

# **Long-term thermal sensitivity of Earth's tropical forests**

Martin J P Sullivan, Simon Lewis, Kofi Affum-Baffoe, Carolina Castilho, Flávia Costa, Aida Cuni Sanchez, Corneille Ewango, Wannes Hubau, Beatriz Marimon, Abel Monteagudo-Mendoza, et al.

## **To cite this version:**

Martin J P Sullivan, Simon Lewis, Kofi Affum-Baffoe, Carolina Castilho, Flávia Costa, et al.. Long-term thermal sensitivity of Earth's tropical forests. Science, 2020, 368 (6493), pp.869-874.  $10.1126/\text{science.aaw}$ 7578. hal-02650649

# **HAL Id: hal-02650649 <https://hal.umontpellier.fr/hal-02650649v1>**

Submitted on 16 Aug 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

This is the author's version of the work. It is posted here by permission of the AAAS for personal use, not for redistribution. The definitive version was published in *Science* on 22 May 2020: Vol. 368, Issue 6493, pp. 869-874, DOI:<https://doi.org/10.1126/science.aaw7578>

Sullivan et al. Thermal sensitivity of tropical forests

## **Long-term thermal sensitivity of Earth's tropical forests**

Martin J. P. Sullivan<sup>1,2</sup>, Simon L. Lewis<sup>1,3</sup>, Kofi Affum-Baffoe<sup>4</sup>, Carolina Castilho<sup>5</sup>, Flávia Costa<sup>6</sup>, Aida Cuni Sanchez<sup>7,8</sup>, Corneille E. N. Ewango<sup>9,10,11</sup>, Wannes Hubau<sup>1,12,13</sup>, Beatriz Marimon<sup>14</sup>, Abel Monteagudo-Mendoza<sup>15</sup>, Lan Qie<sup>16</sup>, Bonaventure Sonké<sup>17</sup>, Rodolfo Vasquez Martinez<sup>15</sup>, Timothy R Baker<sup>1</sup>, Roel J. W. Brienen<sup>1</sup>, Ted R. Feldpausch<sup>18</sup>, David Galbraith<sup>1</sup>, Manuel Gloor<sup>1</sup>, Yadvinder Malhi<sup>19</sup>, Shin-Ichiro Aiba<sup>20</sup>, Miguel N. Alexiades<sup>21</sup>, Everton C. Almeida<sup>22</sup>, Edmar Almeida de Oliveira<sup>23</sup>, Esteban Álvarez Dávila<sup>24</sup>, Patricia Alvarez Loayza<sup>25</sup>, Ana Andrade<sup>26</sup>, Simone Aparecida Vieira<sup>27</sup>, Luiz Aragão<sup>28</sup>, Alejandro Araujo-Murakami<sup>29</sup>, Eric J.M.M. Arets<sup>30</sup>, Luzmila Arroyo<sup>31</sup>, Peter Ashton<sup>32</sup>, Gerardo Aymard C.<sup>33</sup>, Fabrício B. Baccaro<sup>34</sup>, Lindsay F. Banin<sup>35</sup>, Christopher Baraloto<sup>36</sup>, Plínio Barbosa Camargo<sup>37</sup>, Jos Barlow<sup>38</sup>, Jorcely Barroso<sup>39</sup>, Jean-François Bastin<sup>40</sup>, Sarah A. Batterman<sup>1,41,42,43</sup>, Hans Beeckman<sup>12</sup>, Serge K. Begne<sup>17,44</sup>, Amy C. Bennett<sup>44</sup>, Erika Berenguer<sup>19,38</sup>, Nicholas Berry<sup>45</sup>, Lilian Blanc<sup>46</sup>, Pascal Boeckx<sup>47</sup>, Jan Bogaert<sup>48</sup>, Damien Bonal<sup>49</sup>, Frans Bongers<sup>50</sup>, Matt Bradford<sup>51</sup>, Francis Q. Brearley<sup>2</sup>, Terry Brncic<sup>52</sup>, Foster Brown<sup>53</sup>, Benoit Burban<sup>54</sup>, José Luís Camargo<sup>26</sup>, Wendeson Castro<sup>55</sup>, Carlos Céron<sup>56</sup>, Sabina Cerruto Ribeiro<sup>57</sup>, Victor Chama Moscoso<sup>15</sup>, Jerôme Chave<sup>58</sup>, Eric Chezeaux<sup>59</sup>, Connie J. Clark<sup>25</sup>, Fernanda Coelho<sup>1</sup>, Murray Collins<sup>61</sup>, James A. Comiskey<sup>62,63</sup>, Fernando Cornejo Valverde<sup>64</sup>, Massiel Corrales Medina<sup>65</sup>, Lola da Costa<sup>66</sup>, Martin Dančák<sup>67</sup>, Greta C. Dargie<sup>1</sup>, Stuart Davies<sup>68</sup>, Nallaret Davila Cardozo<sup>69</sup>, Thales de Haulleville<sup>12,48</sup>, Marcelo Brilhante de Medeiros<sup>70</sup>, Jhon del Aguila Pasquel<sup>71</sup>, Géraldine Derroire<sup>72</sup>, Anthony Di Fiore<sup>73</sup>, Jean-Louis Doucet<sup>74</sup>, Aurélie Dourdain<sup>72</sup>, Vincent Droissant<sup>75</sup>, Luisa Fernanda Duque<sup>76</sup>, Romeo Ekoungoulou<sup>77</sup>, Fernando Elias<sup>78</sup>, Terry Erwin<sup>79</sup>, Adriane Esquivel-Muelbert<sup>80</sup>, Sophie Fauset<sup>81</sup>, Joice Ferreira<sup>82</sup>, Gerardo Flores Llampazo<sup>83</sup>, Ernest Foli<sup>84</sup>, Andrew Ford<sup>51</sup>, Martin Gilpin<sup>1</sup>, Jefferson S. Hall<sup>85</sup>, Keith C. Hamer<sup>86</sup>, Alan C. Hamilton<sup>87</sup>, David J. Harris<sup>88</sup>, Terese B. Hart<sup>89,90</sup>, Radim Hédl<sup>91,92</sup>, Bruno Herault<sup>72</sup>, Rafael Herrera<sup>93</sup>, Niro Higuchi<sup>6</sup>, Annette Hladik<sup>94</sup>, Eurídice Honorio Coronado<sup>71</sup>, Isau Huamantupa-Chuquimaco<sup>95</sup>, Walter Huaraca Huasco<sup>95</sup>, Kathryn J. Jeffery<sup>96</sup>, Eliana Jimenez-Rojas<sup>97</sup>, Michelle Kalamandeen<sup>1</sup>, Marie-Noel Kamdem<sup>11,13,17,98</sup>, Elizabeth Kearsley<sup>99</sup>, Ricardo Keichi Umetsu<sup>100</sup>, Lip Khoon Kho Khoon<sup>101</sup>, Timothy Killeen<sup>102</sup>, Kanehiro Kitayama<sup>103</sup>, Bente Klitgaard<sup>104</sup>, Nicolas Labrière<sup>58</sup>, William Laurance<sup>105</sup>, Susan Laurance<sup>105</sup>, Miguel E. Leal<sup>106</sup>, Aurora Levesley<sup>1</sup>, Adriano J. N. Lima<sup>6</sup>, Janvier Lisingo<sup>11</sup>, Aline P. Lopes<sup>107,108</sup>, Gabriela Lopez-Gonzalez<sup>1</sup>, Tom Lovejoy<sup>109</sup>, Jon Lovett<sup>1</sup>, Richard Lowe<sup>110</sup>, William E. Magnusson<sup>111</sup>, Jagoba Malumbres-Olarte<sup>112,113</sup>, Ângelo Gilberto Manzatto<sup>114</sup>, Ben Hur Marimon Junior<sup>115</sup>, Andrew R. Marshall<sup>8,116,117</sup>, Toby Marthews<sup>118</sup>, Simone Matias de Almeida Reis<sup>14,19</sup>, Colin Maycock<sup>119</sup>, Karina Melgaço<sup>1</sup>, Casimiro Mendoza<sup>120</sup>, Faizah Metali<sup>121</sup>, Vianet Mihindou<sup>122,123</sup>, William Milliken<sup>104</sup>, Edward Mitchard<sup>124</sup>, Paulo S. Morandi<sup>14</sup>, Hannah L. Mossman<sup>2</sup>, Laszlo Nagy<sup>125</sup>, Henrique Nascimento<sup>6</sup>, David Neill<sup>126</sup>, Reuben Nilus<sup>127</sup>, Percy Núñez Vargas<sup>95</sup>, Walter Palacios<sup>128</sup>, Nadir Pallqui Camacho<sup>1,95</sup>, Julie Peacock<sup>1</sup>, Colin Pendry<sup>129</sup>, Maria Cristina Peñuela Mora<sup>130</sup>, Georgia C. Pickavance<sup>1</sup>, John Pipoly<sup>131</sup>, Nigel Pitman<sup>132</sup>, Maureen Playfair<sup>133</sup>, Lourens Poorter<sup>134</sup>, John R. Poulsen<sup>25</sup>, Axel D. Poulsen<sup>135</sup>, Richard Preziosi<sup>2</sup>, Adriana Prieto<sup>136</sup>, Richard Primack<sup>137</sup>, Hirma Ramírez-Angulo<sup>138</sup>, Jan Reitsma<sup>139</sup>, Maxime Réjou-Méchain<sup>75</sup>, Zorayda Restrepo Correa<sup>140</sup>, Thaiane Rodrigues de Sousa<sup>6</sup>, Lily Rodriguez Bayona<sup>141</sup>, Anand Roopsind<sup>142</sup>, Agustín Rudas<sup>136</sup>, Ervan Rutishauser<sup>42,143</sup>, Kamariah Abu Salim<sup>121</sup>, Rafael P. Salomão<sup>144,145</sup>, Juliana Schietti<sup>6</sup>, Douglas Sheil<sup>146</sup>, Richarlly C. Silva<sup>57,147</sup>, Javier Silva Espejo<sup>148</sup>, Camila Silva Valeria<sup>38</sup>, Marcos Silveira<sup>57</sup>, Murielle Simo-Droissart<sup>17</sup>, Marcelo Fragomeni Simon<sup>70</sup>, James Singh<sup>149</sup>, Yahn Carlos Soto Shareva<sup>15</sup>, Clement Stahl<sup>54</sup>, Juliana Stropp<sup>150</sup>, Rahayu Sukri<sup>121</sup>, Terry Sunderland<sup>151,152</sup>, Martin Svátek<sup>153</sup>, Michael D. Swaine<sup>154</sup>, Varun Swamy<sup>155</sup>, Hermann Taedoumg<sup>17</sup>, Joey Talbot<sup>1</sup>, James Taplin<sup>156</sup>, David Taylor<sup>157</sup>, Hans ter Steege<sup>158,159</sup>, John Terborgh<sup>25</sup>, Raquel Thomas<sup>142</sup>, Sean C. Thomas<sup>160</sup>, Armando Torres-Lezama<sup>161</sup>, Peter Umunay<sup>162,163</sup>, Luis Valenzuela Gamarra<sup>15</sup>, Geertje van der Heijden<sup>164</sup>, Peter van der Hout<sup>165</sup>, Peter van der Meer<sup>166</sup>, Mark van Nieuwstadt<sup>167</sup>, Hans Verbeeck<sup>99</sup>, Ronald Vernimmen<sup>168</sup>, Alberto Vicentini<sup>6</sup>, Ima Célia Guimarães Vieira<sup>145</sup>, Emilio Vilanova Torre<sup>169</sup>, Jason Vleminckx<sup>36</sup>, Vincent Vos<sup>171</sup>, Ophelia Wang<sup>172</sup>, Lee J. T. White<sup>123,173,174</sup>, Simon Willcock<sup>175</sup>, John T. Woods<sup>176</sup>, Verginia Wortel<sup>177</sup>, Kenneth Young<sup>178</sup>, Roderick Zagt<sup>179</sup>, Lise Zemagho<sup>17</sup>, Pieter A. Zuidema<sup>50</sup>, Joeri A. Zwerts<sup>177,180</sup>, Oliver L. Phillips<sup>1</sup>

