Long-term decline of the Amazon carbon sink

R.J.W. Brienen^{1*}, O.L. Phillips^{1*}, T.R. Feldpausch^{1,2}, E. Gloor¹, T.R. Baker¹, J. Lloyd^{3,4}, G. Lopez-Gonzalez¹, A. Monteagudo-Mendoza⁵, Y. Malhi⁶, S.L. Lewis^{1,5}, R. Vásquez Martinez⁵, M. Alexiades⁸, E. Álvarez Dávila⁹, P. Alvarez-Loayza¹⁰, A. Andrade¹¹, L.E.O.C. Aragão^{2,12}, A. Araujo-Murakami¹³, E.J.M.M. Arets¹⁴, L. Arroyo¹³, G.A. Aymard C.¹⁵, C. Baraloto¹⁷, J. Barroso¹⁸, D. Bonal¹⁹, R.G.A. Boot²⁰, J.L. Camargo¹¹, C.V. Castilho²¹, V. Chama²², K.J. Chao¹, J. Chave²⁴, J.A. Comiskey²⁵, F. Cornejo Valverde²⁶, L. da Costa²⁷, E.A. Oliveira²⁸, A. Di Fiore²⁹, T.L. Erwin³⁰, S. Fauset¹, M. Forsthofer²⁸, E.S. Grahame¹, N. Groot¹, B. Hérault³¹, N. Higuchi¹¹, E. Honorio C.¹, H. Keeling¹, T.J. Killeen³², W.F. Laurance³³, S. Laurance³³, J. Licona³⁴, W.E. Magnusson³⁵, B.S. Marimon²⁸, B.H. Marimon-Junior²⁸, C. Mendoza³⁶, D.A. Neill³⁷, E.M. Nogueira³⁵, P. Núñez²², N.C. Pallaqui Camacho²², A. Parada¹³, G. Pardo³⁸, J. Peacock³⁹, M. Peña-Claros^{34,40}, G.C. Pickavance¹, N.C.A. Pitman^{10,41}, L. Poorter⁴⁰, A. Prieto⁴², C.A. Quesada³⁵, F. Ramírez⁴³, H. Ramírez-Angulo⁴⁴, Z. Restrepo⁴⁵, A. Roopsind⁴⁶, A. Rudas⁴², R.P. Salomão⁴⁷, M. Schwarz¹, N. Silva⁴⁸, J.E. Silva-Espejo²², M. Silveira⁴⁹, J. Stropp⁵⁰, J Talbot¹, H. ter Steege⁵¹, J. Teran-Aguilar⁵², J. Terborgh¹⁰, R. Thomas-Caesar⁴⁶, M. Toledo³⁴, M. Torello-Raventos^{53,33}, R.K. Umetsu, ²⁸, G.M.F. van der Heijden^{54,55}, P. van der Hout ⁵⁶, I.C. Guimarães Vieira⁴⁷, S.A.Vieira⁵⁷, E. Vilanova⁵⁸, V. Vos^{59,38}, R.J. Zagt²⁰

- 1 School of Geography, University of Leeds, Leeds, LS2 9JT, UK
- 2 College of Life and Environmental Sciences, University of Exeter, Rennes Drive, Exeter, EX4 4RJ, UK
- 3 Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK
- 4 School of Marine and Tropical Biology, James Cook University, Cairns, 4870 Qld, Australia
- 5 Jardín Botánico de Missouri, Prolongacion Bolognesi Mz.e, Lote 6, Oxapampa, Pasco, Peru
- 6 Environmental Change Institute, School of Geography and the Environment, University of Oxford, UK
- 7 Department of Geography, University College London, Pearson Building, Gower Street, WC1E 6BT, UK
- 8 School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury CT1 3EH, UK
- 9 Servicios Ecosistemicos y Cambio Climático, Jardín Botánico de Medellín, Medellín, Colombia
- 10 Center for Tropical Conservation, Duke University, Box 90381, Durham, NC 27708, USA
- 11 Biological Dynamics of Forest Fragment Project (INPA & STRI), C.P. 478, Manaus, AM 69011-970, Brazil
- 12 National Institute for Space Research (INPE), São José dos Campos, São Paulo, Brazil
- Museo de Historia Natural Noel Kempff Mercado, Universidad Autonoma Gabriel Rene Moreno, Casilla
 2489, Av. Irala 565, Santa Cruz, Bolivia
- 14 Alterra, Wageningen University and Research Centre, PO box 47, 6700 AA Wageningen, The Netherlands
- 15 UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, Estado Portuguesa, Venezuela 3350
- Biodiversiteit en Ecosysteem Dynamica, University of Amsterdam, Postbus 94248, 1090 GE Amsterdam,
 The Netherlands

