3% to plot-level  
901 carbon gains. Carbon Losses are affected by the same census interval bias, hence we corrected this  
902 bias by accounting for (i) the additional carbon losses from the trees that were recruited and then  
903 died within the same interval, and (ii) the additional carbon losses resulting from the growth of the  
904 trees that died in the interval<sup>6,15,63</sup>. These two components are calculated in the same way as for  
905 Carbon gains and typically add <3% to plot-level carbon losses.

906

907 Carbon gains include both gains from the growth of surviving stems and new recruits. Separating  
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<sup>-1</sup> yr<sup>-1</sup>;  
911 CI: 0.16-0.18 versus Amazon: 0.27 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; CI: 0.25-0.28, p<0.001; two-way Wilcoxon test),  
912 but this is compensated by carbon gains from survivors being significantly larger in Africa (2.33 Mg  
913 C ha<sup>-1</sup> yr<sup>-1</sup>; CI: 2.27-2.39) than in the Amazon (2.13 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; CI: 2.09-2.17, p=0.014).  
914 Therefore, gains overall (sum of gains from surviving stems and newly recruited stems) are  
915 indistinguishable between the continents (Africa: 2.57 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; CI: 2.51-2.67 vs Amazon: 2.46  
916 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; CI: 2.41-2.50, p=0.460; two-way Wilcoxon test).

917

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

919 The estimated mean and uncertainty in carbon gains, carbon losses and the net carbon sink of the  
920 African plots from 1983-2014 (Figure 1, Extended Data Figure 7 and Extended Data Figure 8) were  
921 calculated following ref.<sup>6</sup> to allow direct comparison with published Amazonian results. First, each  
922 census interval value was interpolated for each 0.1-yr period within the census interval. Then, for  
923 each 0.1-yr period between 1983 and 2014, we calculated a weighted mean of all plots monitored at

924 that time, using the square root of plot area as a weighting factor<sup>6</sup>. Confidence intervals for each 0.1-  
925 yr period were bootstrapped.

926

927 Trends in carbon gains, losses and the net carbon sink over time were assessed using linear mixed  
928 effects models (lmer function in R, lme4 package<sup>72</sup>), providing the linear slopes reported in Figure 1.  
929 These models regress the mid-point of each census interval against the value of the response variable  
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  
932 previously published Amazon analyses<sup>6</sup>, because models did not converge due to some plots having  
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.<sup>13</sup>. The following  
936 weighting removes all pattern in the residuals: Weight=  $3\sqrt{\text{length}_{\text{int}}} + 4\sqrt{\text{plotsize}} - 1$  (equation 3),  
937 where  $\text{length}_{\text{int}}$  is the length of the census interval, in years. Significance was assessed by regressing  
938 the residuals of the net carbon sink model against the weights ( $p=0.702$ ).

939

940 Differences in long-term slopes between the two continents for carbon gains, carbon losses and net  
941 carbon sink, reported in the main text, were also assessed using linear mixed effects models, as  
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  
945 interaction would indicate that the slopes differ between continents. The statistical significance of  
946 continental differences in slope were assessed using the F-statistic (Anova function in R, car  
947 package<sup>73</sup>). Shortening the common time window to the 20 years when the continents are best-  
948 sampled, 1991.5 to 2011.5, gave very similar results, including a divergent continental sink ( $p=0.04$ ).

949

950 **Continental and Pan-Tropical Carbon Sink Estimates**

951 The per unit area total net carbon sink (in  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) for each time period in Table 1 (each  
952 decade between 1980 and 2010; and 2010-2015) is the sum of three components. The first  
953 component is the per unit area aboveground carbon sink from living trees and lianas with  $\text{DBH} \geq 100$   
954 mm. For Africa we use the per unit area net carbon sink values presented in this paper. For  
955 Amazonia, we use data in ref.<sup>6</sup>. For Southeast Asia, we use inventory data collected using similar  
956 standardised methods from 49 plots in ref.<sup>15</sup>. For each time window, we use all plots for which  
957 census dates overlap the period, weighted by the square root of plot area, as for the solid lines in  
958 Figure 1. The second component is the per unit area aboveground carbon sink from living trees and  
959 lianas with  $\text{DBH} < 100$  mm. This is calculated as 5.19%, 9.40% and 5.46% of the first component (i.e.  
960 aboveground carbon of large living trees) in Africa, Amazonia and Southeast Asia respectively<sup>13,74</sup>.  
961 The third component is the per unit area belowground carbon sink in live biomass, i.e. roots. This is  
962 calculated as 25%, 37% and 17% of the aboveground carbon of living trees with  $\text{DBH} \geq 100$  mm in  
963 Africa<sup>13</sup>, Amazonia<sup>6</sup> and Southeast Asia<sup>75</sup> respectively.

964

965 For each time period in Table 1 we calculated the continental-scale total carbon sink ( $\text{Pg C yr}^{-1}$ ) by  
966 multiplying the per unit area total net carbon sink described above by the area of intact forest on each  
967 continent at that time interval (in ha) reported in Extended Data Table 2. Decades are calculated from  
968 1990.01 to 1999.99. For comparability with previous continental-sink results, we used continental  
969 values of intact forest area for 1990, 2000 and 2010 as published in ref.<sup>1</sup>, i.e. total forest area minus  
970 forest regrowth. We used the 1990-2010 data to fit an exponential model for each continent and used  
971 this model to estimate intact forest area for 1980 and 2015.

972

973 Finally, in the main text we calculated the proportion of anthropogenic  $\text{CO}_2$  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<sub>2</sub> emissions. Total anthropogenic CO<sub>2</sub> 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<sup>-1</sup> in the 1990s, 9.0 Pg C yr<sup>-1</sup> in the 2000s, and 11.1 Pg C yr<sup>-1</sup>  
977 in the 2010s (ref.<sup>21</sup>, 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  
984 of dead trees. We did this by calculating total forest carbon loss (Mg C ha<sup>-1</sup> yr<sup>-1</sup>) for each year  
985 between 1950-2015, using the mean 1983-2015 records from Figure 1 and assuming constant losses  
986 prior to 1983 (1.9 and 1.5 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for Africa and Amazonia respectively). Then, for each focal  
987 year between 1950-2015, we calculated how much carbon was released to the atmosphere in the  
988 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  
989 focal year;  $y_t$  is the carbon released to the atmosphere at  $t$  years from the focal year; and -0.17 yr<sup>-1</sup> is  
990 a constant decomposition rate calculated for tropical forests in the Amazon<sup>45</sup>. For example, carbon  
991 loss was 1.95 Mg C ha<sup>-1</sup> in 1990 in African forests (Figure 1), from which 0.31 Mg C ha<sup>-1</sup> was  
992 released to the atmosphere in 1991; 0.26 Mg C ha<sup>-1</sup> in 1992; 0.22 Mg C ha<sup>-1</sup> in 1993; 0.07 Mg C ha<sup>-1</sup>  
993 in 2000 and 0.01 Mg C ha<sup>-1</sup> in 2010. Hence, of the full 1.95 Mg C ha<sup>-1</sup> dead tree biomass from 1990,  
994 ~50% was released to the atmosphere after 4 yrs, ~85% after 10 yrs, and ~97% after 20 years.  
995 Finally, for each year between 1983 and 2015, the total contribution to the atmosphere from carbon  
996 losses was calculated as the sum of all carbon contributions released at that year, from all total yearly  
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.