## Affiliations:

- <sup>1</sup> School of Geography, University of Leeds, Leeds, UK
- <sup>2</sup> Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK
- <sup>3</sup> Department of Geography, University College London, London, UK
- <sup>4</sup> Mensuration Unit, Forestry Commission of Ghana, Kumasi, Ghana
- <sup>5</sup> Embrapa Roraima, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil
- 6 Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil
- <sup>7</sup> Department of Ecosystem Science and Sustainability, Colorado State University, USA
- <sup>8</sup> Department of Environment and Geography, University of York, York, UK
- <sup>9</sup> DR Congo Programme, Wildlife Conservation Society, Kisangani, Democratic Republic of Congo
- <sup>10</sup> Centre de Formation et de Recherche en Conservation Forestiere (CEFRECOF), Epulu, Democratic Republic of Congo
- <sup>11</sup> Faculté de Gestion de Ressources Naturelles Renouvelables, Université de Kisangani, Kisangani, Democratic Republic of Congo
- <sup>12</sup> Service of Wood Biology, Royal Museum for Central Africa, Tervuren, Belgium
- <sup>13</sup> Department of Environment, Laboratory of Wood Technology (Woodlab), Ghent University, Ghent, Belgium
- <sup>14</sup> Faculdade de Ciências Agrárias, Biológicas e Sociais Aplicadas, Universidade do Estado de Mato Grosso, Nova Xavantina-MT, Brazil
- <sup>15</sup> Jardín Botánico de Missouri, Oxapampa, Peru
- <sup>16</sup> School of Life Sciences, University of Lincoln, Lincoln, UK
- <sup>17</sup> Plant Systematics and Ecology Laboratory, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon
- <sup>18</sup> Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
- <sup>19</sup> Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK
- <sup>20</sup> Graduate School of Science and Engineering, Kagoshima University, Japan
- <sup>21</sup> School of Anthropology and Conservation, University of Kent, Canterbury, UK
- <sup>22</sup> Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará, Santarém PA, Brazil
- <sup>23</sup> Universidade do Estado de Mato Grosso, Cáceres MT, Brazil
- <sup>24</sup> Escuela de Ciencias Agrícolas, Pecuarias y del Medio Ambiente, National Open University and Distance, Colombia
- <sup>25</sup> Center for Tropical Conservation, Nicholas School of the Environment, Duke University, Durham, NC, USA
- <sup>26</sup> Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
- <sup>27</sup> Universidade Estadual de Campinas, Campinas SP, Brazil
- <sup>28</sup> National Institute for Space Research (INPE), São José dos Campos-SP, Brazil
- <sup>29</sup> Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia
- <sup>30</sup> Wageningen Environmental Research, Wageningen, The Netherlands
- <sup>31</sup> Dirección de la Carrera de Biología, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia
- <sup>32</sup> Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA
- <sup>33</sup> Programa de Ciencias del Agro y el Mar, Herbario Universitario, Barinas, Venezuela
- <sup>34</sup> Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Brazil
- Centre of Ecology and Hydrology, Penicuik, UK
- International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Florida, FL, USA
- Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, São Paulo, SP, Brazil
- Lancaster Environment Centre, Lancaster University, Lancaster, UK
- Centro Multidisciplinar, Universidade Federal do Acre, Cruzeiro do Sul AC, Brazil
- Institure of Integrative Biology, ETH Zurich, Zurich, Switzerland
- Priestley International Centre for Climate, University of Leeds, Leeds, UK
- Smithsonian Tropical Research Institute, Panama, Panama
- Cary Institute of Ecosystem Studies, Millbrook, NY, USA
- School of Geography, School of Geography, Leeds, UK
- The Landscapes and Livelihoods Group, Edinburgh, UK
- UR Forest& Societies, CIRAD, Montpellier, France
- Isotope Bioscience Laboratory-ISOFYS, Ghent University, Gent, Belgium
- Gembloux Agro-Bio Tech, University of Liège, Liège, Belgium
- UMR Silva, INRA, Nancy, France
- <sup>50</sup> Department of Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands
- CSIRO, Canberra, Australia
- Congo Programme, Wildlife Conservation Society, Brazzavile, Republic of Congo
- Woods Hole Research Center, Falmouth, MA, USA
- Ecologie des Forêts de Guyane (ECOFOG), INRA, Kourou, French Guiana
- Programa de Pós-Graduação Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre, Rio Branco - AC, Brazil
- Herbario Alfredo Paredes, Universidad Central del Ecuador, Quito, Ecuador
- Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco AC, Brazil
- Laboratoire Évolution et Diversité Biologique UMR 5174 (CNRS/IRD/UPS), CNRS, Toulouse, France
- Rougier-Gabon, Libreville, Gabon
- Nicholas School of the Environment, Duke University, Durham, NC, USA
- <sup>61</sup> Grantham Research Institute on Climate Change and the Environment, London, UK
- Inventory & Monitoring Program, National Park Service, Fredericksburg, VA, USA
- Smithsonian Institution, Washington, DC, USA
- Proyecto Castaña, Made de Dios, Peru
- Universidad Nacional de San Agustín de Arequipa, Arequipa, Peru
- Instituto de Geociências, Faculdade de Meteorologia, Universidade Federal do Para, Belém PA, Brazil
- <sup>67</sup> Faculty of Science, Department of Ecology and Environmental Sciences, Palacký University Olomouc, Olomouc, Czech Republic
- Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Panama, Panama
- Facultad de Ciencias Biológicas, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru
- Embrapa Genetic Resources & Biotechnology, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil
- Instituto de Investigaciones de la Amazonía Peruana, Iquitos, Peru
- Ecologie des Forêts de Guyane (ECOFOG), CIRAD, Kourou, French Guiana
- Department of Anthropology, The University of Texas at Austin, Austin, TX, USA
- Forest Resources Management, Gembloux Agro-Bio Tech, University of Liège, Liège, Belgium
- AMAP Lab, IRD, CIRAD, CNRS, INRA, Univ Montpellier, Montpellier, France
- Socioecosistemas y Cambio Climatico, Fundacion con Vida, Medellín, Colombia
- School of Forestry, Beijing Forestry University, Beijing, China
- Institute of Biological Sciences, Universidade Federal do Pará, Belém PA, Brazil
- National Museum of Natural History, Smithsonian Institute, Washington, DC, USA
- School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK
- School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK
- Embrapa Amazônia Oriental, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil
- Universidad Nacional Jorge Basadre de Grohmann (UNJBG), Tacna, Peru
- Forestry Research Institute of Ghana (FORIG), Kumasi, Ghana
- Smithsonian Institution Forest Global Earth Observatory (ForestGEO), Smithsonian Tropical Research Institute, Washington, DC, USA
- 86 School of Biology, University of Leeds, Leeds, UK
- 128 Busbridge Lane, Godalming, Surrey, UK
- Royal Botanic Garden Edinburgh, Edinburgh, UK
- Lukuru Wildlife Research Foundation, Kinshasa, Democratic Republic of Congo
- <sup>90</sup> Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT, USA
- <sup>91</sup> Institute of Botany, Czech Academy of Sciences, Brno, Czech Republic
- <sup>92</sup> Department of Botany, Palacký University in Olomouc, Olomouc, Czech Republic
- Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela
- Département Hommes, natures, sociétés, Muséum National d'Histoire Naturel, Paris, France
- Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru
- <sup>96</sup> Biological and Environmental Sciences, University of Stirling, Stirling, UK
- Instituto IMANI, Universidad Nacional de Colombia, Leticia, Colombia
- <sup>98</sup> Faculty of Science, Department of Botany and Plant Physiology, University of Buea, Buea, Cameroon
- <sup>99</sup> Department of Environment, Computational & Applied Vegetation Ecology (Cavelab), Ghent University, Ghent, Belgium
- PELD, Universidade do Estado de Mato Grosso, Nova Xavantina-MT, Brazil
- Tropical Peat Research Institute, Malaysian Palm Oil Board, Kuala Lumpur, Malaysia
- Agteca, Santa Cruz, Bolivia
- Graduate School of Agriculture, Kyoto University, Japan
- Royal Botanic Gardens Kew, Richmond, London, UK
- <sup>105</sup> Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Sciences, James Cook University, Australia
- Uganda Programme, Wildlife Conservation Society, Kampala, Uganda
- Remote Sensing Division, National Institute for Space Research (INPE), São José dos Campos-SP, Brazil
- Department of Ecology, University of Brasília, Brasília, Brazil
- Environmental Science and Policy, George Mason University, Fairfax, VA, USA
- Botany Department, University of Ibadan, Ibadan, Nigeria
- Coordenação da Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Mauaus, Brazil
- <sup>112</sup> cE3c Centre for Ecology, Evolution and Environmental Changes / Azorean Biodiversity Group, Universidade dos Açores, Angra do Heroísmo, Azores, Portugal
- LIBRe Laboratory for Integrative Biodiversity Research, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
- Laboratório de Biogeoquímica Ambiental Wolfgang C. Pfeiffer, Universidade Federal de Rondônia, Porto Velho - RO, Brazil
- Faculdade de Ciências Agrárias, Biológicas e Sociais Aplicadas, Universidad do Estado de Mato Grosso, Nova Xavantina-MT, Brazil
- Tropical Forests and People Research Centre, University of the Sunshine Coast, Australia
- Flamingo Land Ltd., North Yorkshire, UK
- Centre for Ecology and Hydrology, Wallingford, UK
- School of International Tropical Forestry, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia
- Escuela de Ciencias Forestales, Unidad Académica del Trópico, Universidad Mayor de San Simón, Sacta, Bolivia
- Faculty of Science, Universiti Brunei Darussalam, Brunei
- Agence Nationale des Parcs Nationaux, Libreville, Gabon
- Ministère de la Forêt, de la Mer, de l'Environnement, Chargé du Plan Climat, Libreville, Gabon
- University of Edinburgh, Edinburgh, UK
- Biologia Vegetal, Universide Estadual de Campinas, Campinas SP, Brazil
- Facultad de Ingeniería Ambiental, Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador
- Forest Research Centre, Sabah Forestry Department, Sepilok, Malaysia
- Carrera de Ingeniería Forestal, Universidad Tecnica del Norte, Ibarra, Ecuador
- Royal Botanical Garden Edinburgh, Edinburgh, UK
- Universidad Regional Amazónica IKIAM, Tena, Ecuador
- <sup>131</sup> Public Communications and Outreach Group, Parks and Recreation Division, Oakland Park, FL, USA
- Keller Science Action Center, Field Museum, Chicago, IL, USA
- Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname
- <sup>134</sup> Department of Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, The Netherlands
- University of Oslo, Oslo, Norway
- Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Leticia, Colombia
- Department of Biology, Boston University, Boston, USA
- Institute of Research for Forestry Development (INDEFOR), Universidad de los Andes, Mérida, Venezuela
- Bureau Waardenburg, Culemborg, The Netherlands
- Socioecosistemas y Cambio Climatico, Fundacion Con Vida, Medellín, Colombia
- Centro de Conservacion, Investigacion y Manejo de Areas Naturales, CIMA Cordillera Azul, Lima, Peru
- Iwokrama International Centre for Rainforest Conservation and Development, Georgetown, Guyana
- Carboforexpert, Geneva, Switzerland
- Universidade Federal Rural da Amazônia/CAPES, Belém PA, Brazil
- Museu Paraense Emílio Goeldi, Belém PA, Brazil
- <sup>146</sup> Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
- Instituto Federal do Acre, Rio Branco AC, Brazil
- Universidad de San Antonio Abad del Cusco, Cusco, Peru
- Guyana Forestry Commission, Georgetown, Guyana
- Federal University of Alagoas, Maceió, Brazil
- Sustainable Landscapes and Food Systems, Center for International Forestry Research, Bogor, Indonesia
- Faculty of Forestry, University of British Columbia, Vancouver, Canada
- <sup>153</sup> Department of Forest Botany, Dendrology and Geobiocoenology, Mendel University in Brno, Brno, Czech Republic
- <sup>154</sup> Department of Plant & Soil Science, School of Biological Sciences, University of Aberdeen, Aberdeen, UK
- Institute for Conservation Research, San Diego Zoo, San Diego, USA
- UK Research & Innovation, Innovate UK, London
- Department of Geography, National University of Singapore, Singapore, Singapore
- Naturalis Biodiversity Center, Leiden, The Netherlands
- Systems Ecology, VU University, Amsterdam, The Netherlands
- Faculty of Forestry, University of Toronto, Toronto, Canada
- Universidad de los Andes, Merida, Colombia
- Wildlife Conservation Society, New York, NY, USA
- <sup>163</sup> Yale School of Forestry & Environmental Studies, Yale University, New Haven, CT, USA
- <sup>164</sup> School of Geography, University of Notingham, Nottingham, UK
- Van der Hoult Forestry Consulting, Rotterdam, The Netherlands
- Van Hall Larenstein University of Applied Sciences, Velp, The Netherlands
- Utrecht University, Utrecht, The Netherlands
- Deltares, Delft, The Netherlands
- <sup>169</sup> School of Environmental and Forest Sciences, University of Washington, Seattle, OR, USA
- Department of Biological Sciences, Florida International University, Florida, FL, USA
- Centro de Investigación y Promoción del Campesinado, La Paz, Bolivia
- <sup>172</sup> School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ, USA
- Institut de Recherche en Ecologie Tropicale, Libreville, Gabon
- School of Natural Sciences, University of Stirling, Stirling, UK
- School of Natural Sciences, University of Bangor, Bangor, UK
- University of Liberia, Monrovia, Liberia
- Forest Management, Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname
- <sup>178</sup> Department of Geography and The Environment, University of Texas at Austin, Austin, TX, USA
- Tropenbos International, Wageningen, The Netherlands
- Biology, Utrecht University, Utrecht, The Netherlands

## **Abstract**



**One sentence summary.** Biome-wide variation in tropical forest carbon stocks and dynamics shows long-term thermal resilience.