- 17 Institut National de la Recherche Agronomique, UMR EcoFoG, Campus Agronomique, 97310 Kourou, French Guiana
- 18 Universidade Federal do Acre, Campus de Cruzeiro do Sul, Rio Branco, Brazil
- 19 INRA, UMR 1137 "Ecologie et Ecophysiologie Forestiere "54280 Champenoux, France
- 20 Tropenbos International, P.O. Box 232, 6700 AE Wageningen, The Netherlands
- 21 Embrapa Roraima, Caixa Postal 133, Boa Vista, RR, CEP 69301-970, Brazil
- 22 Universidad Nacional San Antonio Abad del Cusco. Av. de la Cultura Nº 733. Cusco, Peru
- 23 International Master Program of Agriculture, College of Agriculture and Natural Resources, National Chung Hsing University, Taichung 40227, Taiwan
- Université Paul Sabatier CNRS, UMR 5174 Evolution et Diversité Biologique, bâtiment 4R1, 31062
 Toulouse, France
- 25 Northeast Region Inventory and Monitoring Program, National Park Service, 120 Chatham Lane, Fredericksburg, VA 22405, USA
- 26 Andes to Amazon Biodiversity Program, Madre de Dios, Perú
- 27 Universidade Federal do Para, Centro de Geociencias, Belem, CEP 66017-970, Para, Brazil
- Universidade do Estado de Mato Grosso, Campus de Nova Xavantina, Caixa Postal 08, CEP 78.690-000,
 Nova Xavantina, MT, Brazil
- 29 Department of Anthropology, University of Texas at Austin, SAC Room 5.150, 2201 Speedway Stop C3200, Austin, TX 78712, USA
- 30 Department of Entomology, Smithsonian Institution, PO Box 37012, MRC 187, Washington, DC 20013-7012, USA
- 31 Cirad, UMR Ecologie des Forêts de Guyane, Campus Agronomique, 97310 Kourou, French Guiana
- 32 World Wildlife Fund, 1250 24th St NW, Washington, DC 20037, USA
- Centre for Tropical Environmental and Sustainability Science (TESS) and School of Marine and Tropical
 Biology, James Cook University, Cairns, Queensland 4878, Australia
- 34 Instituto Boliviano de Investigacion Forestal, CP 6201, Santa Cruz de la Sierra, Bolivia
- 35 National Institute for Research in Amazonia (INPA), C.P. 478, Manaus, Amazonas, CEP 69011-970, Brazil
- 36 FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta, Bolivia
- Universidad Estatal Amazónica, Facultad de Ingeniería Ambiental, Paso lateral km 2 1/2 via Napo, Puyo,
 Pastaza, Ecuador
- 38 Universidad Autonoma del Beni, Campus Universitario, Av. Ejército Nacional, final, Riberalta, Beni, Bolivia
- 39 Department of Agriculture, Askham Bryan College, York, UK
- Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen,
 The Netherlands
- 41 The Field Museum, 1400 South Lake Shore Drive, Chicago, IL 60605–2496, USA
- 42 Doctorado Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Colombia
- 43 Universidad Nacional de la Amazonía Peruana, Iquitos, Loreto, Perú
- 44 Universidad de Los Andes, Facultad de Ciencias Forestales y Ambientales, Mérida, Venezuela
- 45 Ecosistemicos y cambio climático (SECC) del Jardín Botánico de Medellin, Medellin, Colopmbia