999

1000 **Predictor Variable Estimates, 1983-2014**

1001 For each census interval of each plot, we examined potential predictor variables that may explain the  
1002 long-term trends in carbon gains and carbon losses, reported in Extended Data Table 1 and main text  
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  
1005 environmental change. The predictor variable estimates for each census need to avoid bias due to  
1006 seasonal variation, for example the intra-annual variability in atmospheric CO<sub>2</sub> concentration. We  
1007 therefore applied the following procedure to avoid seasonal variability impacts on long-term trends:  
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  
1011 intervals of a plot do not overlap. The resulting sequence of non-overlapping census intervals was  
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 CO<sub>2</sub> concentration (CO<sub>2</sub>), mean annual temperature (MAT), and  
1018 drought intensity, which we quantified as maximum climatological water deficit (MCWD)<sup>14,20,76,77</sup>.

1019

1020 Atmospheric CO<sub>2</sub> concentration (CO<sub>2</sub>, in ppm) is estimated as the mean of the monthly mean values  
1021 from the Mauna Loa record<sup>78</sup> over the census interval. While atmospheric CO<sub>2</sub> concentration is  
1022 highly correlated with time ( $R^2=0.98$ ), carbon gains are slightly better correlated with CO<sub>2</sub>  
1023 ( $R_{adj}^2=0.0027$ ) than with time ( $R_{adj}^2=0.0025$ ).

1024

1025 Mean Annual Temperature (MAT, in °C) was derived from the temporally resolved (1901-2015)  
1026 dataset of monthly mean temperature from the Climatic Research Unit (CRU TS version 4.03; ~3025  
1027 km<sup>2</sup> resolution; released 15 May 2019; <https://crudata.uea.ac.uk/cru/data/hrg/>)<sup>79</sup>. We downscaled the  
1028 data to ~1 km<sup>2</sup> resolution using the WorldClim dataset<sup>51,80</sup>, by subtracting the difference in mean  
1029 monthly temperature, and applying this monthly correction to all months<sup>81</sup>. We then calculated MAT  
1030 for each census interval of each plot using the downscaled monthly CRU record.

1031

1032 Maximum Climatological Water Deficit (MCWD, in mm) was derived from the ~3025 km<sup>2</sup>  
1033 resolution Global Precipitation Climatology Centre dataset (GPCC version 6.0) that includes many  
1034 more rain gauges than CRU in tropical Africa<sup>82,83</sup>. As GPCC ends in 2013 we combined it with  
1035 satellite-based Tropical Rainfall Measurement Mission data (TRMM 3B43 V7 product, ~757 km<sup>2</sup>  
1036 resolution)<sup>84</sup>. The fit for the overlapping time period (1998-2013) was used to correct the systematic  
1037 difference between GPCC and TRMM: GPCC' = a+b\*GPCC, with GPCC' the adjusted GPCC  
1038 record and a and b different parameters for each month of the year and for each continent.  
1039 Precipitation was then downscaled to ~1 km<sup>2</sup> resolution using the WorldClim dataset<sup>51,80</sup>, by dividing  
1040 by the ratio in mean monthly rainfall, and applying this monthly correction to all months<sup>81</sup>. For each  
1041 census interval we extracted monthly precipitation values and estimated evapotranspiration (ET) to  
1042 calculate monthly Climatological Water Deficit (CWD), a commonly used metric of dry season  
1043 intensity for tropical forests<sup>14,76,77</sup>. Monthly CWD values were calculated for each subsequent series  
1044 of 12 months (complete years)<sup>77</sup>. 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:  
1047 CWD<sub>i</sub>= ET - P<sub>i</sub> + CWD<sub>i-1</sub>, where negative CWD<sub>i</sub> values were set to zero<sup>77</sup> (no drought conditions).  
1048 This procedure was repeated for each subsequent complete 12 months. We then calculated the annual  
1049 MCWD as the largest monthly CWD value for every complete year within the census interval, with

1050 the MCWD of a census interval being the mean of the annual MCWD values within the census  
1051 interval. Larger MCWD indicates more severe water deficits.

1052

1053 We assume ET is 100 mm month<sup>-1</sup> on both continents, based on measurements from Amazonia<sup>76,77</sup>,  
1054 more limited measurements from West Africa summarized in ref.<sup>85</sup>, predictive skill<sup>86</sup>, and use in past  
1055 studies on both continents<sup>14,87</sup>. MCWD therefore represents a precipitation-driven dry season deficit,  
1056 as ET remains constant. An alternative assessment, using a data-driven ET product<sup>88,89</sup>, gave a mean  
1057 ET of 95 and 98 mm month<sup>-1</sup> for the African and Amazonian plot networks respectively. Using these  
1058 values did not affect the results.

1059

1060 To calculate the environmental change of potential predictor variables, CO<sub>2</sub>-change (in ppm yr<sup>-1</sup>),  
1061 MAT-change (in °C yr<sup>-1</sup>) and MCWD-change (in mm yr<sup>-1</sup>), we selected an optimum period over  
1062 which to calculate the change, derived empirically by assessing the correlation of carbon gains (all  
1063 plots, all censuses) with the change in each environmental variable, using linear mixed effects  
1064 models (lmer function in R, lme4 package<sup>72</sup>). The annualised change in the environmental variable  
1065 was calculated as the change between the focal interval and a prior interval (termed the baseline  
1066 period) with a lengthening time window ranging from 1 year through to 80 years prior to the focal  
1067 interval (i.e. 80 linear mixed effects models per variable). We calculated AIC for each model and  
1068 selected the interval length with the lowest AIC. Thus, MAT-change (in °C yr<sup>-1</sup>) = (MAT<sub>i</sub>-  
1069 MAT<sub>b</sub>)/(date<sub>i</sub>-date<sub>b</sub>), where MAT<sub>i</sub> is the MAT over the focal census interval calculated using the  
1070 procedure described above, MAT<sub>b</sub> is the MAT over a baseline period prior to the focal interval, date<sub>i</sub>  
1071 is the mid-date of the focal census interval and date<sub>b</sub> is the mid-date of the baseline period. The lmer  
1072 results show that the baseline period for MAT-change is 5 years and for CO<sub>2</sub>-change it is 56 years,  
1073 while MCWD showed no clear trend, so MCWD-change was not included in the models (see  
1074 Extended Data Figure 3). All three results conform to a priori theoretical expectations. For CO<sub>2</sub> a

1075 maximum response to an integrated 56 years of change is expected because forest stands will  
1076 respond most strongly to CO<sub>2</sub> when most individuals have grown under the new rapidly changing  
1077 condition, which should be at its maximum at a time approximately equivalent to the carbon  
1078 residence time of a forest stand<sup>30,90</sup> (mean of 62 years in this dataset). For MAT, 5 years is consistent  
1079 with experiments showing temperature acclimation of leaf- and plant-level photosynthetic and  
1080 respiration processes over half-decadal timescales<sup>31,91</sup>. MCWD has no overall trend suggesting that  
1081 once a drought ends, its impact on tree growth fades rapidly, as seen in other studies<sup>14,92</sup>. Also in the  
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 old-  
1087 growth forests, mean WD (in g cm<sup>-3</sup>) is inversely related to resource availability<sup>28,93,94</sup>, as is seen in  
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  
1090 end of the census interval, to be consistent with the previous Amazon analysis<sup>6</sup>. Carbon residence  
1091 time (CRT, in yrs) is a measure of the time that fixed carbon stays in the system. CRT is a potential  
1092 correlate of the impact of past carbon gains on later carbon losses<sup>30</sup>. To avoid circularity in the  
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  
1098 equation employed for use in the carbon loss model (based on gains) is the standard formula used to  
1099 calculate CRT and is retained in the minimum adequate model (see below and Table 2). The non-

1100 standard CRT equation (based on losses) used in the carbon gain model is not retained in the  
1101 minimum adequate model (see below).