## Main text

 The response of tropical terrestrial carbon to environmental change is a critical component of global climate models (*1*). Land-atmosphere feedbacks depend on the balance of positive biomass growth 17 stimulation by  $CO<sub>2</sub>$  fertilisation (i.e.  $\beta$ ) and negative responses to warmer temperatures and any 18 change in precipitation (i.e.  $\gamma$ ). Yet the climate response is so poorly constrained that it remains one of the largest uncertainties in Earth system models (*2, 3*), with the temperature sensitivity of tropical land 20 carbon stocks alone differing by  $> 100$  Pg C  $^{\circ}$ C<sup>-1</sup> among models (2). Such uncertainty impedes our understanding of the global carbon cycle, limiting our ability to simulate the future of the Earth system under different long-term climate mitigation strategies. A critical long-term control on tropical 23 land-atmosphere feedbacks is the sensitivity to climate  $(\gamma)$  of tropical forests, where c. 40 % of the world's vegetation carbon resides (*4*). The sensitivity of tropical biomass carbon stocks, their rate of production and their persistence to

 environmental change can all be estimated by relating their short-term and inter-annual responses to variation in climate (*5-7*). These sensitivities are then used to constrain longer-term projections of climate responses (*2*). Such approaches typically find that higher minimum temperatures are strongly associated with slower tree growth and reduced forest carbon stocks, likely due to increased respiration at higher temperatures (*7-9*). Tropical forest carbon is also sensitive to precipitation (*10*), with, for example, elevated tree mortality occurring during drought events (*11*).

 Yet, the sensitivity of ecosystems to inter-annual fluctuations may be an unreliable guide to their longer-term responses to climate change. Such responses will also be influenced by physiological acclimation (*12*), changes in demographic rates (*13*), and shifts in species composition (*14*). For example, both respiration and photosynthesis can acclimate under sustained temperature increases (*15-17*), and tropical trees exhibit physiological plasticity (*18*) and shifts in species composition (*14*) under sustained drought. These processes could mean that tropical forests are less sensitive to climate than estimates derived from inter-annual variability imply. An alternative, complimentary approach to assessing sensitivity to climate is to measure and analyse spatial variation in tropical ecosystems across climate gradients as a space-for-time substitution. Such biome-wide spatial variation in forest

 carbon stocks, fluxes and persistence offers a unique and largely unexplored window into the potential equilibrium sensitivity of tropical forest vegetation to warming, as it captures real-world vegetation responses that allow for physiological and ecological adaptation (*12*).

 To assess the long-term climate controls on tropical forest growth and carbon stocks, here we have assembled, measured, and analysed a pan-tropical network of 590 permanent, long-term inventory plots (Fig. 1, see Figs. S1-2 for ability to capture biome climate space). Our analysis combines standardised measurements from across South American, African, Asian and Australian tropical lowland forests (273, 239, 61 and 17 plots respectively). For every plot we calculated aboveground carbon stocks (*19*). Then, to better assess the dynamic controls on aboveground carbon stocks, we also computed the rate of carbon gained by the system (aboveground woody carbon production, 51 calculated as tree growth plus newly recruited trees, in Mg C ha<sup>-1</sup> yr<sup>-1</sup>), and its longevity in living biomass (carbon residence time, calculated as the ratio of stocks to gains, in years).

 We find considerable variation in biomass carbon among continents, with lower stocks per unit area in South America compared with the Paleotropics even after accounting for environmental variables (Fig. 1). Continents with high carbon stocks had either large carbon gains (Asia), or long carbon residence times (Africa, Fig. 1). Because of these differences among continents, which are potentially due to differences in evolutionary history (*20*), we analyse the environmental drivers of spatial variation in carbon stocks while accounting for biogeographical differences. We fitted linear models with explanatory variables representing hypothesised mechanistic controls of climate on tropical forest carbon (Table S1). We also included soil covariates, continent intercepts and eigenvectors describing spatial relationships amongst plots to account for other sources of variation (*21*).

 Forest carbon stocks were most strongly related to maximum temperature (-5.9 % per 1°C increase in 63 maximum temperature, 95 % CI = -8.6 to -3.1 %, Fig. 2, equivalent to 9.1 Mg C ha<sup>-1 o</sup>C<sup>-1</sup> for a stand 64 with the mean carbon stocks in our dataset,  $154.6 \text{ Mg C} \text{ ha}^{-1}$ ), followed by rainfall (+2.4 % per 100 65 mm increase in precipitation in the driest quarter, 95 % CI =  $0.6 - 4.3$  %, Fig. 2), with no statistically significant relationship with minimum temperature, wind speed or cloud cover (Fig 2). The effects of maximum temperature and precipitation are also evident in an analysis considering a wider suite of



72 carbon gains in hotter forests (-4.0 % per 1 $\degree$ C, 95% CI = -6.2 to -1.8 %, Fig. 2) while the positive effect of precipitation emerges through longer carbon residence times in wetter forests (3.3 % per 100 74 mm, 95 % CI =  $0.9 - 5.7$  %, Fig. 2). Carbon residence time also increased with the proportion of clay in the soil (Fig. 2). The additive effects of precipitation and temperature on carbon stocks were 76 modified by an interaction between them  $(\Delta AIC = 15.4$  comparing full linear model with or without interaction), with temperature effects more negative when precipitation is low (Fig. S6). The 78 interaction was through shortening carbon residence time  $(\Delta AIC = 11.9)$  rather than reducing carbon 79 gains (model without interaction better,  $\triangle$  AIC = 1.4).

 An alternative analysis using decision tree algorithms (*22*) also showed maximum temperature and precipitation to be important (Fig. S7). This decision tree approach, which can capture complex non- linear relationships (*22*), indicated potential non-linearity in the relationships between carbon stocks and both temperature and precipitation, with the positive effect of increasing dry season precipitation on residence times strengthening when precipitation was low, and the negative effect of maximum temperature intensifying at high temperatures (Fig. S7).

 We further investigated non-linearity in the temperature relationship using breakpoint regression 87 (supported over linear regression based on lower AIC,  $\triangle$  AIC = 15.0), which revealed that above 32.2 88 °C (95 % CI = 31.7 – 32.6 °C) the relationship between carbon stocks and maximum temperature 89 became more negative (cooler than breakpoint: -3.8 %  $^{\circ}C^{-1}$ , warmer than breakpoint: -14.7 %  $^{\circ}C^{-1}$ , Fig. 3). By partitioning carbon stocks into their production and persistence we find that this non-91 linearity reflects changes to carbon residence time ( $\Delta$  AIC = 10.6) rather than gains ( $\Delta$  AIC = 1.7). Overall, our results thus indicate two separate climate controls on carbon stocks: a negative linear effect of maximum temperature through reduced carbon gains, and a non-linear negative effect of

 maximum temperature, ameliorated by high dry-season precipitation, through reduced carbon residence time.

 The effect of temperature on carbon residence time only emerges when dry season precipitation is low, so is consistent with theoretical expectations that negative effects of temperature on tree longevity are exacerbated by moisture limitation rather than being independent of it (i.e. due to increased respiration costs alone) (*23*). This could occur through high vapour pressure deficits in hot and dry forests increasing mortality risk by causing hydraulic stress (*23, 24*), or carbon starvation due to limited photosynthesis as a result of stomatal closure (*23*). Notably, the temperature-precipitation interaction we find for aboveground stocks is in the opposite direction to temperature-precipitation interactions reported for soil carbon. In soils, moisture limitation suppresses the temperature response of heterotrophic respiration (*25*), while in trees moisture limitation enhances the mortality risks of high temperatures.

 The temperature effects on biomass carbon stocks and gains are primarily due to maximum rather 107 than minimum temperature. This is consistent with high daytime temperatures reducing  $CO<sub>2</sub>$  assimilation rates, for example due to increased photorespiration or longer duration of stomatal closure (*26, 27*), whereas if negative temperature effects were to have increased respiration rates there should be a stronger relationship with minimum (i.e. night-time) temperature. Critically, minimum temperature is unrelated to aboveground carbon stocks both pan-tropically and in the one continent, South America, where maximum and minimum temperature are largely decoupled (*r* = 0.33; Fig. S8). While carbon gains are negatively related to minimum temperature (Fig S9) this bivariate relationship is weaker than with maximum temperature, and disappears once the effects of other variables are accounted for (Fig. 2). Finally, in Asia, the tropical region which experiences the warmest minimum temperatures of all, both carbon stocks and carbon gains are highest (Fig. 1, Fig. S11).

 Overall our results suggest that tropical forests have considerable potential to acclimate and adapt to the effects of night-time minimum temperatures, but are clearly sensitive to the effects of daytime

maximum temperature. This is consistent with ecophysiological observations suggesting that the

acclimation potential of respiration (*15*) is greater than that of photosynthesis (*17*). The temperature

 sensitivity revealed by our analysis is also considerably weaker than the short-term sensitivities associated with inter-annual climate variation (*8*). For example, by relating short-term annual climate 123 anomalies to responses in plots, the effect of a  $1^{\circ}$ C increase in temperature on carbon gains has been estimated as more than three-fold our long-term, pantropical result (*28*). This stronger long-term thermal resilience is likely due to a combination of individual acclimation and plasticity (*15-17*), differences in species' climate responses (*29*) leading to shifts in community composition due to changing demographic rates (*12*) and the immigration of species with higher performance at high temperatures (*12*).

 Our pantropical analysis of the sensitivity to climate of aboveground carbon stocks, gains and persistence shows that warming reduces carbon stocks and gains from woody productivity in tropical forests. Using a reference carbon stock map (*30*) and applying our estimated temperature sensitivity (including non-linearity) while holding other variables constant leads to a biome-wide reduction of 14.1 Pg C in live biomass (including scaling to estimate carbon in roots) for a 1°C increase in 134 maximum temperature (95 % CI =  $6.9 - 20.7$  Pg). In comparison, coupled climate-carbon cycle 135 models (2) give a median tropical land temperature sensitivity of 53 Pg C  $^{\circ}$ C<sup>-1</sup> (95 % CI = 19.7 – 86.3 Pg), although these also incorporate the response of heterotrophic respiration and fire. In the future, reporting Earth System Model outputs for live biomass carbon separate from other changes would assist in comparing model outcomes with direct observations.

139 Our results suggest that global surface temperature increases of  $2^{\circ}C$  above pre-industrial levels will 140 cause a potential biome-wide loss of 35.3 Pg C (95 % CI = 20.9 – 49.0 Pg) based on responses to warming from the 1970-2000 baseline (*31*). The greatest reductions in carbon stocks are projected in South America, where baseline temperatures and future warming are both highest (Fig. 4, Fig. S12). This warming would push 71 % of the biome beyond the thermal threshold – maximum temperature of 32.2°C – where larger reductions in biomass are expected. Of course, growth stimulation by carbon dioxide (*32*) will partially or wholly offset the effect of this temperature increase, depending on both 146 the level of atmospheric carbon dioxide that limits warming to  $2^{\circ}$ C above pre-industrial levels and the fertilization effect of this carbon dioxide on tropical trees. Using a variety of published estimates of

 the carbon dioxide fertilization effect (Table S3), partial or full amelioration is expected in the Paleotropics, although reductions in forest carbon stocks are predicted in South America in all scenarios (Fig. S15).

 The long-term climate sensitivities derived from our pan-tropical field measurements incorporate ecophysiological and ecological adaptation, and so provide a model-independent estimate of the long- term quasi-equilibrium response of tropical vegetation to climate, which can inform long-term model predictions (*33*). We note that the thermal adaptation measured here may not be fully realised because (i) the speed of temperature rises may exceed species' adaptive capabilities, (ii) habitat fragmentation may limit species' ability to track changes in the environment, and (iii) other human impacts such as logging and fire can increase the vulnerability of forest carbon stocks to high temperatures. Predictions based on short-term inter-annual sensitivity and our long-term pan-tropical sensitivity likely represent the upper and lower bounds of transient responses to rising temperatures over the coming decades. While many tropical forests are under severe threat of conversion, our results show that, in the long-run, tropical forests that remain intact can continue to store high levels of carbon under high temperatures. Achieving the biome-wide climate resilience potential we document depends on limiting heating and on large-scale conservation and restoration to protect biodiversity and allow species to move.

