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Long-term thermal sensitivity of Earth's tropical forests

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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 Mg C ha^{-1} °C^{-1}), primarily by reducing woody productivity, and

7 with a greater rate of decline in the hottest forests (>32.2 °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.

7

13   <u>Main text</u>

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_2 fertilisation (i.e. β) and negative responses to warmer temperatures and any

17   change in precipitation (i.e. γ). 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 Pg C $°C^{-1}$ 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 (γ) 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

8

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 Mg C ha^{-1} 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°C increase in

62 maximum temperature, 95 % CI = -8.6 to -3.1 %, Fig. 2, equivalent to -9.1 Mg C ha^{-1} °C^{-1} for a stand

63 with the mean carbon stocks in our dataset, 154.6 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 Mg C ha^{-1} 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

9

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 (Δ 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 (Δ AIC = 11.9) rather than reducing carbon gains (model without interaction better, Δ 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, Δ 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 % $°C^{-1}$, warmer than breakpoint: -14.7 % $°C^{-1}$,

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 (Δ AIC = 10.6) rather than gains (Δ AIC = 1.7).

93   Overall, our results thus indicate two separate climate controls on carbon stocks: a negative linear

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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_2

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

11

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 $°C^{-1}$),

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_2 fertilisation is expected to reduce temperature induced

12

148 carbon losses from biomass across the tropics (Table S3), our analysis indicates that CO_2 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.

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412 **Supplementary Materials:**

413 Materials and Methods

414 Figures S1-S15

415 Tables S1-S3

416 References (32-85)

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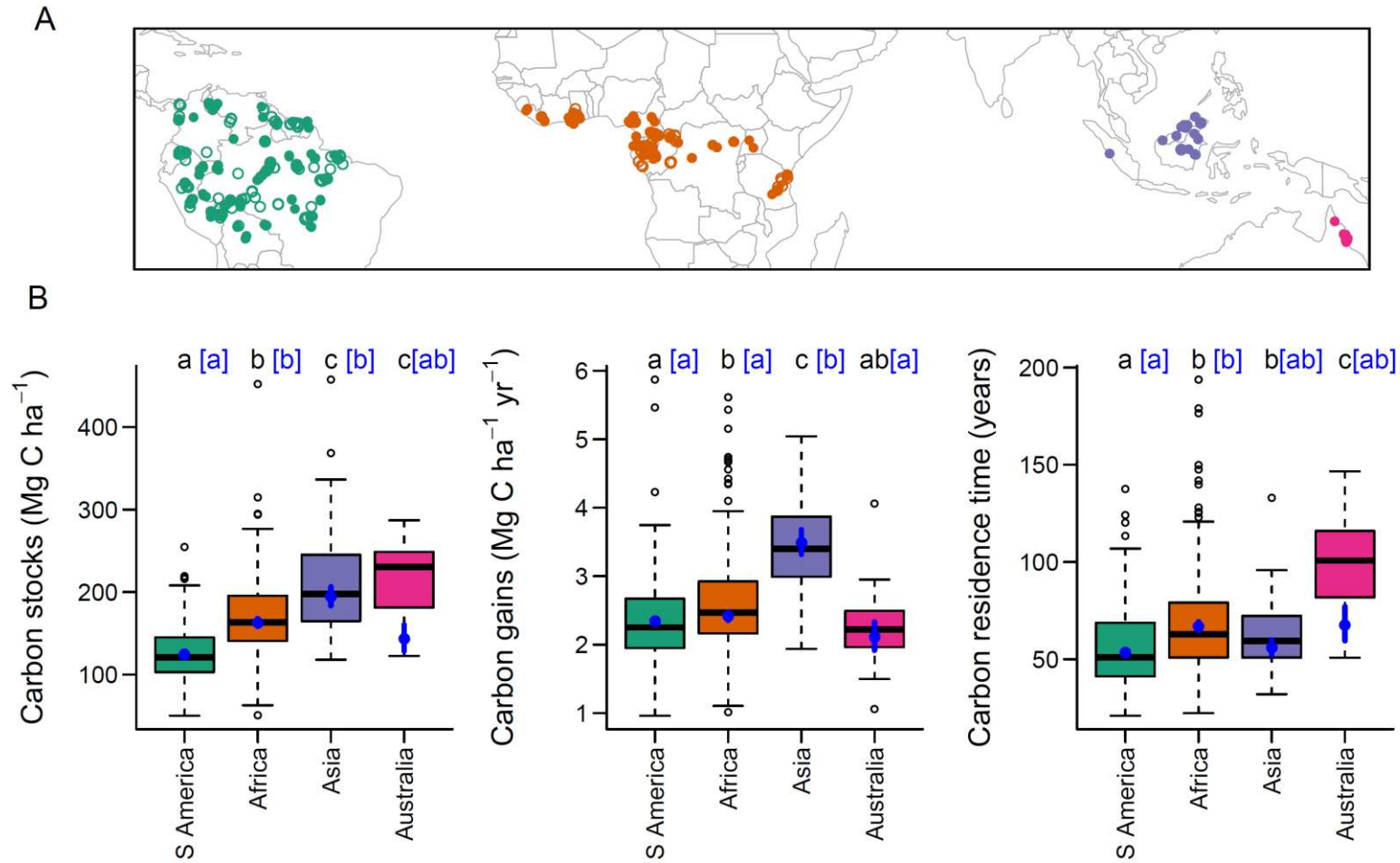
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419 **Figure 1.** Spatial variation in tropical forest carbon. (A) Our plot network. Filled symbols show multi-census plots used in the main analysis, open symbols
420 show single-census plots used as an independent dataset. (B) Variation in carbon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

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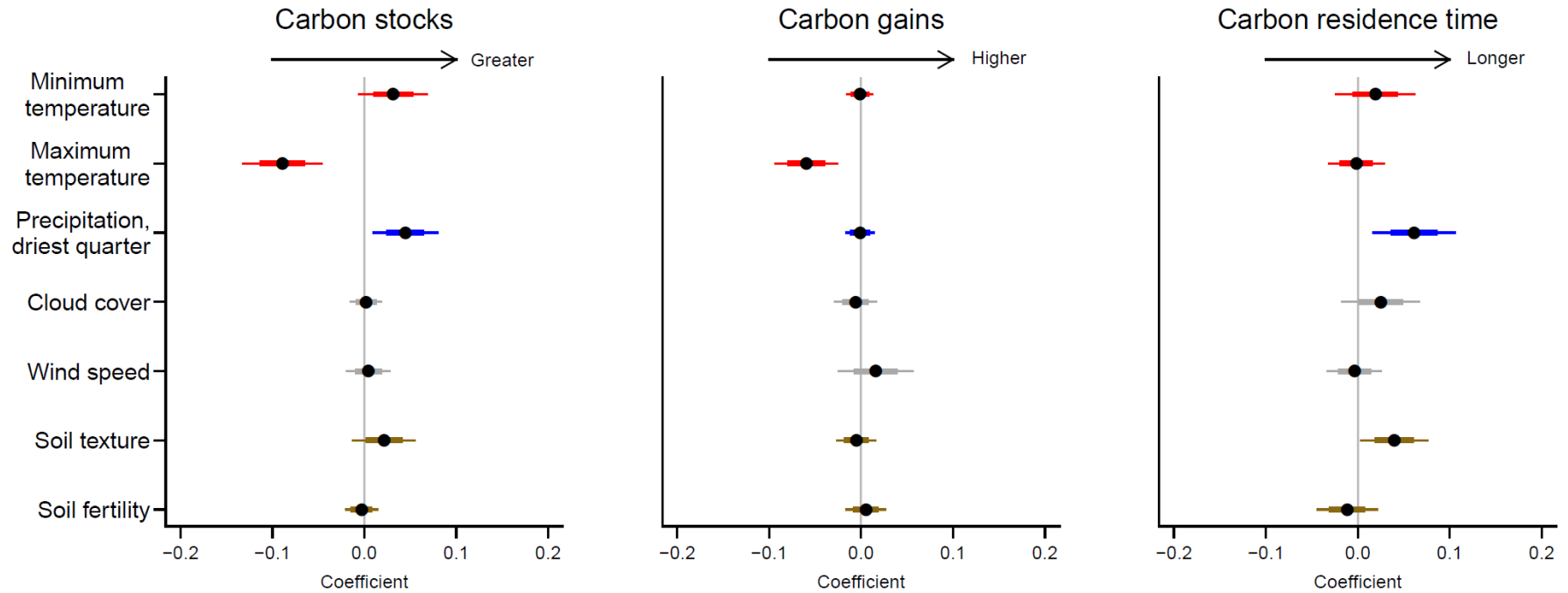
Figure 2. Correlates of spatial variation in tropical forest carbon. Points show coefficients from model-averaged general linear models. Variables that did not occur in well-supported models are shrinkage adjusted towards zero. Coefficients are standardised so that they represent change in the response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