1102

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  
1105 that impact theory-driven models of photosynthesis and respiration as predictor variables: CO<sub>2</sub>,  
1106 MAT, and MCWD. One model had carbon gains as the response variable, the other had carbon  
1107 losses as the response variable (both in Mg C ha<sup>-1</sup> yr<sup>-1</sup>). Models were fitted using the lme function in  
1108 R, with maximum likelihood (NLME package<sup>95</sup>). All census intervals within all plots were used,  
1109 weighted by plot size and census length (using equation 3 above). Plot identity was included as a  
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 package<sup>62</sup>).  
1112 Carbon gain values were normally distributed but carbon loss values required a power-law  
1113 transformation ( $\lambda = 0.361$ ) to meet normality criteria. Multi-parameter models are: carbon gains =  
1114 intcp + a $\times$ CO<sub>2</sub> + b $\times$ MAT + c $\times$ MCWD (model 1); carbon losses = intcp + a $\times$ CO<sub>2</sub> + b $\times$ MAT +  
1115 c $\times$ MCWD (model 2); where intcp is the estimated model intercept, and a, b, and c are model  
1116 parameters giving the slope of relationships with environmental predictor variables. For multi-  
1117 parameter model outputs see Extended Data Table 1, for single-parameter relationships, Figure 2.

1118

1119 The second pair of models include the same environmental predictors (CO<sub>2</sub>, MAT, MCWD), plus  
1120 their rate of change (CO<sub>2</sub>-change, MAT-change, but not MCWD-change as explained above), and  
1121 forest attributes that may alter how forests respond (WD, CRT), as described above. We also  
1122 evaluated the possible inclusion of a differential continent effect of each variable in the full model.  
1123 We first constructed models with only a single predictor variable, and allowed different slopes in  
1124 each continent. Next, if removal of the continent-specific slope (using stepAIC function in R, MASS

1125 package<sup>96</sup>) decreased model Akaike Information Criterion (AIC) then the continent-specific slope  
1126 was not included in the full model for that variable. Only MCWD showed a significant differential  
1127 continent-specific slope. This implies that forests on both continents have common responses to CO<sub>2</sub>,  
1128 CO<sub>2</sub>-change, MAT, MAT-change, WD and CRT, but respond differently to differences in MCWD.  
1129 This is likely because wet-adapted species are much rarer in Africa than in Amazonia as a result of  
1130 large differences in past climate variation<sup>34</sup>. Lastly, we allowed different intercepts for the two  
1131 continents to potentially account for differing biogeographical or other continent-specific factors. For  
1132 the carbon loss model, we applied the same continent-specific effects for slope as for the carbon gain  
1133 model. Carbon loss values were transformed using a power-law transformation ( $\lambda = 0.361$ ) to meet  
1134 normality criteria.

1135

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 all-  
1138 subsets regression<sup>97,98</sup>. To do so, we first generated a set of models with all possible combinations  
1139 (subsets) of fixed effect terms in the global model using the dredge function of the MuMIn package  
1140 in R<sup>99</sup>. We then chose the best-ranked simplified model based on the AICc criterion, hereafter called  
1141 “minimum adequate carbon gain/loss model”, reported in Table 2. The minimum adequate models  
1142 are: carbon gains = intcp $\times$ continent + a $\times$ CO<sub>2</sub>-change + b $\times$ MAT + c $\times$ MAT-change +  
1143 d $\times$ MCWD $\times$ continent + e $\times$ WD (model 3); carbon losses = intcp + a $\times$ CO<sub>2</sub>-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.

1147

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

1150 and 0.132 respectively, which is almost double the weight of the second ranked models (0.152 and  
1151 0.075 respectively). In Supplementary Table 2 we also used the model.avg function of the MuMIn  
1152 package to calculate a weighted mean of the coefficients of the best-ranked models together  
1153 representing a cumulative weight-sum of 0.95 (i.e. a 95% confidence subset). Supplementary Table 2  
1154 (model-averaged) and main text Table 2 (best-ranked) model parameters are very similar.  
1155 Supplementary Tables 3 and 4 report the complete sets of carbon gains and loss models that  
1156 contribute to the model average results.

1157

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 CO<sub>2</sub>-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  
1163 models result in similar predictions of the net carbon sink over the 1983-2040 period: the future net  
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  
1166 respectively. The Amazon sink reaches zero in 2041 using model-averaged parameters compared to  
1167 2035 using the best-ranked models.

1168

## 1169 **Estimating Future Predictor Variables to 2040**

1170 To calculate future modelled trends in carbon gains and losses (Figure 3), we first estimated annual  
1171 records of the predictor variables (CO<sub>2</sub>-change, MAT, MAT-change, MCWD, WD and CRT) to  
1172 2040 (Extended Data Figure 5).

1173

1174 To do so we first calculated annual records for the period of the observed trends for each plot  
1175 location (i.e. from 1983-2014 in Africa and 1983-2011.5 in Amazonia). For CO<sub>2</sub>-change, MAT,  
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  
1179 plot locations in Africa, and separately the mean annual value of each predictor variable from the  
1180 321 plot locations in Amazonia (i.e. solid lines in ED Figure 5). For each predictor variable, we  
1181 calculated annual records of upper and lower confidence intervals by respectively adding and  
1182 subtracting 2 $\sigma$  to the mean of each annual value (shaded area in ED Figure 5).

1183

1184 Secondly, for each predictor variable we parameterised a linear model for each continent using the  
1185 annual records for the period of the observed trends. Then for each predictor variable, the continent-  
1186 specific linear regression models were used to estimate predictor variables for each plot location  
1187 from 2014 to 2040 in Africa and from 2011.5 to 2040 in the Amazon (dotted lines in Extended Data  
1188 Figure 5). For each predictor variable, we calculated annual records of upper and lower confidence  
1189 intervals by respectively adding and subtracting 2 $\sigma$  to the slope of each linear model (shaded area  
1190 around dotted lines in ED Figure 5).

1191

## 1192 **Estimating Future Carbon Gain, Loss and Net Carbon Sink**

1193 We used the minimum adequate models (Table 2) to predict annual records of carbon gain, carbon  
1194 loss and the carbon sink for the plot networks in Africa and Amazonia over the period 1983 through  
1195 to 2040 (Figure 3). We extracted fitted carbon gain and loss values using the mean annual records for  
1196 each predictor variable (predictSE.lme function, AICcmodavg package<sup>100</sup>). Upper and lower  
1197 confidence intervals were calculated accounting for uncertainties in the model (both fixed and  
1198 random effects) and predictor variables using the 2 $\sigma$  upper and lower confidence interval for each

1199 predictor variable (using predictSE.lme). Finally the net carbon sink was calculated by subtracting  
1200 the losses from the gains. To obtain sink values in the future in Table 1, annual per unit area sink  
1201 predictions, from Figure 3, were averaged over each decade and multiplied by the future forest area,  
1202 as described above.

1203

1204 To test the sensitivity of the future predictions in Figure 3, we reran the analysis by modifying future  
1205 trajectories of predictor variables one at a time, while keeping all others the same, to assess the mean  
1206 C sink over 2010-15 and 2030 (averaging at 2030 is not necessary as trends in MAT-change and  
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  
1212 bounds represent deviations of  $>2$  sigma from observed trends. Change in MAT also alters MAT-  
1213 change, so we present the sensitivity of both parameters together.

