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Sullivan, MJP

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## 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>, Jérôme 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 Brillhante 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 Hédli<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<sup>101</sup>, Timothy Killeen<sup>102</sup>, Kanehiro Kitayama<sup>103</sup>, Bente Klitgaard<sup>104</sup>, Alexander Koch<sup>105</sup>, Nicolas Labrière<sup>58</sup>, William Laurance<sup>106</sup>, Susan Laurance<sup>106</sup>, Miguel E. Leal<sup>107</sup>, Aurora Levesley<sup>1</sup>, Adriano J. N. Lima<sup>6</sup>, Janvier Lisingo<sup>11</sup>, Aline P. Lopes<sup>108,109</sup>, Gabriela Lopez-Gonzalez<sup>1</sup>, Tom Lovejoy<sup>110</sup>, Jon Lovett<sup>1</sup>, Richard Lowe<sup>111</sup>, William E. Magnusson<sup>112</sup>, Jagoba Malumbres-Olarte<sup>113,114</sup>, Ângelo Gilberto Manzatto<sup>115</sup>, Ben Hur Marimon Junior<sup>116</sup>, Andrew R. Marshall<sup>8,117,118</sup>, Toby Marthews<sup>119</sup>, Simone Matias de Almeida Reis<sup>14,19</sup>, Colin Maycock<sup>120</sup>, Karina Melgaço<sup>1</sup>, Casimiro Mendoza<sup>121</sup>, Faizah Metali<sup>122</sup>, Vianet Mihindou<sup>123,124</sup>, William Milliken<sup>104</sup>, Edward Mitchard<sup>125</sup>, Paulo S. Morandi<sup>14</sup>, Hannah L. Mossman<sup>2</sup>, Laszlo Nagy<sup>126</sup>, Henrique Nascimento<sup>6</sup>, David Neill<sup>127</sup>, Reuben Nilus<sup>128</sup>, Percy Núñez Vargas<sup>95</sup>, Walter Palacios<sup>129</sup>, Nadir Pallqui Camacho<sup>1,95</sup>, Julie Peacock<sup>1</sup>, Colin Pendry<sup>130</sup>, Maria Cristina Peñuela Mora<sup>131</sup>, Georgia C. Pickavance<sup>1</sup>, John Pipoly<sup>132</sup>, Nigel Pitman<sup>133</sup>, Maureen Playfair<sup>134</sup>, Lourens Poorter<sup>135</sup>, John R. Poulsen<sup>25</sup>, Axel D. Poulsen<sup>136</sup>, Richard Preziosi<sup>2</sup>, Adriana Prieto<sup>137</sup>, Richard Primack<sup>138</sup>, Hirma Ramírez-Angulo<sup>139</sup>, Jan Reitsma<sup>140</sup>, Maxime Réjou-Méchain<sup>75</sup>, Zorayda Restrepo Correa<sup>141</sup>, Thaianie Rodrigues de Sousa<sup>6</sup>, Lily Rodriguez Bayona<sup>142</sup>, Anand Roopsind<sup>143</sup>, Agustín Rudas<sup>137</sup>, Ervan Rutishauser<sup>42,144</sup>, Kamariah Abu Salim<sup>122</sup>, Rafael P. Salomão<sup>145,146</sup>, Juliana Schiatti<sup>6</sup>, Douglas Sheil<sup>147</sup>, Richarlly C. Silva<sup>57,148</sup>, Javier Silva Espejo<sup>149</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>150</sup>, Yahn Carlos Soto Shareva<sup>15</sup>, Clement Stahl<sup>54</sup>, Juliana Stropp<sup>151</sup>, Rahayu Sukri<sup>122</sup>, Terry Sunderland<sup>152,153</sup>, Martin Svátek<sup>154</sup>, Michael D. Swaine<sup>155</sup>, Varun Swamy<sup>156</sup>, Hermann Taedoum<sup>17</sup>, Joey Talbot<sup>1</sup>, James Taplin<sup>157</sup>, David Taylor<sup>158</sup>, Hans ter Steege<sup>159,160</sup>, John Terborgh<sup>25</sup>, Raquel Thomas<sup>143</sup>, Sean C. Thomas<sup>161</sup>, Armando Torres-Lezama<sup>162</sup>, Peter Umunay<sup>163,164</sup>, Luis Valenzuela Gamarra<sup>15</sup>, Geertje van der Heijden<sup>165</sup>, Peter van der Hout<sup>166</sup>, Peter van der Meer<sup>167</sup>, Mark van Nieuwstadt<sup>168</sup>, Hans Verbeeck<sup>99</sup>, Ronald Vernimmen<sup>169</sup>, Alberto Vicentini<sup>6</sup>, Ima Célia Guimarães Vieira<sup>146</sup>, Emilio Vilanova Torre<sup>170</sup>, Jason Vleminckx<sup>36</sup>, Vincent Vos<sup>172</sup>, Ophelia Wang<sup>173</sup>, Lee J. T. White<sup>124,174,175</sup>, Simon Willcock<sup>176</sup>, John T. Woods<sup>177</sup>, Verginia Wortel<sup>178</sup>, Kenneth Young<sup>179</sup>, Roderick Zagt<sup>180</sup>, Lise Zemagho<sup>17</sup>, Pieter A. Zuidema<sup>50</sup>, Joeri A. Zwarts<sup>178,181</sup>, Oliver L. Phillips<sup>1</sup>

Affiliations:

- 1 School of Geography, University of Leeds, Leeds, UK
- 2 Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK
- 3 Department of Geography, University College London, London, UK
- 4 Mensuration Unit, Forestry Commission of Ghana, Kumasi, Ghana
- 5 Embrapa Roraima, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil
- 6 Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil
- 7 Department of Ecosystem Science and Sustainability, Colorado State University, USA
- 8 Department of Environment and Geography, University of York, York, UK
- 9 DR Congo Programme, Wildlife Conservation Society, Kisangani, Democratic Republic of Congo
- 10 Centre de Formation et de Recherche en Conservation Forestiere (CEFRECOF), Epulu, Democratic Republic of Congo
- 11 Faculté de Gestion de Ressources Naturelles Renouvelables, Université de Kisangani, Kisangani, Democratic Republic of Congo
- 12 Service of Wood Biology, Royal Museum for Central Africa, Tervuren, Belgium
- 13 Department of Environment, Laboratory of Wood Technology (Woodlab), Ghent University, Ghent, Belgium
- 14 Faculdade de Ciências Agrárias, Biológicas e Sociais Aplicadas, Universidade do Estado de Mato Grosso, Nova Xavantina-MT, Brazil
- 15 Jardín Botánico de Missouri, Oxapampa, Peru
- 16 School of Life Sciences, University of Lincoln, Lincoln, UK
- 17 Plant Systematics and Ecology Laboratory, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon
- 18 Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
- 19 Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK
- 20 Graduate School of Science and Engineering, Kagoshima University, Japan
- 21 School of Anthropology and Conservation, University of Kent, Canterbury, UK
- 22 Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará, Santarém - PA, Brazil
- 23 Universidade do Estado de Mato Grosso, Cáceres - MT, Brazil
- 24 Escuela de Ciencias Agrícolas, Pecuarias y del Medio Ambiente, National Open University and Distance, Colombia
- 25 Center for Tropical Conservation, Nicholas School of the Environment, Duke University, Durham, NC, USA
- 26 Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
- 27 Universidade Estadual de Campinas, Campinas - SP, Brazil
- 28 National Institute for Space Research (INPE), São José dos Campos-SP, Brazil
- 29 Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia
- 30 Wageningen Environmental Research, Wageningen, The Netherlands
- 31 Dirección de la Carrera de Biología, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia
- 32 Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA
- 33 Programa de Ciencias del Agro y el Mar, Herbario Universitario, Barinas, Venezuela
- 34 Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Brazil

- 35 Centre of Ecology and Hydrology, Penicuik, UK
- 36 International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Florida, FL, USA
- 37 Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, São Paulo, SP, Brazil
- 38 Lancaster Environment Centre, Lancaster University, Lancaster, UK
- 39 Centro Multidisciplinar, Universidade Federal do Acre, Cruzeiro do Sul - AC, Brazil
- 40 Institute of Integrative Biology, ETH Zurich, Zurich, Switzerland
- 41 Priestley International Centre for Climate, University of Leeds, Leeds, UK
- 42 Smithsonian Tropical Research Institute, Panama, Panama
- 43 Cary Institute of Ecosystem Studies, Millbrook, NY, USA
- 44 School of Geography, School of Geography, Leeds, UK
- 45 The Landscapes and Livelihoods Group, Edinburgh, UK
- 46 UR Forest & Societies, CIRAD, Montpellier, France
- 47 Isotope Bioscience Laboratory-ISOFYS, Ghent University, Ghent, Belgium
- 48 Gembloux Agro-Bio Tech, University of Liège, Liège, Belgium
- 49 UMR Silva, INRA, Nancy, France
- 50 Department of Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands
- 51 CSIRO, Canberra, Australia
- 52 Congo Programme, Wildlife Conservation Society, Brazzaville, Republic of Congo
- 53 Woods Hole Research Center, Falmouth, MA, USA
- 54 Ecologie des Forêts de Guyane (ECOFOG), INRA, Kourou, French Guiana
- 55 Programa de Pós-Graduação Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre, Rio Branco - AC, Brazil
- 56 Herbario Alfredo Paredes, Universidad Central del Ecuador, Quito, Ecuador
- 57 Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco - AC, Brazil
- 58 Laboratoire Évolution et Diversité Biologique - UMR 5174 (CNRS/IRD/UPS), CNRS, Toulouse, France
- 59 Rougier-Gabon, Libreville, Gabon
- 60 Nicholas School of the Environment, Duke University, Durham, NC, USA
- 61 Grantham Research Institute on Climate Change and the Environment, London, UK
- 62 Inventory & Monitoring Program, National Park Service, Fredericksburg, VA, USA
- 63 Smithsonian Institution, Washington, DC, USA
- 64 Proyecto Castaña, Madre de Dios, Peru
- 65 Universidad Nacional de San Agustín de Arequipa, Arequipa, Peru
- 66 Instituto de Geociências, Faculdade de Meteorologia, Universidade Federal do Pará, Belém - PA, Brazil
- 67 Faculty of Science, Department of Ecology and Environmental Sciences, Palacký University Olomouc, Olomouc, Czech Republic
- 68 Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Panama, Panama
- 69 Facultad de Ciencias Biológicas, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru
- 70 Embrapa Genetic Resources & Biotechnology, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil
- 71 Instituto de Investigaciones de la Amazonía Peruana, Iquitos, Peru
- 72 Ecologie des Forêts de Guyane (ECOFOG), CIRAD, Kourou, French Guiana

- 73 Department of Anthropology, The University of Texas at Austin, Austin, TX, USA  
74 Forest Resources Management, Gembloux Agro-Bio Tech, University of Liège, Liège, Belgium  
75 AMAP Lab, IRD, CIRAD, CNRS, INRA, Univ Montpellier, Montpellier, France  
76 Socioecosistemas y Cambio Climatico, Fundacion con Vida, Medellín, Colombia  
77 School of Forestry, Beijing Forestry University, Beijing, China  
78 Institute of Biological Sciences, Universidade Federal do Pará, Belém - PA, Brazil  
79 National Museum of Natural History, Smithsonian Institute, Washington, DC, USA  
80 School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK  
81 School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK  
82 Embrapa Amazônia Oriental, Brazilian Agricultural Research Corporation (EMBRAPA), Brasília, Brazil  
83 Universidad Nacional Jorge Basadre de Grohmann (UNJBG), Tacna, Peru  
84 Forestry Research Institute of Ghana (FORIG), Kumasi, Ghana  
85 Smithsonian Institution Forest Global Earth Observatory (ForestGEO), Smithsonian Tropical Research Institute, Washington, DC, USA  
86 School of Biology, University of Leeds, Leeds, UK  
87 128 Busbridge Lane, Godalming, Surrey, UK  
88 Royal Botanic Garden Edinburgh, Edinburgh, UK  
89 Lukuru Wildlife Research Foundation, Kinshasa, Democratic Republic of Congo  
90 Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT, USA  
91 Institute of Botany, Czech Academy of Sciences, Brno, Czech Republic  
92 Department of Botany, Palacký University in Olomouc, Olomouc, Czech Republic  
93 Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela  
94 Département Hommes, natures, sociétés, Muséum National d'Histoire Naturel, Paris, France  
95 Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru  
96 Biological and Environmental Sciences, University of Stirling, Stirling, UK  
97 Instituto IMANI, Universidad Nacional de Colombia, Leticia, Colombia  
98 Faculty of Science, Department of Botany and Plant Physiology, University of Buea, Buea, Cameroon  
99 Department of Environment, Computational & Applied Vegetation Ecology (Cavelab), Ghent University, Ghent, Belgium  
100 PELD, Universidade do Estado de Mato Grosso, Nova Xavantina-MT, Brazil  
101 Tropical Peat Research Institute, Malaysian Palm Oil Board, Kuala Lumpur, Malaysia  
102 Agteca, Santa Cruz, Bolivia  
103 Graduate School of Agriculture, Kyoto University, Japan  
104 Royal Botanic Gardens Kew, Richmond, London, UK  
105 Department of Earth Sciences, University of Hong Kong, HKSAR  
106 Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Sciences, James Cook University, Australia  
107 Uganda Programme, Wildlife Conservation Society, Kampala, Uganda  
108 Remote Sensing Division, National Institute for Space Research (INPE), São José dos Campos-SP, Brazil  
109 Department of Ecology, University of Brasília, Brasília, Brazil  
110 Environmental Science and Policy, George Mason University, Fairfax, VA, USA

- 111 Botany Department, University of Ibadan, Ibadan, Nigeria
- 112 Coordenação da Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil
- 113 cE3c – Centre for Ecology, Evolution and Environmental Changes / Azorean Biodiversity Group, Universidade dos Açores, Angra do Heroísmo, Azores, Portugal
- 114 LIBRe – Laboratory for Integrative Biodiversity Research, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
- 115 Laboratório de Biogeoquímica Ambiental Wolfgang C. Pfeiffer, Universidade Federal de Rondônia, Porto Velho - RO, Brazil
- 116 Faculdade de Ciências Agrárias, Biológicas e Sociais Aplicadas, Universidad do Estado de Mato Grosso, Nova Xavantina-MT, Brazil
- 117 Tropical Forests and People Research Centre, University of the Sunshine Coast, Australia
- 118 Flamingo Land Ltd., North Yorkshire, UK
- 119 Centre for Ecology and Hydrology, Wallingford, UK
- 120 School of International Tropical Forestry, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia
- 121 Escuela de Ciencias Forestales, Unidad Académica del Trópico, Universidad Mayor de San Simón, Sacta, Bolivia
- 122 Faculty of Science, Universiti Brunei Darussalam, Brunei
- 123 Agence Nationale des Parcs Nationaux, Libreville, Gabon
- 124 Ministère de la Forêt, de la Mer, de l'Environnement, Chargé du Plan Climat, Libreville, Gabon
- 125 University of Edinburgh, Edinburgh, UK
- 126 Biologia Vegetal, Universidade Estadual de Campinas, Campinas - SP, Brazil
- 127 Facultad de Ingeniería Ambiental, Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador
- 128 Forest Research Centre, Sabah Forestry Department, Sepilok, Malaysia
- 129 Carrera de Ingeniería Forestal, Universidad Técnica del Norte, Ibarra, Ecuador
- 130 Royal Botanical Garden Edinburgh, Edinburgh, UK
- 131 Universidad Regional Amazónica IKIAM, Tena, Ecuador
- 132 Public Communications and Outreach Group, Parks and Recreation Division, Oakland Park, FL, USA
- 133 Keller Science Action Center, Field Museum, Chicago, IL, USA
- 134 Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname
- 135 Department of Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, The Netherlands
- 136 University of Oslo, Oslo, Norway
- 137 Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Leticia, Colombia
- 138 Department of Biology, Boston University, Boston, USA
- 139 Institute of Research for Forestry Development (INDEFOR), Universidad de los Andes, Mérida, Venezuela
- 140 Bureau Waardenburg, Culemborg, The Netherlands
- 141 Socioecosistemas y Cambio Climático, Fundación Con Vida, Medellín, Colombia
- 142 Centro de Conservación, Investigación y Manejo de Áreas Naturales, CIMA Cordillera Azul, Lima, Peru
- 143 Iwokrama International Centre for Rainforest Conservation and Development, Georgetown, Guyana
- 144 Carboforexpert, Geneva, Switzerland
- 145 Universidade Federal Rural da Amazônia/CAPES, Belém - PA, Brazil
- 146 Museu Paraense Emílio Goeldi, Belém - PA, Brazil
- 147 Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