### **References and Notes**

- 168 1. P. M. Cox, R. A. Betts, C. D. Jones, S. A. Spall, I. J. Totterdell, Acceleration of global warming
- due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184 (2000).
- 2. P. M. Cox *et al.*, Sensitivity of tropical carbon to climate change constrained by carbon
- dioxide variability. *Nature* **494**, 341-344 (2013).
- 3. B. B. B. Booth *et al.*, High sensitivity of future global warming to land carbon cycle processes.
- *Environmental Research Letters* **7**, 024002 (2012).
- 4. K.-H. Erb *et al.*, Unexpectedly large impact of forest management and grazing on global
- vegetation biomass. *Nature* **553**, 73 (2017).
- 176 5. W. Wang *et al.*, Variations in atmospheric CO<sub>2</sub> growth rates coupled with tropical
- temperature. *Proceedings of the National Academy of Sciences* **110**, 13061 (2013).
- 6. J. Liu *et al.*, Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. *Science* **358**, eaam5690 (2017).
- 7. D. A. Clark, S. C. Piper, C. D. Keeling, D. B. Clark, Tropical rain forest tree growth and
- atmospheric carbon dynamics linked to interannual temperature variation during 1984–
- 2000. *Proceedings of the National Academy of Sciences* **100**, 5852 (2003).
- 8. W. R. L. Anderegg *et al.*, Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink. *Proceedings of the National Academy of Sciences* **112**, 15591-15596
- (2015).
- 9. A. Ballantyne *et al.*, Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. *Nature Climate Change* **7**, 148 (2017).
- 10. J. K. Green *et al.*, Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature* **565**, 476-479 (2019).
- 11. O. L. Phillips *et al.*, Drought Sensitivity of the Amazon Rainforest. *Science* **323**, 1344 (2009).

- 191 12. M. D. Smith, A. K. Knapp, S. L. Collins, A framework for assessing ecosystem dynamics in
- response to chronic resource alterations induced by global change. *Ecology* **90**, 3279-3289 (2009).
- 13. J. H. Brown, T. J. Valone, C. G. Curtin, Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences* **94**, 9729-9733
- (1997).
- 14. S. Fauset *et al.*, Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters* **15**, 1120-1129 (2012).
- 15. A. Gunderson Carla, H. O'Hara Keiran, M. Campion Christina, V. Walker Ashley, T. Edwards
- Nelson, Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a
- warming climate. *Global Change Biology* **16**, 2272-2286 (2010).
- 16. M. Slot *et al.*, Thermal acclimation of leaf respiration of tropical trees and lianas: response to experimental canopy warming, and consequences for tropical forest carbon balance. *Global Change Biology* **20**, 2915-2926 (2014).
- 17. F. Ow Lai, L. Griffin Kevin, D. Whitehead, S. Walcroft Adrian, H. Turnbull Matthew, Thermal
- acclimation of leaf respiration but not photosynthesis in Populus deltoides×nigra. *New*
- *Phytologist* **178**, 123-134 (2008).
- 18. T. F. Domingues *et al.*, Ecophysiological plasticity of Amazonian trees to long-term drought. *Oecologia* **187**, 933-940 (2018).

210 19. See suplimentary materials.

- 20. J. W. F. Slik *et al.*, Phylogenetic classification of the world's tropical forests. *Proceedings of the National Academy of Sciences* **115**, 1837 (2018).
- 21. S. Dray, P. Legendre, P. R. Peres-Neto, Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* **196**, 483-
- 493 (2006).
- 22. L. Breiman, Random Forests. *Machine Learning* **45**, 5-32 (2001).

- 23. N. McDowell *et al.*, Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist* **219**, 851-869 (2018).
- 24. G. Fontes Clarissa *et al.*, Dry and hot: the hydraulic consequences of a climate change–type
- drought for Amazonian trees. *Philosophical Transactions of the Royal Society B: Biological*
- *Sciences* **373**, 20180209 (2018).
- 25. P. Ciais *et al.*, Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529-533 (2005).
- 26. M. E. Dusenge, A. G. Duarte, D. A. Way, Plant carbon metabolism and climate change:
- elevated CO2 and temperature impacts on photosynthesis, photorespiration and respiration.
- *New Phytologist* **221**, 32-49 (2019).
- 227 27. S. Pau, M. Detto, Y. Kim, C. J. Still, Tropical forest temperature thresholds for gross primary productivity. *Ecosphere* **9**, e02311 (2018).
- 28. D. A. Clark, D. B. Clark, S. F. Oberbauer, Field-quantified responses of tropical rainforest
- aboveground productivity to increasing CO2 and climatic stress, 1997-2009. *Journal of*

*Geophyical Research - Biogeosciences.* **118**, 783-794 (2013).

- 29. W. R. L. Anderegg *et al.*, Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* **561**, 538-541 (2018).
- 234 30. V. Avitabile *et al.*, An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology* **22**, 1406-1420 (2016).
- 31. S. E. Fick, R. J. Hijmans, WorldClim 2: new 1-km spatial resolution climate surfaces for global
- land areas. *International Journal of Climatology* **37**, 4302-4315 (2017).
- 32. S. Piao *et al.*, Evaluation of terrestrial carbon cycle models for their response to climate
- variability and to CO2 trends. *Global Change Biology* **19**, 2117-2132 (2013).
- 33. L. M. Mercado *et al.*, Large sensitivity in land carbon storage due to geographical and
- temporal variation in the thermal response of photosynthetic capacity. *New Phytologist* **218**,

1462-1477 (2018).

- Additional references cited in suplementary materials 34. A. B. Anderson, White-sand vegetation of Brazilian Amazonia. *Biotropica* **13**, 199-210 (1981). 245 35. S. R. Pezeshki, Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. *Trees* **5**, 180-186 (1991). 36. O. L. Phillips, T. R. Baker, T. R. Feldpausch, R. J. W. Brienen, *RAINFOR Field Manual for Plot Establishment and Remeasurement* (University of Leeds, 2001). 37. J. Talbot *et al.*, Methods to estimate aboveground wood productivity from long-term forest inventory plots. *Forest Ecology and Management* **320**, 30-38 (2014). 38. D. B. Clark, D. A. Clark, Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**, 185-198 (2000). 39. G. Lopez-Gonzalez, S. L. Lewis, M. Burkitt, O. L. Phillips, ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science* **22**, 610-613 (2011). 40. G. Lopez-Gonzalez, S. L. Lewis, M. Burkitt, T. R. Baker, O. L. Phillips, ForestPlots.net Database. [www.forestplots.net.](http://www.forestplots.net/) (2009). 41. R. J. W. Brienen *et al.*, Long-term decline of the Amazon carbon sink. *Nature* **519**, 344-348 (2015). 42. J. Chave *et al.*, Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* **20**, 3177-3190 (2014). 43. J. Chave *et al.*, Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351-366 (2009).
- 44. A. E. Zanne *et al.* Data from: Towards a worldwide wood economics spectrum.
- <https://datadryad.org/stash/dataset/doi:10.5061/dryad.234> (Dryad Data Repository, 2009).
- 45. R. C. Goodman *et al.*, Amazon palm biomass and allometry. *Forest Ecology and Management* **310**, 994-1004 (2013).

- 46. M. J. P. Sullivan *et al.*, Field methods for sampling tree height for tropical forest biomass estimation. *Methods in Ecology and Evolution* **9**, 1179-1189 (2018).
- 270 47. S. C. Thomas, Asymptotic height as a predictor of growth and allometric characteristics in malaysian rain forest trees. *American Journal of Botany* **83**, 556-566 (1996).
- 48. T. R. Feldpausch *et al.*, Tree height integrated into pantropical forest biomass estimates.
- *Biogeosciences* **9**, 3381-3403 (2012).
- 49. T. S. Kohyama, T. I. Kohyama, D. Sheil, Definition and estimation of vital rates from repeated censuses: Choices, comparisons and bias corrections focusing on trees. *Methods in Ecology and Evolution* **9**, 809-821 (2018).
- 50. A. R. Martin, M. Doraisami, S. C. Thomas, Global patterns in wood carbon concentration across the world's trees and forests. *Nature Geoscience* **11**, 915-920 (2018).
- 51. D. Galbraith *et al.*, Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity* **6**, 139-157 (2013).
- 281 52. G. Lopez-Gonzalez, M. J. P. Sullivan, T. R. Baker. BiomasaFP: R package for analysing data downloaded from ForestPlots.net (2015).
- 53. R. J. Hijmans, S. Phillips, J. Leathwick, J. Elith, dismo: Species distribution modeling. R package version 1.0-12. (2015).
- 54. A. M. Wilson, W. Jetz, Remotely Sensed High-Resolution Global Cloud Dynamics for
- Predicting Ecosystem and Biodiversity Distributions. *PLOS Biology* **14**, e1002415 (2016).
- 55. M. New, D. Lister, M. Hulme, I. Makin, A high-resolution data set of surface climate over global land areas. *Climate Research* **21**, 1-25 (2002).
- 56. T. Hengl *et al.*, SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE* **12**, e0169748 (2017).
- 57. P. R. Peres-Neto, P. Legendre, Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography* **19**, 174-184 (2010).
- 58. S. L. Lewis *et al.*, Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003 (2009).
- 59. K. Barton, MuMIn: Multi-Model Inference. R package version 1.12.1. http://CRAN.R-project.org/package=MuMIn (2015).
- 60. V. M. R. Muggeo, Estimating regression models with unknown break-points. *Statistics in Medicine* **22**, 3055-3071 (2003).
- 61. A. Liaw, M. Wiener, Classificiation and Regression by randomForest. *R News* **2**, 18-22 (2002).
- 62. D. M. Olson *et al.*, Terrestrial Ecoregions of the World: A New Map of Life on EarthA new
- global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity.
- *BioScience* **51**, 933-938 (2001).
- 63. M. C. Hansen *et al.*, High-Resolution Global Maps of 21st-Century Forest Cover Change.
- *Science* **342**, 850-853 (2013).
- 64. R. Jackson *et al.*, A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**, 389-411 (1996).
- 65. S. S. Saatchi *et al.*, Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences* **108**, 9899-9904 (2011).
- 66. A. Baccini *et al.*, Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change* **2**, 182-185 (2012).
- 67. E. T. A. Mitchard *et al.*, Uncertainty in the spatial distribution of tropical forest biomass: a comparison of pan-tropical maps. *Carbon Balance and Management* **8**, 10 (2013).
- 
- 68. E. T. Mitchard *et al.*, Markedly divergent estimates of A mazon forest carbon density from
- ground plots and satellites. *Global Ecology and Biogeography* **23**, 935-946 (2014).
- 315 69. R. J. Hijmans. WorldClim Future Climate Dat[a https://www.worldclim.org/cmip5v1.](https://www.worldclim.org/cmip5v1) (2005).
- 70. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution
- interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**,

1965-1978 (2005).

- 71. B. Kirtman *et al.*, Near-term climate change: projections and predictability. (2013).
- 72. H. D. Matthews, K. Caldeira, Stabilizing climate requires near-zero emissions. *Geophysical Research Letters* **35**, (2008).
- 73. M. Meinshausen *et al.*, The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change* **109**, 213 (2011).
- 
- 74. W. Kolby Smith *et al.*, Large divergence of satellite and Earth system model estimates of global terrestrial CO2 fertilization. *Nature Climate Change* **6**, 306 (2015).
- 75. D. W. Kicklighter *et al.*, A first-order analysis of the potential role of CO2 fertilization to affect
- the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus B:*
- *Chemical and Physical Meteorology* **51**, 343-366 (1999).
- 76. Y. Malhi *et al.*, The linkages between photosynthesis, productivity, growth and biomass in
- lowland Amazonian forests. *Global Change Biology* **21**, 2283-2295 (2015).
- 77. C. Terrer *et al.*, Nitrogen and phosphorus constrain the CO2 fertilization of global plant biomass. *Nature Climate Change* **9**, 684-689 (2019).
- 78. E. Bartholome, A. S. Belward, GLC2000: a new approach to global land cover mapping from
- Earth observation data. *International Journal of Remote Sensing* **26**, 1959-1977 (2005).
- 79. J. Chave *et al.*, Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**, 87-99 (2005).
- 80. M. Slot, K. Winter, In situ temperature response of photosynthesis of 42 tree and liana
- species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall
- regimes. *New Phytologist* **214**, 1103-1117 (2017).
- 81. Y. Malhi, The productivity, metabolism and carbon cycle of tropical forest vegetation.
- *Journal of Ecology* **100**, 65-75 (2012).
- 82. E. A. Graham, S. S. Mulkey, K. Kitajima, N. G. Phillips, S. J. Wright, Cloud cover limits net CO2
- uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the*
- *National Academy of Sciences* **100**, 572-576 (2003).

- 83. W. F. Laurance, T. J. Curran, Impacts of wind disturbance on fragmented tropical forests: A
- review and synthesis. *Austral Ecology* **33**, 399-408 (2008).