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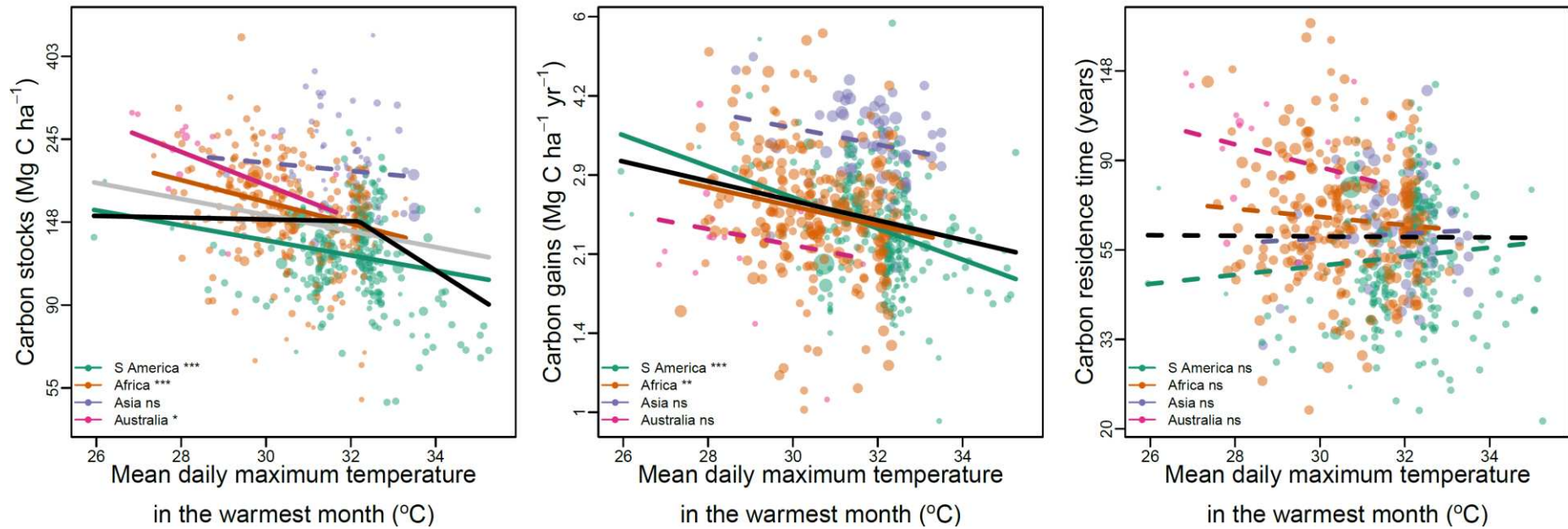
Figure 3. Temperature effects on tropical forest carbon stocks, carbon gains from woody productivity and carbon residence time. Black lines show the best pan-tropical relationships accounting for environmental covariates. The grey line shows the additional linear pan-tropical relationship for carbon stocks. Coloured lines show bivariate relationships within each continent. Statistically significant relationships are shown with solid lines, non-significant with dashed lines. 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 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 better sampled continents. For carbon residence time, relationships with temperature are non-significant but there is a statistically significant interaction between maximum temperature and precipitation in the driest quarter (Figure S6). Relationships with other variables are shown in Fig. S8-S10. *** P < 0.001, ** P < 0.01, * P < 0.05, ns P ≥ 0.05

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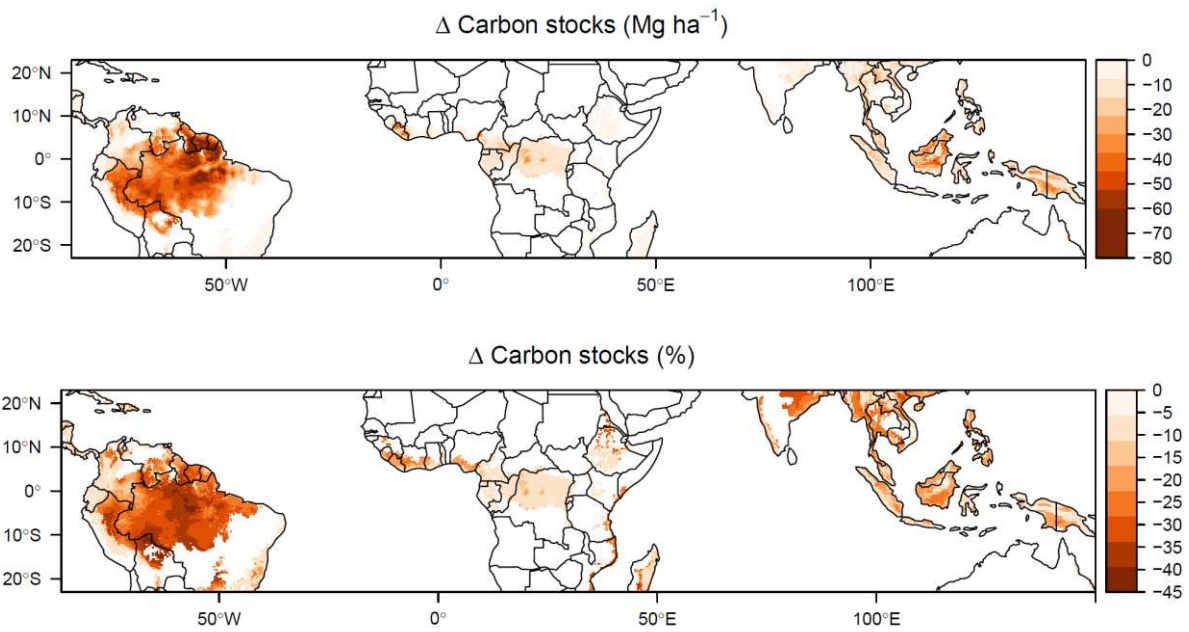
446

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_2 (see Fig. S15 for analysis incorporating this).

453

454

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

456   **Forests**

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470   Collins[61], James A. Comiskey[62,63], Fernando Cornejo Valverde[64], Massiel Corrales Medina[65], Lola da
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483   Lovett[1], Richard Lowe[111], William E. Magnusson[112], Jagoba Malumbres-Olarte[113,114], Ângelo Gilberto
484   Manzatto[115], Ben Hur Marimon Junior[116], Andrew R. Marshall[8,117,118], Toby Marthews[119], Simone Matias de
485   Almeida Reis[14,19], Colin Maycock[120], Karina Melgaço[1], Casimiro Mendoza[121], Faizah Metali[122], Vianet
486   Mihindou[123,124], William Milliken[104], Edward Mitchard[125], Paulo S. Morandi[14], Hannah L. Mossman[2], Laszlo
487   Nagy[126], Henrique Nascimento[6], David Neill[127], Reuben Nilus[128], Percy Núñez Vargas[95], Walter Palacios[129],
488   Nadir Pallqui Camacho[1,95], Julie Peacock[1], Colin Pendry[130], Maria Cristina Peñuela Mora[131], Georgia C.
489   Pickavance[1], John Pipoly[132], Nigel Pitman[133], Maureen Playfair[134], Lourens Poorter[135], John R. Poulsen[25],
490   Axel D. Poulsen[136], Richard Preziosi[2], Adriana Prieto[137], Richard Primack[138], Hirma Ramírez-Angulo[139], Jan
491   Reitsma[140], Maxime Réjou-Méchain[75], Zorayda Restrepo Correa[141], Thaiane Rodrigues de Sousa[6], Lily
492   Rodriguez Bayona[142], Anand Roopsind[143], Agustín Rudas[137], Ervan Rutishauser[42,144], Kamariah Abu
493   Salim[122], Rafael P. Salomão[145,146], Juliana Schietti[6], Douglas Sheil[147], Richarlly C. Silva[57,148], Javier Silva
494   Espejo[149], Camila Silva Valeria[38], Marcos Silveira[57], Murielle Simo-Droissart[17], Marcelo Fragomeni
495   Simon[70], James Singh[150], Yahn Carlos Soto Shareva[15], Clement Stahl[54], Juliana Stropp[151], Rahayu Sukri[122],
496   Terry Sunderland[152,153], Martin Svátek[154], Michael D. Swaine[155], Varun Swamy[156], Hermann Taedoumg[17],
497   Joey Talbot[1], James Taplin[157], David Taylor[158], Hans ter Steege[159,160], John Terborgh[25], Raquel Thomas[143],
498   Sean C. Thomas[161], Armando Torres-Lezama[162], Peter Umunay[163,164], Luis Valenzuela Gamarra[15], Geertje
499   van der Heijden[165], Peter van der Hout[166], Peter van der Meer[167], Mark van Nieuwstadt[168], Hans Verbeeck[99],
500   Ronald Vernimmen[169], Alberto Vicentini[6], Ima Célia Guimarães Vieira[146], Emilio Vilanova Torre[170], Jason
501   Vleminckx[36], Vincent Vos[172], Ophelia Wang[173], Lee J. T. White[124,174,175], Simon Willcock[176], John T.
502   Woods[177], Verginia Wortel[178], Kenneth Young[179], Roderick Zagt[180], Lise Zemagho[17], Pieter A. Zuidema[50],
503   Joeri A. Zwerts[178,181], Oliver L. Phillips[1]

504

2

Supporting information for Sullivan et al.

505 **This file includes:**

506 Materials and Methods

507 Figures S1 – S15

508 Tables S1 – S2

509

3

510 **Materials and Methods**

511 <u>Forest census data</u>

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 ≥ 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 supress 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 ≥ 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_{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 ≥ 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 (≤ 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).