- 148 Instituto Federal do Acre, Rio Branco - AC, Brazil
- 149 Universidad de San Antonio Abad del Cusco, Cusco, Peru
- 150 Guyana Forestry Commission, Georgetown, Guyana
- 151 Federal University of Alagoas, Maceió, Brazil
- 152 Sustainable Landscapes and Food Systems, Center for International Forestry Research, Bogor, Indonesia
- 153 Faculty of Forestry, University of British Columbia, Vancouver, Canada
- 154 Department of Forest Botany, Dendrology and Geobiocoenology, Mendel University in Brno, Brno, Czech Republic
- 155 Department of Plant & Soil Science, School of Biological Sciences, University of Aberdeen, Aberdeen, UK
- 156 Institute for Conservation Research, San Diego Zoo, San Diego, USA
- 157 UK Research & Innovation, Innovate UK, London
- 158 Department of Geography, National University of Singapore, Singapore, Singapore
- 159 Naturalis Biodiversity Center, Leiden, The Netherlands
- 160 Systems Ecology, VU University, Amsterdam, The Netherlands
- 161 Faculty of Forestry, University of Toronto, Toronto, Canada
- 162 Universidad de los Andes, Merida, Colombia
- 163 Wildlife Conservation Society, New York, NY, USA
- 164 Yale School of Forestry & Environmental Studies, Yale University, New Haven, CT, USA
- 165 School of Geography, University of Nottingham, Nottingham, UK
- 166 Van der Hout Forestry Consulting, Rotterdam, The Netherlands
- 167 Van Hall Larenstein University of Applied Sciences, Velp, The Netherlands
- 168 Utrecht University, Utrecht, The Netherlands
- 169 Deltares, Delft, The Netherlands
- 170 School of Environmental and Forest Sciences, University of Washington, Seattle, OR, USA
- 171 Department of Biological Sciences, Florida International University, Florida, FL, USA
- 172 Centro de Investigación y Promoción del Campesinado, La Paz, Bolivia
- 173 School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ, USA
- 174 Institut de Recherche en Ecologie Tropicale, Libreville, Gabon
- 175 School of Natural Sciences, University of Stirling, Stirling, UK
- 176 School of Natural Sciences, University of Bangor, Bangor, UK
- 177 University of Liberia, Monrovia, Liberia
- 178 Forest Management, Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname
- 179 Department of Geography and The Environment, University of Texas at Austin, Austin, TX, USA
- 180 Tropenbos International, Wageningen, The Netherlands
- 181 Biology, Utrecht University, Utrecht, The Netherlands

1 **Abstract**

2 The sensitivity of tropical forest carbon to climate is a key uncertainty in predicting global climate  
3 change. While short-term drying and warming are known to impact forests it is unknown if such effects  
4 translate into long-term responses. Here we analyse 590 permanent plots measured across the tropics to  
5 derive the equilibrium climate controls on forest carbon. Maximum temperature is the most important  
6 predictor of aboveground biomass ( $-9.1 \text{ Mg C ha}^{-1} \text{ }^\circ\text{C}^{-1}$ ), primarily by reducing woody productivity, and  
7 with a greater rate of decline in the hottest forests ( $>32.2 \text{ }^\circ\text{C}$ ). Our results nevertheless reveal greater  
8 thermal resilience than observations of short-term variation imply. To realise the long-term climate  
9 adaptation potential of tropical forests requires both protecting them and stabilising the Earth's climate.

10

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



13 Main text

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

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

31 Yet the sensitivity of ecosystems to inter-annual fluctuations may be an unreliable guide to their  
32 longer-term responses to climate change. Such responses will also be influenced by physiological  
33 acclimation (12), changes in demographic rates (13), and shifts in species composition (14). For  
34 example, both respiration and photosynthesis can acclimate under sustained temperature increases  
35 (15-17), and tropical trees exhibit physiological plasticity (18) and shifts in species composition (14)  
36 under sustained drought. These processes could mean that tropical forests are less sensitive to climate  
37 than estimates derived from inter-annual variability imply. An alternative, complimentary approach to  
38 assessing sensitivity to climate is to measure and analyse spatial variation in tropical ecosystems  
39 across climate gradients as a space-for-time substitution. Such biome-wide spatial variation in forest

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

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

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

61 Forest carbon stocks were most strongly related to maximum temperature (-5.9 % per  $1^\circ\text{C}$  increase in  
62 maximum temperature, 95 % CI = -8.6 to -3.1 %, Fig. 2, equivalent to  $-9.1 \text{ Mg C ha}^{-1} \text{ }^\circ\text{C}^{-1}$  for a stand  
63 with the mean carbon stocks in our dataset,  $154.6 \text{ Mg C ha}^{-1}$ ), followed by rainfall (+2.4 % per 100  
64 mm increase in precipitation in the driest quarter, 95 % CI = 0.6 – 4.3 %, Fig. 2, equivalent to  $0.04$   
65  $\text{Mg C ha}^{-1} \text{ mm}^{-1}$  for a stand with the mean carbon stocks in our dataset), with no statistically  
66 significant relationship with minimum temperature, wind speed or cloud cover (Fig 2). The effects of

67 maximum temperature and precipitation are also evident in an analysis considering a wider suite of  
68 climate variables than those tied to hypothesised mechanisms (Fig. S3), and in an additional  
69 independent pantropical dataset of 223 single-census plots (for which carbon gains and residence time  
70 cannot be assessed, Fig. S4).

71 The negative effect of maximum temperature on aboveground carbon stocks mainly reflects reduced  
72 carbon gains with increasing temperature (-4.0 % per 1°C, 95% CI = -6.2 to -1.8 %, Fig. 2) while the  
73 positive effect of precipitation emerges through longer carbon residence times with increasing  
74 precipitation in the driest quarter (3.3 % per 100 mm, 95 % CI = 0.9 – 5.7 %, Fig. 2). Carbon  
75 residence time also increased with the proportion of clay in the soil (Fig. 2). The additive effects of  
76 precipitation and temperature on carbon stocks were modified by an interaction between them ( $\Delta$  AIC  
77 = 15.4 comparing full linear model with or without interaction), with temperature effects more  
78 negative when precipitation is low (Fig. S6). The interaction was through shortening carbon residence  
79 time ( $\Delta$  AIC = 11.9) rather than reducing carbon gains (model without interaction better,  $\Delta$  AIC =  
80 1.4).

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

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

94 effect of maximum temperature through reduced carbon gains, and a non-linear negative effect of  
95 maximum temperature, ameliorated by high dry-season precipitation, through reduced carbon  
96 residence time.

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

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

118 Overall our results suggest that tropical forests have considerable potential to acclimate and adapt to  
119 the effects of night-time minimum temperatures, but are clearly sensitive to the effects of daytime  
120 maximum temperature. This is consistent with ecophysiological observations suggesting that the

121 acclimation potential of respiration (15) is greater than that of photosynthesis (17). The temperature  
122 sensitivity revealed by our analysis is also considerably weaker than short-term sensitivities  
123 associated with inter-annual climate variation (8). For example, by relating short-term annual climate  
124 anomalies to responses in plots, the effect of a 1°C increase in temperature on carbon gains has been  
125 estimated as more than three-fold our long-term, pantropical result (28). This stronger long-term  
126 thermal resilience is likely due to a combination of individual acclimation and plasticity (15-17),  
127 differences in species' climate responses (29) leading to shifts in community composition due to  
128 changing demographic rates (12) and the immigration of species with higher performance at high  
129 temperatures (12).

130 Our pantropical analysis of the sensitivity to climate of aboveground forest carbon stocks, gains and  
131 persistence shows that warming reduces carbon stocks and gains from woody productivity. Using a  
132 reference carbon stock map (30) and applying our estimated temperature sensitivity (including non-  
133 linearity) while holding other variables constant leads to an eventual biome-wide reduction of 14.1 Pg  
134 C in live biomass (including scaling to estimate carbon in roots) for a 1°C increase in maximum  
135 temperature (95 % CI = 6.9 – 20.7 Pg). This compares with a large range of projected sensitivities in  
136 the subset of coupled climate carbon cycle models that report vegetation carbon (1 – 58 Pg C °C<sup>-1</sup>),  
137 although we note that these models have not been run to equilibrium (see SI Methods).

138 Our results suggest that stabilising global surface temperatures at 2°C above pre-industrial levels will  
139 cause a potential long-term biome-wide loss of 35.3 Pg C (95 % CI = 20.9 – 49.0 Pg, estimates with  
140 alternative baseline biomass maps 24.0 – 28.4 Pg, Fig. S12). The greatest long-term reductions in  
141 carbon stocks are projected in South America, where baseline temperatures and future warming are  
142 both highest (Fig. 4, Fig. S13). This warming would push 71 % of the biome beyond the thermal  
143 threshold – maximum temperature of 32.2°C – where larger long-term reductions in biomass are  
144 expected (Fig. S14). Of course, growth stimulation by carbon dioxide (31) will partially or wholly  
145 offset the effect of this temperature increase, depending on both the level of atmospheric carbon  
146 dioxide that limits warming to 2°C above pre-industrial levels and the fertilization effect of this  
147 carbon dioxide on tropical trees. Although CO<sub>2</sub> fertilisation is expected to reduce temperature induced

148 carbon losses from biomass across the tropics (Table S3), our analysis indicates that CO<sub>2</sub> fertilisation  
149 is not enough to offset long-term temperature induced carbon losses within Amazonia (Fig. S15).

150 The long-term climate sensitivities derived from our pan-tropical field measurements incorporate  
151 ecophysiological and ecological adaptation, and so provide an estimate of the long-term, quasi-  
152 equilibrium, response of tropical vegetation to climate. We note that this thermal adaptation potential  
153 may not be fully realised in future responses because (i) the speed of temperature rises may exceed  
154 species' adaptive capabilities, (ii) habitat fragmentation may limit species' ability to track changes in  
155 the environment, and (iii) other human impacts such as logging and fire can increase the vulnerability  
156 of forest carbon stocks to high temperatures. While many tropical forests are under severe threat of  
157 conversion, our results show that, in the long-run, tropical forests that remain intact can continue to  
158 store high levels of carbon under high temperatures. Achieving the biome-wide climate resilience  
159 potential we document depends on limiting heating and on large-scale conservation and restoration to  
160 protect biodiversity and allow species to move.

161

162

163 **References and Notes**

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348

349

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399 conceived the RAINFOR, AfriTRON and T-FORCES forest census network programmes; M.J.P.S.,  
400 O.L.P. and S.L.L. conceived and designed the study. L.A., A.A.-M., T.R.B., R.J.W.B., S.K.B., K.A-

401 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.,  
402 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.,  
403 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.  
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406 the collection of field data, M.J.P.S. analysed the data, M.J.P.S., O.L.P. and S.L.L. wrote the  
407 manuscript with contributions from other authors. All co-authors commented on or approved the  
408 manuscript. **Competing interests:** The authors declare no competing financial interests. **Data and**  
409 **materials availability:** Plot-level input data and R scripts will be deposited as a data package on  
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411

412 **Supplementary Materials:**

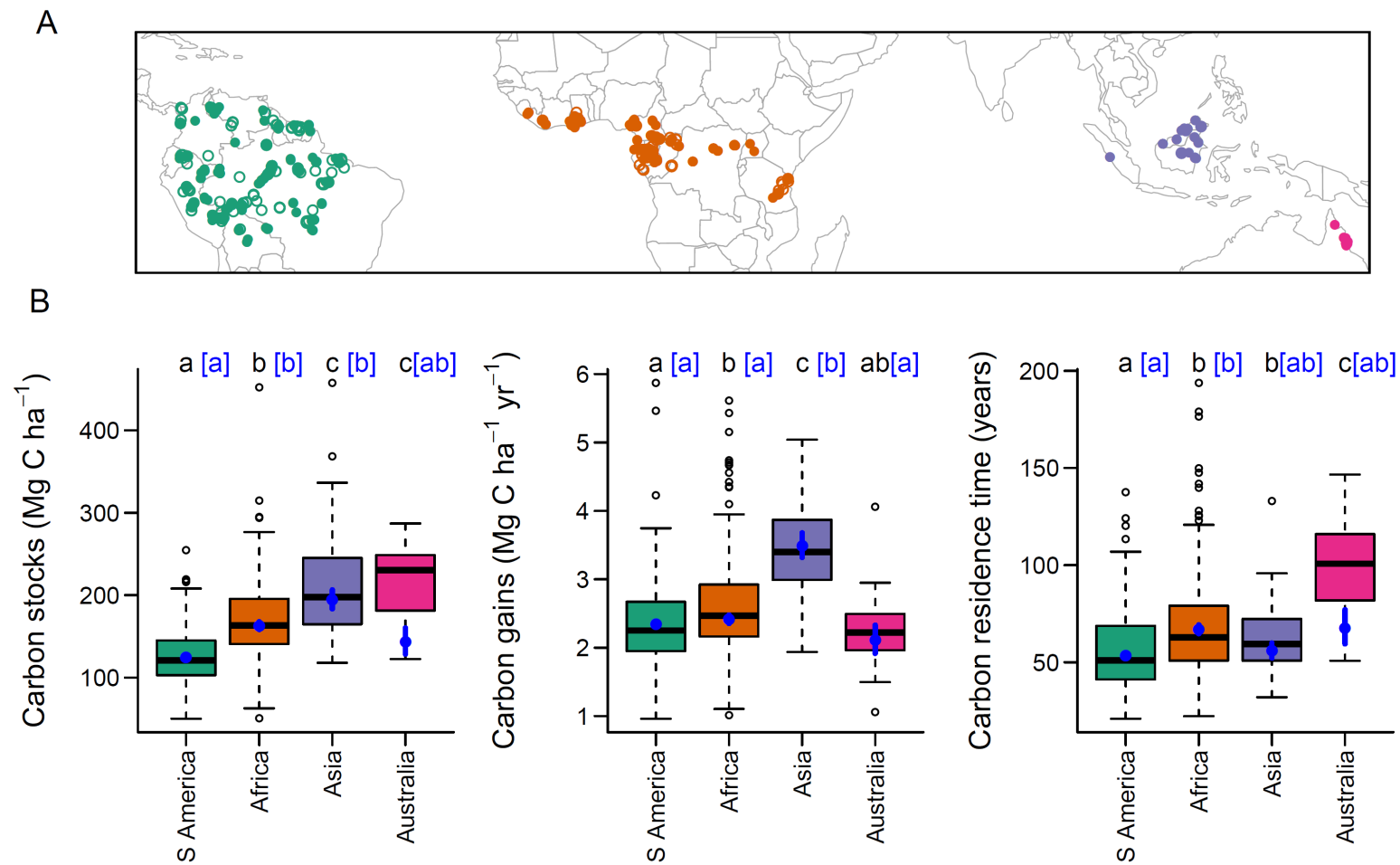
413 Materials and Methods

414 Figures S1-S15

415 Tables S1-S3

416 References (32-85)

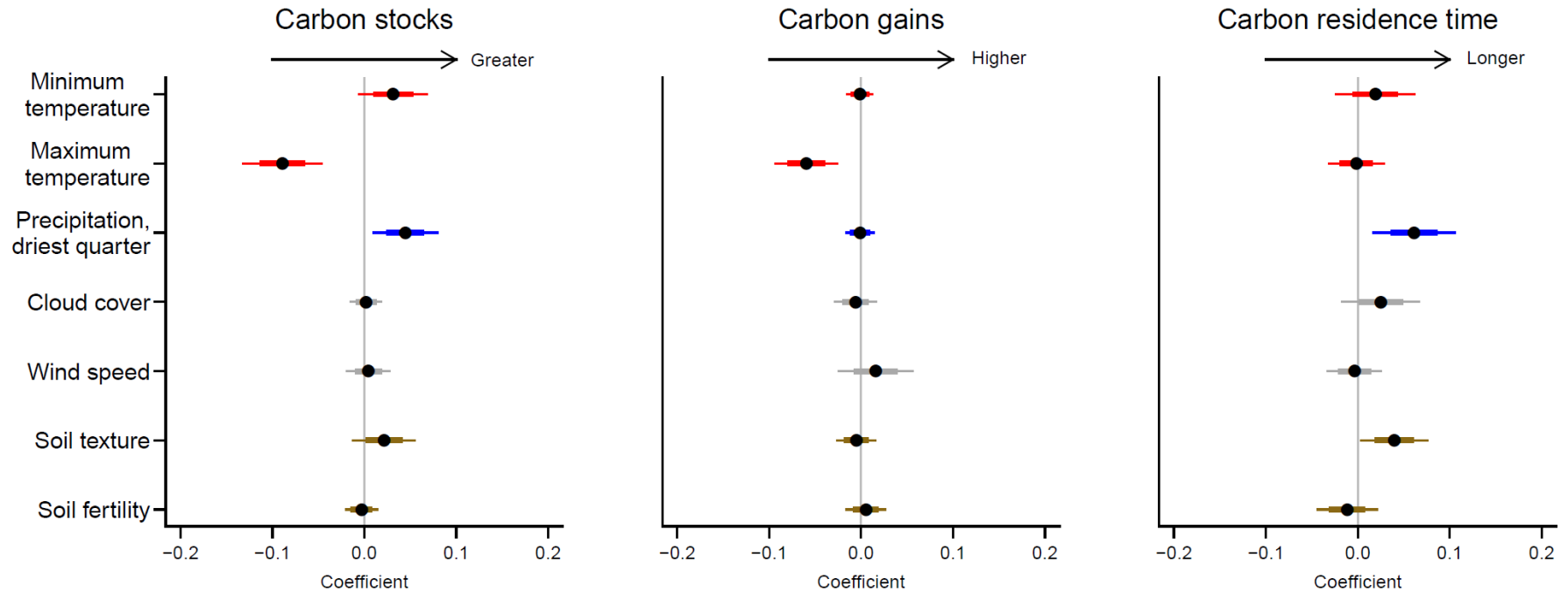
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418

419 **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  
 420 show single-census plots used as an independent dataset. (B) Variation in carbon among continents. Boxplots show raw variation while blue points show  
 421 estimated mean values ( $\pm$  SE) after accounting for environmental variation. Letters denote statistically significant differences between continents ( $P < 0.05$ )  
 422 based on raw data (black) or accounting for environmental effects (blue, square brackets).