 **Acknowledgements:** This paper is a product of the RAINFOR, AfriTRON and T-FORCES networks, and is facilitated by ForestPlots.net technology for data management which promotes science synergies across countries and continents. While these initiatives have been supported by numerous people and grants since their inception we are particularly indebted to hundreds of institutions, field assistants and local communities for help in establishing and maintaining the plots. For additional assistance with access to datasets we thank Jon Lloyd, Carlos Quesada, Michel Baisie, Olaf Banki, Wemo Betian, Vincent Bezard, Rene Boot, Mireille Breuer-Ndoundou Hockemba, Ezequiel Chavez, Douglas Daly, Armandu Daniels, Darcy Galiano Cabrera, Toby Gardner, Paolo Graca, Andrew Graham, Olivier Hardy, Eduardo Hase, David Hilvert, Muhammad Idhamsyah, Phillipe Jeanmart, Cisquet Keibou Opepa, Jeanette Kemp, Wilmar Lopez Oviedo, Jean-Remy Makana, Faustin Mbaya Mpanya Lukasu, Irina Mendoza Polo, Edi Mirmanto, Sam Moore, Jacques Mukinzi, Pétrus Naisso, Lucas Ojo, Raimunda Oliveira de Araújo, Sonia Cesarina Palacios Ramos, Alexander Parada Gutierrez, Guido Pardo, Marielos Peña-Claros, Freddy Ramirez Arevalo, Antonio Lima, Rodrigo Sierra, Natalino Silva, Marc Steininger, Marisol Toledo, John Tshibamba Mukendi, Darlington Tuagben , Hannsjoerg Woell and Ishak Yassir. We thank Jon Lloyd, Carlos Quesada for discussions and three anonymous reviewers for helpful comments and suggestions. **Funding:** The networks have been supported by multiple grants, most notably the European Research Council (ERC Advanced Grant 291585 – 'T-FORCES'), the Gordon and Betty Moore Foundation (#1656 'RAINFOR' and Monitoring Protected Areas in Peru to Increase Forest Resilience to Climate Change), the David and Lucile Packard Foundation, the European Union's Seventh Framework Programme (283080 – 'GEOCARBON', 282664 – 'AMAZALERT'), the Natural Environment Research Council (NERC grants NE/D005590/1 – 'TROBIT', NE/F005806/1 – 'AMAZONICA', NERC Urgency Grants and a NERC New Investigators Grant), the NERC/ State of São Paulo Research Foundation (FAPESP) consortium grants 'BIO-RED' (NE/N012542/1, 2012/51872-5) and 'ECOFOR' (NE/K016431/1, 2012/51509-8), the Royal Society, the Centre for International Forestry (CIFOR) and Gabon's National Parks Agency (ANPN). Additional data were included from the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution and the Wildlife Conservation Society, and partly funded by these institutions, the Gordon and Betty Moore Foundation, and other donors. M.J.P.S. was supported by the ERC (T-FORCES), NERC ('BIO-RED') and the Royal Society (CH160091), S.L.L. by a Royal Society University Research Fellowship, ERC Advanced Grant and a Phillip Leverhulme Prize, and O.L.P. by an ERC Advanced Grant and a Royal Society Wolfson Research Merit Award. We thank the National Council for Science and Technology Development of Brazil (CNPq) for support to the Cerrado/Amazonia Transition Long-Term Ecology Project (PELD/403725/2012-7), the PPBio Phytogeography of Amazonia/Cerrado Transition project (CNPq/PPBio/457602/2012-0) and a Productivity Grant to B.S.M. and B.H.M-J.. Funding for plots in the Udzungwa Mountains (Tanzania) was obtained from the Leverhulme Trust under the Valuing the Arc project. This study is contribution number XXX to the Technical Series (TS) of the BDFFP (INPA – STRI). Data from RAINFOR, AfriTRON and T-FORCES are stored and curated by ForestPlots.net, a cyber-infrastructure initiative hosted at the University of Leeds that unites permanent plot records and their contributing scientists from the world's tropical forests. The development of ForestPlots.net and curation of most data analysed here was funded by several grants to O.L.P. (principally from NERC NE/B503384/1, NE/N012542/1 BIO-RED, ERC AdG 291585 T- FORCES', and Gordon and Betty Moore Foundation #1656, 'RAINFOR'), E.G. ('GEOCARBON', and NE/F005806/1 'AMAZONICA'), T.R.B. (Gordon and Betty Moore Foundation 'Monitoring Protected Areas in Peru to Increase Forest Resilience to Climate Change'), S.L.L. (Royal Society

- University Research Fellowship; NERC New Investigators Award; Phillip Leverhulme Prize), and
- D.G. (NERC NE/N004655/1, 'TREMOR'). **Author contributions:** O.L.P., S.L.L. and Y.M.
- conceived the RAINFOR, AfriTRON and T-FORCES forest census network programmes; M.J.P.S.,
- S.L.L. and O.L.P. conceived and designed the study. L.A., A.A.-M., T.R.B., R.J.W.B., S.K.B., K.A-
- B., F.C., C.C., E.A.D., A.C.S., C.E.N.E., T.R.F., W.H., S.L.L., A.M.M., B.S.M., O.L.P., L.Q., B.S.,
- T.S., R.V. and L.J.T.W. coordinated data collection with the help of most co-authors. O.L.P., T.R.B.,
- G.L.-G. and S.L.L. conceived and managed ForestPlots.net; O.L.P., T.R.B., D.G., E.G. and S.L.L.
- funded it, and R.B., T.F., G.L.-G., A.L., G.C.P. and M.J.P.S. helped develop it. M.J.P.S., T.R.B.,
- W.H., S.L.L., A.E.-M., and L.Q. contributed tools to analyse data. All authors collected or supported
- the collection of field data, M.J.P.S. analysed the data, M.J.P.S., S.L.L. and O.L.P. wrote the
- manuscript with contributions from other authors. All co-authors commented on or approved the
- manuscript. **Competing interests:** The authors declare no competing financial interests. **Data and**
- **materials availability:** Plot-level input data and R scripts will be deposited as a data package on ForestPlots.net (doi-xxx).

## **Supplementary Materials:**

- Materials and Methods
- Figures S1-S15
- Tables S1-S3
- References (34-83)



 **Figure 1.** Spatial variation in tropical forest carbon. (A) Our plot network. Filled symbols show multi-census plots used in the main analysis, open symbols show single-census plots used as an independent dataset. (B) Variation in carbon among continents. Boxplots show raw variation while blue points show

417 estimated mean values  $(\pm SE)$  after accounting for environmental variation. Letters denote statistically significant differences between continents ( $P < 0.05$ )

based on raw data (black) or accounting for environmental effects (blue, square brackets).



 **Figure 2.** Correlates of spatial variation in tropical forest carbon. Points show coefficients from model-averaged general linear models. Variables that did not occur in well-supported models are shrinkage adjusted towards zero. Coefficients are standardised so that they represent change in the response variable for one standard deviation change in the explanatory variable. Error bars show standard errors (thick lines) and 95% confidence intervals (thin lines). Soil texture 424 is represented by the percentage clay, and soil fertility by cation exchange capacity. The full models explained 44.1 %, 31.4 % and 30.9 % of spatial variation in carbon stocks, gains and residence time respectively. Coefficients are shown in Table S2. Results are robust to using an alternative allometry to estimate tree biomass (Fig. S5).







 **Figure 3.** Temperature effects on tropical forest carbon stocks (left) and carbon gains from woody productivity (right). Black lines show the best pan-tropical relationships accounting for environmental covariates. The grey line shows the additional linear pan-tropical relationship for carbon stocks. Coloured lines show bivariate relationships within each continent. Statistically significant relationships are shown with solid lines, non-significant with dashed lines. Symbol point size is proportional to weights used in model fitting based on plot size and monitoring length, see SI Materials and Methods. Linear and break-point pan-tropical relationships are all statistically significant (*P* < 0.001), as are better sampled continents. Relationships with other variables are shown in Fig. S8-S10. \*\*\* *P* < 0.001, \*\* *P* < 0.01, \* *P* < 0.05, ns *P* ≥ 0.05.





 **Figure 4.** Long-term change in carbon stocks due to global surface temperature warming of approximately 2°C. Future temperatures come from an ensemble of 15 climate models for RCP4.5, 445 2040-2060, which give global mean surface temperatures  $\sim 1.9^{\circ}$ C above pre-industrial. Maps show the predicted absolute and relative change in tropical forest carbon stocks if global temperatures equilibrated at these new levels, based on the increase in maximum temperature from 1970-2000 baseline climate. Note parts of the biome become warmer than currently observed in our dataset (Fig. S13). See Fig. S14 for predictions using alternative carbon reference maps. Predictions are based on temperature alone and do not include precipitation changes (for which future patterns of change are 451 uncertain) or potential moderation via elevated  $CO<sub>2</sub>$  (see Fig. S15).