1214

1215 Additionally, for CO<sub>2</sub>-change and MAT, we also calculated future slopes under three future  
1216 Representative Concentration Pathway (RCP) scenarios<sup>38</sup> with different radiative forcing in 2100:  
1217 RCP2.6, 4.5, and 8.5. Future RCP CO<sub>2</sub>-change slopes (ppm yr<sup>-1</sup>) were calculated using RCP CO<sub>2</sub>  
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  
1220 resolution data for current<sup>80</sup> and future<sup>51</sup> climate from WorldClim, and averaged over 19 CMIP5  
1221 models. We subtracted the mean 2040-2060 climate MAT (i.e. 2050) from the mean 1970-2000  
1222 climate MAT (i.e. 1985), divided by 65 years to give the annual rate of change. We then calculated a  
1223 mean slope over all plots per continent. Finally, to avoid mismatches between RCP-derived values of

1224 CO<sub>2</sub> and MAT and the observed records we removed any difference in intercept between the RCP  
1225 trends and observed trends, so the RCP trends were a continuation of the end-point of the observed  
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  
1229 slope, Supplementary Table 5 reports the absolute decline in the sink in each continent in 2030  
1230 compared to the 2010-15 mean sink. This shows that the future sink strength is sensitive to future  
1231 environmental conditions, but within both RCP scenarios and our bounds of possibility we show a  
1232 decline in the sink strength in both continents over the 2020s.

1233

#### 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](http://dx.doi.org/10.5521/Forestplots.net/2019_1)

1237

#### 1238 **References (Methods only)**

1239 51 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution  
1240 interpolated climate surfaces for global land areas. International Journal of Climatology **25**,  
1241 1965-1978, doi:10.1002/joc.1276 (2005).

1242 52 Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M. & Phillips, O. L. ForestPlots.net: a web  
1243 application and research tool to manage and analyse tropical forest plot data. Journal of  
1244 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-DataPackage-  
1250 20151201235855\_1254. (2011).

1251 56 Rovero, F., Marshall, A. & Martin, E. Udzungwa TEAM Site. Data Set Identifier: TEAM-  
1252 DataPackage-20151130235007\_5069. (2009).

1253 57 Hockemba, M. B. N. Nouabalé Ndoki TEAM Site. Data Set Identifier: TEAM-DataPackage-  
1254 20151201235855\_1254. (2010).

1255 58 Anderson-Teixeira, K. J. et al. CTFS-ForestGEO: a worldwide network monitoring forests in  
1256 an era of global change. *Global Change Biology* **21**, 528-549, doi:10.1111/gcb.12712 (2015).

1257 59 Gourlet-Fleury, S. et al. Tropical forest recovery from logging: a 24 year silvicultural  
1258 experiment from Central Africa. *Philosophical Transactions of the Royal Society B-*  
1259 *Biological 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).

1267 63 Lopez-Gonzalez, G., Sullivan, M. & Baker, T. BiomasaFP package. Tools for analysing data  
1268 downloaded from ForestPlots.net. R package version 0.2.1. Available at  
1269 <http://www.forestplots.net/en/resources/analysis>. (2017).

1270 64 Phillips, O., Baker, T., Brienen, R. & Feldpausch, T. RAINFOR field manual for plot  
1271 establishment and remeasurement. Available at  
1272 [http://www.rainfor.org/upload/ManualsEnglish/RAINFOR\\_field\\_manual\\_version\\_2016.pdf](http://www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_2016.pdf).  
1273 (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).

1277 66 Sullivan, M. J. P. et al. Field methods for sampling tree height for tropical forest biomass  
1278 estimation. *Methods in Ecology and Evolution* **9**, 1179-1189, doi:10.1111/2041-210X.12962  
1279 (2018).

1280 67 Feldpausch, T. R. et al. Tree height integrated into pantropical forest biomass estimates.  
1281 *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**, 351-  
1283 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).

1286 70 Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration  
1287 across the world's trees and forests. *Nature Geoscience* **11**, 915-920, doi:10.1038/s41561-  
1288 018-0246-x (2018).

1289 71 Kohyama, T. S., Kohyama, T. I., Sheil, D. & Rees, M. Definition and estimation of vital rates  
1290 from repeated censuses: Choices, comparisons and bias corrections focusing on trees.  
1291 *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. *lme4: Linear mixed-effects models using*  
1293 *Eigen and S4.Rpackage version, 1.0-4. Available at* [http://www.inside-  
1294 r.org/packages/lme4/versions/1-0-4.](http://www.inside-r.org/packages/lme4/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).

1299 75 Yuen, J. Q., Ziegler, A. D., Webb, E. L. & Ryan, C. M. Uncertainty in below-ground carbon  
1300 biomass for major land covers in Southeast Asia. *Forest Ecology and Management* **310**, 915-  
1301 926, doi:10.1016/j.foreco.2013.09.042 (2013).

1302 76 Aragão, L. E. O. C. et al. Spatial patterns and fire response of recent Amazonian droughts.  
1303 *Geophysical Research Letters* **34**, 1-5, doi:10.1029/2006gl028946 (2007).

1304 77 Aragão, L. E. O. C. et al. Environmental change and the carbon balance of Amazonian  
1305 forests. *Biological Reviews* **89**, 913-931, doi:10.1111/brv.12088 (2014).

1306 78 Tans, P. & Keeling, R. Mauna Loa CO<sub>2</sub> monthly mean data. Available at  
1307 <http://www.esrl.noaa.gov/gmd/ccgg/trends/>. (2016).

1308 79 Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of  
1309 monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of*  
1310 *Climatology* **34**, 623–642 doi:10.1002/joc.3711 (2014).

1311 80 Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for  
1312 global land areas. *International Journal of Climatology* **37**, 4302-4315, doi:10.1002/joc.5086  
1313 (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).

1316 82 Schneider, 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).

1321 84 Huffman, G. J. et al. The TRMM Multisatellite Precipitation Analysis (TMPA): Quasi-  
1322 Global, Multiyear, Combined-Sensor Precipitation Estimates at Fine Scales. *Journal of*  
1323 *Hydrometeorology* **8**, 38-55, doi:10.1175/jhm560.1 (2007).

1324 85 Kume, T. et al. Ten-year evapotranspiration estimates in a Bornean tropical rainforest.  
1325 Agricultural and Forest Meteorology **151**, 1183-1192, doi:10.1016/j.agrformet.2011.04.005  
1326 (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).

1331 87 James, R., Washington, R. & Rowell, D. P. Implications of global warming for the climate of  
1332 African rainforests. Philosophical transactions of the Royal Society of London. Series B,  
1333 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).

1336 89 Jung, M. et al. Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and  
1337 sensible heat derived from eddy covariance, satellite, and meteorological observations.  
1338 Journal of Geophysical Research **116**, doi:10.1029/2010jg001566 (2011).

1339 90 Lloyd, J. & Farquhar, G. D. The CO<sub>2</sub> dependence of photosynthesis, plant growth responses  
1340 to elevated atmospheric CO<sub>2</sub> 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).

1343 91 Aspinwall, M. J. et al. Convergent acclimation of leaf photosynthesis and respiration to  
1344 prevailing ambient temperatures under current and warmer climates in *Eucalyptus*  
1345 *tereticornis*. New Phytol **212**, 354-367, doi:10.1111/nph.14035 (2016).

1346 92 Bonal, D., Burban, B., Stahl, C., Wagner, F. & Héault, B. The response of tropical  
1347 rainforests to drought—lessons from recent research and future prospects. Annals of Forest  
1348 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  
1350 relation to their genesis. *Biogeosciences* **7**, 1515-1541, doi:10.5194/bg-7-1515-2010 (2010).

1351 94 Baker, T. R., Swaine, M.D., Burslem, D.F.R.P. Variation in tropical forest growth rates:  
1352 combined effects of functional group composition and resource availability. *Perspectives in  
1353 Plant Ecology, Evolution and Systematics* **6**, 21-36, doi:10.1078/1433-8319-00040 (2003).