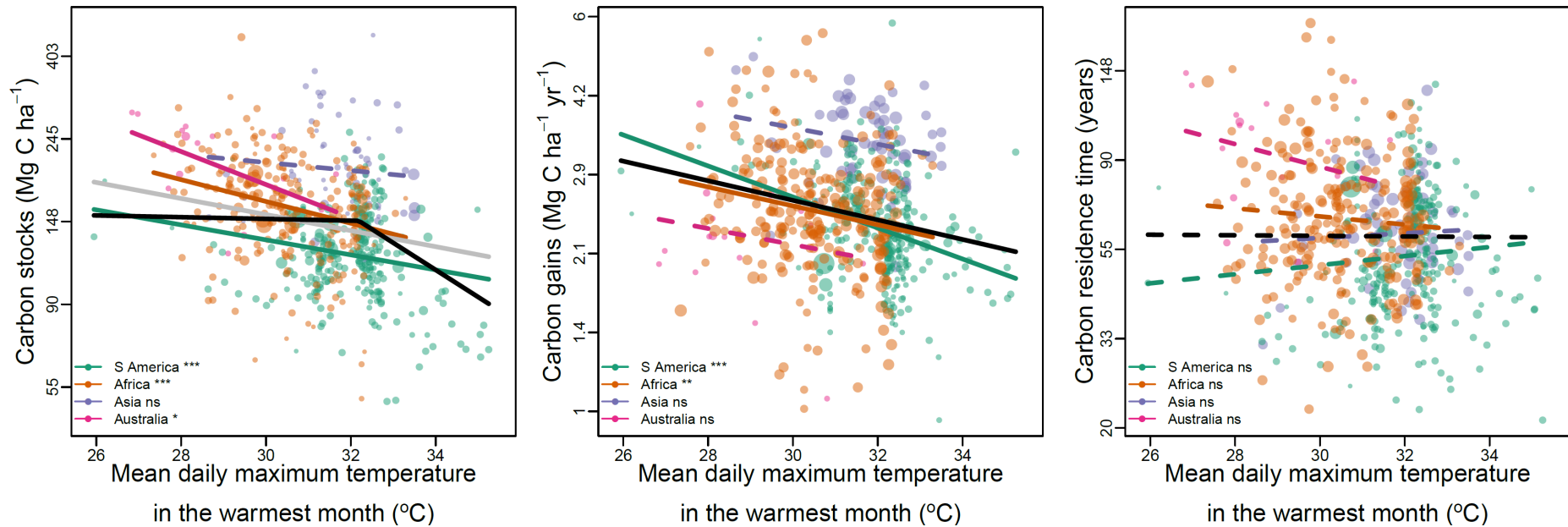
423  
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426



427

428 **Figure 2.** Correlates of spatial variation in tropical forest carbon. Points show coefficients from model-averaged general linear models. Variables that did not  
429 occur in well-supported models are shrinkage adjusted towards zero. Coefficients are standardised so that they represent change in the response variable for  
430 one standard deviation change in the explanatory variable. Error bars show standard errors (thick lines) and 95% confidence intervals (thin lines). Soil texture  
431 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  
432 in carbon stocks, gains and residence time respectively. Coefficients are shown in Table S2. Results are robust to using an alternative allometry to estimate  
433 tree biomass (Fig. S5).

434



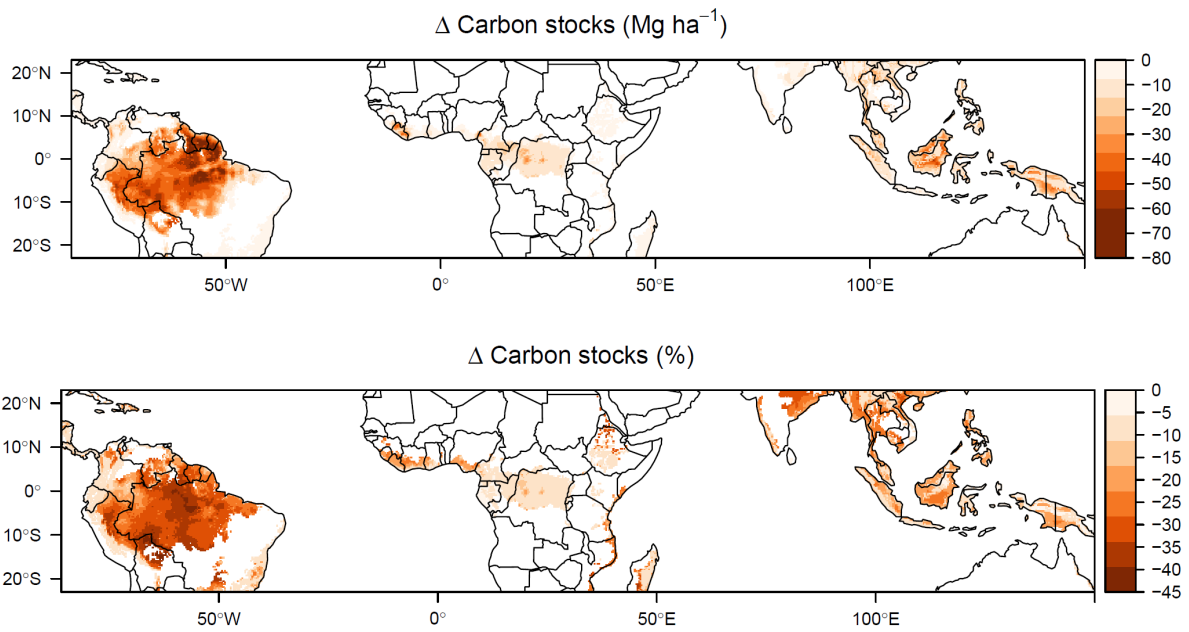
435

436

437 **Figure 3.** Temperature effects on tropical forest carbon stocks, carbon gains from woody productivity and carbon residence time. Black lines show the best  
 438 pan-tropical relationships accounting for environmental covariates. The grey line shows the additional linear pan-tropical relationship for carbon stocks.  
 439 Coloured lines show bivariate relationships within each continent. Statistically significant relationships are shown with solid lines, non-significant with  
 440 dashed lines. Note that the y-axis is on a log-scale. Symbol point size is proportional to weights used in model fitting based on plot size and monitoring  
 441 length, see SI Materials and Methods. For stocks and gains linear and break-point pan-tropical relationships are all statistically significant ( $P < 0.001$ ), as are  
 442 better sampled continents. For carbon residence time, relationships with temperature are non-significant but there is a statistically significant interaction  
 443 between maximum temperature and precipitation in the driest quarter (Figure S6). Relationships with other variables are shown in Fig. S8-S10. \*\*\*  $P <$   
 444 0.001, \*\*  $P < 0.01$ , \*  $P < 0.05$ , ns  $P \geq 0.05$



445



446

447 **Figure 4.** Long-term change in carbon stocks due to global surface temperature warming of  
448 approximately 2°C. Maps show the predicted absolute and relative change in tropical forest carbon  
449 stocks. Note that parts of the biome become warmer than currently observed in our dataset (Fig. S14).  
450 See Fig. S12 for predictions using alternative carbon reference maps. Predictions are based on  
451 temperature alone and do not include precipitation changes (for which future patterns of change are  
452 uncertain) or potential moderation via elevated CO<sub>2</sub> (see Fig. S15 for analysis incorporating this).

453

454

455 **Supporting information for Long-term thermal Sensitivity of the Earth's Tropical**456 **Forests**

457 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  
458 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-  
459 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.  
460 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>,  
461 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>,  
462 Patricia Alvarez Loayza<sup>25</sup>, Ana Andrade<sup>26</sup>, Simone Aparecida Vieira<sup>27</sup>, Luiz Aragão<sup>28</sup>, Alejandro Araujo-  
463 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.  
464 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  
465 Barroso<sup>39</sup>, Jean-François Bastin<sup>40</sup>, Sarah A. Batterman<sup>1,41,42,43</sup>, Hans Beekman<sup>12</sup>, Serge K. Begne<sup>17,44</sup>, Amy  
466 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  
467 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  
468 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  
469 Chama Moscoso<sup>15</sup>, Jérôme Chave<sup>58</sup>, Eric Chezeaux<sup>59</sup>, Connie J. Clark<sup>25</sup>, Fernanda Coelho<sup>1</sup>, Murray  
470 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  
471 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  
472 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  
473 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  
474 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  
475 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>,  
476 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 Hédí<sup>91,92</sup>, Bruno  
477 Hérault<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  
478 Huamantupa-Chuquimaco<sup>95</sup>, Walter Huaraca Huasco<sup>95</sup>, Kathryn J. Jeffery<sup>96</sup>, Eliana Jimenez-Rojas<sup>97</sup>,  
479 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  
480 Khoon Kho Khoon<sup>101</sup>, Timothy Killeen<sup>102</sup>, Kanehiro Kitayama<sup>103</sup>, Bente Klitgaard<sup>104</sup>, Alexander Koch<sup>105</sup>,  
481 Nicolas Labrière<sup>58</sup>, William Laurance<sup>106</sup>, Susan Laurance<sup>106</sup>, Miguel E. Leal<sup>107</sup>, Aurora Levesley<sup>1</sup>, Adriano  
482 J. N. Lima<sup>6</sup>, Janvier Lisingo<sup>11</sup>, Aline P. Lopes<sup>108,109</sup>, Gabriela Lopez-Gonzalez<sup>1</sup>, Tom Lovejoy<sup>110</sup>, Jon  
483 Lovett<sup>1</sup>, Richard Lowe<sup>111</sup>, William E. Magnusson<sup>112</sup>, Jagoba Malumbres-Olarte<sup>113,114</sup>, Ângelo Gilberto  
484 Manzatto<sup>115</sup>, Ben Hur Marimon Junior<sup>116</sup>, Andrew R. Marshall<sup>8,117,118</sup>, Toby Marthews<sup>119</sup>, Simone Matias de  
485 Almeida Reis<sup>14,19</sup>, Colin Maycock<sup>120</sup>, Karina Melgaço<sup>1</sup>, Casimiro Mendoza<sup>121</sup>, Faizah Metali<sup>122</sup>, Vianet  
486 Mihindou<sup>123,124</sup>, William Milliken<sup>104</sup>, Edward Mitchard<sup>125</sup>, Paulo S. Morandi<sup>14</sup>, Hannah L. Mossman<sup>2</sup>, Laszlo  
487 Nagy<sup>126</sup>, Henrique Nascimento<sup>6</sup>, David Neill<sup>127</sup>, Reuben Nilus<sup>128</sup>, Percy Núñez Vargas<sup>95</sup>, Walter Palacios<sup>129</sup>,  
488 Nadir Pallqui Camacho<sup>1,95</sup>, Julie Peacock<sup>1</sup>, Colin Pendry<sup>130</sup>, Maria Cristina Peñuela Mora<sup>131</sup>, Georgia C.  
489 Pickavance<sup>1</sup>, John Pipoly<sup>132</sup>, Nigel Pitman<sup>133</sup>, Maureen Playfair<sup>134</sup>, Lourens Poorter<sup>135</sup>, John R. Poulsen<sup>25</sup>,  
490 Axel D. Poulsen<sup>136</sup>, Richard Preziosi<sup>2</sup>, Adriana Prieto<sup>137</sup>, Richard Primack<sup>138</sup>, Hirma Ramírez-Angulo<sup>139</sup>, Jan  
491 Reitsma<sup>140</sup>, Maxime Réjou-Méchain<sup>75</sup>, Zorayda Restrepo Correa<sup>141</sup>, Thaianie Rodrigues de Sousa<sup>6</sup>, Lily  
492 Rodriguez Bayona<sup>142</sup>, Anand Roopsind<sup>143</sup>, Agustín Rudas<sup>137</sup>, Ervan Rutishauser<sup>42,144</sup>, Kamariah Abu  
493 Salim<sup>122</sup>, Rafael P. Salomão<sup>145,146</sup>, Juliana Schiatti<sup>6</sup>, Douglas Sheil<sup>147</sup>, Richarlly C. Silva<sup>57,148</sup>, Javier Silva  
494 Espejo<sup>149</sup>, Camila Silva Valeria<sup>38</sup>, Marcos Silveira<sup>57</sup>, Murielle Simo-Droissant<sup>17</sup>, Marcelo Fragomeni  
495 Simon<sup>70</sup>, James Singh<sup>150</sup>, Yahn Carlos Soto Shareva<sup>15</sup>, Clement Stahl<sup>54</sup>, Juliana Stropp<sup>151</sup>, Rahayu Sukri<sup>122</sup>,  
496 Terry Sunderland<sup>152,153</sup>, Martin Svátek<sup>154</sup>, Michael D. Swaine<sup>155</sup>, Varun Swamy<sup>156</sup>, Hermann Taedoum<sup>17</sup>,  
497 Joey Talbot<sup>1</sup>, James Taplin<sup>157</sup>, David Taylor<sup>158</sup>, Hans ter Steege<sup>159,160</sup>, John Terborgh<sup>25</sup>, Raquel Thomas<sup>143</sup>,  
498 Sean C. Thomas<sup>161</sup>, Armando Torres-Lezama<sup>162</sup>, Peter Umunay<sup>163,164</sup>, Luis Valenzuela Gamarra<sup>15</sup>, Geertje  
499 van der Heijden<sup>165</sup>, Peter van der Hout<sup>166</sup>, Peter van der Meer<sup>167</sup>, Mark van Nieuwstadt<sup>168</sup>, Hans Verbeek<sup>99</sup>,  
500 Ronald Vernimmen<sup>169</sup>, Alberto Vicentini<sup>6</sup>, Ima Célia Guimarães Vieira<sup>146</sup>, Emilio Vilanova Torre<sup>170</sup>, Jason  
501 Vleminckx<sup>36</sup>, Vincent Vos<sup>172</sup>, Ophelia Wang<sup>173</sup>, Lee J. T. White<sup>124,174,175</sup>, Simon Willcock<sup>176</sup>, John T.  
502 Woods<sup>177</sup>, Verginia Wortel<sup>178</sup>, Kenneth Young<sup>179</sup>, Roderick Zagt<sup>180</sup>, Lise Zemagho<sup>17</sup>, Pieter A. Zuidema<sup>50</sup>,  
503 Joeri A. Zwarts<sup>178,181</sup>, Oliver L. Phillips<sup>1</sup>

504

505 **This file includes:**

506 Materials and Methods

507 Figures S1 – S15

508 Tables S1 – S2

509

## 510 **Materials and Methods**

### 511 Forest census data

512 Our plots come from the RAINFOR, AfriTRON, and T-FORCES networks. Forest inventory plots  
513 were located in lowland (<1200 m), old-growth, closed-canopy forests that were not known to have  
514 been subject to anthropogenic disturbance through fire or selective logging. Plots characterised  
515 floristically as dry forest were not included, as were plots that received less than 1200 mm  
516 precipitation each year. We also did not include plots in white sand, swamp and seasonally flooded  
517 forests, as we expect these to experience marked edaphic constraints (extreme nutrient limitation for  
518 white sand forests (32), stress caused by hypoxic conditions for swamp and seasonally flooded forests  
519 (33)). All plots were  $\geq 0.2$  ha (median size = 1 ha) and were monitored for at least two years (median  
520 monitoring period = 9.7 years). All censuses were prior to the 2015-16 very strong El Niño event, as  
521 we expected that event to suppress carbon gains relative to the long-term mean.