## 454 **Supporting information for Long-term thermal Sensitivity of the Earth's Tropical**  455 **Forests**

456 Martin J. P. Sullivan<sup>1,2</sup>, Simon L. Lewis<sup>1,3</sup>, Kofi Affum-Baffoe<sup>4</sup>, Carolina Castilho<sup>5</sup>, Flávia Costa<sup>6</sup>, Aida 457 Cuni Sanchez<sup>7,8</sup>, Corneille E. N. Ewango<sup>9,10,11</sup>, Wannes Hubau<sup>1,12,13</sup>, Beatriz Marimon<sup>14</sup>, Abel Monteagudo-458 Mendoza<sup>15</sup>, Lan Qie<sup>16</sup>, Bonaventure Sonké<sup>17</sup>, Rodolfo Vasquez Martinez<sup>15</sup>, Timothy R Baker<sup>1</sup>, Roel J. W. 459 Brienen<sup>1</sup>, Ted R. Feldpausch<sup>18</sup>, David Galbraith<sup>1</sup>, Manuel Gloor<sup>1</sup>, Yadvinder Malhi<sup>19</sup>, Shin-Ichiro Aiba<sup>20</sup>, 460 Miguel N. Alexiades<sup>21</sup>, Everton C. Almeida<sup>22</sup>, Edmar Almeida de Oliveira<sup>23</sup>, Esteban Álvarez Dávila<sup>24</sup>, 461 Patricia Alvarez Loayza<sup>25</sup>, Ana Andrade<sup>26</sup>, Simone Aparecida Vieira<sup>27</sup>, Luiz Aragão<sup>28</sup>, Alejandro Araujo-462 Murakami<sup>29</sup>, Eric J.M.M. Arets<sup>30</sup>, Luzmila Arroyo<sup>31</sup>, Peter Ashton<sup>32</sup>, Gerardo Aymard C.<sup>33</sup>, Fabrício B. 463 Baccaro<sup>34</sup>, Lindsay F. Banin<sup>35</sup>, Christopher Baraloto<sup>36</sup>, Plínio Barbosa Camargo<sup>37</sup>, Jos Barlow<sup>38</sup>, Jorcely 464 Barroso<sup>39</sup>, Jean-François Bastin<sup>40</sup>, Sarah A. Batterman<sup>1,41,42,43</sup>, Hans Beeckman<sup>12</sup>, Serge K. Begne<sup>17,44</sup>, Amy C. Bennett<sup>44</sup>, Erika Berenguer<sup>19,38</sup>, Nicholas Berry<sup>45</sup>, Lilian Blanc<sup>46</sup>, Pascal Boeckx<sup>47</sup>, Jan Bogaert<sup>48</sup>, Damien 466 Bonal<sup>49</sup>, Frans Bongers<sup>50</sup>, Matt Bradford<sup>51</sup>, Francis Q. Brearley<sup>2</sup>, Terry Brncic<sup>52</sup>, Foster Brown<sup>53</sup>, Benoit 467 Burban<sup>54</sup>, José Luís Camargo<sup>26</sup>, Wendeson Castro<sup>55</sup>, Carlos Céron<sup>56</sup>, Sabina Cerruto Ribeiro<sup>57</sup>, Victor 468 Chama Moscoso<sup>15</sup>, Jerôme Chave<sup>58</sup>, Eric Chezeaux<sup>59</sup>, Connie J. Clark<sup>25</sup>, Fernanda Coelho<sup>1</sup>, Murray 469 Collins<sup>61</sup>, James A. Comiskey<sup>62,63</sup>, Fernando Cornejo Valverde<sup>64</sup>, Massiel Corrales Medina<sup>65</sup>, Lola da 470 Costa<sup>66</sup>, Martin Dančák<sup>67</sup>, Greta C. Dargie<sup>1</sup>, Stuart Davies<sup>68</sup>, Nallaret Davila Cardozo<sup>69</sup>, Thales de 471 Haulleville<sup>12,48</sup>, Marcelo Brilhante de Medeiros<sup>70</sup>, Jhon del Aguila Pasquel<sup>71</sup>, Géraldine Derroire<sup>72</sup>, Anthony 472 Di Fiore<sup>73</sup>, Jean-Louis Doucet<sup>74</sup>, Aurélie Dourdain<sup>72</sup>, Vincent Droissant<sup>75</sup>, Luisa Fernanda Duque<sup>76</sup>, Romeo 473 Ekoungoulou<sup>77</sup>, Fernando Elias<sup>78</sup>, Terry Erwin<sup>79</sup>, Adriane Esquivel-Muelbert<sup>80</sup>, Sophie Fauset<sup>81</sup>, Joice 474 Ferreira<sup>82</sup>, Gerardo Flores Llampazo<sup>83</sup>, Ernest Foli<sup>84</sup>, Andrew Ford<sup>51</sup>, Martin Gilpin<sup>1</sup>, Jefferson S. Hall<sup>85</sup>, 475 Keith C. Hamer<sup>86</sup>, Alan C. Hamilton<sup>87</sup>, David J. Harris<sup>88</sup>, Terese B. Hart<sup>89,90</sup>, Radim Hédl<sup>91,92</sup>, Bruno 476 Herault<sup>72</sup>, Rafael Herrera<sup>93</sup>, Niro Higuchi<sup>6</sup>, Annette Hladik<sup>94</sup>, Eurídice Honorio Coronado<sup>71</sup>, Isau 477 Huamantupa-Chuquimaco<sup>95</sup>, Walter Huaraca Huasco<sup>95</sup>, Kathryn J. Jeffery<sup>96</sup>, Eliana Jimenez-Rojas<sup>97</sup>, 478 Michelle Kalamandeen<sup>1</sup>, Marie-Noel Kamdem<sup>11,13,17,98</sup>, Elizabeth Kearsley<sup>99</sup>, Ricardo Keichi Umetsu<sup>100</sup>, Lip 479 Khoon Kho Khoon<sup>101</sup>, Timothy Killeen<sup>102</sup>, Kanehiro Kitayama<sup>103</sup>, Bente Klitgaard<sup>104</sup>, Nicolas Labrière<sup>58</sup>, 480 William Laurance<sup>105</sup>, Susan Laurance<sup>105</sup>, Miguel E. Leal<sup>106</sup>, Aurora Levesley<sup>1</sup>, Adriano J. N. Lima<sup>6</sup>, Janvier 481 Lisingo<sup>11</sup>, Aline P. Lopes<sup>107,108</sup>, Gabriela Lopez-Gonzalez<sup>1</sup>, Tom Lovejoy<sup>109</sup>, Jon Lovett<sup>1</sup>, Richard Lowe<sup>110</sup>, 482 William E. Magnusson<sup>111</sup>, Jagoba Malumbres-Olarte<sup>112,113</sup>, Ângelo Gilberto Manzatto<sup>114</sup>, Ben Hur Marimon 483 Junior<sup>115</sup>, Andrew R. Marshall<sup>8,116,117</sup>, Toby Marthews<sup>118</sup>, Simone Matias de Almeida Reis<sup>14,19</sup>, Colin 484 Maycock<sup>119</sup>, Karina Melgaço<sup>1</sup>, Casimiro Mendoza<sup>120</sup>, Faizah Metali<sup>121</sup>, Vianet Mihindou<sup>122,123</sup>, William 485 Milliken<sup>104</sup>, Edward Mitchard<sup>124</sup>, Paulo S. Morandi<sup>14</sup>, Hannah L. Mossman<sup>2</sup>, Laszlo Nagy<sup>125</sup>, Henrique 486 Nascimento<sup>6</sup>, David Neill<sup>126</sup>, Reuben Nilus<sup>127</sup>, Percy Núñez Vargas<sup>95</sup>, Walter Palacios<sup>128</sup>, Nadir Pallqui 487 Camacho<sup>1,95</sup>, Julie Peacock<sup>1</sup>, Colin Pendry<sup>129</sup>, Maria Cristina Peñuela Mora<sup>130</sup>, Georgia C. Pickavance<sup>1</sup>, John 488 Pipoly<sup>131</sup>, Nigel Pitman<sup>132</sup>, Maureen Playfair<sup>133</sup>, Lourens Poorter<sup>134</sup>, John R. Poulsen<sup>25</sup>, Axel D. Poulsen<sup>135</sup>, 489 Richard Preziosi<sup>2</sup>, Adriana Prieto<sup>136</sup>, Richard Primack<sup>137</sup>, Hirma Ramírez-Angulo<sup>138</sup>, Jan Reitsma<sup>139</sup>, 490 Maxime Réjou-Méchain<sup>75</sup>, Zorayda Restrepo Correa<sup>140</sup>, Thaiane Rodrigues de Sousa<sup>6</sup>, Lily Rodriguez 491 Bayona<sup>141</sup>, Anand Roopsind<sup>142</sup>, Agustín Rudas<sup>136</sup>, Ervan Rutishauser<sup>42,143</sup>, Kamariah Abu Salim<sup>121</sup>, Rafael 492 P. Salomão<sup>144,145</sup>, Juliana Schietti<sup>6</sup>, Douglas Sheil<sup>146</sup>, Richarlly C. Silva<sup>57,147</sup>, Javier Silva Espejo<sup>148</sup>, Camila 493 Silva Valeria<sup>38</sup>, Marcos Silveira<sup>57</sup>, Murielle Simo-Droissart<sup>17</sup>, Marcelo Fragomeni Simon<sup>70</sup>, James Singh<sup>149</sup>, 494 Yahn Carlos Soto Shareva<sup>15</sup>, Clement Stahl<sup>54</sup>, Juliana Stropp<sup>150</sup>, Rahayu Sukri<sup>121</sup>, Terry Sunderland<sup>151,152</sup>, 495 Martin Svátek<sup>153</sup>, Michael D. Swaine<sup>154</sup>, Varun Swamy<sup>155</sup>, Hermann Taedoumg<sup>17</sup>, Joey Talbot<sup>1</sup>, James 496 Taplin<sup>156</sup>, David Taylor<sup>157</sup>, Hans ter Steege<sup>158,159</sup>, John Terborgh<sup>25</sup>, Raquel Thomas<sup>142</sup>, Sean C. Thomas<sup>160</sup>, 497 Armando Torres-Lezama<sup>161</sup>, Peter Umunay<sup>162,163</sup>, Luis Valenzuela Gamarra<sup>15</sup>, Geertje van der Heijden<sup>164</sup>, 498 Peter van der Hout<sup>165</sup>, Peter van der Meer<sup>166</sup>, Mark van Nieuwstadt<sup>167</sup>, Hans Verbeeck<sup>99</sup>, Ronald 499 Vernimmen<sup>168</sup>, Alberto Vicentini<sup>6</sup>, Ima Célia Guimarães Vieira<sup>145</sup>, Emilio Vilanova Torre<sup>169</sup>, Jason 500 Vleminckx<sup>36</sup>, Vincent Vos<sup>171</sup>, Ophelia Wang<sup>172</sup>, Lee J. T. White<sup>123,173,174</sup>, Simon Willcock<sup>175</sup>, John T. 501 Woods<sup>176</sup>, Verginia Wortel<sup>177</sup>, Kenneth Young<sup>178</sup>, Roderick Zagt<sup>179</sup>, Lise Zemagho<sup>17</sup>, Pieter A. Zuidema<sup>50</sup>, 502 Joeri A. Zwerts<sup>177,180</sup>, Oliver L. Phillips<sup>1</sup>

- 503
- 504

## **This file includes:**

- Materials and Methods
- Figures S1 S15
- 508 Tables  $S1 S3$

## **Materials and Methods**

### Forest census data

 Our plots come from the RAINFOR, AfriTRON, and T-FORCES networks. Forest inventory plots were located in lowland (<1200 m), old-growth, closed-canopy forests that were not known to have been subject to anthropogenic disturbance through fire or selective logging. Plots characterised floristically as dry forest were not included, as were plots that received less than 1200 mm precipitation each year. We also did not include plots in white sand, swamp and seasonally flooded forests, as we expect these to experience marked edaphic constraints (extreme nutrient limitation for white sand forests (*34*), stress caused by hypoxic conditions for swamp and seasonally flooded forests 519 (*35*)). All plots were  $\geq$  0.2 ha (median size = 1 ha) and were monitored for at least two years (median monitoring period = 9.7 years). All censuses were prior to the 2015-16 very strong El Niño event, as we expected that event to supress carbon gains relative to the long-term mean. Forest inventory plots were sampled using standardised protocols (*36*), where all live stems with

523 diameter  $\geq 100$  mm were measured at 1.3 m or 50 cm above buttresses and deformities. Trees were tagged so that the same tree could be identified in subsequent censuses. In some cases the point of diameter measurement (POM) had to be moved due to upward growth of buttresses and deformities. For these trees we use the Dmean approach from Talbot et al. (*37*).

In a few cases (6 plots) the minimum diameter measured changed over time, or palms and

*Phenakospermum* were excluded in some censuses. For these, we estimated aboveground biomass

(AGB, subsequently converted to carbon stocks) and aboveground woody production (AGWP,

subsequently converted to carbon gains) using a minimum diameter or taxonomic protocol that could

be consistently applied across censuses, and scaled these values by the aboveground biomass ratio

532 between that protocol and all stems  $\geq 100$  mm protocol for censuses when all stems were measured.

Some plots had nested designs where the plot was split into subplots with different minimum diameter

protocols (69 plots). For these, we only analysed the area conforming to our minimum diameter

535 protocol. For analysis, we grouped small  $(\leq 0.5 \text{ ha})$  plots within 1 km of each other, and also grouped



 available from every plot, so to ensure consistent treatment of plots height-diameter models were constructed for each biogeographic region. We fitted three parameter asymptotic models (*47*) of the form

564 
$$
H = a(1-\exp(-bD^C)),
$$
 [3]

 where *a*, *b* and *c* are estimated parameters ('Weibull' models, *48*). We fitted these models either treating each observation equally or with case weights proportional to each trees' basal area. These weights give more importance to large trees during model fitting. We selected the best fitting of these models, determining this as the model that minimised prediction error of stand biomass when calculated with estimated heights or observed heights (*46*). Weibull models were implemented using 570 the nls function in R with default settings. Starting values of  $a = 25$ ,  $b = 0.05$  and  $c = 0.7$  were chosen following trial and error as they led to regular model convergence. Where models did not converge this was usually because the height-diameter relationship did not reach an asymptote, so in these cases 573 we used the log-log model  $ln(H) = a + b(ln(D))$  to estimate height, where *b* gives the scaling exponent of a power law relationship between height and diameter. We checked if models gave unrealistic predictions by applying models to predict the height of all trees in the biogeographic region, and excluded models that predicted any tree height 10 % higher than the tallest tree we recorded in that continent.

## Estimating above-ground woody production

 We estimated AGWP following Talbot et al. (*37*). AGWP is comprised of four components, (1) the sum of growth of surviving trees, (2) the sum of AGB of new recruits, (3) the sum of unobserved growth of trees that died during a census interval and (4) the sum of growth of unobserved recruits that entered then died during a census interval. Accounting for the latter two components is necessary to avoid census-interval length effects, as more AGWP in these components will be missed due to the greater mortality of trees that accumulates over longer census intervals.

 Components 3 and 4 can be estimated using two quantities that can be calculated from observed stem- dynamics in each plot; per-area annual recruitment (*Ra*) and per-capita annual mortality (*ma*). Per- capita mortality is calculated from the ratio of surviving stems to initial stems, using equation 5 in Kohyama et al. (*49*). Per-area annual recruitment is calculated using estimated mortality rates and the observed change in the number of stems over a census interval, using equation 11 of Kohyama et al. (*49*).

 To estimate the unobserved growth of stems that died during a census interval, we first use plot-level per-capita mortality rates (*ma*) to estimate how many trees are expected to have died in each year of the census interval, and from that calculate the mean number of years that trees that died during the 595 census interval would have lived before death. The diameter of tree at death ( $D_{\text{death}}$ ) can then be estimated as

$$
597 \qquad D_{\text{death}} = D_{\text{start}} \times G \times Y_{\text{mean}} \tag{4}
$$

598 where  $D_{\text{start}}$  is the diameter at the start of the census interval, *G* is the plot-level median growth rate of the size class the tree was in at the start of the census interval (size classes are defined as *D* < 200 mm,  $400 \text{ mm} > D \ge 200 \text{ mm}$ , and  $D \ge 400 \text{ mm}$ ) and  $Y_{mean}$  is the mean number of years trees survived in the census interval before dying. The diameter at death is then converted to AGB at death using allometric equations (equation 1, except for ferns and monocots where equation 2 is used), and the unobserved growth is calculated as the difference between AGB at death and AGB at the start of the census.