4

544

545   <u>Estimating above-ground biomass</u>

546   Diameter measurements were converted to estimates of aboveground biomass (AGB). For dicot trees

547   we used the allometric equation

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

549   from Chave et al. (40), where ρ 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   $\ln(AGB) = -3.3488 + 2.7483.\ln(D)$,   [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 ≤ 90 m, diameters ≥ 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   $H = a(1-\exp(-bD^C))$,   [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

5

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

577   continent.

578

579   <u>Estimating above-ground woody production</u>

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_{death}) can then be

596   estimated as

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

598   where D_{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 mm > D ≥ 200 mm, and D ≥ 400 mm) and Y_{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_{surv}) is

6

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    $D_{death} = 100 + (G \times Y_{mean-rec})$ [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   <u>Obtaining environmental data</u>

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

7

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 – vapour

646 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 ~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 (°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 <u>Statistical analysis</u>

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 colinearity within this set of explanatory variables using

671 variance inflation factors (VIF) and pairwise correlations. Because of colinearity, 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

8

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 the 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, Area $^{1/3}$; carbon gains, Monitoring length $^{1/7}$; carbon residence time, Area $^{1/9}$ + Monitoring

693 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 Δ 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

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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 <u>Validation with independent single-census plot dataset</u>

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.

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742   <u>Scaling results to the biome</u>

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 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 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°C increase to all

773   locations. Secondly, we assessed the consequence of global temperatures stabilizing 1.5°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°C above pre-industrial levels. For the

776   latter two we obtained data from CMIP5 climate models, using downscaled future climate projections

11

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_2 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_2 concentrations of 443

797   ppm and 487 ppm respectively (72). We cannot assess the effect of CO_2 on biomass from our spatial

798   dataset, so instead used independent estimates of CO_2 effects from other sources. Firstly, we obtained

799   CO_2 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_2 concentration. To

802   propagate this through to changes in AGB under future CO_2 conditions we first estimated the

803   logarithmic dependency of NPP on CO_2 (74) by substituting values of NPP and CO_2 at time zero and t

804   (from (73)) into the equation,

805     $$NPP_t = NPP_0 \left[1 + \beta \ln\left(\frac{[CO_2]_t}{[CO_2]_0}\right) \right]$$ 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_2 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^{-1} yr^{-1} (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    $$\frac{dM_{wood}}{dt} = \alpha_{wood} N_P - \frac{M_{wood}}{\tau_{wood}}$$ Equation 8

814   where M_{wood} is woody biomass, N_p is NPP, α_{wood} is the allocation of NPP to wood (taken as 0.33, the

815   mean value across nine plots from (75)) and τ_{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_2 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_2 effects.

821   The effects of CO_2 in earth system models have been reported to be larger than those deduced from

822   satellite data or CO_2 enrichment experiments (73), so we also ran the above model using changes in

823   NPP reported from a synthesis of free-air CO_2 enrichment experiments conducted in forests (73).

824   Finally, we looked at the impact of using CO_2 effects derived from a recent large meta-analysis of

825   CO_2 enrichment experiments (76), which reported a 12.5 % increase in biomass of tropical trees for a

826   250 ppm increase in CO_2 concentration. As this relationship was reported to be linear (76) we used

827   linear interpolation to estimate the change in biomass under CO_2 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_2 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_2 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_2 (76).

835   <u>Temperature sensitivity of CMIP5 models</u>

836   The temperature sensitivity (γ_{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_2 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_2 concentration, but in the uncoupled simulation temperature is not directly

841   affected by this increase in CO_2.

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 ($\Delta Cveg_C$)

847   and uncoupled ($\Delta Cveg_U$) simulation, and this was then divided by the change in tropical land

848   temperature (ΔT) to obtain the temperature sensitivity of the model,

849    $\gamma_{LT} = (\Delta Cveg_C - \Delta Cveg_U) / \Delta T$ Equation 9.

850   We calculated the temperature sensitivity of the six CMIP5 models that report vegetation carbon:

851   CESM-1-BGC (γ_{LT} = -0.7 Pg C °C^{-1}), GFDL-ESM2M (γ_{LT} = -58.4 Pg C °C^{-1}), HadGEM2-ES (γ_{LT} = -

852   9.2 Pg C °C^{-1}), IPSL-CM5A-LR (γ_{LT} = -11.3 Pg C °C^{-1}), MPI-ESM-LR (γ_{LT} = -22.8 Pg C °C^{-1}) and

853   NorESM1-ME (γ_{LT} = -1.0 Pg C °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.
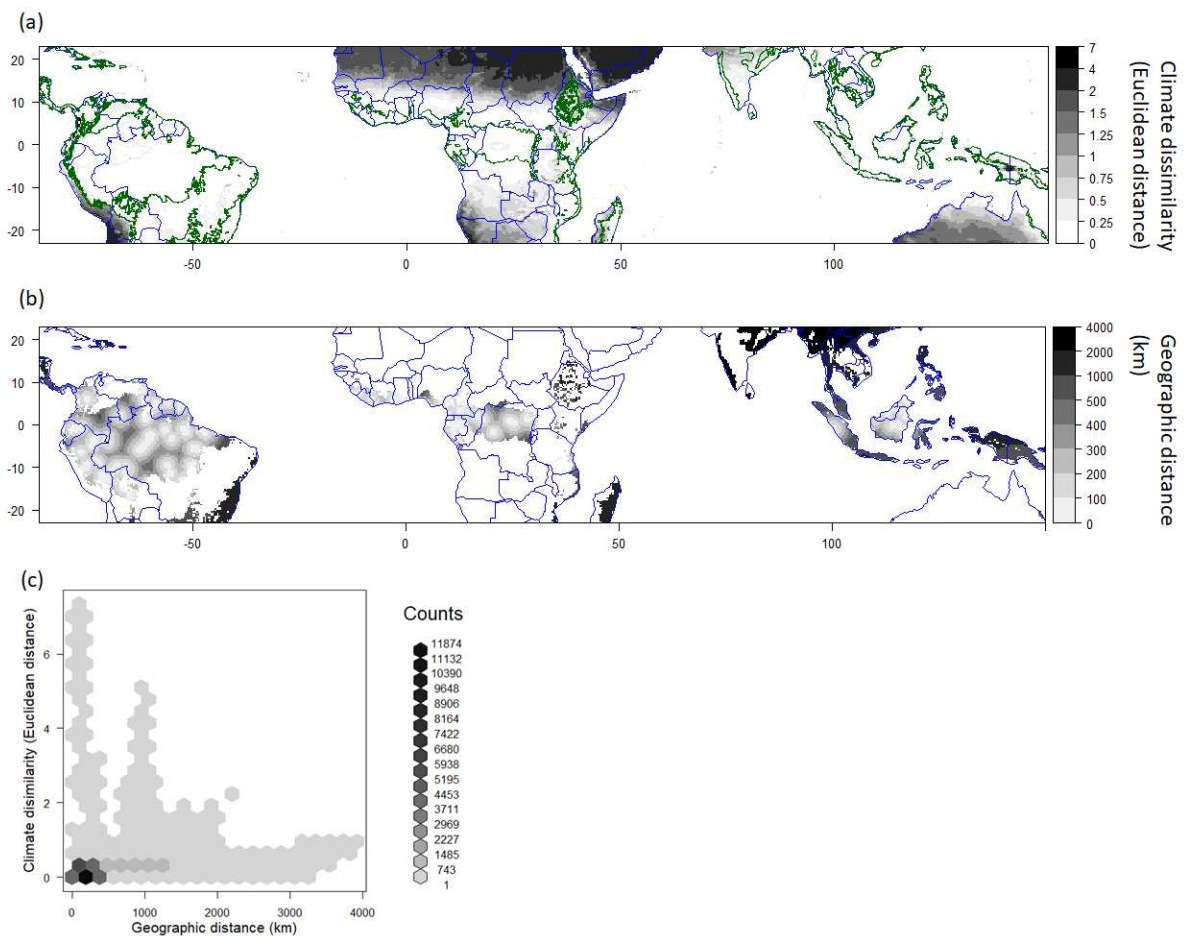
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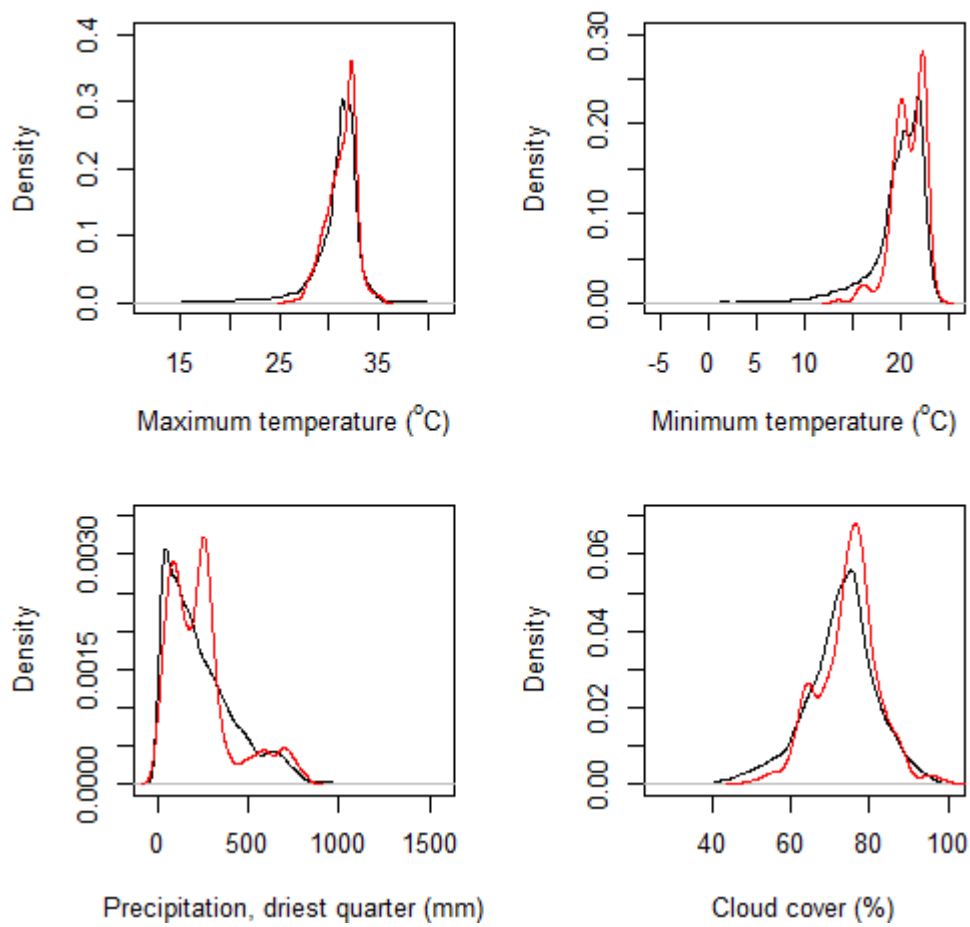
Figure S1. Climate space represented by our plot network. Red lines show the probability density