522 Forest inventory plots were sampled using standardised protocols (34), 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  
524 tagged so that the same tree could be identified in subsequent censuses. In some cases the point of  
525 diameter measurement (POM) had to be moved due to upward growth of buttresses and deformities.  
526 For these trees we use the  $D_{\text{mean}}$  approach from Talbot et al. (35).

527 In a few cases (6 plots) the minimum diameter measured changed over time, or palms and  
528 *Phenakospermum* were excluded in some censuses. For these, we estimated aboveground biomass  
529 (AGB, subsequently converted to carbon stocks) and aboveground woody production (AGWP,  
530 subsequently converted to carbon gains) using a minimum diameter or taxonomic protocol that could  
531 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.  
533 Some plots had nested designs where the plot was split into subplots with different minimum diameter  
534 protocols (69 plots). For these, we only analysed the area conforming to our minimum diameter  
535 protocol. For analysis, we grouped small ( $\leq 0.5$  ha) plots within 1 km of each other, and also grouped  
536 contiguous larger plots (18 plots), as these will experience equivalent climate and larger plots are less  
537 sensitive to stochastic tree fall events (36).

538 Data were curated in ForestPlots.net (37, 38), or were subject to equivalent offline handling, and  
539 experienced the same quality control procedures. Details of quality control procedures are described  
540 in Brienen et al. (39). Our final dataset consists of 590 sampling units (hereafter plots) covering 637.2  
541 ha, with 2.2 million measurements of 670,499 unique stems. For validating models of carbon stocks  
542 an additional dataset of 223 single-census plots using the same measurement protocols was assembled  
543 from the same networks (see section “Validation with independent single-census plot dataset” below).

544

545 Estimating above-ground biomass

546 Diameter measurements were converted to estimates of aboveground biomass (AGB). For dicot trees  
547 we used the allometric equation

$$548 \text{ AGB} = 0.673 \times (\rho D^2 H)^{0.976}, \quad [1]$$

549 from Chave et al. (40), where  $\rho$  is wood density (from (41, 42)) and  $H$  is tree height estimated using  
550 allometric equations described below. For monocots and tree ferns, we used a palm-specific  
551 allometric equation

$$552 \ln(\text{AGB}) = -3.3488 + 2.7483 \cdot \ln(D), \quad [2]$$

553 from Goodman et al. (43), where  $D$  is the measured diameter.

554 The heights of a subset of trees in our dataset were measured in the field, either with a laser  
555 rangefinder, hypsometer, or clinometer, or directly by climbing the tree. We filtered this dataset to  
556 stems with measured diameters, height  $\leq 90$  m, diameters  $\geq 90$  mm DBH, as height-diameter  
557 allometries of saplings differ from those of more mature trees, and to stems that were not broken,  
558 leaning or fallen. This gave a total of 78,899 height measurements. We used this dataset to fit local  
559 height-diameter allometric models, as these refine AGB estimates by capturing spatial variation in  
560 height-diameter allometries missed by large-scale allometric models (44). Height data were not  
561 available from every plot, so to ensure consistent treatment of plots height-diameter models were  
562 constructed for each biogeographic region. We fitted three parameter asymptotic models (45) of the  
563 form

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

565 where  $a$ ,  $b$  and  $c$  are estimated parameters ('Weibull' models, 46). We fitted these models either  
566 treating each observation equally or with case weights proportional to each trees' basal area. These  
567 weights give more importance to large trees during model fitting. We selected the best fitting of these  
568 models, determining this as the model that minimised prediction error of stand biomass when  
569 calculated with estimated heights or observed heights (44). 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  
571 following trial and error as they led to regular model convergence. Where models did not converge  
572 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  
574 of a power law relationship between height and diameter. We checked if models gave unrealistic  
575 predictions by applying models to predict the height of all trees in the biogeographic region, and

576 excluded models that predicted any tree height 10 % higher than the tallest tree we recorded in that  
577 continent.

578

579 Estimating above-ground woody production

580 We estimated AGWP following Talbot et al. (35). AGWP is comprised of four components, (1) the  
581 sum of growth of surviving trees, (2) the sum of AGB of new recruits, (3) the sum of unobserved  
582 growth of trees that died during a census interval and (4) the sum of growth of unobserved recruits  
583 that entered then died during a census interval. Accounting for the latter two components is necessary  
584 to avoid census-interval length effects, as more AGWP in these components will be missed due to the  
585 greater mortality of trees that accumulates over longer census intervals.

586 Components 3 and 4 can be estimated using two quantities that can be calculated from observed stem-  
587 dynamics in each plot; per-area annual recruitment ( $R_a$ ) and per-capita annual mortality ( $m_a$ ). Per-  
588 capita mortality is calculated from the ratio of surviving stems to initial stems, using equation 5 in  
589 Kohyama et al. (47). Per-area annual recruitment is calculated using estimated mortality rates and the  
590 observed change in the number of stems over a census interval, using equation 11 of Kohyama et al.  
591 (47).

592 To estimate the unobserved growth of stems that died during a census interval, we first use plot-level  
593 per-capita mortality rates ( $m_a$ ) to estimate how many trees are expected to have died in each year of  
594 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  
596 estimated as

$$597 \quad D_{\text{death}} = D_{\text{start}} \times G \times Y_{\text{mean}} \quad [4]$$

598 where  $D_{\text{start}}$  is the diameter at the start of the census interval,  $G$  is the plot-level median growth rate of  
599 the size class the tree was in at the start of the census interval (size classes are defined as  $D < 200$  mm,  
600  $400 \text{ mm} > D \geq 200$  mm, and  $D \geq 400$  mm) and  $Y_{\text{mean}}$  is the mean number of years trees survived in  
601 the census interval before dying. The diameter at death is then converted to AGB at death using  
602 allometric equations (equation 1, except for ferns and monocots where equation 2 is used), and the  
603 unobserved growth is calculated as the difference between AGB at death and AGB at the start of the  
604 census.

605 To estimate the growth of recruits that were not observed because they died during the census  
606 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  
608 that recruit in a given year, and the probability of each recruit surviving until the next census ( $P_{\text{surv}}$ ) is

609  $P_{surv} = (1 - m_a)^T$ , 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  
611 census interval gives the total number of unobserved recruits in that census interval. We then need to  
612 estimate how long each recruit was alive for. From  $m_a$  we can calculate the number of recruits in a  
613 given year that died in each subsequent year, and from this calculate the mean life-span of recruits in a  
614 given year that died before the next census. The average life-span of unobserved recruits ( $Y_{mean-rec}$ ) is  
615 the weighted mean of each cohort's lifespan, weighted by the number of unobserved recruits in each  
616 year. Diameter at death is given in mm by

$$617 \quad D_{death} = 100 + (G \times Y_{mean-rec}) \quad [5]$$

618 where  $G$  is the plot-level median growth rate of the smallest size class (i.e.  $D < 200$  mm).  
619 Aboveground biomass of recruits at the time of death is estimated using equation 1. These corrections  
620 for unobserved growth have a marginal impact on AGWP calculations, collectively accounting on  
621 average for just 2.3 % of estimated plot-level AGWP.

622 AGB was calculated for each census, and AGWP was calculated for each census interval, and the  
623 time-weighted mean of each was taken to give one value per plot. We used a time-weighted mean to  
624 give greater importance to AGB estimates separated by longer census-intervals, as these will be more  
625 independent. Estimates of AGB and AGWP were converted to carbon stocks and carbon gains by  
626 multiplying by 0.456 (48). Carbon residence time was then estimated as carbon stocks /carbon gains,  
627 and represents the length of time carbon resides in living biomass before being passed to the litter and  
628 necromass pools (49). Calculations to estimate AGB and AGWP were performed using the R package  
629 BiomasaFP (50).

630

### 631 Obtaining environmental data

632 Most climate data were obtained from climate data from Worldclim2 (51) as it provides the highest  
633 resolution (~ 1 km) pantropical climate data, although we note that some regions, such as central  
634 Africa, have limited station data. We extracted monthly data for the following variables: mean daily  
635 minimum temperature, mean daily maximum temperature, precipitation, solar radiation and wind  
636 speed, In addition to calculating the standard series of 19 bioclimatic variables, using the dismo R  
637 package (52), we calculated 1) mean daily maximum temperature,  $BIO1 + BIO2/2$ , 2) mean daily  
638 minimum temperature,  $BIO1 - BIO2/2$ , 3) maximum cumulative water deficit as the minimum across  
639 the year of monthly cumulative water deficit  $W$ ,

$$640 \quad W_i = W_{i-1} - \min(0, P_i - 100), \quad [6]$$

641 where  $P$  is monthly precipitation in mm, and 100 represents measured evapotranspiration. This  
642 calculation was run for a year from the wettest month in the year, starting at a water deficit of zero, 4)  
643 the number of months where monthly cumulative water deficit was negative, 5) the number of months  
644 where monthly precipitation was below 100 mm (i.e. less than evapotranspiration), 6) mean annual  
645 solar radiation, 7) mean annual wind speed, and 8) vapour pressure deficit ( $VPD = SVP - \text{vapour}$   
646  $\text{pressure}$ , where saturated vapour pressure,  $SVP, = 0.611 \times e^{(17.502 \text{ temperature}) / (\text{temperature} + 240.97)}$ ). We also  
647 obtained data on cloud frequency at  $\sim 1$  km resolution from Wilson & Jetz (53), who processed twice-  
648 daily MODIS satellite images. Temperature values were adjusted for differences in altitude between  
649 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  
651 temperature ( $^{\circ}\text{C}$ ) and  $A$  is altitude (m). Temperature values were also corrected for systematic  
652 warming trends. To do this, the mean annual temperature in each grid-cell in each year was extracted  
653 from the CRU TS 3.24 dataset (54), and robust linear regression used to estimate grid-cell specific  
654 warming rates. These were used to adjust Worldclim2 temperature values for the difference between  
655 the midpoint of plot monitoring and the midpoint of the Worldclim2 climatology.

656 Data on soil texture and chemistry was obtained at 1 km resolution from the SoilGrids dataset (55),  
657 with this resolution selected to match the resolution of the climate data. From this we extracted CEC,  
658 representing soil fertility, and percentage clay, representing soil texture. For each soil variable we  
659 calculated the depth-weighted average for 0 – 30 cm.

## 660 Statistical analysis

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

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

669 We selected explanatory variables to represent hypothesised ways in which climate could affect  
670 carbon stocks (Table S1). We assessed collinearity within this set of explanatory variables using  
671 variance inflation factors (VIF) and pairwise correlations. Because of collinearity, we had to exclude  
672 VPD, total precipitation, use only one of MCWD and precipitation in the driest quarter, and could  
673 include both minimum and maximum temperature but not mean annual temperature. We used  
674 precipitation in the driest quarter rather than MCWD as the latter is zero truncated and so is less  
675 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  $VIF < 3$ ).

678 To account for variation other than in climate we also included soil variables relating to texture (%  
679 clay) and fertility (CEC), and included continent specific intercepts to account for biogeographic  
680 variation in carbon. To account for unmeasured environmental gradients (e.g. soil variation not  
681 captured by the SoilGrids variables), we used Moran's eigenvector maps as explanatory variables,  
682 selecting eigenvectors that corresponded to positive spatial autocorrelation in the distance matrix (56).  
683 These variables act as a proxy for unmeasured spatial gradients by capturing positive spatial  
684 associations between plots.

685 Plots differed in their area and the length of time they were monitored for. This is likely to affect the  
686 variance of carbon stocks, carbon gains and carbon residence time, as smaller plots or plots only  
687 monitored for short periods are more likely to be sensitive to the mortality of a few large trees. To  
688 account for this, we used case weights relating to plot area and monitoring period. Following Lewis et  
689 al. (57), we selected weights by relating residuals from our linear models to plot area and to plot  
690 monitoring period, and subsequently assessing which root transformation of plot area/ monitoring  
691 period removed the pattern in the residuals when used as a weight. Selected weights were: carbon  
692 stocks,  $\text{Area}^{1/3}$ ; carbon gains,  $\text{Monitoring length}^{1/7}$ ; carbon residence time,  $\text{Area}^{1/9} + \text{Monitoring}$   
693  $\text{length}^{1/12} - 1$ .

694 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  $\Delta \text{AIC} < 4$ , using  
696 full averaging so variables that do not appear in the model get the value of zero for their coefficients.  
697 This means that model averaged coefficients of terms with limited support exhibit shrinkage towards  
698 zero. Multi-model inference was performed using the MuMIn R package (58).

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

705 To assess whether the temperature carbon relationship was non-linear we used breakpoint regression  
706 implemented in the segmented R package (59). This estimates a breakpoint in the explanatory variable  
707 at which the slope of the relationship with the response variable changes. We estimated the breakpoint  
708 for the mean daily maximum temperature in the warmest month variable in the full model with a  
709 temperature-precipitation interaction described above. We assessed the support for the breakpoint by

710 comparing the AIC of the model with a breakpoint with the AIC of a model with a linear relationship.  
711 We repeated this with carbon gains and carbon residence time as response variables.

712 We also analysed spatial variation in carbon stocks as a function of the above climate and soil  
713 variables and spatial eigenvectors using Random Forest decision tree algorithms (22) implemented  
714 using the randomForest R package (60). We assessed variable importance by calculating the average  
715 increase in node purity across all decision trees (measured by residual sum of squares) when using the  
716 variable to split the data. We assessed modelled relationships between response and explanatory  
717 variables using partial plots, which show predicted change in the response variable, averaged across  
718 trees, when changing the explanatory variable and holding all other variables constant.

719 To compliment this analysis based on relationships expected *a priori*, we also performed an  
720 exploratory analysis to assess whether other climate variables excluded from the full general linear  
721 models had an effect on carbon. To do this, we fitted linear models to assess the bivariate relationship  
722 of carbon with each climate variable, with continent also included as an explanatory variable to  
723 account for biogeographic variation in forest characteristics.

724

#### 725 Validation with independent single-census plot dataset

726 We assessed whether the relationships with environmental variables identified in the analyses of  
727 multi-census plot data described above held when applied to an additional dataset of 223 single-  
728 census plots. As the single-census data were not used in any of the analyses above they did not  
729 influence modelling decisions, so provide an independent test of the relationships identified with the  
730 multi-census plot analysis.

731 Single-census plots were extracted from the ForestPlots.net database (37, 38) using the same plot-  
732 selection criteria as for the multi-census plots, except that censuses during or following the 2015-16  
733 strong El Niño were included in the single-census plot dataset as we expected that carbon stocks,  
734 unlike gains, would still remain close to their long-term mean.

735 We fitted a general linear model with the five climate explanatory variables, soil fertility and texture,  
736 continent and spatial eigenvector, and model averaging of all subsets of this model as described for  
737 the multi-census plots. We performed this analysis using just the single-census plots and a combined  
738 dataset of single and multi-census plots.

739

740

741

742 Scaling results to the biome

743 We applied the non-linear relationship between carbon stocks and mean daily maximum temperature  
744 in the warmest month identified by the breakpoint regression to estimate the total change in carbon  
745 stock due to temperature effects alone for different scenarios of temperature increase. We delimited  
746 the biome extent using the WWF tropical and subtropical moist broadleaved forest biome (61),  
747 restricted to tropical latitudes, and further refined it by excluding grid-cells with  $< 50 \text{ Mg C ha}^{-1}$  using  
748 data from (30), as these are unlikely to be forest. Calculations were conducted at 10-minute  
749 resolution. The non-linear relationship between temperature and carbon means that the change in  
750 biomass for a given increase in temperature will depend on the baseline temperature. For each grid-  
751 cell we predicted the percentage change in carbon for a given temperature increase from the baseline  
752 temperature in that grid-cell based on the non-linear relationship identified in our statistical model,  
753 holding all other variables constant. We then used a reference carbon stock map (30) to convert  
754 percentage change to change in carbon stocks per hectare (in  $\text{Mg ha}^{-1}$ ). To calculate change in carbon  
755 stocks for the whole grid-cell, we multiplied change per hectare by the area of the grid-cell in  
756 hectares, and then adjusted this by the proportion of the grid-cell that was forested by multiplying by  
757 2014 forest cover (62). Total change for the biome (in Pg) was calculated by summing these grid-cell  
758 level values. Uncertainty due to our statistical model was assessed by generating multiple predictions  
759 by resampling model parameters (breakpoint threshold, slope below breakpoint, slope above  
760 breakpoint), and extracting quantiles from the resultant distribution of predicted change values.  
761 Aboveground biomass carbon values were scaled to include root biomass based on a root to shoot  
762 ratio of 0.19 in tropical evergreen forests (63).