1354 95 Pinheiro, J. C. & Bates, D. M. *Mixed-Effects Models in S and S-PLUS*. First edn, 528  
1355 (Springer, 2000).

1356 96 Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S*. Fourth edn, 498  
1357 (Springer, 2002).

1358 97 Olejnik, S., Mills, J. & Keselman, H. Using Wherry's Adjusted  $R^2$  and Mallow's Cp for  
1359 Model Selection From All Possible Regressions. *The Journal of Experimental Education* **68**,  
1360 365-380, doi:10.1080/00220970009600643 (2000).

1361 98 Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. Why do we still use  
1362 stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* **75**, 1182-1189,  
1363 doi:10.1111/j.1365-2656.2006.01141.x (2006).

1364 99 Bartoń, K. MuMIn: Multi-Model Inference. Tools for performing model selection and model  
1365 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).

1368 101 Mayaux, P., De Grandi, G. & Malingreau, J.-P. Central African Forest Cover Revisited: A  
1369 Multisatellite Analysis. *Remote Sensing of Environment* **71**, 183–196, doi:10.1016/S0034-  
1370 4257(99)00073-5 (2000).

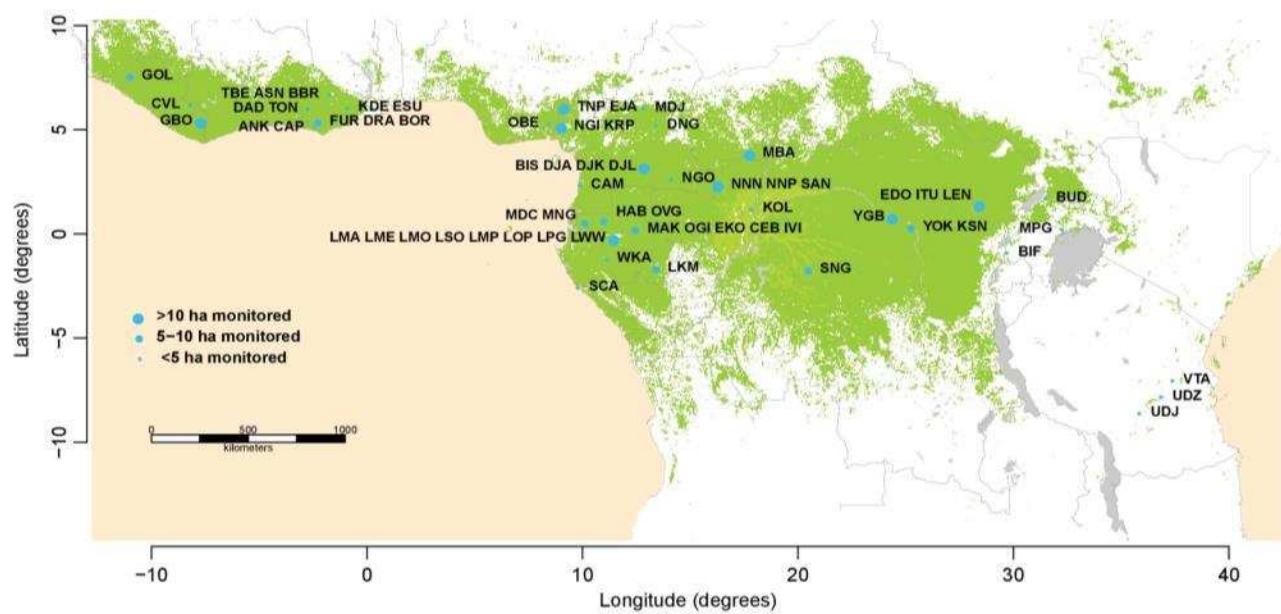
1371

1372 **Author Information**

1373 Correspondence and requests for materials should be addressed to W.H. ([whubau@gmail.com](mailto:whubau@gmail.com)). The  
1374 authors declare no competing financial interests. Supplementary Information is available online for  
1375 this paper.