function of each variable in our multi-census plot network. Black lines show the probability density

across 10 minute grid-cells in the biome, restricted to areas with forest cover in GLC 2000 (80).

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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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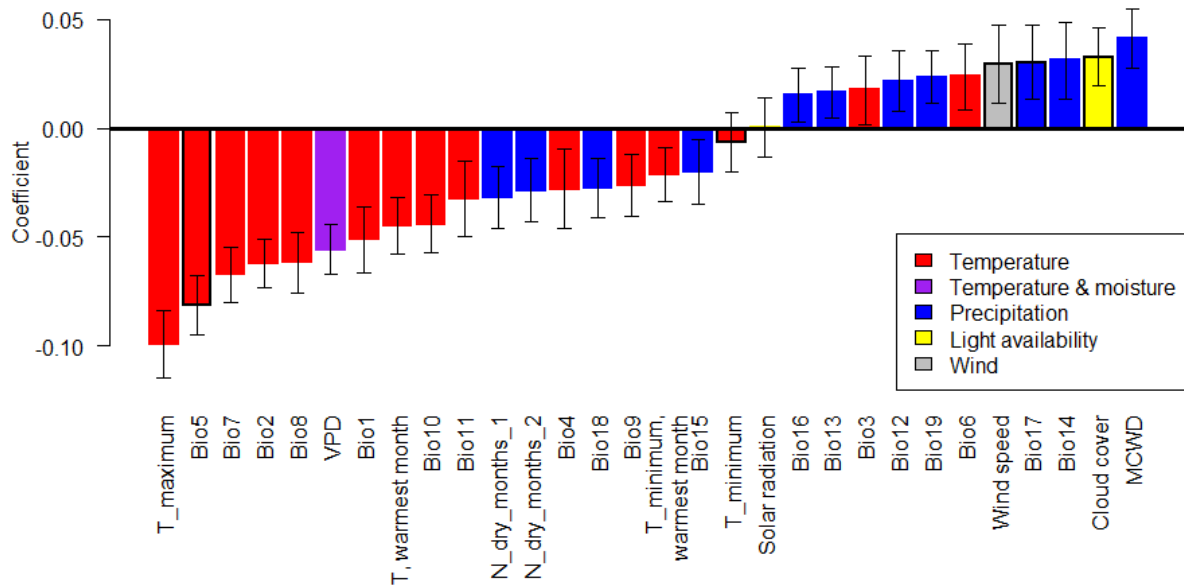
879 **Figure S3.** Relationships between individual climate variables and tropical forest aboveground carbon
880 stocks. Standardised coefficients are from models with the climate variable and continent as
881 explanatory variables and show change in ln(carbon) for a standard deviation change in the
882 explanatory variable. Error bars show standard errors. Variables used in the main analysis have black
883 outlines. Full variable names are: T_maximum – mean daily maximum temperature, Bio5 – mean
884 daily maximum temperature in the warmest month, Bio7 – annual temperature range, Bio2 – mean
885 diurnal temperature range, Bio8 – mean temperature in the wettest quarter, VPD – vapour pressure
886 deficit, Bio1 – mean annual temperature, Bio10 – mean temperature in the warmest quarter, Bio11 –
887 mean temperature in the coldest quarter, N_dry_months_1 – number of months with negative
888 cumulative water deficit, N_dry_months_2 – number of months where precipitation is less than
889 evapotranspiration, Bio4 – temperature seasonality, Bio18 – precipitation in the warmest quarter, Bio9
890 – mean temperature in the driest quarter, T_minimum warmest month – mean daily minimum
891 temperature in the warmest month, Bio15 – precipitation seasonality, T_minimum – mean daily
892 minimum temperature, Bio16 – precipitation in the wettest quarter, Bio13 – precipitation in the
893 wettest month, Bio3 – isothermality, Bio12 – annual precipitation, Bio19 – precipitation in the coldest
894 quarter, Bio6 – mean daily minimum temperature in the coldest month, Wind speed – mean daily
895 wind speed, Bio17 – precipitation in the driest quarter, Bio14 – precipitation in the driest month,
896 Cloud cover – proportion of MODIS passes with cloud present, MCWD – maximum cumulative
897 water deficit (note this is negative when water deficit is high, so a positive relationship with MCWD
898 indicates higher carbon when water deficits are less).

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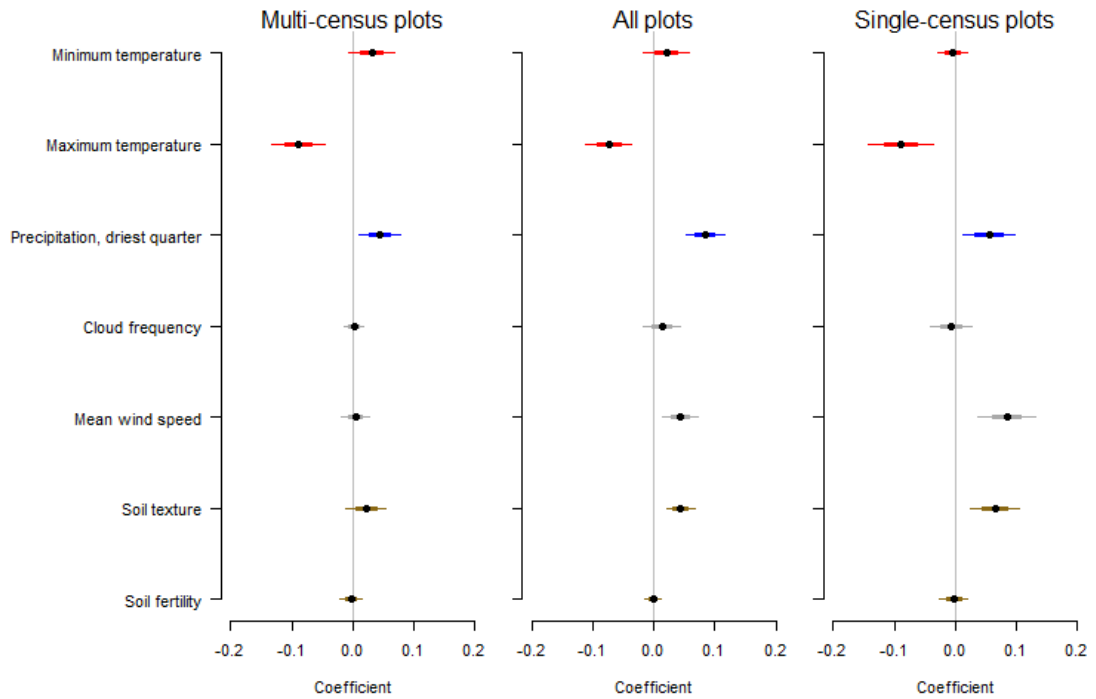
Figure S4. Validation of tropical forest carbon stock sensitivity model against an independent dataset of 223 single-census plots from our networks measured with the same protocols. Model-averaged shrinkage adjusted coefficients from multiple regression models of biomass carbon stocks as a function of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