763 The Avitabile et al (30) aboveground biomass map was chosen to provide reference carbon stocks.  
764 While other maps have previously been produced by Saatchi et al. (64) and Baccini et al. (65) we  
765 selected the Avitabile map because it synthesises the earlier maps (see Mitchard et al. (66) for  
766 discussion of substantial differences between these maps) and is anchored by more field data.  
767 Importantly, the Avitabile map reproduces spatial patterns in aboveground biomass that have been  
768 described from field data but are absent in the Saatchi or Baccini maps, including the much higher  
769 biomass density of north-east Amazonian forests due to tall trees and very high wood density (67).  
770 Nevertheless, we also investigated the consequences of using the Saatchi or Baccini maps for our  
771 estimates of biomewide thermal sensitivity and spatial patterns of change in carbon stocks (Fig S15).

772 We investigated three temperature change scenarios. Firstly, we applied a  $1^\circ\text{C}$  increase to all  
773 locations. Secondly, we assessed the consequence of global temperatures stabilizing  $1.5^\circ\text{C}$  above pre-  
774 industrial levels for the equilibrium temperature response of tropical forest carbon. Finally, we  
775 assessed the consequence of global temperatures stabilizing  $2^\circ\text{C}$  above pre-industrial levels. For the  
776 latter two we obtained data from CMIP5 climate models, using downscaled future climate projections

777 based on the Worldclim climatology (68). As downscaling was performed using Worldclim version  
 778 1.4 (69) and our statistical models use Worldclim version 2, we calculated the warming anomaly in  
 779 each grid-cell from the current Worldclim version 1.4 conditions, and applied this to the Worldclim 2  
 780 data to obtain future temperature. RCP scenarios and time-points were chosen to give global  
 781 temperature increases that best match 1.5°C and 2°C above pre-industrial. Importantly, these future  
 782 climate projections were used to capture the spatially varying nature of warming, and our predictions  
 783 relate to the long-term response of vegetation if the climate stabilised at these new warming levels,  
 784 rather than being predictions of transient responses at these specific time-points. For 1.5°C we used  
 785 RCP 2.6 averaged for 2040-2060 (median temperature increase across models = 1.5°C, (70)). For  
 786 2°C, we used RCP 2.6 averaged for 2040-2060 (median temperature increase models = 1.9°C (70)).  
 787 Note that predicted increases in maximum temperatures were often considerably greater than the  
 788 global increase, especially in South America. For both scenarios we used the median predicted  
 789 temperature change for each grid-cell from an ensemble of 15 models (BCC-CSM1-1, CCSM4,  
 790 CNRM-CM5, GFDL-CM3, GFDL-ESM2G, GISS-E2-R, HadGEM2-AO, HadGEM-ES, IPSL-  
 791 CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3,  
 792 NorESM1-M).

793 We assessed the potential for long-term carbon dioxide growth stimulation to offset these long-term  
 794 temperature effects. We used CO<sub>2</sub> concentrations from the RCP scenarios and time-points described  
 795 above, which approximate the long-term concentrations if the climate stabilised at the new  
 796 temperatures (71). Thus the 1.5°C and 2°C scenarios were associated with CO<sub>2</sub> concentrations of 443  
 797 ppm and 487 ppm respectively (72). We cannot assess the effect of CO<sub>2</sub> on biomass from our spatial  
 798 dataset, so instead used independent estimates of CO<sub>2</sub> effects from other sources. Firstly, we obtained  
 799 CO<sub>2</sub> only effects on net primary production (NPP) extracted from an ensemble of CMIP5 earth system  
 800 models by (73). This gives the proportional change in NPP for evergreen forests (note that this also  
 801 includes boreal forests) over 1980-2010, standardised to a 100 ppm increase in CO<sub>2</sub> concentration. To  
 802 propagate this through to changes in AGB under future CO<sub>2</sub> conditions we first estimated the  
 803 logarithmic dependency of NPP on CO<sub>2</sub> (74) by substituting values of NPP and CO<sub>2</sub> at time zero and  $t$   
 804 (from (73)) into the equation,

$$805 \quad NPP_t = NPP_0 \left[ 1 + \beta \ln \left( \frac{[CO_2]_t}{[CO_2]_0} \right) \right] \quad \text{Equation 7}$$

806 This equation can be used to compute NPP annually given an initial NPP estimate and a time series of  
 807 atmospheric CO<sub>2</sub> concentrations (from a combination of the observed record from pre-industrial and  
 808 the RCP 4.5 scenario, modified so that it stabilises at 487 or 443 ppm depending on warming  
 809 scenario). Initial pre-industrial NPP was back-calculated from present-day values using Equation 7,  
 810 with 13.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (mean of nine Amazon plots where NPP has been measured, from (75)) used

811 for present-day NPP. To propagate NPP into change in woody biomass (following (49)) we used the  
812 equation

$$813 \quad \frac{dM_{\text{wood}}}{dt} = \alpha_{\text{wood}} N_{\text{P}} - \frac{M_{\text{wood}}}{\tau_{\text{wood}}} \quad \text{Equation 8}$$

814 where  $M_{\text{wood}}$  is woody biomass,  $N_p$  is NPP,  $\alpha_{\text{wood}}$  is the allocation of NPP to wood (taken as 0.33, the  
815 mean value across nine plots from (75)) and  $\tau_{\text{wood}}$  is the residence time of woody biomass, taken as  
816 59.1 years (the median value across plots used in this study). This model (equations 7 and 8) was run  
817 from pre-industrial to 2500, enabling us to see the equilibrium effect of increased CO<sub>2</sub> concentrations  
818 on biomass, assuming temporally invariant allocation and residence time. We calculated the  
819 proportional change in biomass from 2000 to 2500, and applied this to the reference carbon stock map  
820 to obtain predicted equilibrium change in aboveground biomass due to CO<sub>2</sub> effects.

821 The effects of CO<sub>2</sub> in earth system models have been reported to be larger than those deduced from  
822 satellite data or CO<sub>2</sub> enrichment experiments (73), so we also ran the above model using changes in  
823 NPP reported from a synthesis of free-air CO<sub>2</sub> enrichment experiments conducted in forests (73).  
824 Finally, we looked at the impact of using CO<sub>2</sub> effects derived from a recent large meta-analysis of  
825 CO<sub>2</sub> enrichment experiments (76), which reported a 12.5 % increase in biomass of tropical trees for a  
826 250 ppm increase in CO<sub>2</sub> concentration. As this relationship was reported to be linear (76) we used  
827 linear interpolation to estimate the change in biomass under CO<sub>2</sub> concentrations associated with each  
828 warming scenario (i.e. 443 and 487 ppm). To estimate long-term changes in biomass accounting for  
829 both temperature and carbon dioxide, we first applied the CO<sub>2</sub> relationship to estimate the change in  
830 biomass due to carbon dioxide growth stimulation, and then assessed the effects of warmer  
831 temperatures from this revised baseline. Our approach allows a simple assessment of CO<sub>2</sub> effects  
832 exploring a range of different effect strengths. Real-world responses will likely be more complex,  
833 with, for example, nutrient limitation potentially affecting the extent to which growth is stimulated by  
834 CO<sub>2</sub> (76).

### 835 Temperature sensitivity of CMIP5 models

836 The temperature sensitivity ( $\gamma_{\text{LT}}$ ) of coupled climate carbon cycle models can be identified by  
837 comparing responses of carbon stocks in coupled and uncoupled simulations forced with a 1%  
838 increase in CO<sub>2</sub> concentrations per year (respectively, these are the 1pctCO2 and esmFixClim  
839 simulations), following Wenzel et al. (77). Both coupled and uncoupled simulations are exposed to  
840 the same increase in CO<sub>2</sub> concentration, but in the uncoupled simulation temperature is not directly  
841 affected by this increase in CO<sub>2</sub>.

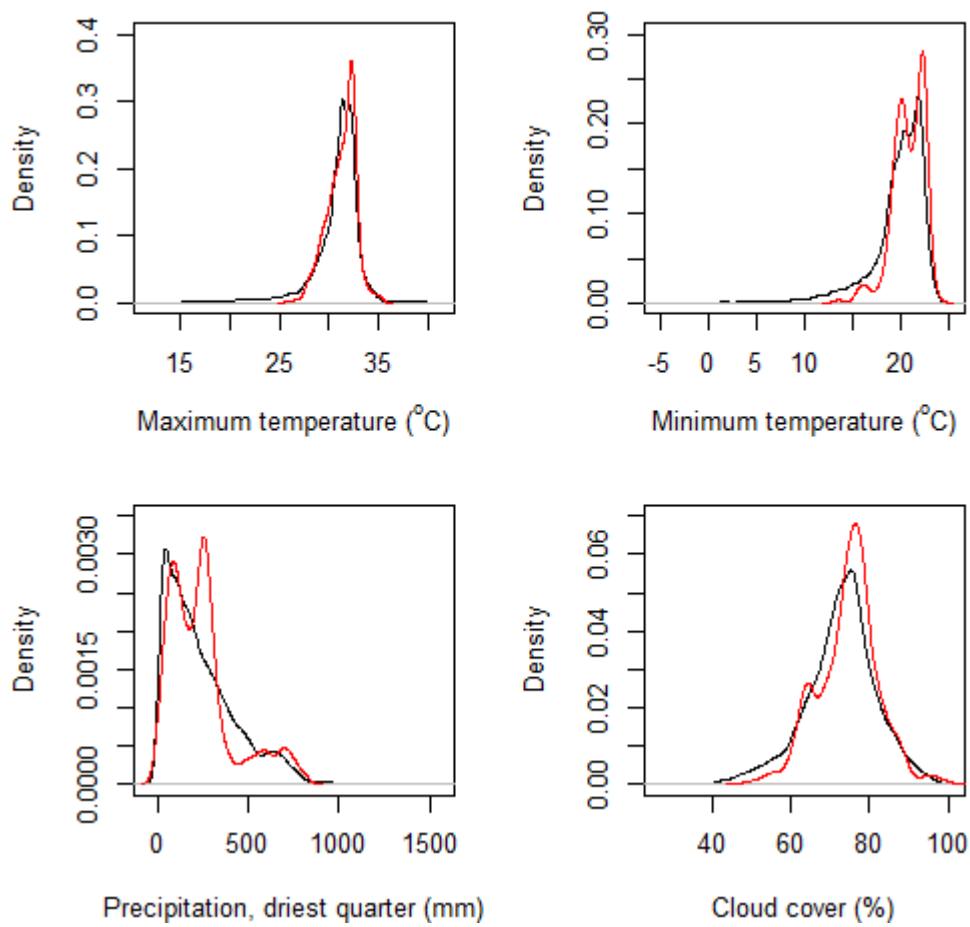
842 Vegetation carbon outputs are reported from six CMIP5 models, each with coupled and uncoupled  
843 simulations (78, 79). For all simulations, we calculated the change in vegetation carbon (the *cVeg*

844 variable) in the tropics between year 110 and year 30 of the experiment, and also calculated the  
845 difference in land temperature (the *tas* variable). The change in vegetation carbon due to temperature  
846 alone was calculated by taking the difference in change in vegetation carbon in the coupled ( $\Delta C_{vegC}$ )  
847 and uncoupled ( $\Delta C_{vegU}$ ) simulation, and this was then divided by the change in tropical land  
848 temperature ( $\Delta T$ ) to obtain the temperature sensitivity of the model,

$$849 \quad \gamma_{LT} = (\Delta C_{vegC} - \Delta C_{vegU}) / \Delta T \quad \text{Equation 9.}$$

850 We calculated the temperature sensitivity of the six CMIP5 models that report vegetation carbon:  
851 CESM-1-BGC ( $\gamma_{LT} = -0.7 \text{ Pg C } ^\circ\text{C}^{-1}$ ), GFDL-ESM2M ( $\gamma_{LT} = -58.4 \text{ Pg C } ^\circ\text{C}^{-1}$ ), HadGEM2-ES ( $\gamma_{LT} = -$   
852  $9.2 \text{ Pg C } ^\circ\text{C}^{-1}$ ), IPSL-CM5A-LR ( $\gamma_{LT} = -11.3 \text{ Pg C } ^\circ\text{C}^{-1}$ ), MPI-ESM-LR ( $\gamma_{LT} = -22.8 \text{ Pg C } ^\circ\text{C}^{-1}$ ) and  
853 NorESM1-ME ( $\gamma_{LT} = -1.0 \text{ Pg C } ^\circ\text{C}^{-1}$ ). Note that the simulations do not run to equilibrium (77), so  
854 changes in carbon stocks due to increased temperature may not be fully realised.

855

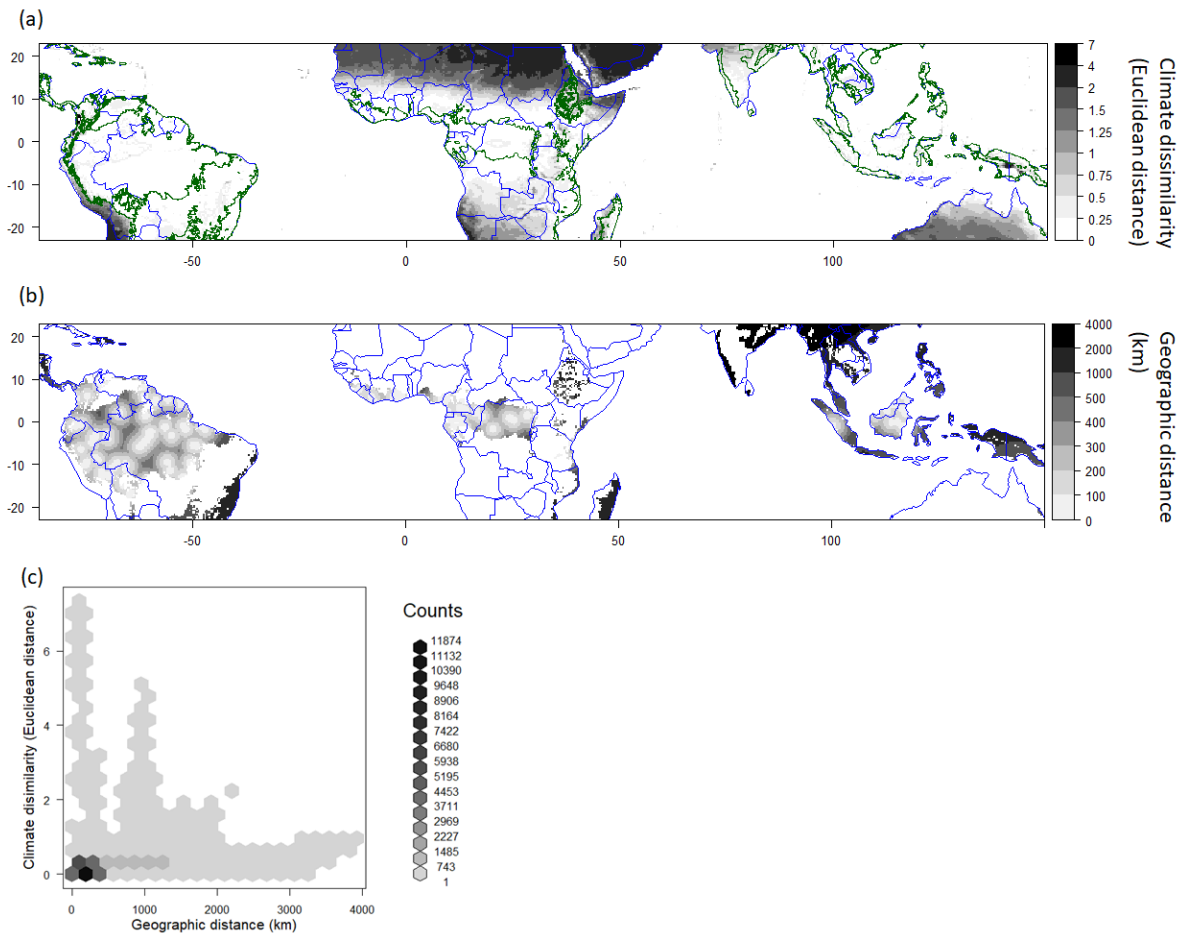


856

857 **Figure S1.** Climate space represented by our plot network. Red lines show the probability density  
858 function of each variable in our multi-census plot network. Black lines show the probability density  
859 across 10 minute grid-cells in the biome, restricted to areas with forest cover in GLC 2000 (80).