- 46 Iwokrama International Centre for Rainforest Conservation and Development, 77 High Street Kingston, Georgetown, Guyana
- 47 Museu Paraense Emilio Goeldi, Av. Magalhães Barata, 376 São Braz, CEP: 66040-170, Belém, PA, Brazil
- 48 UFRA, Av. Presidente Tancredo Neves 2501, Belém, Pará, Brasil
- 49 Museu Universitário, Universidade Federal do Acre, Rio Branco AC 69910-900, Brazil
- 50 European Commission DG Joint Research Centre, Institute for Environment and Sustainability, Via Enrico Fermi 274, 21010 Ispra, Italy
- 51 NCB Naturalis, PO Box, 2300 RA, Leiden, The Netherlands
- 52 Museo de Historia Natural Alcide D'Orbigny, Av. Potosi no 1458, Cochabamba, Bolivia
- 53 School of Earth and Environmental Science, James Cook University, Cairns, Qld 4870, Australia
- 54 University of Winsconsin, Milwaukee, WI 53202, USA
- 55 Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá
- 56 Van der Hout Forestry Consulting, Jan Trooststraat 6, 3078 HP Rotterdam, the Netherlands
- 57 Universidade Estadual de Campinas, NEPAM, Rua dos Flamboyants, 155- Cidade Universitária Zeferino Vaz, CAMPINAS, CEP 13083-867, Sao Paulo, Brazil
- 58 Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Mérida, Venezuela
- 59 PROMAB, Casilla 107, Riberalta, Beni, Bolivia

* These authors contributed equally to this work

Corresponding author: Roel Brienen, School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK, Tel. ++ 44 113 343 3381, e-mail: r.brienen@leeds.ac.uk

Atmospheric CO₂ records indicate that the land surface has acted as a strong global carbon sink over recent decades^{1,2}, with a substantial fraction of this sink likely located in the tropics³, particularly in the Amazon⁴. Nevertheless, it is unclear how the terrestrial carbon sink will evolve as climate and atmospheric composition continue to change. Here we analyse the historic evolution of the biomass dynamics of the Amazon rainforest over three decades using a distributed network of 321 plots. While this analysis confirms that the Amazon has acted as a long-term net biomass sink, we find a long-term decreasing trend of carbon accumulation. Rates of net increase in above ground biomass declined by a third during the last decade compared to the 1990s. This is a consequence of growth rate increases levelling off recently, while biomass mortality persistently increased throughout leading to a shortening of carbon residence times. Potential drivers for the mortality, resulting in shortened tree longevity⁵. The observed decline of the Amazon sink diverges markedly from the recent increase in terrestrial carbon uptake at the global scale^{1,2}, and is contrary to expectations based on models⁶.

The direction and magnitude of the response of the Earth's land surface to increasing levels of atmospheric CO₂ and a warming climate are important determinants of future atmospheric CO₂ levels and thus greenhouse warming^{6,7}. One of the largest vegetation carbon pools on Earth is the Amazon forest, storing ca. 150-200 Pg C in living biomass and soils⁸. Earlier studies based on forest inventories in the Amazon Basin showed the tropical forest here to be acting as a strong carbon sink with an estimated annual uptake of 0.42-0.65 Pg C yr⁻¹ for 1990-2007, ca. 25% of the residual terrestrial carbon sink^{3,4}. There is however substantial uncertainty as to how the Amazon forest will respond to future climatic and atmospheric composition changes. Some earlier modelling studies predicted a large-scale dieback of the Amazon rainforest⁹, while more recent studies predict a carbon sink well into the 21st century due to a CO₂ fertilization effect⁶. The realism of such model predictions remains low due to uncertainty associated both with future climate and with vegetation responses^{6,7} in particular changes in forest dynamics^{5,10}. Thus, ground-based observations of tropical forest responses are critical to examine what changes are actually occurring and what to expect in the future. Here, we analyse the longest and largest spatially distributed time-series of forest dynamics for tropical South America.

Our analysis is based on 321 inventory plots lacking signs of recent anthropogenic impacts within the RAINFOR network⁴. The sites are distributed throughout the Amazon basin and cover all major forest types, soils and climates (Extended Data Fig. 1, Extended Data Table 1). For each plot (mean size 1.2 hectare) all trees with stem diameter greater than 100 mm were identified, and allometric equations applied to convert tree diameter, height and wood density to woody biomass or carbon⁸. Net biomass change was estimated for each census interval as the difference between standing biomass at the end and the beginning of the interval divided by the census length. We also derived forest woody productivity (hereafter "productivity") from the sum of biomass growth of surviving trees and trees that recruited (i.e., reached a diameter ≥ 100 mm), and mortality from the biomass of trees that died between censuses, allowing for census-interval effects (see Methods Section online). Plots were measured on average 5

times and the mean measurement period was 3 years. We show trends since 1983, the first year with measurements for 25 plots, up to mid-2011.