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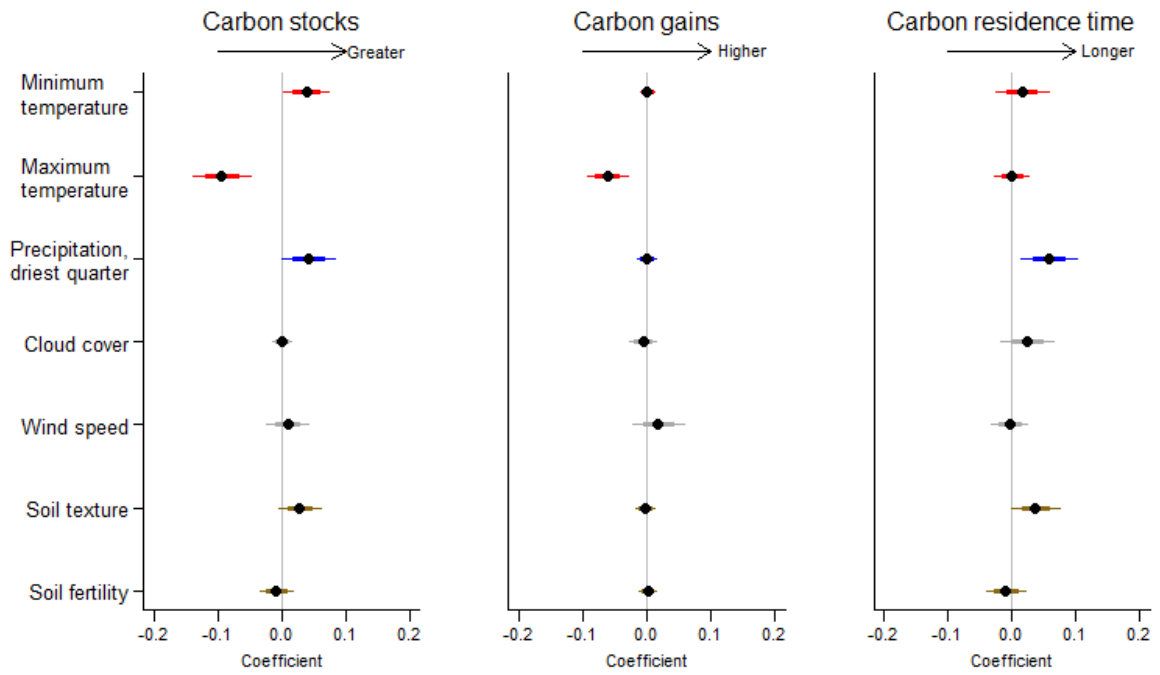
914 **Figure S5.** As Figure 2, but with aboveground biomass estimated using the Chave et al. 2005 (81)
915 moist forest allometric equation, which does not include a height term and is instead based on a third-
916 order polynomial relationship between diameter and aboveground biomass. This indicates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

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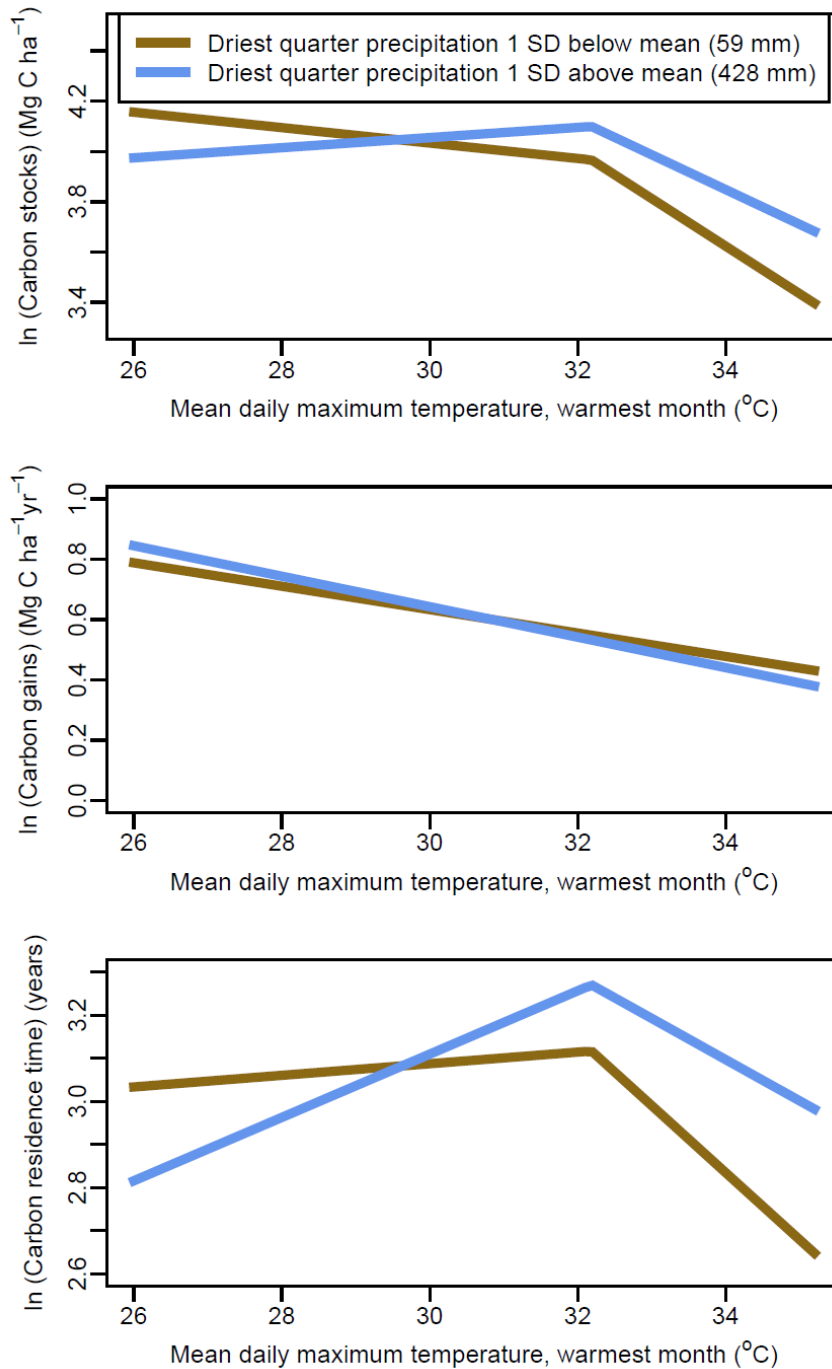
Figure S6. Interaction between mean daily maximum temperature in the warmest month and precipitation in the driest quarter in determining aboveground tropical forest carbon stocks, gains and residence time. Modelled relationships with temperature are shown holding precipitation either one standard deviation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