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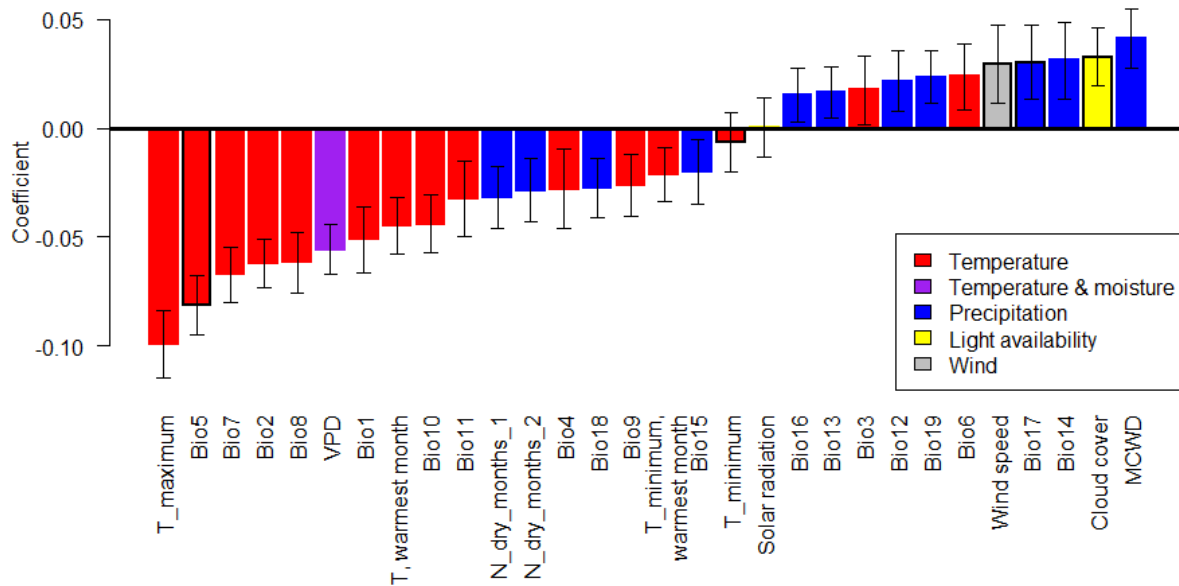


862

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



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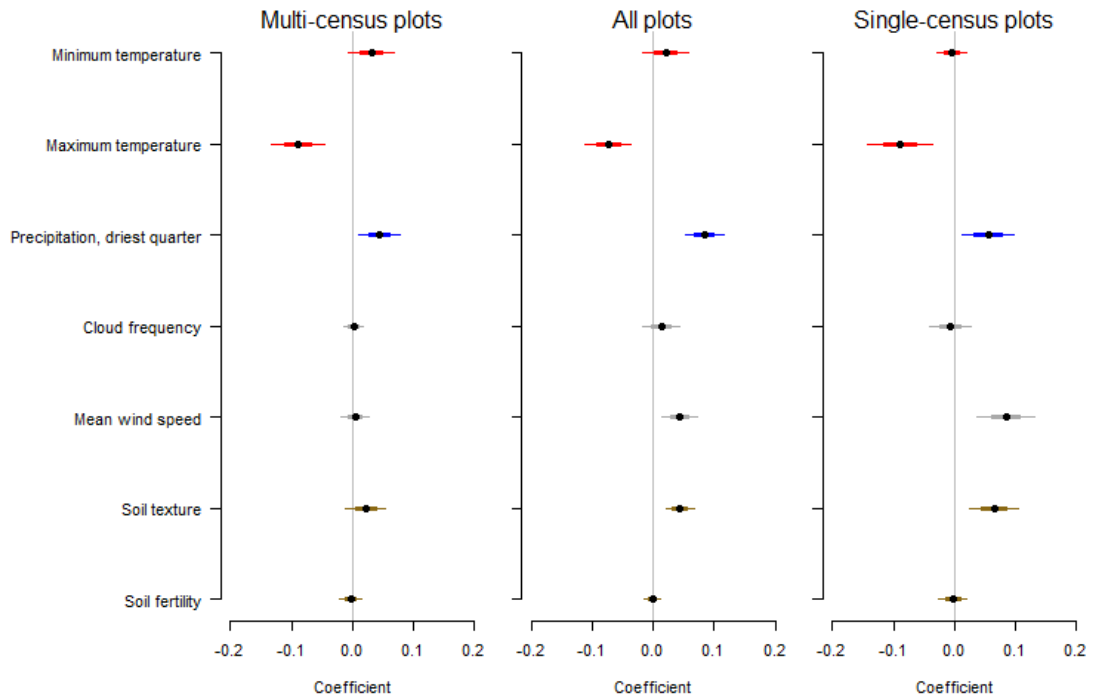
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**Figure S3.** Relationships between individual climate variables and tropical forest aboveground carbon stocks. Standardised coefficients are from models with the climate variable and continent as explanatory variables and show change in  $\ln(\text{carbon})$  for a standard deviation change in the explanatory variable. Error bars show standard errors. Variables used in the main analysis have black 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 deficit, Bio1 – mean annual temperature, Bio10 – mean temperature in the warmest quarter, Bio11 – mean temperature in the coldest quarter, N\_dry\_months\_1 – number of months with negative cumulative water deficit, N\_dry\_months\_2 – 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 temperature in the warmest month, Bio15 – 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).

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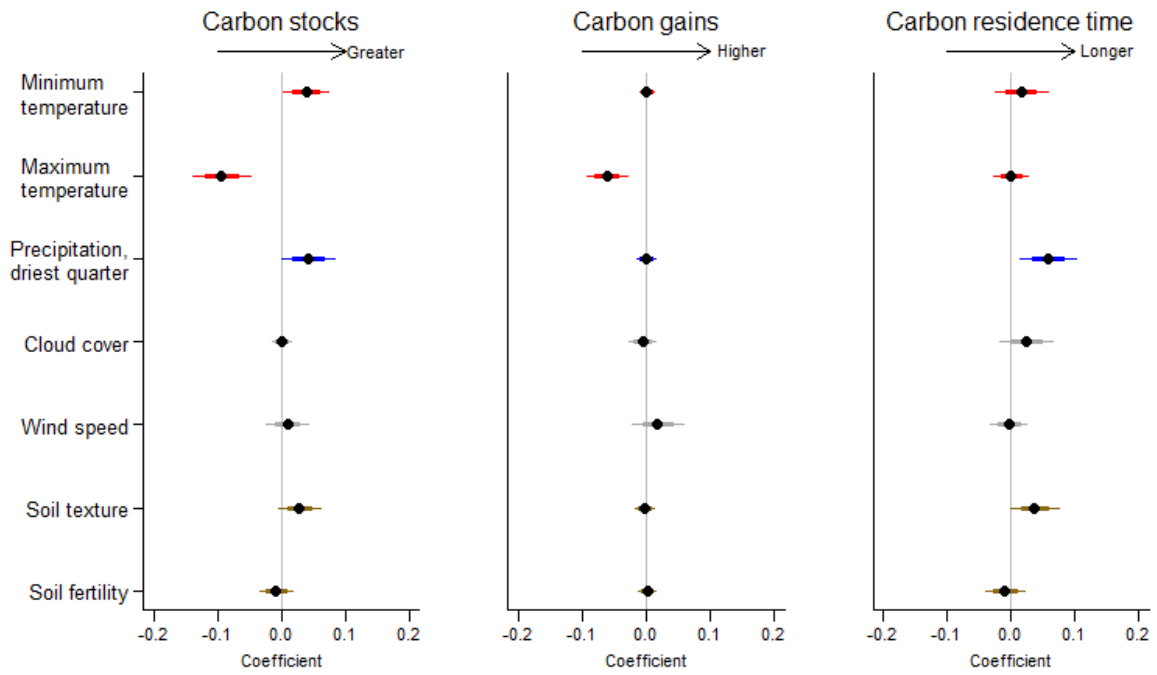
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902

903 **Figure S4.** Validation of tropical forest carbon stock sensitivity model against an independent dataset  
 904 of 223 single-census plots from our networks measured with the same protocols. Model-averaged  
 905 shrinkage adjusted coefficients from multiple regression models of biomass carbon stocks as a  
 906 function of climate, soil, biogeography and spatial eigenvectors. Models were either fitted to the  
 907 multi-census plot dataset (as in Fig. 2), to the single-census plot dataset, or to the combined dataset.  
 908 This analysis shows that the relationships identified to be most important in the main multi-census  
 909 plot analysis (i.e. the negative relationship between carbon stocks and maximum temperature and  
 910 positive relationship with precipitation in the driest quarter) are also found in an independent dataset,  
 911 which was not used for preliminary analysis so did not influence the choice of explanatory variables.

912



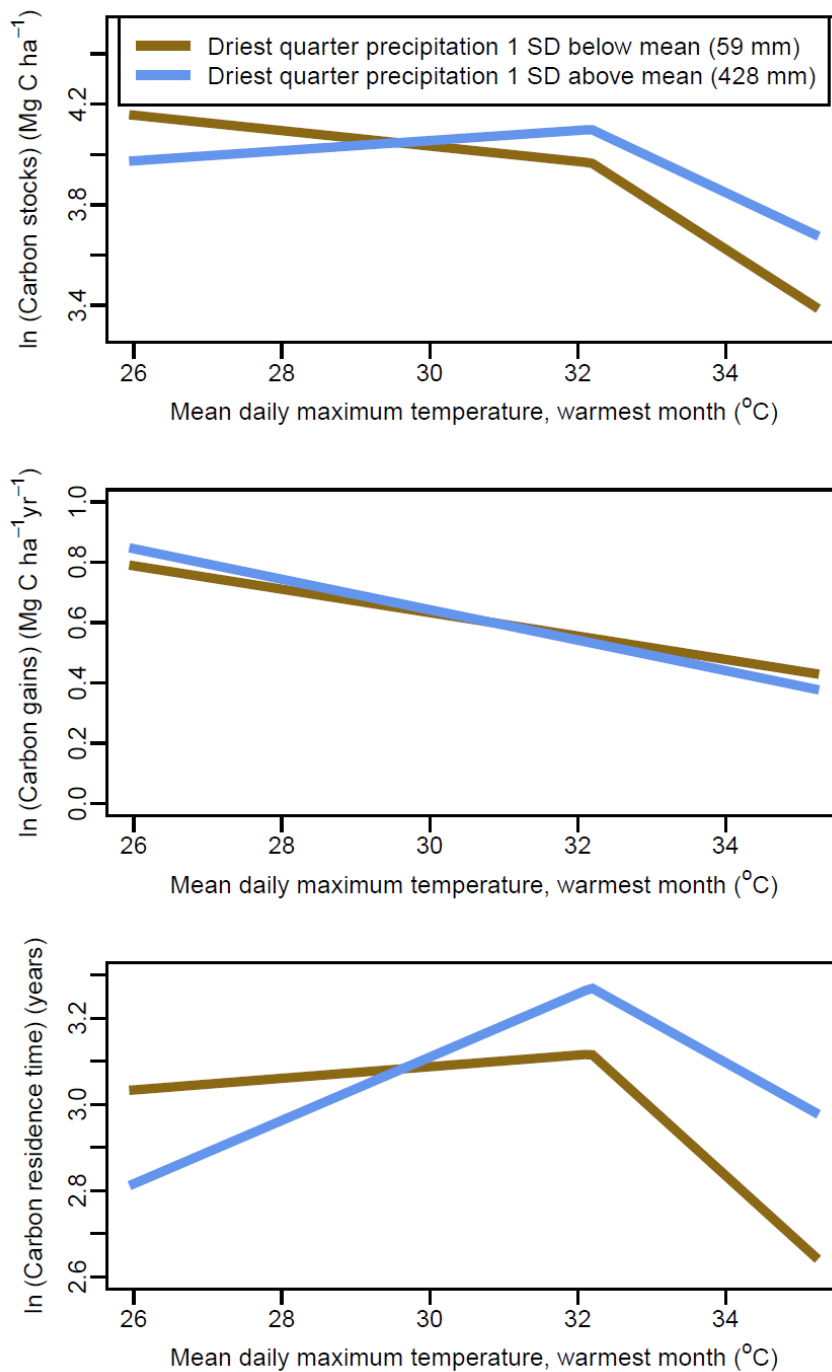
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914 **Figure S5.** As Figure 2, but with aboveground biomass estimated using the Chave et al. 2005 (81)  
915 moist forest allometric equation, which does not include a height term and is instead based on a third-  
916 order polynomial relationship between diameter and aboveground biomass. This indicates that our  
917 results are robust to using an alternative allometry to estimate aboveground biomass.

918

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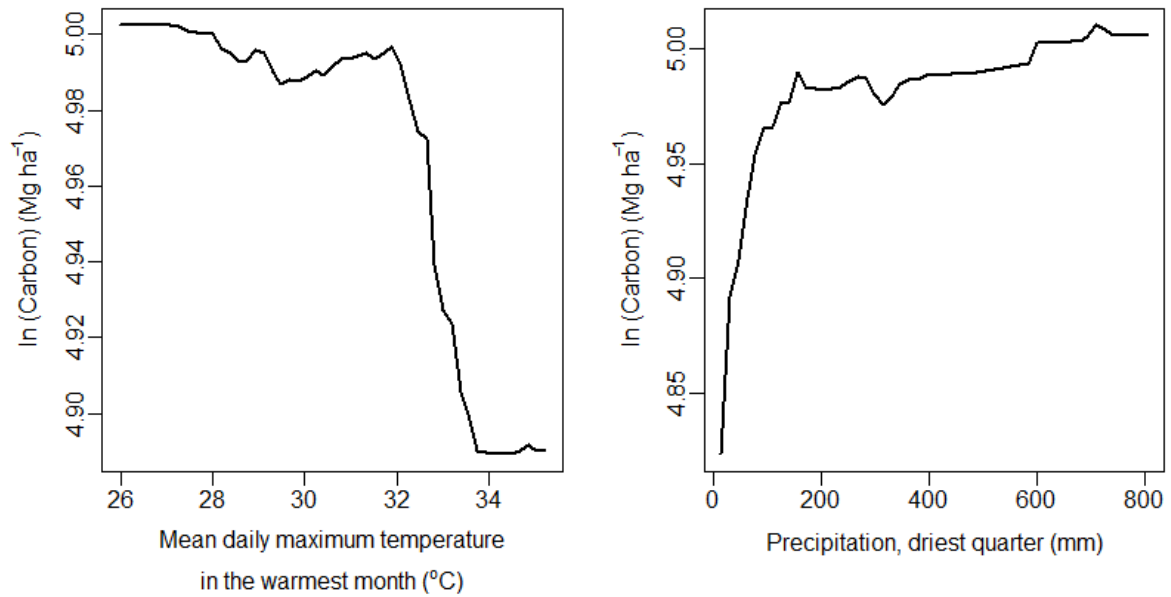
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921

922 **Figure S6.** Interaction between mean daily maximum temperature in the warmest month and  
 923 precipitation in the driest quarter in determining aboveground tropical forest carbon stocks, gains and  
 924 residence time. Modelled relationships with temperature are shown holding precipitation either one  
 925 standard deviation above or below the mean. Models with breakpoints are shown for carbon stocks  
 926 and residence time as they were found to be better supported based on lower AIC ( $\Delta AIC > 2$ ). Note  
 927 that the temperature-carbon relationship is steeper when precipitation is low for carbon stocks and  
 928 (above the breakpoint threshold) carbon residence time, but does not change with precipitation for  
 929 carbon gains. Response curves are predicted with continent set as Africa.