1376

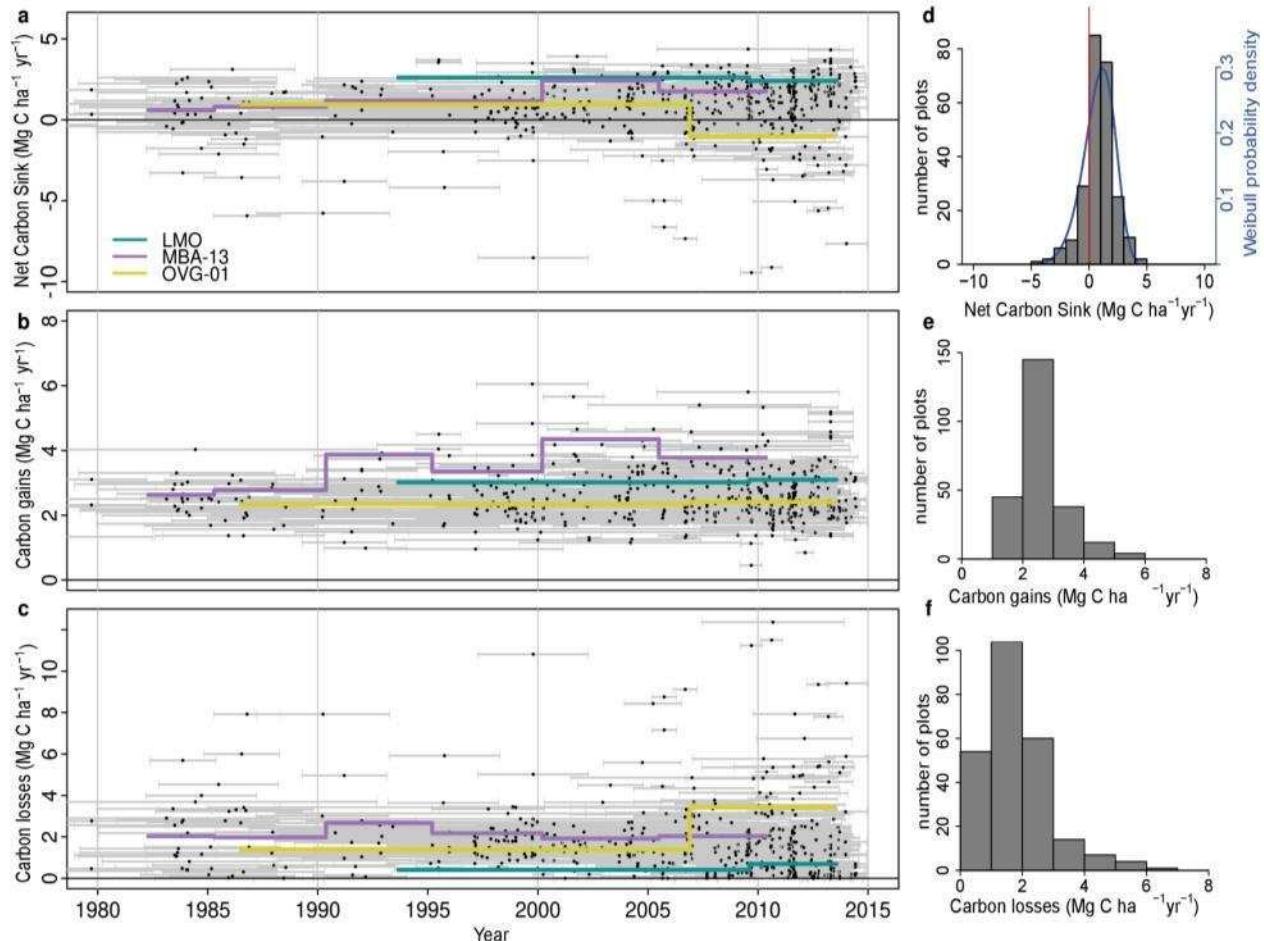
1377 **Extended Data Figures**



1378

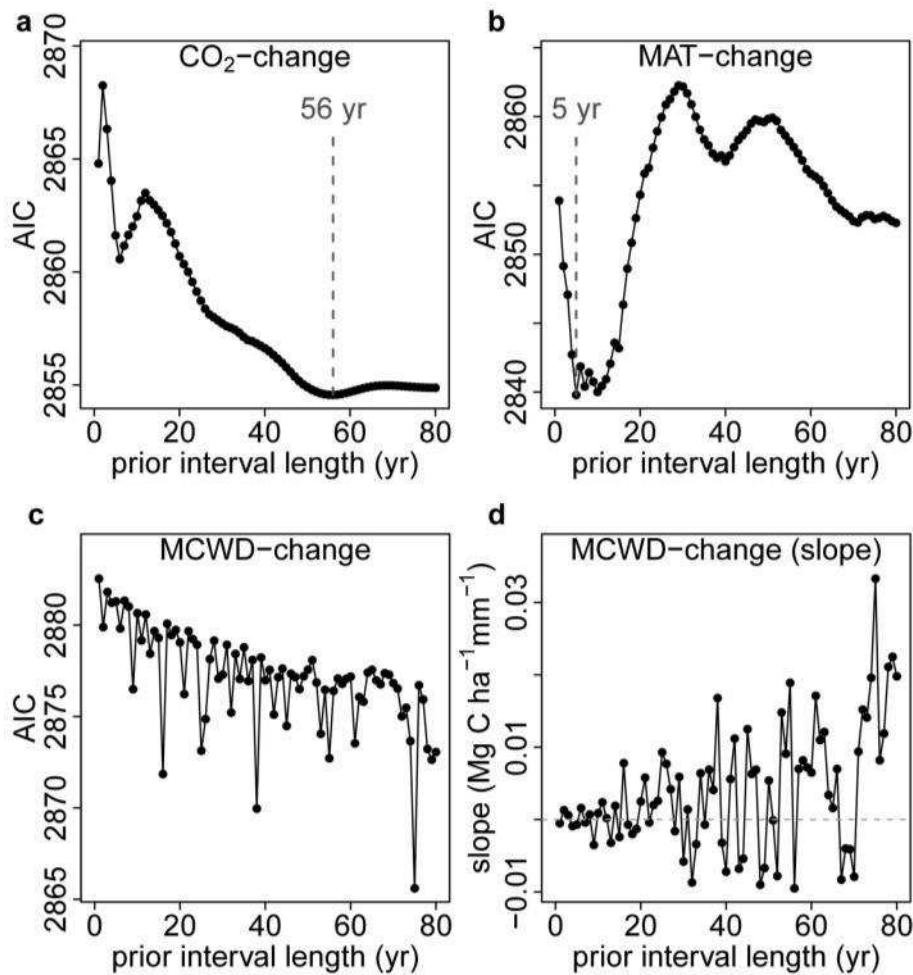
1379 **Extended Data Figure 1. Map showing the locations of the 244 plots included in this study.**

1380 Dark green represents all lowland closed-canopy forests, submontane forests and forest-agriculture  
1381 mosaics; light green shows swamp forests and mangroves<sup>101</sup>, blue circles represent plot clusters,  
1382 referred to by three-letter codes (see Supplementary Table 1 for the full list of plots). Clusters <50  
1383 km apart are shown as one point for display only, with the circlesize corresponding to sampling  
1384 effort in terms of hectares monitored.



1385

1386 **Extended Data Figure 2. Long-term above-ground carbon dynamics of 244 African intact**  
 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  
 1389 biomass carbon change (a), carbon gains (from woody production from tree growth and newly  
 1390 recruited stems) (b), and carbon losses (from tree mortality) (c). Examples of time series for three  
 1391 individual plots are shown in purple, yellow and green. Associated histograms show the distribution  
 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 t-  
 1394 test:  $p < 0.001$ ), carbon gains (e), and carbon losses (f).



1395

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 CO<sub>2</sub>,**  
 1398 **temperature (as MAT) or drought (as MCWD), each calculated over ever-longer prior**  
 1399 **intervals.** Panels show AIC from linear mixed effects models of carbon gains from 565 plots and  
 1400 corresponding, atmospheric CO<sub>2</sub> (CO<sub>2</sub>-change) (a), Mean Annual Temperature (MAT-change) (b),  
 1401 and Maximum Climatological Water Deficit (MCWD-change) (c). For CO<sub>2</sub> the AIC minimum was  
 1402 observed when predicting the carbon gain from the change in CO<sub>2</sub> calculated over a 56 year long  
 1403 prior interval length. We use this length of time to calculate our CO<sub>2</sub>-change parameter. Such a value  
 1404 is expected because forest stands will respond most strongly to CO<sub>2</sub> when most individuals have  
 1405 grown under the new rapidly changing condition, which should be at its maximum at a time  
 1406 approximately equivalent to the carbon residence time of a forest stand<sup>30,90</sup> (mean of 62 years in this

1407 pooled African and Amazonian dataset). For MAT the AIC minimum was 5 years, which we use as  
1408 the prior interval to calculate our MAT-change parameter. This length is consistent with experiments  
1409 showing temperature acclimation of leaf- and plant-level photosynthetic and respiration processes  
1410 over approximately half-decadal timescales<sup>31,91</sup>. For MCWD the AIC minimum is not obvious, while  
1411 the slope of the correlation, shown in panel (d), shows no overall trend and oscillates between  
1412 positive or negative values, meaning there is no relationship between carbon gains and the change in  
1413 MCWD over intervals longer than 1 year; thus MCWD-change is not included in our models. This  
1414 result suggests that once a drought ends, its impact on tree growth fades rapidly, as seen in other  
1415 studies<sup>14,92</sup>. Also in the moist tropics wet-season rainfall is expected to re-charge soil water, hence  
1416 lagged impacts of droughts are not expected.