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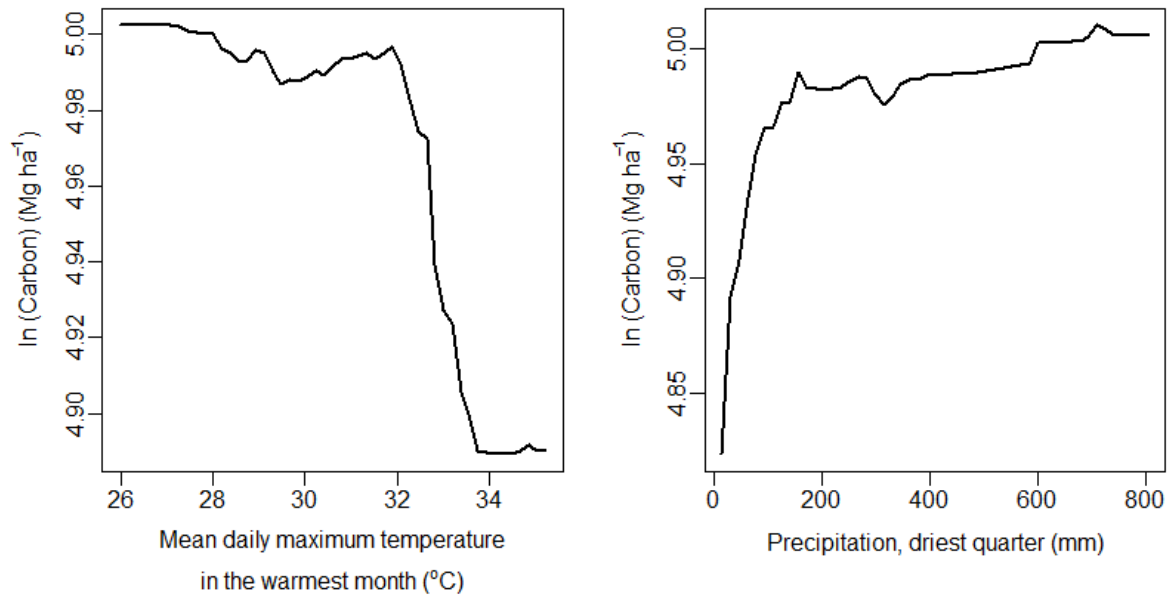
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932 **Figure S7.** Partial relationships between tropical forest carbon stocks and the two climate variables
933 identified to be most important by the random forest decision tree algorithm. Partial plots show
934 predicted values of carbon stocks 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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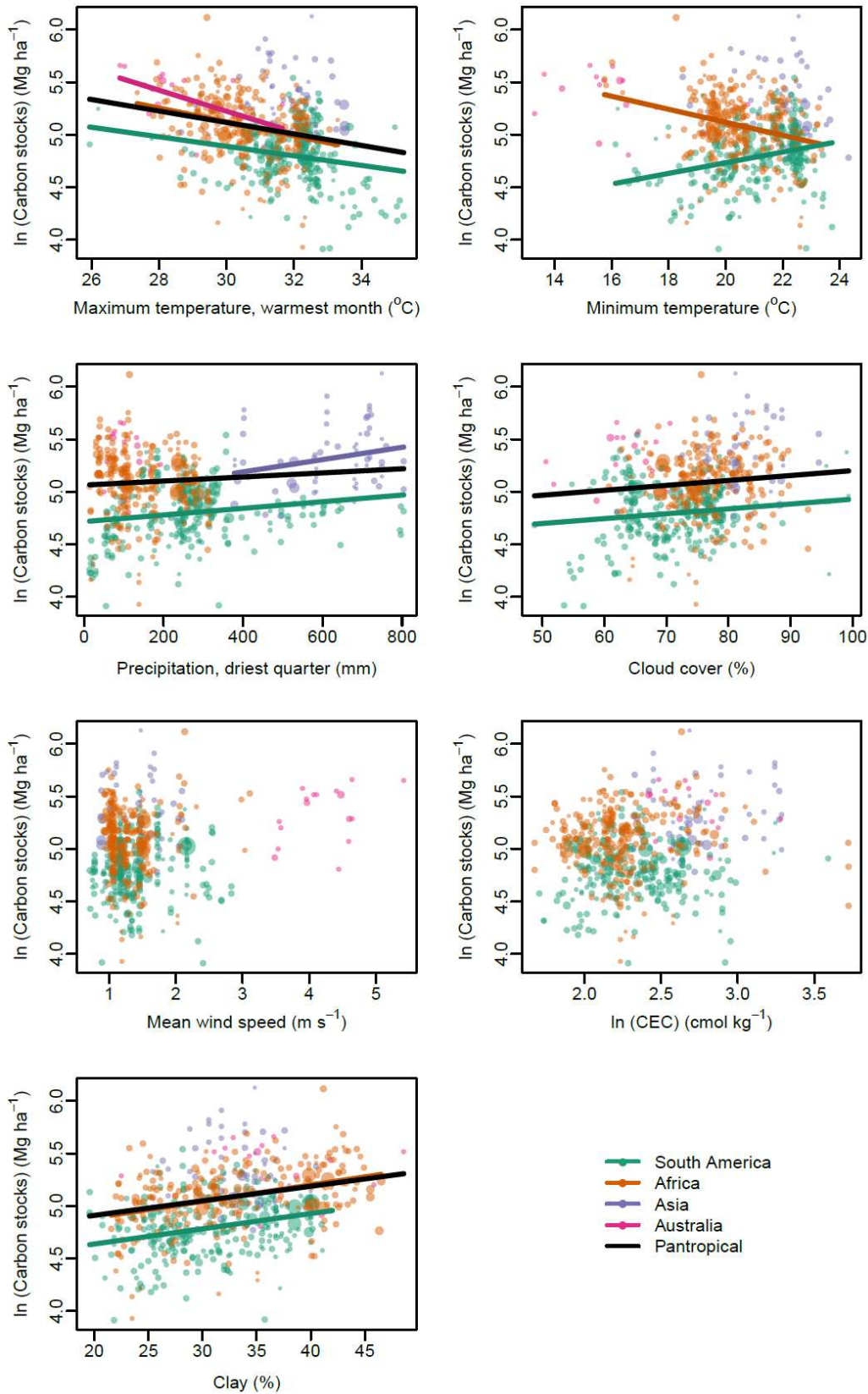
Figure S8. Relationships between aboveground tropical forest carbon stocks and environmental predictors. Symbols and colours as in Fig. 3. Coloured lines show bivariate relationships in each continent, and black lines show pan-tropical relationships also accounting for the effect of continent. Lines are only plotted where statistically significant.