Our data show that forests continued to act as a biomass sink from 1983 to 2011.5, but also reveal a longterm decline in the net rate of biomass increase throughout the census period (Fig. 1a). The decline in net biomass change is due to a strong long-term increase in mortality rates (Fig. 1c), and occurred despite a long-term increase in productivity (Fig. 1b). While mortality increased throughout the period, productivity increases have recently stalled showing no significant trend since 2000 (Extended Data Fig. 3). These time trends are based on a varying set of plots over time (Extended Data Fig. 4), but this siteswitching does not alter the results (see Methods Section Online). The observed trends also emerge from a separate plot-by-plot analysis (Fig. 2), with increases in mortality exceeding productivity gains by approximately two to one. Trends are rarely significant at the individual plot level due to the stochastic nature of local forest dynamics, but the mean slopes of net change, productivity and mortality all differ significantly from zero. Changes in forest dynamics were not geographically limited to a particular area, but occurred throughout the lowland South American tropics (Fig. 2). Whilst rates of change vary depending on the precise plot set, time window and analytical approach used, the trends remain robust (cf. Figs. 1 and 2, Extended Data Fig. 3).

Artefactual explanations have been offered to explain trends in biomass dynamics from plot measurements^{11,12}. Principally, it has been suggested that previously reported net biomass increases⁴ could be driven by recovery of forests from local disturbances¹¹. However, contrary to observations from recovering neotropical forests¹³ and successional studies¹⁴, the plots have collectively experienced increased biomass growth (Fig. 1), accelerated stem recruitment and death (Extended Data Fig. 6), and show no net change in wood density or stem numbers (cf. Fig. 3b,c). It is thus unlikely that the overall patterns would be driven by simultaneous recovery from disturbances. Alternatively, increases in mortality have been proposed to arise due to biased selection of plots in mature forest patches, which over time accumulate disturbances¹². This explanation is contrary to the observation that forests and trees have continued to get bigger (Extended Data Fig. 5a). In addition, if this were driving the network-wide pattern, then the observed trends should disappear if data are reanalysed using only the first interval of each plot, but instead they persist. In sum, the data suggest that trends are unlikely due to artefactual explanations of forests recovering from disturbances or selection of mature forest patches (see Methods Section online for a more complete exploration of these potential biases).

What then could be driving the observed long-term changes? The levelling off of productivity in the most recent decade (Fig. 1b, Extended Data Fig. 3f) could be due either to a relaxation of the growth stimulus itself, or to the onset of a counteracting factor depressing growth rates. The recent demonstration of Amazon-wide carbon sink suppression during a drought year¹⁵ indicates one possible driver. Tropical drought is also often associated with higher temperatures, which may further contribute to reducing productivity¹⁶ and carbon uptake¹⁷. The last decade in Amazonia has seen several droughts¹⁸ and warming¹⁹, which coincide closely with the stalling productivity across Amazon forests.

The increased rate of biomass mortality is driven by an increasing number of trees dying per year (Extended Data Fig. 6c), rather than an increase in the size of the dying trees (Extended Data Fig. 5c). Several mechanisms may explain this increase in loss of biomass due to tree mortality, with recent climate events being an obvious candidate. The plot data clearly show short-term peaks in the size of dying trees during the anomalously dry years 2005 and 2010 (Extended data figure 5c). These are consistent with results from rainfall exclusion experiments in Amazonia^{20,21} and observations⁴ showing that large tropical trees are vulnerable to drought stress²⁰. However, our data lack the signature expected if drought were the dominant driver of the increasing loss of biomass due to mortality in Amazonia. That is, there has been no long-term change in the size of dead trees (Extended data figure 5c), living trees have continued to get bigger (Extended data Fig. 5a), and the increase in stem mortality predates the drought of 2005 (Extended Data Fig. 6c).