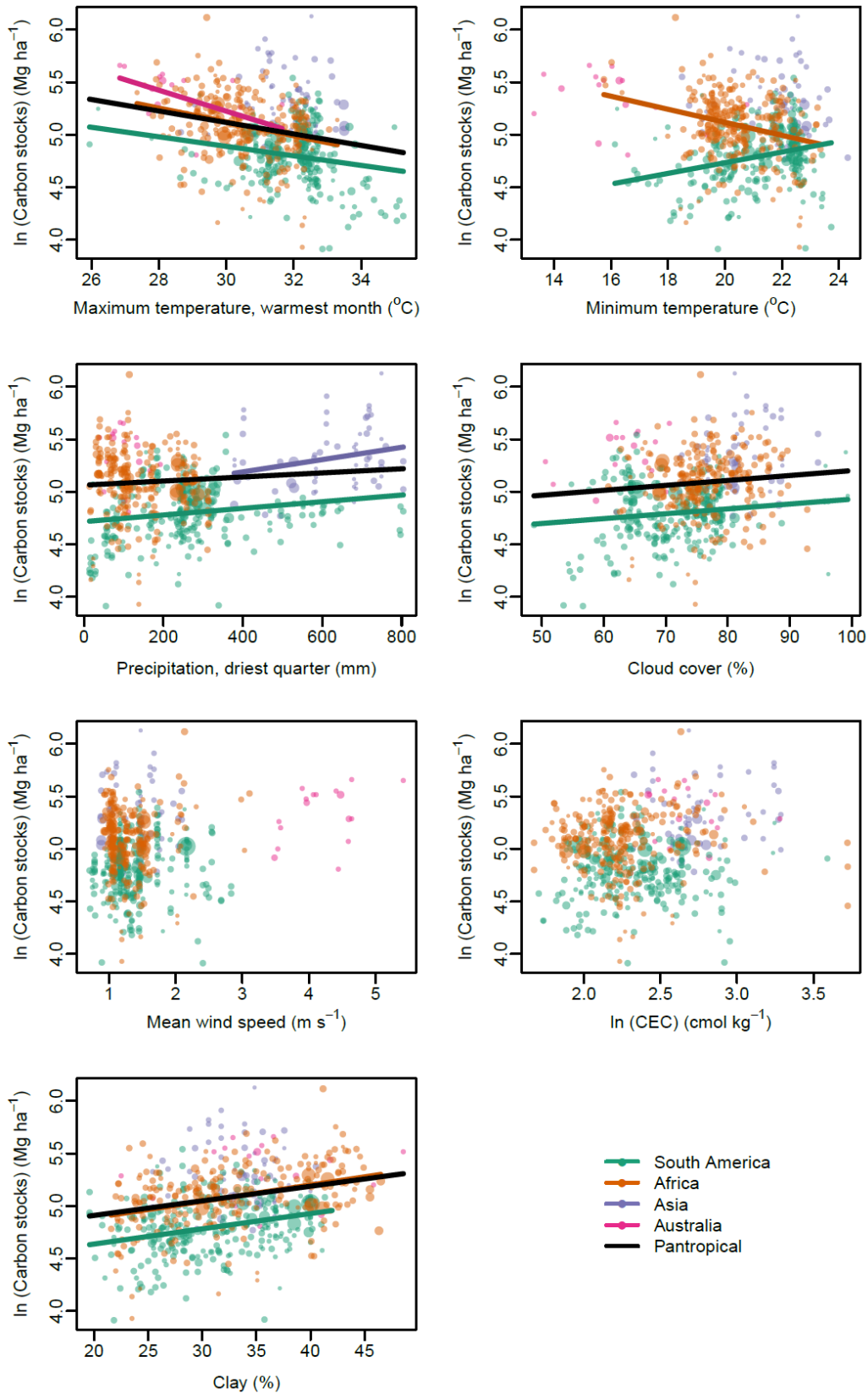
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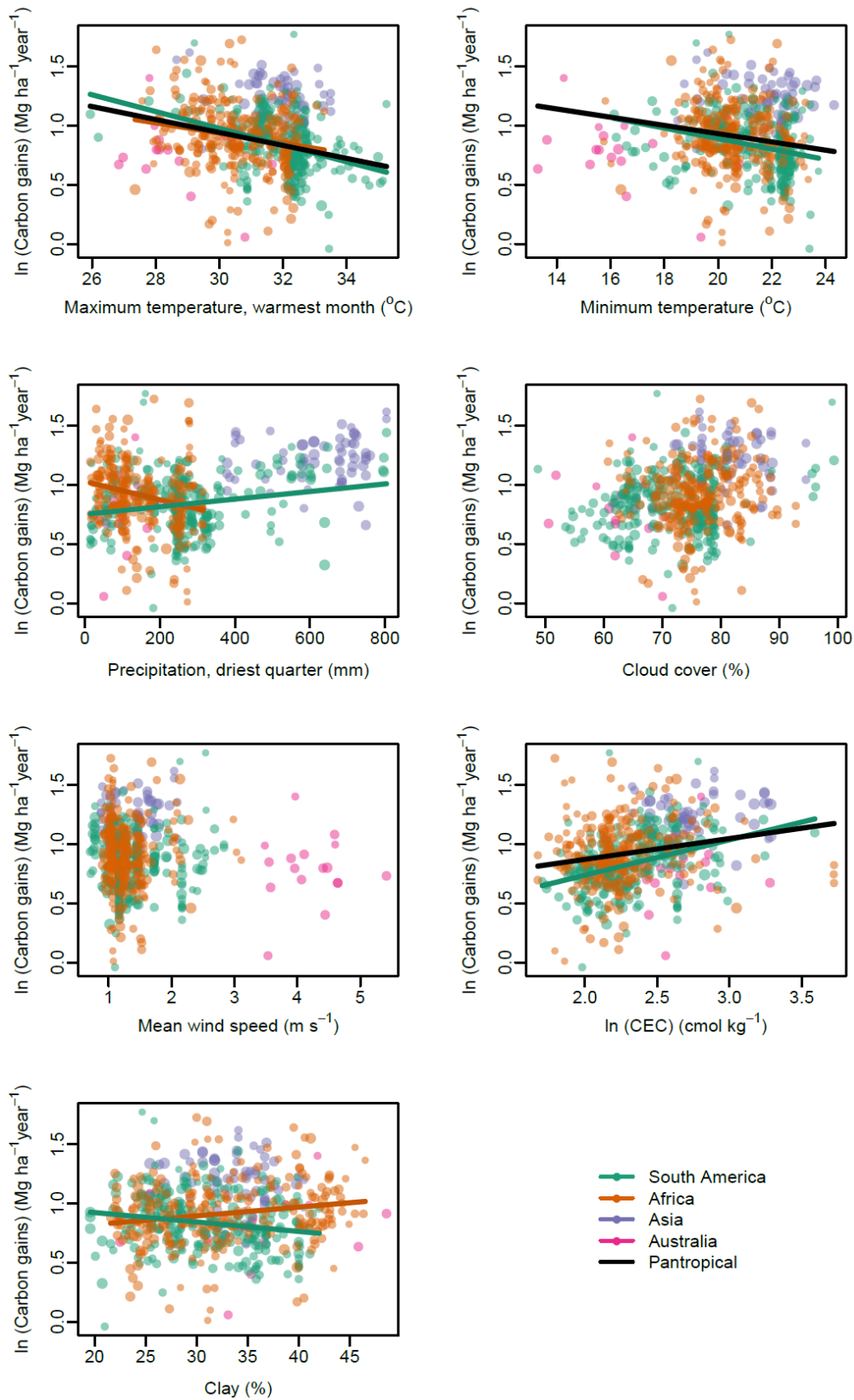
932 **Figure S7.** Partial relationships between tropical forest carbon stocks and the two climate variables  
933 identified to be most important by the random forest decision tree algorithm. Partial plots show  
934 predicted values of carbon stocks averaged across an ensemble of decision tree models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

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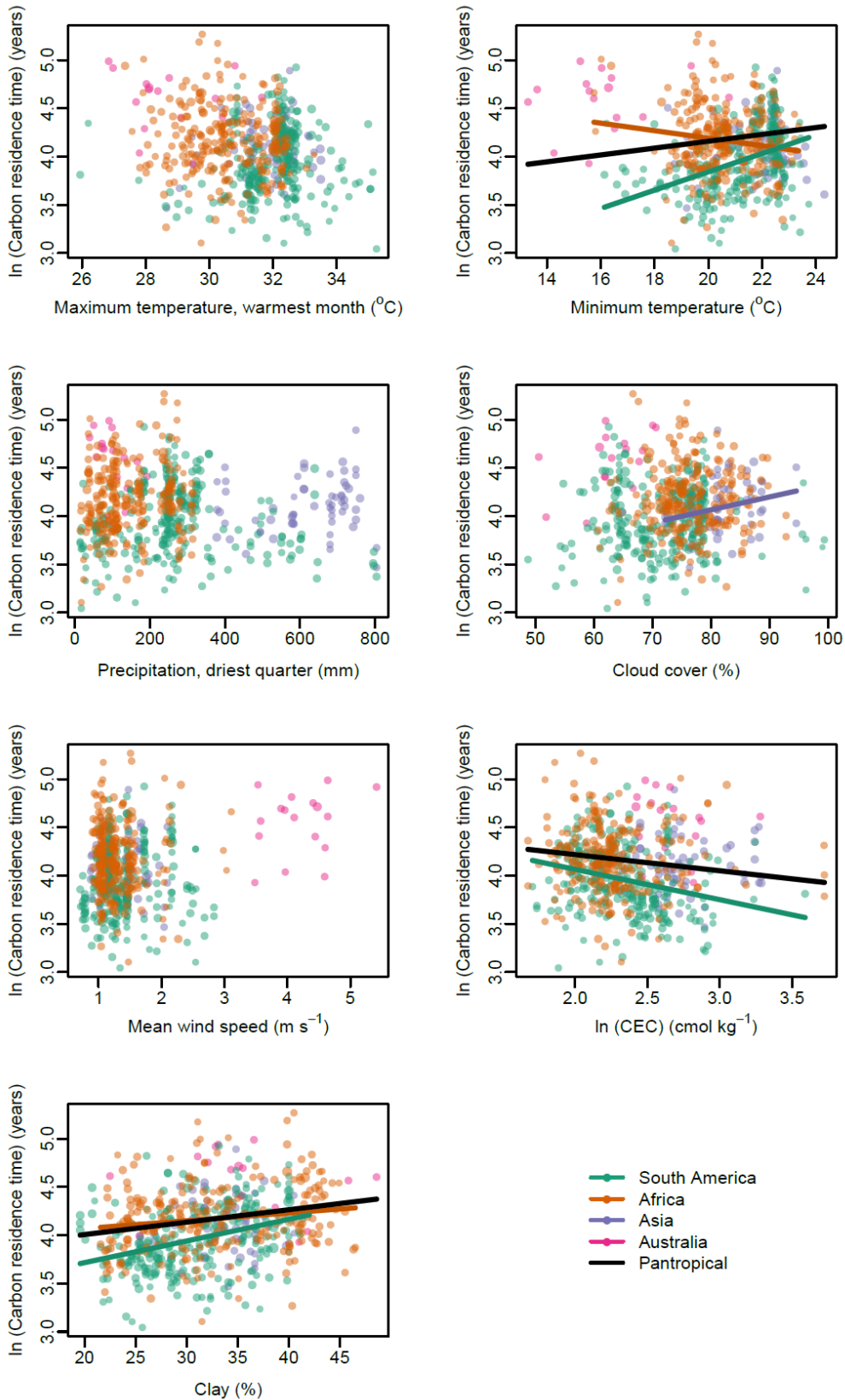
942 **Figure S8.** Relationships between aboveground tropical forest carbon stocks and environmental  
 943 predictors. Symbols and colours as in Fig. 3. Coloured lines show bivariate relationships in each  
 944 continent, and black lines show pan-tropical relationships also accounting for the effect of continent.  
 945 Lines are only plotted where statistically significant.



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948 **Figure S9.** As Fig. S8, but showing relationships with carbon gains.

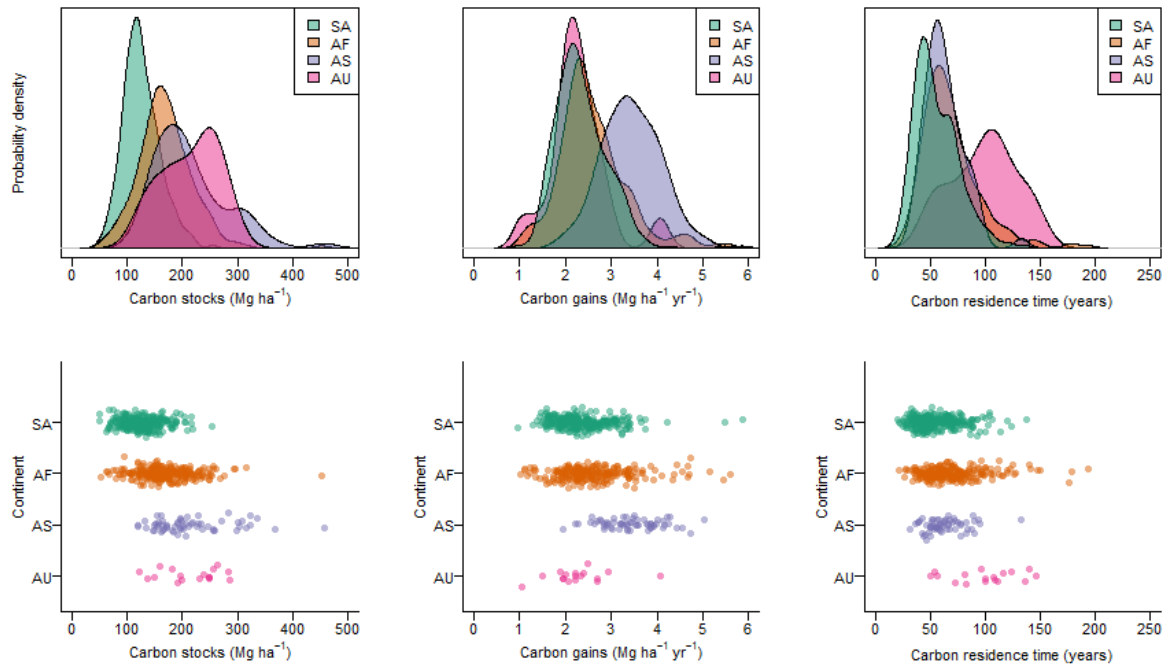


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950 **Figure S10.** As Fig. S8, but showing relationships with carbon residence time.

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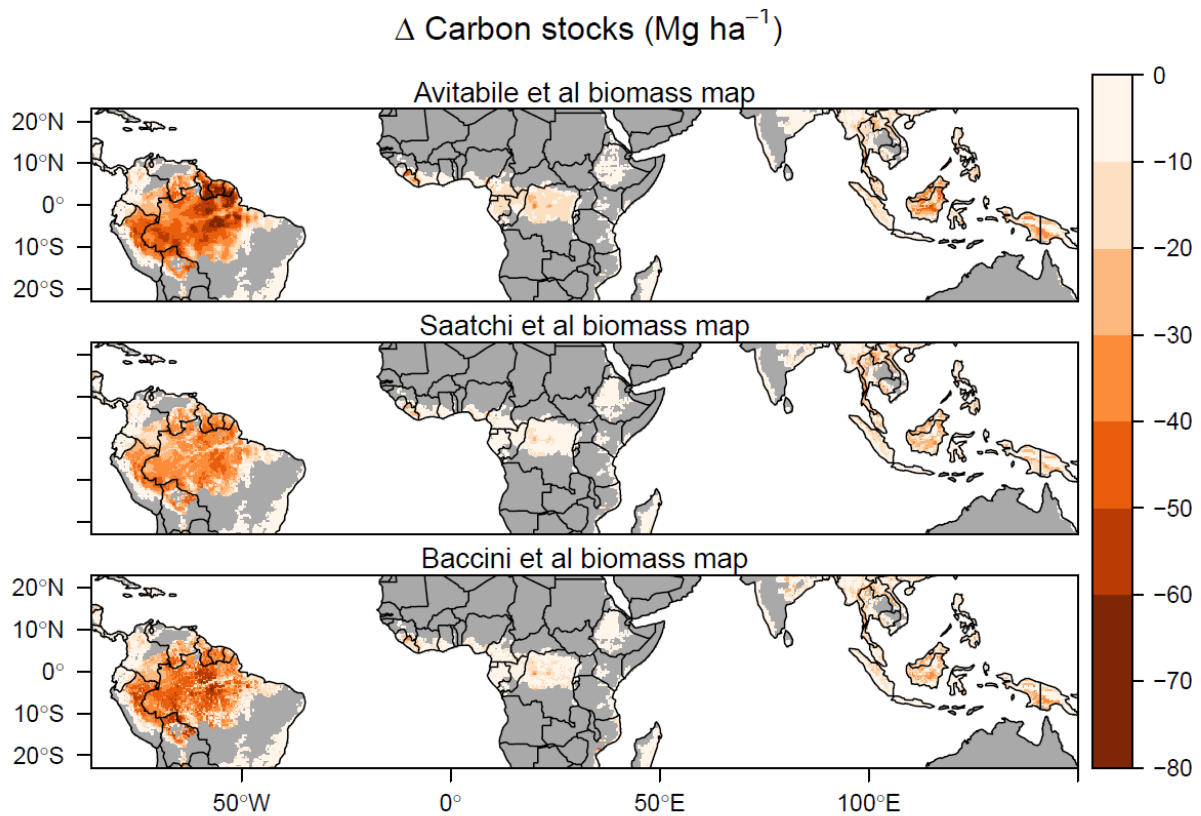




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953 **Figure S11.** Variation in tropical forest aboveground carbon stocks, gains and residence time within  
 954 and amongst continents. Data are presented as empirical probability density functions (top row) and  
 955 dot-plots showing raw data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

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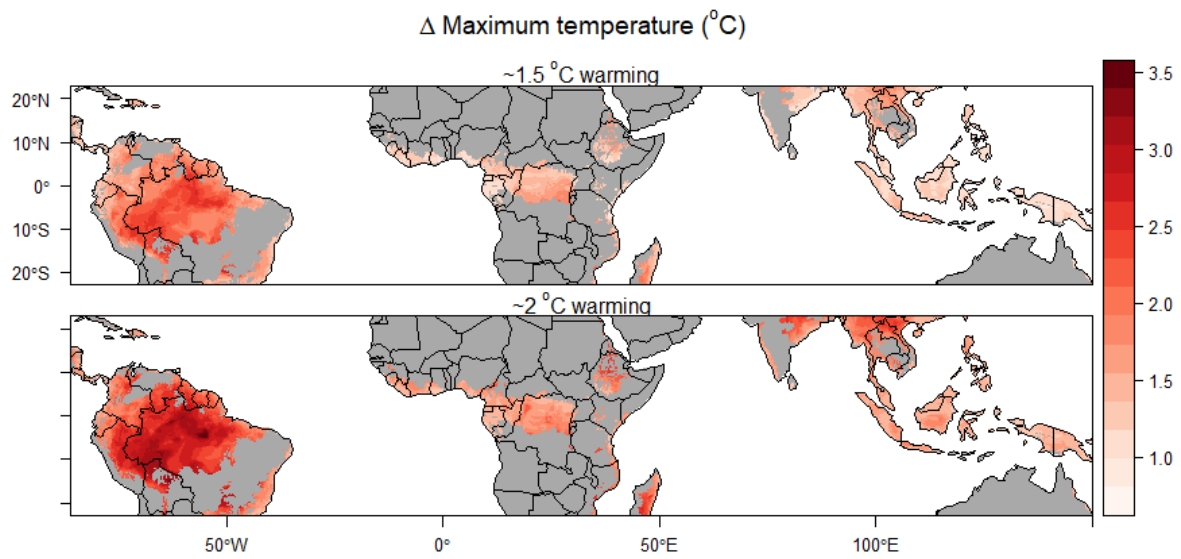
958

959 **Figure S12.** Effect of using earlier biomass reference maps for estimates of change in long-term  
960 carbon stocks for global temperature increases of  $\sim 2^\circ\text{C}$ . Using aboveground biomass stock maps from  
961 Saatchi et al. (64) and Baccini et al. (65) predicted biome-wide reductions in biomass carbon stocks  
962 are 24.0 Pg (95 % CI = 5.8 – 39.6) and 28.4 Pg (95 % CI = 16.1 – 37.5) respectively. Under the  $\sim$   
963 1.5 $^\circ\text{C}$  warming scenario these are 18.4 Pg (5.8 – 30.5) and 21.1 Pg (10.2 – 29.4) respectively. Results  
964 in the main text use the 2016 Avitabile et al. baseline map (30) – see methods for justification.