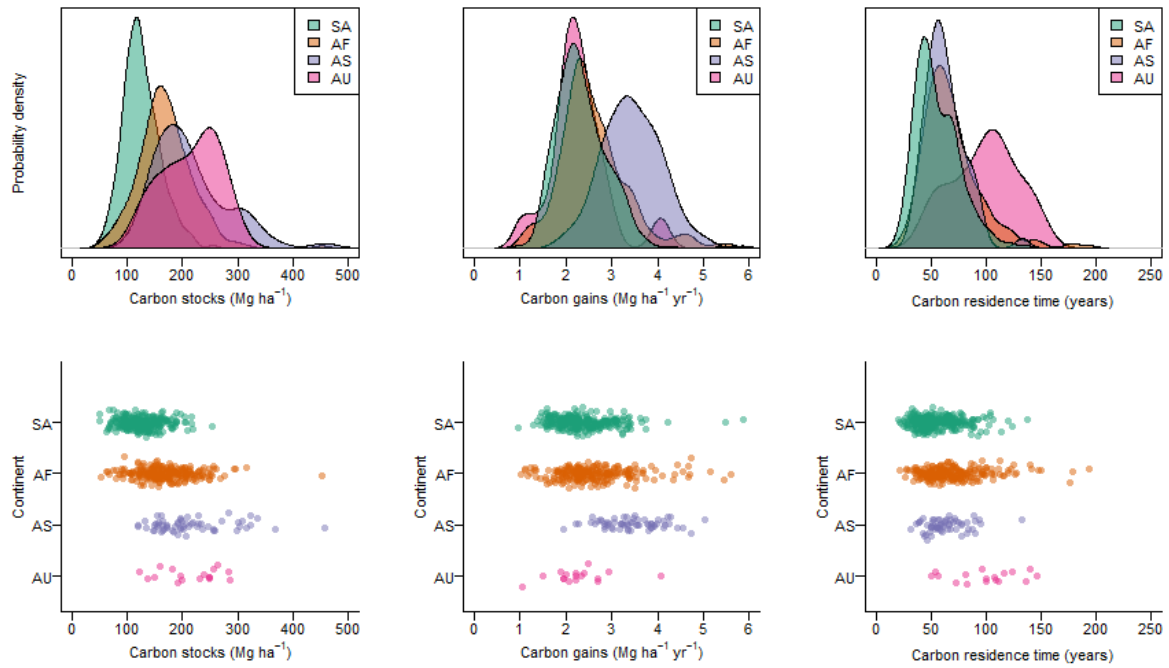
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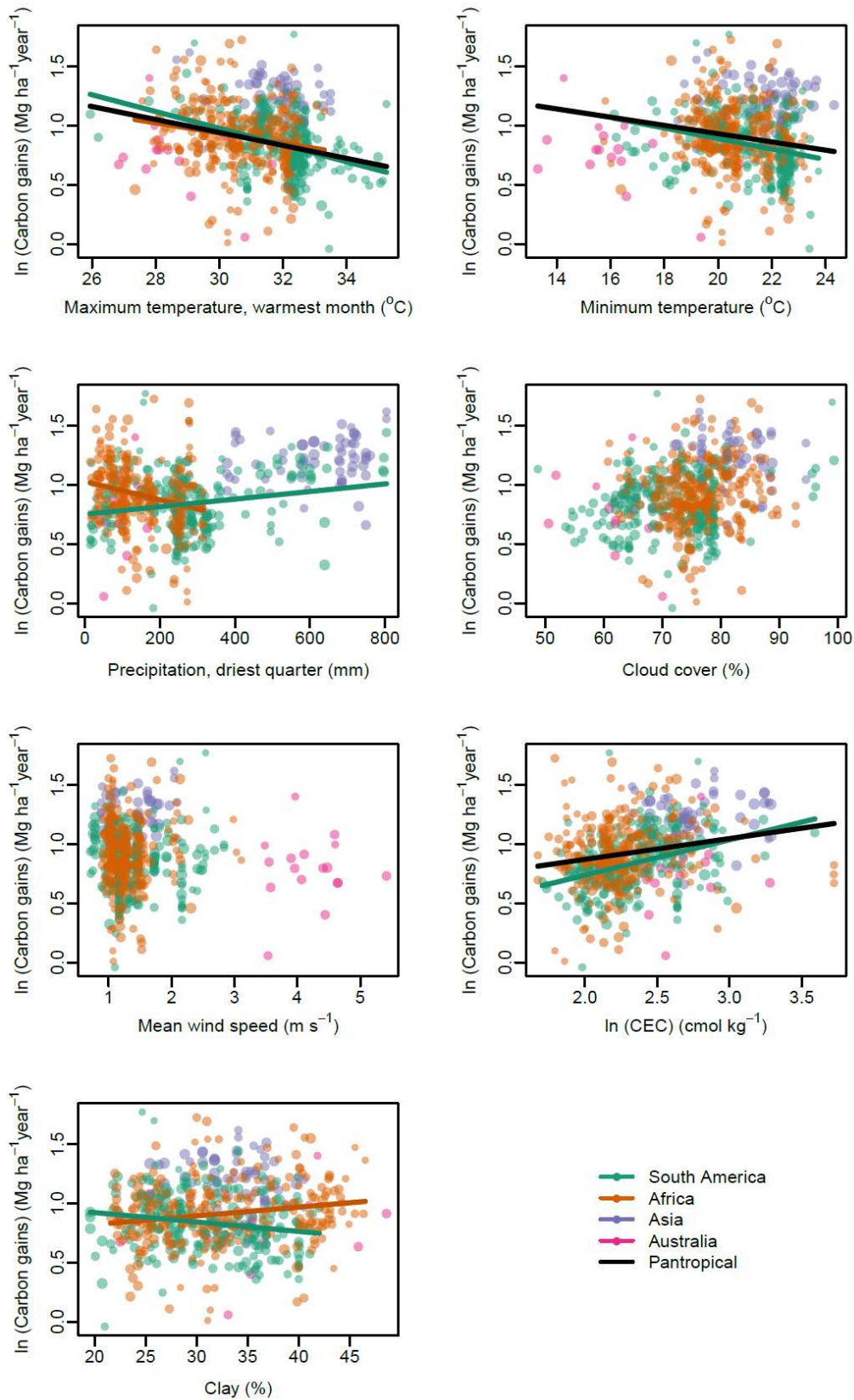
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948 **Figure S9.** As Fig. S8, but showing relationships with carbon gains.
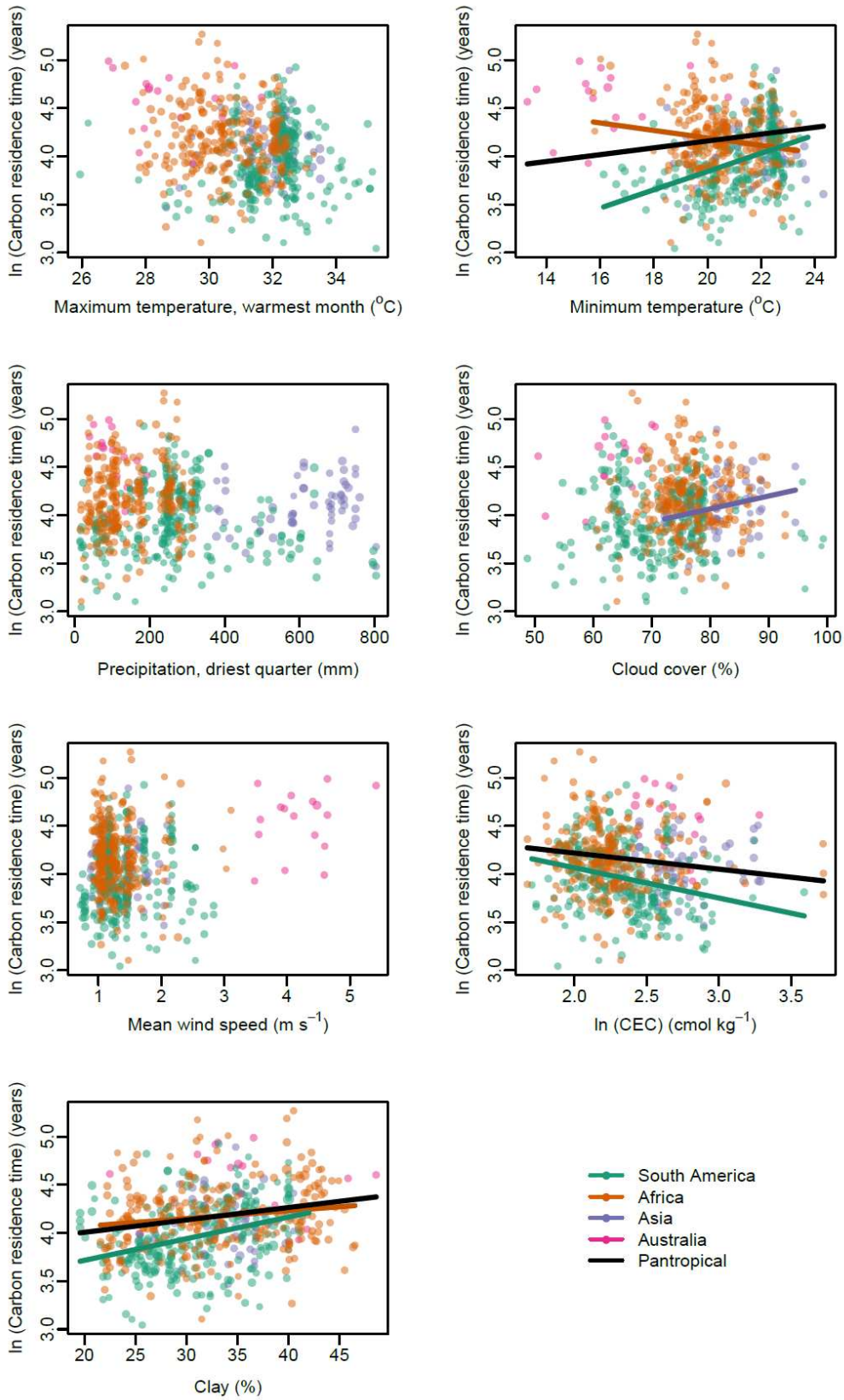
Figure S10. As Fig. S8, but showing relationships with carbon residence time.
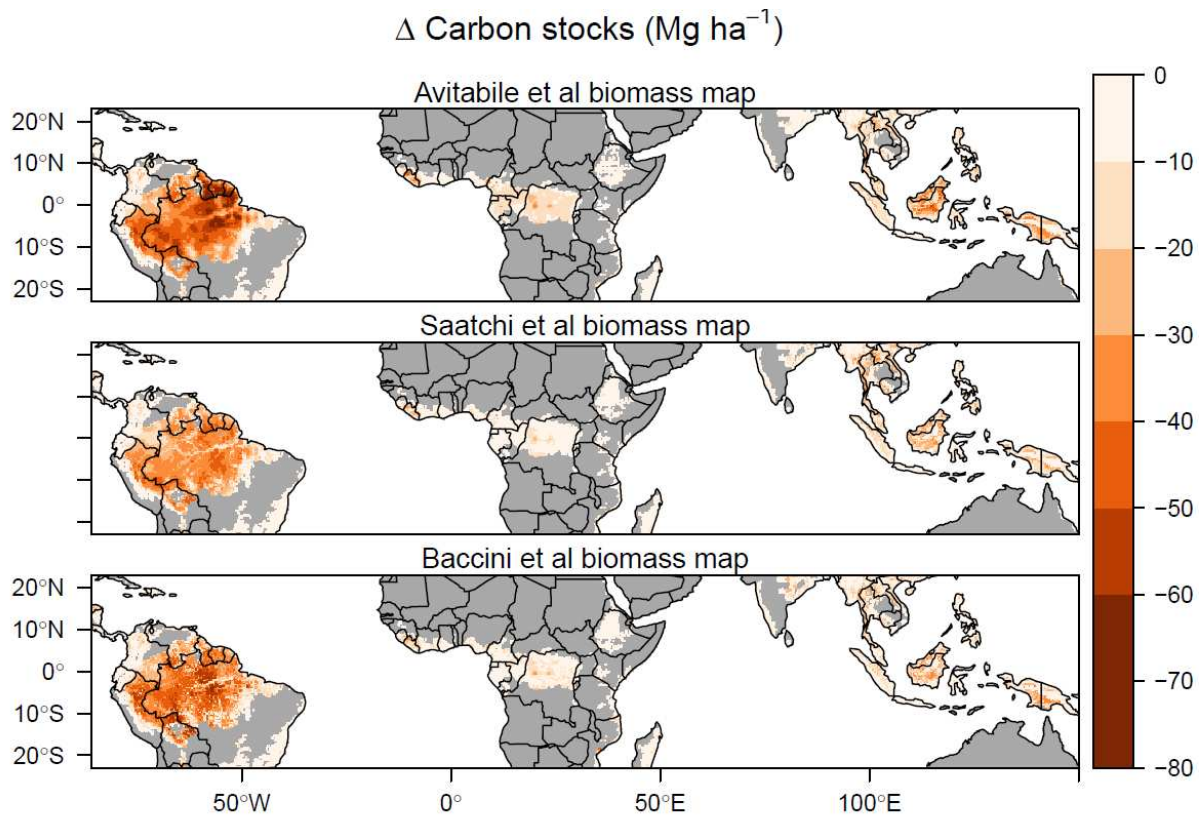
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Figure S11. Variation in tropical forest aboveground carbon stocks, gains and residence time within and amongst continents. Data are presented as empirical probability density functions (top row) and dot-plots showing raw data points for all our multi-census plots (bottom row). SA = South America, AF = Africa, AS = Asia, AU = Australia.