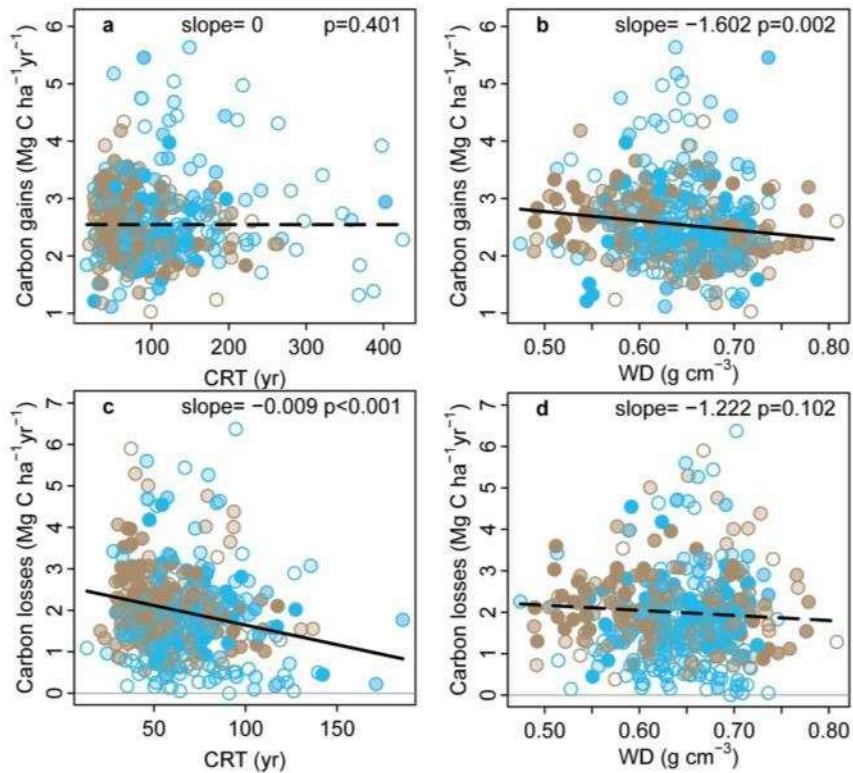
1417

1418

1419

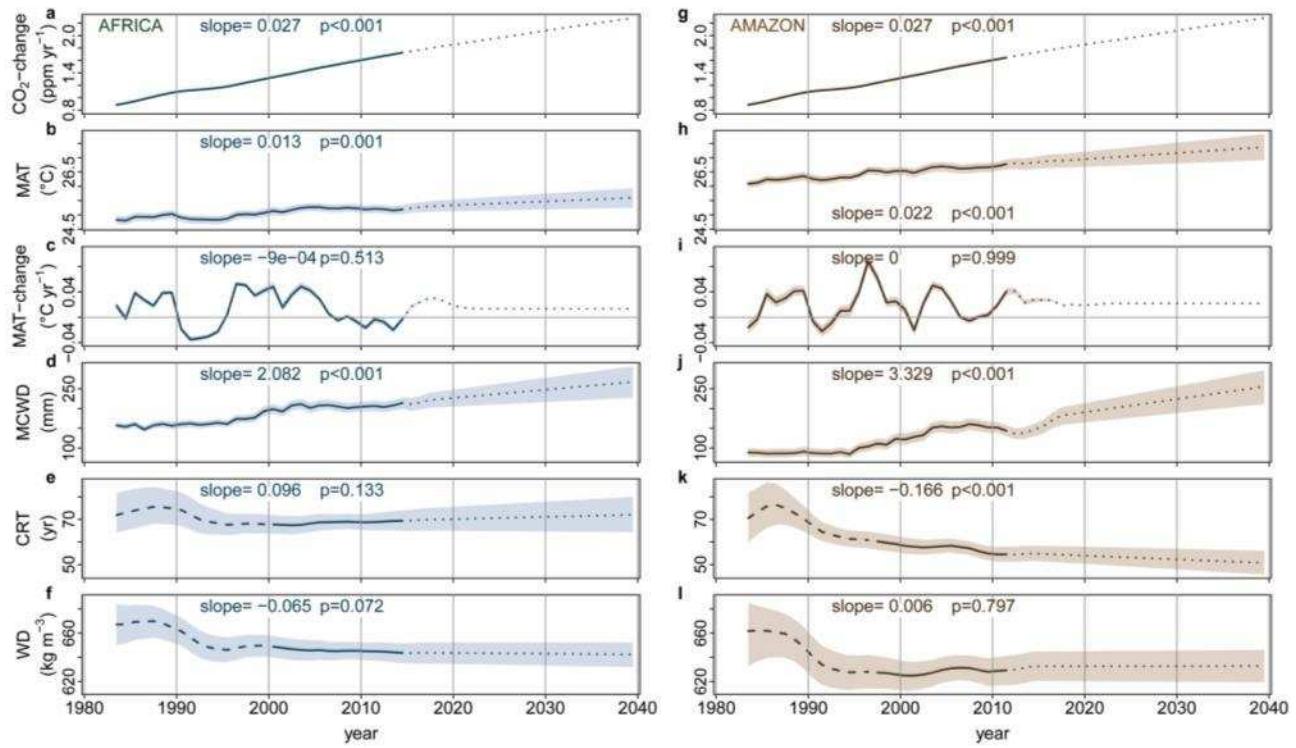
1420

1421



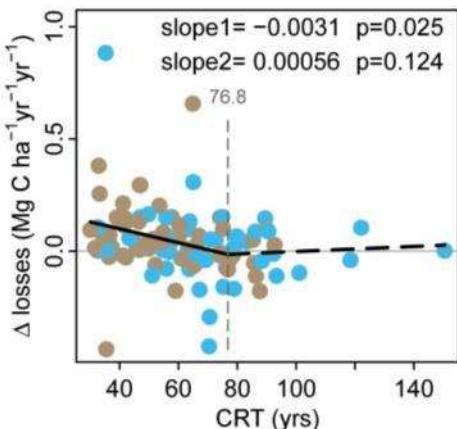
1422

1423 **Extended Data Figure 4. Potential forest dynamics-related drivers of carbon gains and losses in**  
 1424 **structurally intact African and Amazonian tropical forest inventory plots.** The aboveground  
 1425 carbon gains, from woody production (**a-b**), and aboveground carbon losses, from tree mortality (**c**-  
 1426 **d**), are plotted against the carbon residence time (CRT), and wood density (WD), for African (blue)  
 1427 and Amazonian (brown) inventory plots. Linear mixed effect models were performed with census  
 1428 intervals ( $n=1566$ ) nested within plots ( $n=565$ ) to avoid pseudo-replication, using an empirically  
 1429 derived weighting based on interval length and plot area (see methods). Significant regression lines  
 1430 for the complete dataset are shown as a solid line; non-significant regressions as a dashed line. Each  
 1431 dot represents a time-weighted mean plot-level value; transparency of the inner part of the dot  
 1432 represents total monitoring length, with empty circles corresponding to plots monitored for  $\leq 5$  years  
 1433 and solid circles for plots monitored for  $>20$  years. Carbon loss data are presented untransformed for  
 1434 comparison with carbon gains; linear mixed effects models on transformed data to fit normality  
 1435 assumptions do not change the significance of the results. Note, CRT is calculated differently for the  
 1436 carbon gains and losses models (see methods).