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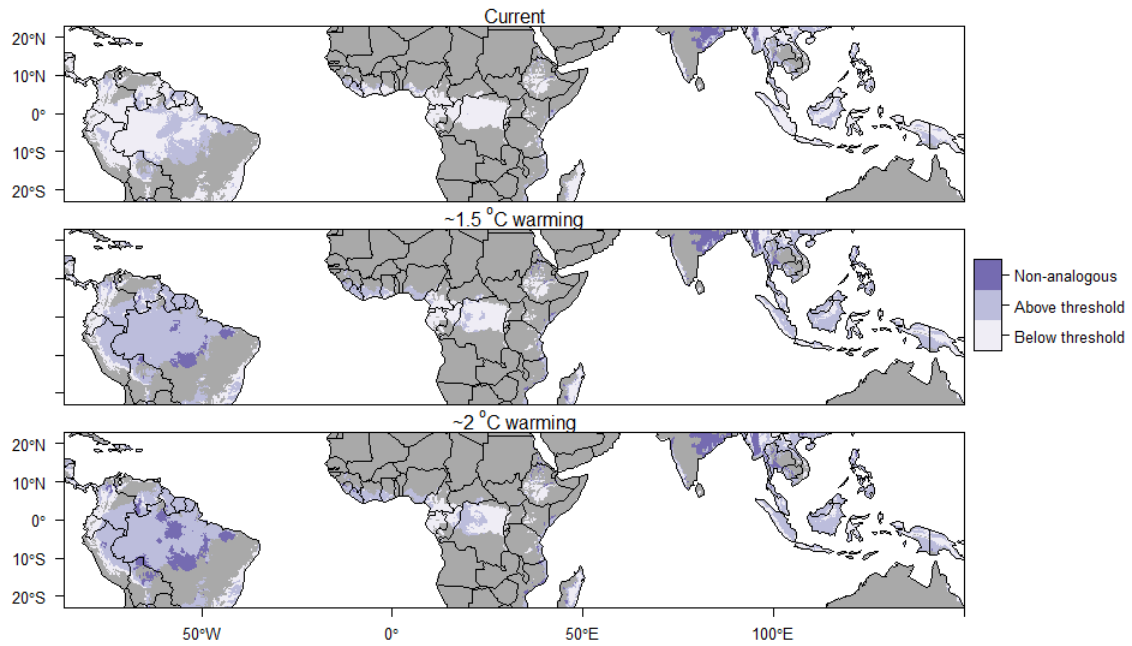
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969 **Figure S13.** Biome-wide change in mean daily maximum temperature in the warmest month from  
 970 present conditions (based on the Worldclim climatology, 1970-2000), given global increases in  
 971 temperature of approximately 1.5 $^{\circ}$ C and 2 $^{\circ}$ C above pre-industrial levels. These levels of global  
 972 temperature increase are obtained from, respectively, RCP 2.6, 2040-2060 and RCP 4.5, 2040-2060 to  
 973 represent the potential spatial pattern of warming associated with global temperatures stabilising at  
 974 these levels. Global temperature increases of 1.5 and 2 $^{\circ}$ C above pre-industrial levels (so  $\sim$ 0.8  $^{\circ}$ C and  
 975  $\sim$ 1.3  $^{\circ}$ C above our current baseline climate) would lead to mean increases in maximum temperature in  
 976 the warmest month across the tropical forest biome of 1.9 $^{\circ}$ C and 2.4 $^{\circ}$ C the current baseline climate  
 977 respectively.

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982 **Figure S14** Areas of the biome above or below the 32.2°C threshold, above which carbon stocks  
 983 decline more rapidly with temperature, under current conditions and two warming scenarios (see Fig.  
 984 4). Areas warmer than any currently observed in our dataset (35.2°C) are also shown (non-analogous  
 985 conditions). Note that even the 1.5°C warming scenario pushes most South American forests above  
 986 the 32.2°C threshold.

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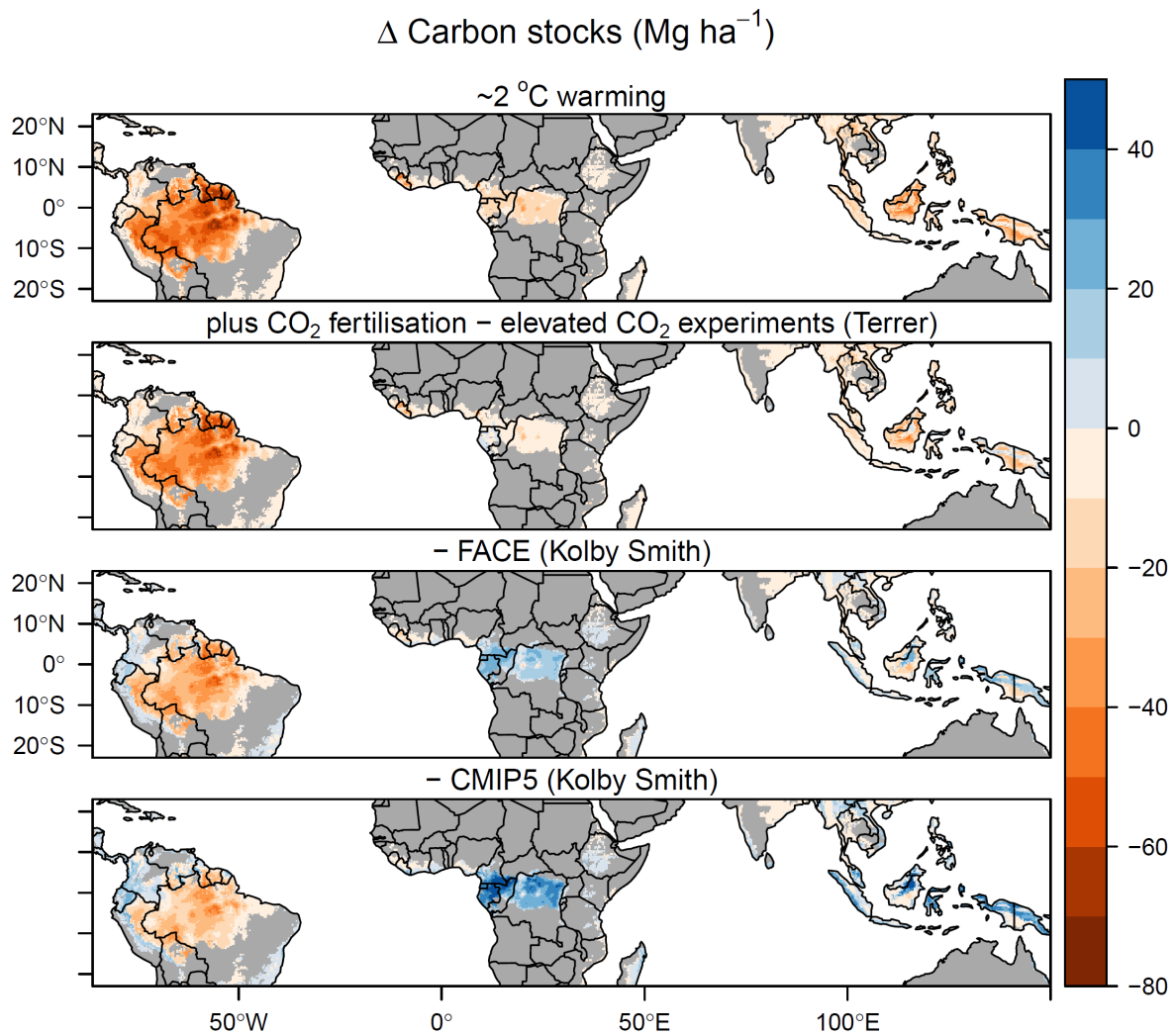
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994 **Figure S15.** Predicted long-term change in aboveground carbon stocks under  $\sim 2^\circ\text{C}$  global warming,  
 995 based on either temperature effects alone or when also accounting for carbon dioxide growth  
 996 stimulation. CO<sub>2</sub> fertilisation effects on equilibrium biomass levels were obtained from a recent  
 997 synthesis of results of elevated CO<sub>2</sub> experiments (Terrer et al. (76)), free-air CO<sub>2</sub> enrichment (FACE)  
 998 experiments (Kolby Smith et al. (73)) and CMIP5 earth system models (Kolby Smith et al. (73)).  
 999 Depending on their strength, CO<sub>2</sub> effects either partially or fully ameliorate the biome-wide negative  
 1000 effects of increasing temperatures on biomass carbon stocks (Table S3), but these carbon stocks are  
 1001 predicted to decline over much of Amazonia even under the strongest CO<sub>2</sub> effect considered.

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1003

1004 **Table S1.** Climate variables selected for analysis and mechanisms by which they can affect carbon stocks.

Climate property	Variable selected for analysis	Mechanism to affect carbon stocks
Daytime temperature	Maximum temperature in the warmest month <sup>1</sup>	High daytime temperatures exceed photosynthesis optima (82), increase evaporative stress, causing stomatal closure and reducing time for photosynthesis (26) and increase risk of mortality through hydraulic failure and/or carbon starvation (23).
Night-time temperature	Mean daily minimum temperature	Respiration rate increases with temperature so proportion of carbon taken through photosynthesis that is allocated to wood should decline with temperature (83). Increased respiration cost could also reduce tree longevity (23). As respiration occurs day and night, and photosynthesis only in the day, nighttime temperature should better reflect respiration effects and daytime temperature better reflect photosynthesis effects.
Moisture availability	Precipitation in the driest quarter <sup>2</sup>	Moisture availability could limit photosynthesis and hence carbon gains, with stomata closing when moisture availability is limiting. The risk of mortality through hydraulic failure or carbon starvation is higher when moisture is limiting (23), and this could also set a limit on potential tree size and hence tree longevity.
Light availability	Cloud frequency	Increased photosynthesis and hence AGWP when light availability is greatest (i.e. cloud cover is low) (84). Alternatively, light availability could have a negative effect due to high evapotranspiration stress when cloud cover is low.
Wind speed	Mean wind speed	Carbon stocks are expected to be lower where physical damage through wind throw or breakage is higher, as carbon is removed more quickly from the system through mortality (85). But there is potential for greater carbon gains if forests are more dynamic.

1005 <sup>1</sup> Mean daily temperature in the warmest month (bio5) was selected instead of mean daily maximum temperature as it was more strongly decoupled from  
1006 other climate variables. VPD could also represent some of these effects, but was too strongly correlation with maximum temperature to include as an  
1007 independent variable.

1008 <sup>2</sup> Moisture availability could also be represented by MCWD (maximum cumulative water deficit) or total precipitation, but only one of the three variables  
1009 could be included in the model due to collinearity. MCWD was excluded as it is zero truncated, so less amenable to regression fitting.

1010

1011 **Table S2.** Coefficients of model-averaged general linear models of carbon stocks, gains and residence time as a function of climate, soil, continent and spatial  
 1012 autocorrelation. Coefficients are AIC weighted averages across models with  $\Delta\text{AIC} < 4$  from the best performing model; variables are given a score of zero if  
 1013 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.

Variable	Carbon stocks				Carbon gains				Carbon residence time			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
Intercept - Africa	4.986	0.010	476.9	<0.001	0.571	0.525	1.09	0.278	3.909	0.688	5.67	<0.001
Minimum temperature	0.031	0.019	1.67	0.096	-0.001	0.007	0.18	0.861	0.019	0.022	0.88	0.381
Maximum temperature, warmest month	-0.089	0.022	4.11	<0.001	-0.060	0.017	3.47	<0.001	-0.001	0.015	0.10	0.924
Precipitation, driest quarter	0.045	0.018	2.54	0.011	-0.001	0.008	0.14	0.887	0.061	0.023	2.70	0.007
Cloud frequency	0.002	0.008	0.24	0.814	-0.006	0.011	0.54	0.592	0.025	0.021	1.17	0.241
Wind speed	0.004	0.012	0.38	0.705	0.016	0.020	0.78	0.437	-0.004	0.015	0.24	0.807
Soil texture (% clay)	0.021	0.017	1.26	0.208	-0.005	0.011	0.49	0.628	0.040	0.018	2.17	0.030
Soil fertility (CEC)	-0.003	0.009	0.34	0.732	0.005	0.011	0.51	0.613	-0.012	0.017	0.70	0.486
MEM1	0.115	0.014	7.96	<0.001	0.319	0.559	0.57	0.569	0.375	0.734	0.51	0.610
MEM2	0.098	0.017	5.67	<0.001	0.083	0.273	0.30	0.762	0.286	0.359	0.80	0.427
MEM3	-0.025	0.014	1.84	0.065	0.014	0.041	0.34	0.735	0.007	0.054	0.12	0.904
MEM4	-0.021	0.011	1.84	0.066	-0.038	0.020	1.84	0.066	-0.002	0.027	0.07	0.945
MEM5	0.027	0.011	2.46	0.014	0.020	0.015	1.33	0.182	0.020	0.020	0.98	0.327
MEM6	0.017	0.011	1.56	0.118	0.025	0.011	2.34	0.019	-0.014	0.014	1.05	0.293
MEM7	0.010	0.011	0.93	0.353	-0.017	0.010	1.61	0.107	0.036	0.014	2.57	0.010
MEM8	-0.072	0.013	5.64	<0.001	0.057	0.012	4.91	<0.001	-0.127	0.016	7.80	0.000
Asia	NA				0.380	0.542	0.70	0.485	-0.753	0.683	1.10	0.271
Australia	NA				-0.173	0.390	0.44	0.658	0.006	0.516	0.01	0.990
South America	NA				0.643	1.164	0.55	0.582	0.542	1.530	0.35	0.724

1015 **Table S3.** Predicted biome-wide changes in long-term biomass carbon stocks (scaled to include root  
 1016 biomass) under global temperature increases of  $\sim 1.5^\circ\text{C}$  and  $\sim 2^\circ\text{C}$ . Changes are based on temperature  
 1017 effects alone, and when also accounting for the effect of increased  $\text{CO}_2$  concentrations on tree growth.  
 1018  $\text{CO}_2$  effects were obtained from a synthesis of results of elevated  $\text{CO}_2$  experiments (Terrer et al. (76)),  
 1019 free-air  $\text{CO}_2$  enrichment (FACE) experiments (Kolby Smith et al. (73)) and CMIP5 earth system  
 1020 models (Kolby Smith et al. (73)). 95% confidence intervals around changes (based on uncertainties in  
 1021 temperature effects alone) are shown in parentheses.

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

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