9

Δ Carbon stocks (Mg ha^{-1})

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

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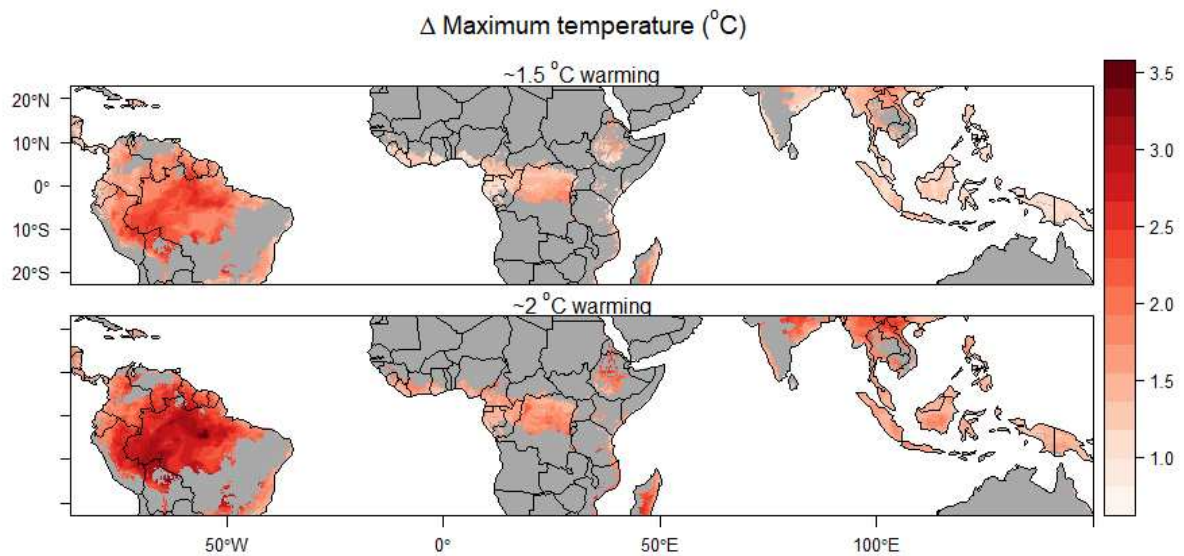
Figure S13. Biome-wide change in mean daily maximum temperature in the warmest month from present conditions (based on the Worldclim climatology, 1970-2000), given global increases in temperature of approximately 1.5°C and 2°C above pre-industrial levels. These levels of global temperature increase are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

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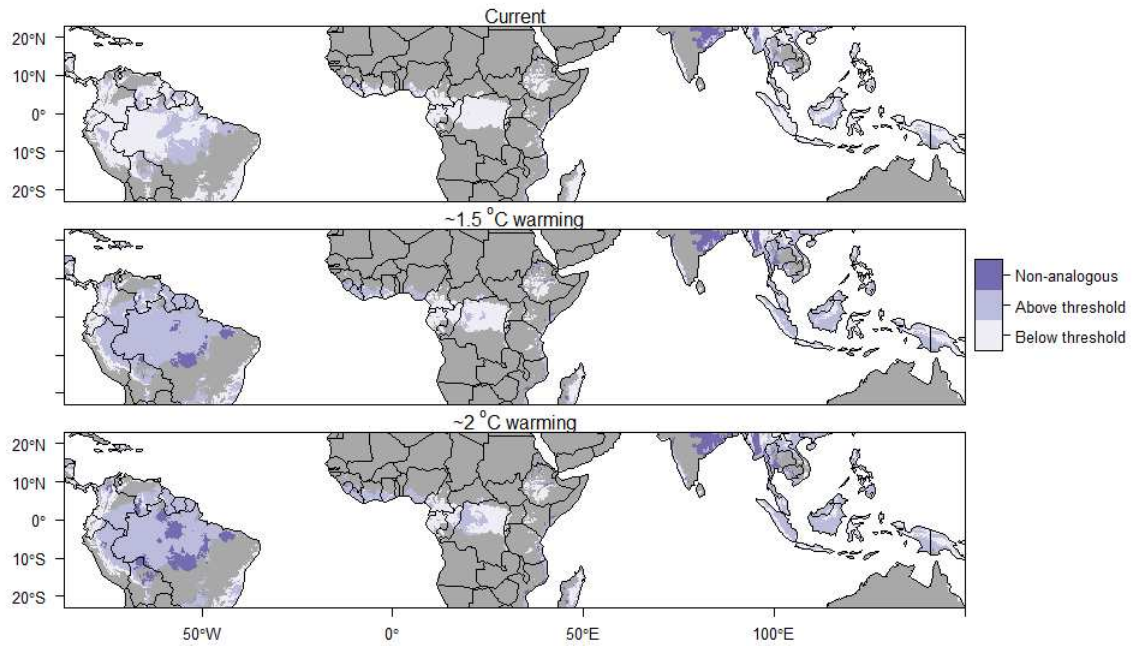
Figure S14 Areas of the biome above or below the 32.2°C threshold, above which carbon stocks decline more rapidly with temperature, under current conditions and two warming scenarios (see Fig. 4). Areas warmer than any currently observed in our dataset (35.2°C) are also shown (non-analogous conditions).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

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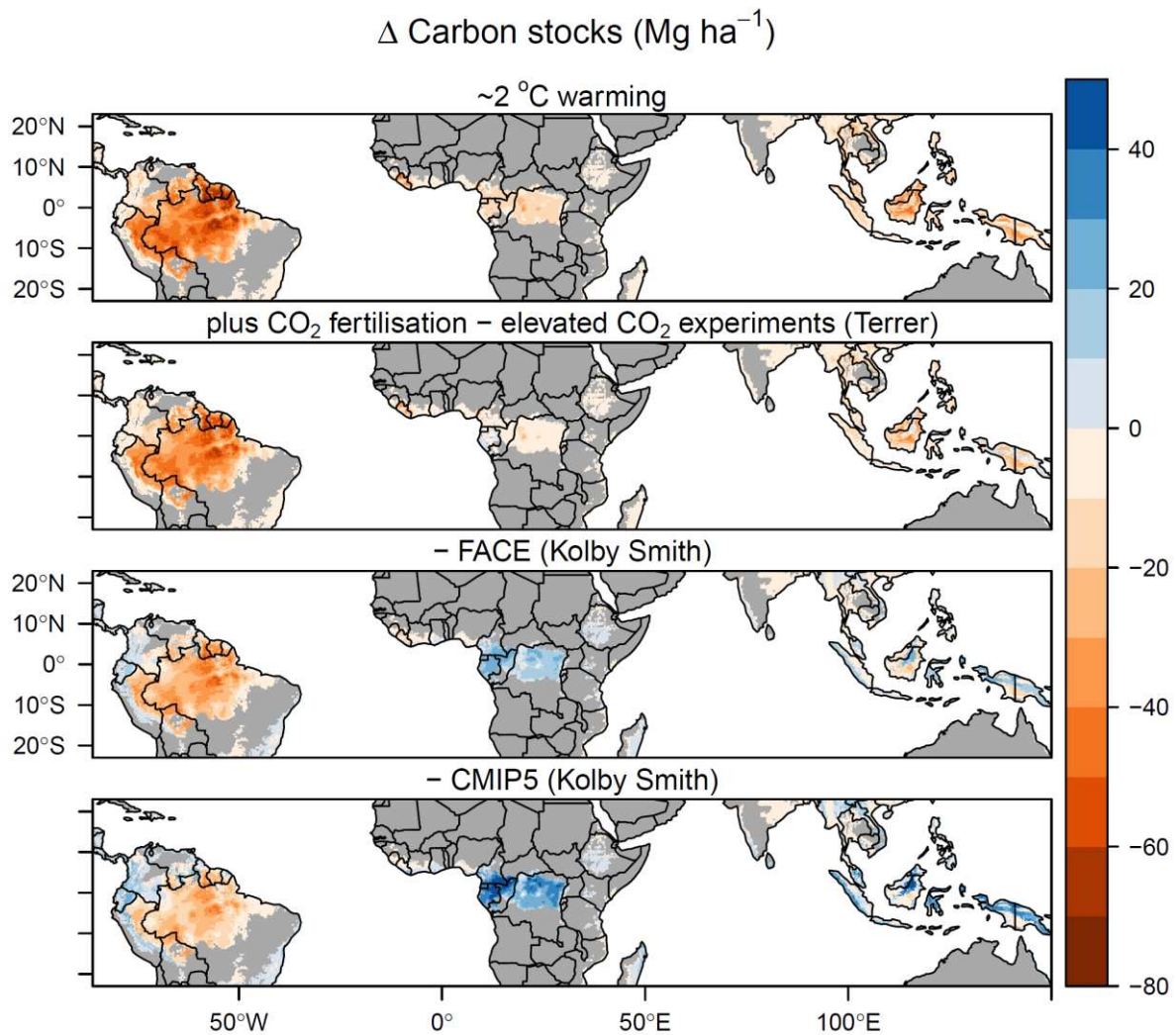
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994 **Figure S15.** Predicted long-term change in aboveground carbon stocks under ~ 2°C global warming,
995 based on either temperature effects alone or when also accounting for carbon dioxide growth
996 stimulation. CO_2 fertilisation effects on equilibrium biomass levels were obtained from a recent
997 synthesis of results of elevated CO_2 experiments (Terrer et al. (76)), free-air CO_2 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_2 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_2 effect considered.

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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[1]	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[2]	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   [1] 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   [2] 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 ΔAIC < 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

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2

1015 **Table S3.** Predicted biome-wide changes in long-term biomass carbon stocks (scaled to include root
1016 biomass) under global temperature increases of ~ 1.5°C and ~ 2°C. Changes are based on temperature
1017 effects alone, and when also accounting for the effect of increased CO_2 concentrations on tree growth.
1018 CO_2 effects were obtained from a synthesis of results of elevated CO_2 experiments (Terrer et al. (76)),
1019 free-air 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_2 effect | Change in biomass carbon stocks (Pg) | |
	~ 1.5°C warming (443 ppm CO_2)	~ 2°C warming (487 ppm CO_2)
None	-26.9 (-38.4 - -15.8)	-35.3 (-49.0 - -20.9)
Terrer et al. elevated CO_2 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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