To estimate the growth of recruits that were not observed because they died during the census

 interval, we first need to estimate the number of unobserved recruits. This can be estimated from per-607 area annual recruitment  $(R_a)$  and per-capita annual mortality  $(m_a)$ :  $R_a$  gives the number of stems per ha that recruit in a given year, and the probability of each recruit surviving until the next census (*Psurv*) is  $P_{\textit{surv}} = (1-m_a)^T$ , where *T* is the number of years remaining in the census interval. The number of 610 recruits in a given year that survive to the next census is  $R_a - P_{surv}R_a$ . Summing this for each year in a census interval gives the total number of unobserved recruits in that census interval. We then need to

 estimate how long each recruit was alive for. From *m<sup>a</sup>* we can calculate the number of recruits in a given year that died in each subsequent year, and from this calculate the mean life-span of recruits in a given year that died before the next census. The average life-span of unobserved recruits (*Ymean-rec*) is the weighted mean of each cohort's lifespan, weighted by the number of unobserved recruits in each year. Diameter at death is given in mm by

$$
617 \qquad D_{\text{death}} = 100 + (G \times Y_{\text{mean-rec}}) \tag{5}
$$

618 where *G* is the plot-level median growth rate of the smallest size class (i.e.  $D < 200$  mm).

Aboveground biomass of recruits at the time of death is estimated using equation 1. These corrections

for unobserved growth have a marginal impact on AGWP calculations, collectively accounting on

average for just 2.3 % of estimated plot-level AGWP.

 AGB was calculated for each census, and AGWP was calculated for each census interval, and the time-weighted mean of each was taken to give one value per plot. We used a time-weighted mean to give greater importance to AGB estimates separated by longer census-intervals, as these will be more independent. Estimates of AGB and AGWP were converted to carbon stocks and carbon gains by multiplying by 0.456 (*50*). Carbon residence time was then estimated as carbon stocks /carbon gains, and represents the length of time carbon resides in living biomass before being passed to the litter and necromass pools (*51*). Calculations to estimate AGB and AGWP were performed using the R package BiomasaFP (*52*).

## Obtaining environmental data

 Most climate data were obtained from climate data from Worldclim2 (*31*) as it provides the highest resolution (~ 1 km) pantropical climate data, although we note that some regions, such as central Africa, have limited station data. We extracted monthly data for the following variables: mean daily minimum temperature, mean daily maximum temperature, precipitation, solar radiation and wind speed, In addition to calculating the standard series of 19 bioclimatic variables, using the dismo R package (*53*), we calculated 1) mean daily maximum temperature, BIO1 + BIO2/2, 2) mean daily

 minimum temperature, BIO1 – BIO2/2, 3) maximum cumulative water deficit as the minimum across the year of monthly cumulative water deficit *W,*

$$
640 \t Wi = Wi-1 - min(0, Pi - 100), \t [6]
$$

 where *P* is monthly precipitation in mm, and 100 represents measured evapotranspiration. This calculation was run for a year from the wettest month in the year, starting at a water deficit of zero, 4) the number of months where monthly cumulative water deficit was negative, 5) the number of months where monthly precipitation was below 100 mm (i.e. less than evapotranspiration), 6) mean annual solar radiation, 7) mean annual wind speed, and 8) vapour pressure deficit (VPD = SVP – vapour 646 pressure, where saturated vapour pressure,  $SVP = 0.611 \times e^{(17.502 \text{ temperature})/(temperature + 240.97)})$ . We also obtained data on cloud frequency at ~1 km resolution from Wilson & Jetz (*54*), who processed twice- daily MODIS satellite images. Temperature values were adjusted for differences in altitude between the plot and the 1 km grid cell used for Worldclim interpolation, as these can differ in topographically 650 diverse regions, using lapse rates, so that  $T_{plot} = T_{worldclim} + 0.005 \times (A_{worldclim} - A_{plot})$ , where *T* is temperature (°C) and *A* is altitude (m). Temperature values were also corrected for systematic warming trends. To do this, the mean annual temperature in each grid-cell in each year was extracted from the CRU TS 3.24 dataset (*55*), and robust linear regression used to estimate grid-cell specific warming rates. These were used to adjust Worldclim2 temperature values for the difference between the midpoint of plot monitoring and the midpoint of the Worldclim2 climatology.

Data on soil texture and chemistry was obtained at 1 km resolution from the SoilGrids dataset (*56*),

with this resolution selected to match the resolution of the climate data. From this we extracted CEC,

representing soil fertility, and percentage clay, representing soil texture. For each soil variable we

659 calculated the depth-weighted average for  $0 - 30$  cm.

Statistical analysis

 We used linear models to relate carbon, carbon gains and carbon residence time to environmental explanatory variables. The role of different explanatory variables was assessed using multi-model inference.

 Response variables were positively skewed and had positive mean-variance relationships, so were log-transformed to meet the assumption of normality and reduce heterogeneity in variances. The log- normal nature of forest carbon stocks and dynamics means that there is greater potential for variation when forests are large, which could be due to the non-linear scaling of tree biomass and tree basal area.

 We selected explanatory variables to represent hypothesised ways in which climate could affect carbon stocks (Table S1). We assessed colinearity within this set of explanatory variables using variance inflation factors (VIF) and pairwise correlations. Because of colinearity, we had to exclude VPD, total precipitation, use only one of MCWD and precipitation in the driest quarter, and could include both minimum and maximum temperature but not mean annual temperature. We used precipitation in the driest quarter rather than MCWD as the latter is zero truncated and so is less amenable to regression analysis. After removing these variables all pairwise correlations (including 676 with soil explanatory variables) were weak enough not to cause problems through collinearity ( $r < 0.6$ ) 677 and  $VIF < 3$ ).

 To account for variation other than in climate we also included soil variables relating to texture (% clay) and fertility (CEC), and included continent specific intercepts to account for biogeographic variation in carbon. To account for unmeasured environmental gradients (e.g. soil variation not captured by the SoilGrids variables), we used Moran's eigenvector maps as explanatory variables, selecting eigenvectors the corresponded to positive spatial autocorrelation in the distance matrix (*57*). These variables act as a proxy for unmeasured spatial gradients by capturing positive spatial associations between plots.

 Plots differed in their area and the length of time they were monitored for. This is likely to affect the variance of carbon stocks, carbon gains and carbon residence time, as smaller plots or plots only monitored for short periods are more likely to be sensitive to the mortality of a few large trees. To account for this, we used case weights relating to plot area and monitoring period. Following Lewis et al. (*58*), we selected weights by relating residuals from our linear models to plot area and to plot monitoring period, and subsequently assessing which root transformation of plot area/ monitoring

 period removed the pattern in the residuals when used as a weight. Selected weights were: carbon 692 stocks, Area <sup>1/3</sup>; carbon gains, Monitoring length <sup>1/7</sup>; carbon residence time, Area <sup>1/9</sup> + Monitoring 693  $length$   $^{1/12}$  -1.

 We fitted all subsets of the general linear model with explanatory variables described above, forcing 695 spatial eigenvectors into all models. We then averaged the subset of models where  $\Delta$  AIC < 4, using full averaging so variables that do not appear in the model get the value of zero for their coefficients. This means that model averaged coefficients of terms with limited support exhibit shrinkage towards zero. Multi-model inference was performed using the MuMIn R package (*59*).

 We assessed whether the two climate variables found to have important additive effects on carbon stocks in this analysis (mean daily maximum temperature in the warmest month and precipitation in the driest quarter) interacted with each other by adding an interaction term between these variables to the full generalised linear model of carbon stocks as a function of other climate and soil variables, continent and spatial eigenvectors. We compared these two models using AIC. We repeated this with carbon gains and carbon residence time as response variables.

 To assess whether the temperature carbon relationship was non-linear we used breakpoint regression implemented in the segmented R package (*60*). This estimates a breakpoint in the explanatory variable at which the slope of the relationship with the response variable changes. We estimated the breakpoint for the mean daily maximum temperature in the warmest month variable in the full model with a temperature-precipitation interaction described above. We assessed the support for the breakpoint by comparing the AIC of the model with a breakpoint with the AIC of a model with a linear relationship. We repeated this with carbon gains and carbon residence time as response variables.

 We also analysed spatial variation in carbon stocks as a function of the above climate and soil variables and spatial eigenvectors using Random Forest decision tree algorithms (*22*) implemented using the randomForest R package (*61*). We assessed variable importance by calculating the average increase in node purity across all decision trees (measured by residual sum of squares) when using the variable to split the data. We assessed modelled relationships between response and explanatory



## 740 Scaling results to the biome

 We applied the relationship between carbon stocks and mean daily maximum temperature in the warmest month identified by the breakpoint regression to estimate the total change in carbon stock due to temperature effects alone for different scenarios of temperature increase. We delimited the biome extent using the WWF tropical and subtropical moist broadleaved forest biome (*62*), restricted 745 to tropical latitudes, and further refined it by excluding grid-cells with  $<$  50 Mg C ha<sup>-1</sup> using data from (*30*), as these are unlikely to be forest. Calculations were conducted at 10-minute resolution. For each grid-cell we predicted the percentage change in carbon for a given temperature increase from our statistical model, holding all other variables constant. We then used a reference carbon stock map (*30*) to convert percentage change to change in carbon stocks per hectare (in Mg ha<sup>-1</sup>). To calculate change in carbon stocks for the whole grid-cell, we multiplied change per hectare by the area of the grid-cell in hectares, and then adjusted this by the proportion of the grid-cell that was forested by multiplying by 2014 forest cover (*63*). Total change for the biome (in Pg) was calculated by summing these grid- cell level values. Uncertainty due to our statistical model was assessed by generating multiple predictions by resampling model parameters (breakpoint threshold, slope below breakpoint, slope above breakpoint), and extracting quantiles from the resultant distribution of predicted change values. Aboveground biomass carbon values were scaled to include root biomass based on a root to shoot ratio of 0.19 in tropical evergreen forests (*64*).

 The Avitabile et al (*30*) aboveground biomass map was chosen to provide reference carbon stocks. While other maps have previously been produced by Saatchi et al. (*65*) and Baccini et al. (*66*) we selected the Avitabile map because it synthesises the earlier maps (see Mitchard et al. (*67*) for discussion of substantial differences between these maps) and is anchored by more field data. Importantly, the Avitabile map reproduces spatial patterns in aboveground biomass that have been described from field data but are absent in the Saatchi or Baccini maps, including the much higher biomass density of north-east Amazonian forests due to tall trees and very high wood density (*68*). Nevertheless, we also investigated the consequences of using the Saatchi or Baccini maps for our estimates of biomewide thermal sensitivity and spatial patterns of change in carbon stocks (Fig S15).

767 We investigated three temperature change scenarios. Firstly, we applied a 1<sup>o</sup>C increase to all locations. Secondly, we assessed the consequence of a 1.5°C increase in global temperature from pre- industrial levels for the equilibrium temperature response of tropical forest carbon. Finally, we assessed the consequence of a 2°C increase in global temperature from pre-industrial levels. For the latter two we obtained data from CMIP5 climate models, using downscaled future climate projections based on the Worldclim climatology (*69*). As downscaling was performed using Worldclim version 1.4 (*70*) and our statistical models use Worldclim version 2, we calculated the warming anomaly in each grid-cell from the current Worldclim version 1.4 conditions, and applied this to the Worldclim 2 data to obtain future temperature. RCP scenarios and time-points were chosen to give global temperature increases that best match 1.5°C and 2°C above pre-industrial. For 1.5°C we used RCP 2.6 averaged for 2040-2060 (median temperature increase across models = 1.5°C, (*71*)). For 2°C, we used RCP 2.6 averaged for 2040-2060 (median temperature increase models = 1.9°C (*71*)). Note that predicted increases in maximum temperatures were often considerably greater than the global increase, especially in South America. For both scenarios we used the median predicted temperature change for each grid-cell from an ensemble of 15 models (BCC-CSM1-1, CCSM4, CNRM-CM5, GFDL-CM3, GFDL-ESM2G, GISS-E2-R, HadGEM2-AO, HadGEM-ES, IPSL-CM5A-LR, MIROC- ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3, NorESM1-M). We assessed the potential for long-term carbon dioxide growth stimulation to offset these long-term 785 temperature effects. We used  $CO<sub>2</sub>$  concentrations from the RCP scenarios and time-points described above, which approximate the long-term concentrations if the climate stabilised at the new 787 temperatures (72). Thus the 1.5°C and  $2^{\circ}$ C scenarios were associated with  $CO_2$  concentrations of 443 788 ppm and 487 ppm respectively  $(73)$ . We cannot assess the effect of  $CO<sub>2</sub>$  on biomass from our spatial 789 dataset, so instead used independent estimates of  $CO<sub>2</sub>$  effects from other sources. Firstly, we obtained CO<sup>2</sup> only effects on net primary production (NPP) extracted from an ensemble of CMIP5 earth system models by (*74*). This gives the proportional change in NPP for evergreen forests (note that this also 792 includes boreal forests) over 1980-2010, standardised to a 100 ppm increase in  $CO<sub>2</sub>$  concentration. To 793 propagate this through to changes in AGB under future  $CO<sub>2</sub>$  conditions we first estimated the