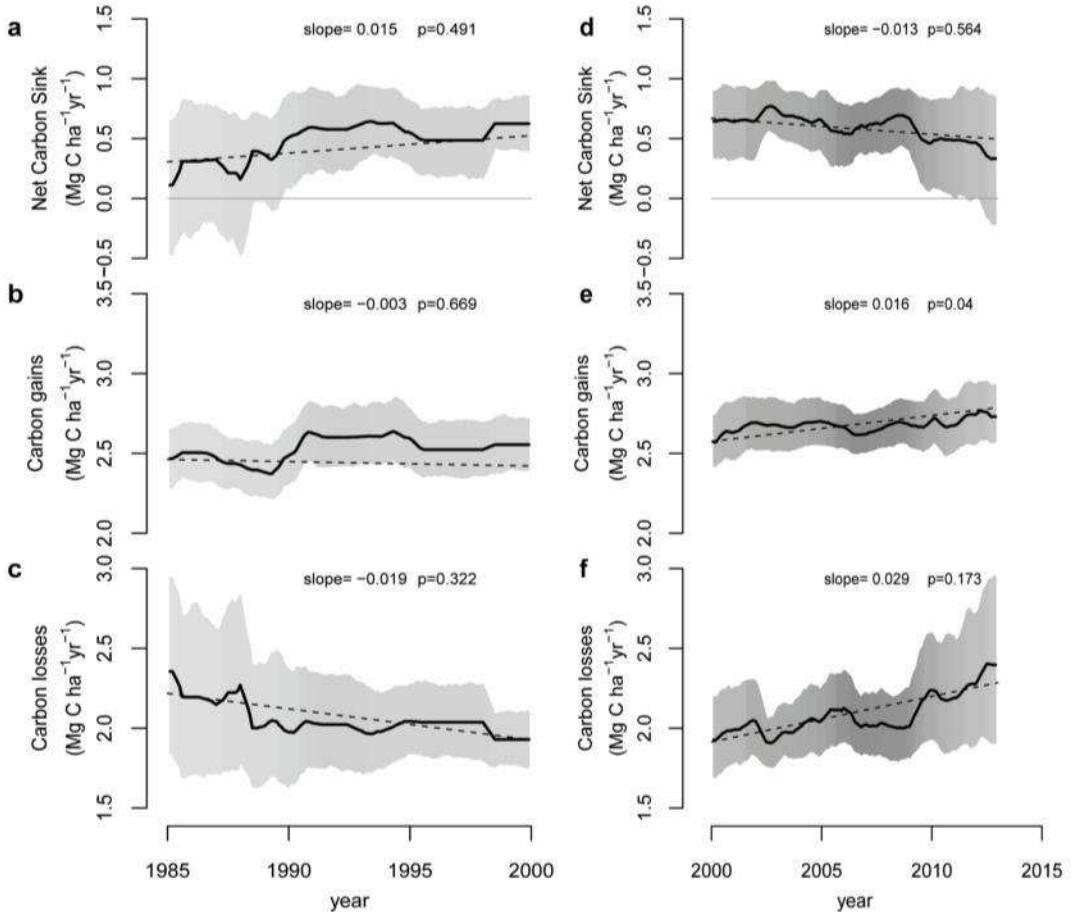
1437

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



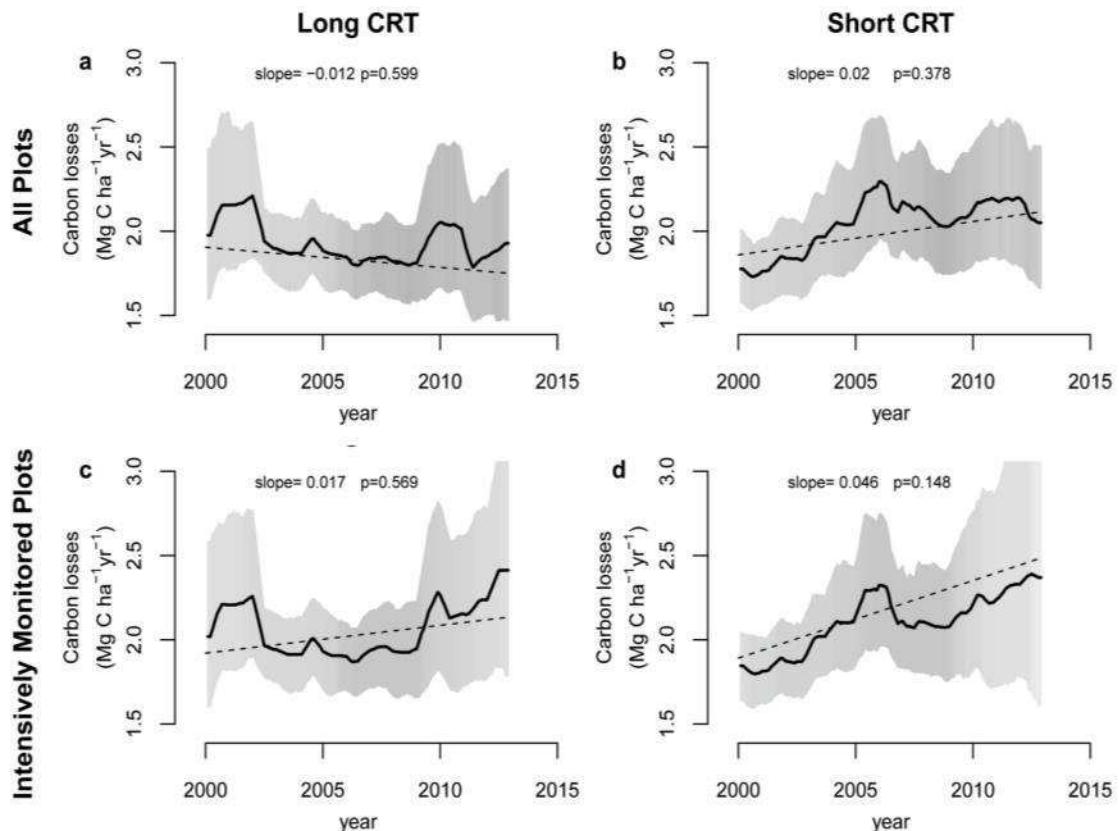
1451

1452 **Extended Data Figure 6. The change in carbon losses versus carbon residence time (CRT) of**  
 1453 **inventory plots in Africa and Amazonia.** For plots with two census intervals, we calculated the  
 1454 change in carbon losses ( $\Delta$ losses, in  $\text{Mg C ha}^{-1} \text{yr}^{-1} \text{yr}^{-1}$ ) as the carbon losses ( $\text{Mg C ha}^{-1} \text{yr}^{-1}$ ) of the  
 1455 second interval minus the carbon losses of the first interval, divided by the difference in mid-interval  
 1456 dates. For plots with more than two intervals, we calculated the change in carbon losses for each pair  
 1457 of subsequent intervals, then calculated the plot-level mean over all pairs, weighted by the time  
 1458 length between mid-interval dates. This analysis includes only plots with at least two census intervals  
 1459 and monitored for  $\geq 20$  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  
 1461 forest carbon losses begin to increase. Plots with  $\text{CRT} < 77$  years show a recent long-term increase in  
 1462 carbon losses, longer CRT plots do not. Blue points are African plots, brown points are Amazonian  
 1463 plots.



1464

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



1476

1477 **Extended Data Figure 8. Twenty-first century trends in aboveground biomass carbon losses**  
 1478 **from African tropical forest inventory plots with either long (left panels) or short (right panels)**  
 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  
 1482 Figure 7, but split into a long-CRT group (**c**), and a short-CRT group (**d**), each containing half the  
 1483 134 plots. Solid lines indicate mean values, shading the 95% CI, as for Figure 1. Dashed lines, slopes  
 1484 and p-values are from linear mixed-effects models, as for Figure 1. Carbon losses increase at a higher  
 1485 rate in the short-CRT than the long-CRT group of plots, in both datasets, although this increase is not  
 1486 statistically significant.

1487

1488

1489

1490 **Extended Data Tables**

1491

1492 **Extended Data Table 1.** Models to predict carbon gains and losses in African and Amazonian  
 1493 tropical forests, including only environmental variables, showing long-term trends that impact  
 1494 theory-driven models of photosynthesis and respiration. Significant values in bold.

| Predictor variable    | Carbon gains, Mg C ha <sup>-1</sup> yr <sup>-1</sup>    |                |         |         |
|-----------------------|---|----------------|---------|---------|
|                       | Parameter value   | Standard Error | t-value | p-value |
| (Intercept)           | 4.694   | 0.739          | 6.354   | 0.000   |
| CO <sub>2</sub> (ppm) | <b>0.005</b>  | 0.001          | 3.196   | 0.001   |
| MAT (°C)              | <b>-0.143</b>   | 0.021          | -6.844  | 0.000   |
| MCWD (mm x1000)       | <b>-1.232</b>   | 0.210          | -5.878  | 0.000   |
| Predictor variable    | Carbon losses, Mg C ha <sup>-1</sup> yr <sup>-1</sup> * |                |         |         |
|                       | Parameter value   | Standard Error | t-value | p-value |
| (Intercept)           | 0.926   | 1.854          | 0.500   | 0.617   |
| CO <sub>2</sub> (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,  $\lambda = 0.361$ .

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       |

1498 \* 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.