794 logarithmic dependency of NPP on  $CO_2$  (75) by substituting values of NPP and  $CO_2$  at time zero and *t* 795 (from (*74*)) into the equation,

$$
796 \quad NPP_t = NPP_0 \left[ 1 + \beta \ln \left( \frac{|co_2|_t}{[co_2]_0} \right) \right]
$$

797 This equation can be used to compute NPP annually given an initial NPP estimate and a time series of 798 atmospheric  $CO<sub>2</sub>$  concentrations (from a combination of the observed record from pre-industrial and 799 the RCP 4.5 scenario, modified so that it stabilises at 487 or 443 ppm depending on warming 800 scenario). Initial pre-industrial NPP was back-calculated from present-day values using Equation 7, 801 with 13.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (mean of nine Amazon plots where NPP has been measured, from (76)) used 802 for present-day NPP. To propagate NPP into change in woody biomass (following (*51*)) we used the 803 equation

$$
804 \quad \frac{dM_{\text{wood}}}{dt} = \alpha_{\text{wood}} N_{\text{P}} - \frac{M_{\text{wood}}}{\tau_{\text{wood}}}
$$

805 where  $M_{wood}$  is woody biomass,  $N_p$  is NPP,  $\alpha_{wood}$  is the allocation of NPP to wood (taken as 0.33, the 806 mean value across nine plots from  $(76)$ ) and  $\tau_{wood}$  is the residence time of woody biomass, taken as 807 59.1 years (the median value across plots used in this study). This model (equations 7 and 8) was run 808 from pre-industrial to 2500, enabling us to see the equilibrium effect of increased  $CO<sub>2</sub>$  concentrations 809 on biomass, assuming temporally invariant allocation and residence time. We calculated the 810 proportional change in biomass from 2000 to 2500, and applied this to the reference carbon stock map 811 to obtain predicted equilibrium change in above ground biomass due to  $CO<sub>2</sub>$  effects.

812 The effects of  $CO<sub>2</sub>$  in earth system models have been reported to be larger than those deduced from 813 satellite data or  $CO_2$  enrichment experiments ( $74$ ), so we also ran the above model using changes in 814 NPP reported from a synthesis of free-air CO<sub>2</sub> enrichment experiments conducted in forests (74). 815 Finally, we looked at the impact of using  $CO<sub>2</sub>$  effects derived from a recent large meta-analysis of 816 CO2 enrichment experiments (*77*), which reported a 12.5 % increase in biomass of tropical trees for a 817 250 ppm increase in CO<sub>2</sub> concentration. As this relationship was reported to be linear (77) we used 818 linear interpolation to estimate the change in biomass under  $CO<sub>2</sub>$  concentrations associated with each

- warming scenario (i.e. 443 and 487 ppm). To estimate long-term changes in biomass accounting for
- 820 both temperature and carbon dioxide, we first applied the  $CO<sub>2</sub>$  relationship to estimate the change in
- biomass due to carbon dioxide growth stimulation, and then assessed the effects of warmer
- 822 temperatures from this revised baseline. Our approach allows a simple assessment of  $CO<sub>2</sub>$  effects
- exploring a range of different effect strengths. Real-world responses will likely be more complex,
- with, for example, nutrient limitation potentially affecting the extent to which growth is stimulated by

CO<sup>2</sup> (*77*).

- 
- 
- 



**Figure S1.** Climate space represented by our plot network. Red lines show the probability density function of each variable in our multi-census plot network. Black lines show the probability density across 10 minute grid-cells in the biome, restricted to areas with forest cover in GLC 2000 (*78*).





 **Figure S2.** Ability of our plot network to represent the climate conditions found in the moist tropical forest biome. (a) Minimum climate dissimilarity (measured as Euclidean distance on climate variables scaled by their standard deviation) between 10 minute grid cells and the multi-census plot network. Climate variables used are the same as in Fig. 2. Green lines indicate the extent of the biome. (b) Geographic distance (km) between grid cells and the multi-census plot network. (c) Relationship between climatic and geographic distance of 10 minute grid cells across the tropical forest biome to our plot network. The lack of relationship between climate dissimilarity and geographical distance, alongside the mostly low climatic dissimilarities, shows that our sampling is sufficient to capture the environmental space of the biome and that we can reasonably extrapolate to geographically distant areas from our plots, which are in any case largely deforested already and hence contribute very little to our projected biome-wide carbon response to climate change. (These tropical moist forest areas that are poorly sampled and largely lost include the Atlantic Forests in Brazil, Andean Forests in western

- South America, eastern Caribbean, Madagascar, and much of tropical South Asia, south China,
- continental Southeast Asia, Philippines, Sumatra and Java).





 **Figure S3.** Relationships between individual climate variables and tropical forest aboveground carbon stocks. Standardised coefficients are from models with the climate variable and continent as explanatory variables and show change in ln(carbon) for a standard deviation change in the explanatory variable. Error bars show standard errors. Variables used in the main analysis have black 856 outlines. Full variable names are: T\_maximum – mean daily maximum temperature, Bio5 – mean daily maximum temperature in the warmest month, Bio7 – annual temperature range, Bio2 – mean diurnal temperature range, Bio8 – mean temperature in the wettest quarter, VPD – vapour pressure 859 deficit, Bio1 – mean annual temperature, Bio10 – mean temperature in the warmest quarter, Bio11 – 860 mean temperature in the coldest quarter, N dry months – number of months with negative 861 cumulative water deficit, N dry months – number of months where precipitation is less than evapotranspiration, Bio4 – temperature seasonality, Bio18 – precipitation in the warmest quarter, Bio9 – mean temperature in the driest quarter, T\_minimum warmest month – mean daily minimum 864 temperature in the warmest month,  $\text{Biol5}$  – precipitation seasonality, T\_minimum – mean daily minimum temperature, Bio16 – precipitation in the wettest quarter, Bio13 – precipitation in the wettest month, Bio3 – isothermality, Bio12 – annual precipitation, Bio19 – precipitation in the coldest quarter, Bio6 – mean daily minimum temperature in the coldest month, Wind speed – mean daily

- wind speed, Bio17 precipitation in the driest quarter, Bio14 precipitation in the driest month,
- Cloud cover proportion of MODIS passes with cloud present, MCWD maximum cumulative
- water deficit (note this is negative when water deficit is high, so a positive relationship with MCWD
- indicates higher carbon when water deficits are less).











 **Figure S5.** As Figure 2, but with aboveground biomass estimated using the Chave et al. 2005 (*79*) moist forest allometric equation, which does not include a height term and is instead based on a third-890 order polynomial relationship between diameter and aboveground biomass. This indicates that our results are robust to using an alternative allometry to estimate aboveground biomass.





**Figure S6.** Interaction between mean daily maximum temperature in the warmest month and

precipitation in the driest quarter in determining aboveground tropical forest carbon stocks. Modelled

relationships with temperature are shown holding precipitation either one standard deviation above or

below the mean. Note that the temperature-carbon relationship is steeper when precipitation is low.



 **Figure S7.** Partial relationships between tropical forest carbon stocks and the two climate variables identified to be most important by the random forest decision tree algorithm. Partial plots show predicted values of carbon stocks averaged across an ensemble of decision tree models when changing the explanatory variable of interest and holding other variables constant. The importance of variables in random forest analysis is assessed by calculating the average increase in node purity across all decision trees (measured by residual sum of squares) when using the variable to split the data. Higher values indicate greater importance. Maximum temperature increased node purity by 4.8 910 and precipitation by 4.7. For all other climate variables increases in node purity were  $<$  3.5.





 **Figure S8.** Relationships between aboveground tropical forest carbon stocks and environmental predictors. Symbols and colours as in Fig. 3. Coloured lines show bivariate relationships in each

- continent, and black lines show pan-tropical relationships also accounting for the effect of continent.
- Lines are only plotted where statistically significant.









**Figure S10.** As Fig. S8, but showing relationships with carbon residence time.



 **Figure S11.** Variation in tropical forest aboveground carbon stocks, gains and residence time within and amongst continents. Data are presented as empirical probability density functions (top row) and dot-plots showing raw data points for all our multi-census plots (bottom row). SA = South America, 928 AF = Africa,  $AS = Asia$ ,  $AU = Australia$ .



 **Figure S12.** Biome-wide change in mean daily maximum temperature in the warmest month from present conditions (based on the Worldclim climatology, 1970-2000), given global increases in 933 temperature of approximately 1.5°C and 2°C above pre-industrial levels. These levels of global temperature increase are obtained from, respectively, RCP 2.6, 2040-2060 and RCP 4.5, 2040-2060. 935 Global temperature increases of 1.5 and  $2^{\circ}$ C above pre-industrial levels (so ~0.8  $^{\circ}$ C and ~1.3  $^{\circ}$ C above our current baseline climate) would lead to mean increases in maximum temperature in the 937 warmest month across the tropical forest biome of 1.9°C and 2.4°C the current baseline climate respectively.





 **Figure S13** Areas of the biome above or below the 32.2°C threshold, above which carbon stocks decline more rapidly with temperature, under current conditions and two warming scenarios (see Fig. 945 4). Areas warmer than any currently observed in our dataset (35.2°C) are also shown (non-analogous 946 conditions). Note that even the 1.5°C warming scenario pushes most South American forests above 947 the 32.2°C threshold.

- 
- 
- 
- 





954 **Figure S14.** Effect of using earlier biomass reference maps for estimates of change in long-term 955 carbon stocks for global temperature increases of ~2°C. Using aboveground biomass stock maps from 956 Saatchi et al. (*65*) and Baccini et al. (*66*) predicted biome-wide reductions in biomass carbon stocks 957 are 24.0 Pg (95 % CI = 5.8 – 39.6) and 28.4 Pg (95 % CI = 16.1 – 37.5) respectively. Under the  $\sim$ 958 1.5°C warming scenario these are 18.4 Pg (5.8 – 30.5) and 21.1 Pg (10.2 – 29.4) respectively. Results 959 in the main text use the 2016 Avitabile et al. baseline map (*30*) – see methods for justification.





972 **Table S1.** Climate variables selected for analysis and mechanisms by which they can affect carbon stocks.



976  $^2$  Moisture availability could also be represented by MCWD (maximum cumulative water deficit) or total precipitation, but only one of the three variables could be included in the model due to collinearity. MCWD was could be included in the model due to collinearity. MCWD was excluded as it is zero truncated, so less amenable to regression fitting.

978



980 autocorrelation. Coefficients are AIC weighted averages across models with ΔAIC < 4 from the best performing model; variables are given a score of zero if 981 they did not appear in a model. NA indicates that a term did not occur in any model in this set. MEM1-8 are spatial eigenvectors.



- 983 **Table S3.** Predicted biome-wide changes in long-term biomass carbon stocks (scaled to include root
- 984 biomass) under global temperature increases of  $\sim 1.5^{\circ}$ C and  $\sim 2^{\circ}$ C. Changes are based on temperature
- 985 effects alone, and when also accounting for the effect of increased  $CO<sub>2</sub>$  concentrations on tree growth.
- 986 CO<sub>2</sub> effects were obtained from a synthesis of results of elevated CO<sub>2</sub> experiments (Terrer et al. (77)),
- 987 free-air CO2 enrichment (FACE) experiments (Kolby Smith et al. (*74*)) and CMIP5 earth system
- 988 models (Kolby Smith et al. (*74*)). 95% confidence intervals around changes (based on uncertainties in

989 temperature effects alone) are shown in parentheses.

| $CO2$ effect                                | Change in biomass carbon stocks (Pg) |                          |  |
|---|--------------------------------------|--------------------------|--|
|   | $\sim 1.5$ °C warming                | $\sim$ 2°C warming       |  |
|   | $(443$ ppm $CO2)$                    | $(487$ ppm $CO2)$        |  |
| None  | $-26.9(-38.4 - 15.8)$                | $-35.3$ $(-49.0 - 20.9)$ |  |
| Terrer et al. elevated $CO2$<br>experiments | $-22.0$ $(-33.0 - 9.9)$              | $-26.3$ $(-37.6 - 11.5)$ |  |
| Kolby Smith et al. FACE<br>experiments      | $-6.2$ ( $-16.8 - 7.7$ )             | $-9.9(-24.3 - 3.9)$      |  |
| Kolby Smith et al. CMIP5<br>models          | $3.9(-8.3-12.6)$                     | $2.0$ (-11.9 – 19.8)     |  |