Alternatively, the increased productivity may have accelerated tree life-cycles so that they now die younger. Large stature is associated with size-related hydraulic²² and mechanical failure²³, reproductive $costs^{24}$, and photosynthetic decline²². Faster growth exposes trees to these size-related risks earlier, as evidenced by tree ring data showing that faster growth shortens lifespans^{25,26}, and by experimental data showing early onset of reproduction under elevated CO_2^{27} . The observed long-term acceleration in stem mortality rates and the plot-level association between productivity and the strength of the increase in biomass loss due to mortality (Extended Data Fig. 8b) are consistent with such a mechanism. While demographic feedbacks are not explicitly included in dynamic global vegetation models¹⁰, our results suggest that they could in fact influence the capacity of forests to gain biomass^{28,29}, with transient rates of ecosystem net carbon accumulation highly sensitive to even small changes in carbon turnover times¹⁰.

Finally, we put our results in a global perspective. According to global records the land carbon sink has increased since the mid-1990s^{1,2}. While tropical land contributed significantly to this global sink during the 1980s and 1990s, our results show that the total net carbon sink into intact Amazon live biomass then decreased by 30% from 0.54 (CI; 0.45-0.63) Pg C yr⁻¹ in the 1990s to 0.38 (CI; 0.22-0.50) Pg C yr⁻¹ in the 2000s (see Methods Section online). If our findings for the Amazon are representative for other tropical forests, and if below-ground pools have responded in the same way as above-ground biomass, then an apparent divergence emerges between a strengthening global terrestrial sink on one hand^{1,2} and a weakening tropical sink on the other. From an atmospheric perspective however, we also note that some of the effects of the Amazon changes are yet to be observed, as little of the carbon resulting from increased mortality is immediately released into the atmosphere³⁰. Rather, dead trees decay slowly, with a fraction also moving into a long-term soil carbon pool. The Amazon forest sink has therefore become increasingly skewed towards gains in the necromass pools. Based on the observed long-term increase in mortality rates, we estimate that the atmosphere has yet to see ≈ 3.8 Pg of the Amazon necromass carbon produced since 1983 (see Methods Section online), representing a 30% increase in necromass stocks. The modelled increase in Amazon necromass is twice the magnitude of the cumulative decadal decline in the live biomass sink from the 1990s to the 2000s (i.e., from 5.5 to 3.9 Pg C).

In summary, we find that the Amazon biomass carbon sink has started to decline, due to recent levelling of productivity increases, combined with a sustained long-term increase in mortality. This behaviour is at odds with expectations from models of a continually strong tropical biomass sink⁶, and underlines how difficult it remains to predict the role of land-vegetation feedbacks in modulating global climate change^{7,10}. Investment in consistent, coordinated long-term monitoring on the ground is fundamental to elucidate the trajectory of the planet's most productive and diverse biome.

Methods summary

Rates of change in net above-ground biomass, productivity and mortality were analysed in two principal ways. The first method calculated the average rate of change across the full set of plots for each month since 1983. Estimates of the long-term trends were performed by regressing the mid-point of each census interval against the rate of change using General Additive Models and Linear Mixed Models. The second method examined averages of slopes of time trends for individual plots using linear regressions. We also calculated regional estimates of net biomass change during the 1990s and 2000s by scaling up net change to the total area of old-growth lowland South American moist forests and to carbon pools that were not directly measured (see Methods Section Online).

Online content Additional methods and extended data display items and Source data are available in the online version of the paper at <u>www.nature.com/nature</u>.

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Figure legends

Figure 1. Trends in net above-ground biomass change, productivity and mortality across all sites. Black lines show the overall mean change 1983-2011 for 321 plots (or 274 units) weighted by plot size, and its bootstrapped confidence interval (shaded area). The red lines indicate the best model fit for the long-term trends using General Additive Mixed Models (GAMM) accounting explicitly for differences in dynamics between plots (red lines = overall mean, broken lines = standard error). Alternative analyses of unvarying subsets of plots that were continuously monitored over shorter time-intervals confirm that the observed trends are not driven by temporal changes in individual sample plot contributions (Extended Data Fig. 4). Estimated long-term (linear) mean slopes and significance levels are indicated, and are robust with regard to the statistical approach applied (i.e., parametric or non-parametric, see Methods Section online). Shading corresponds to the number of plots that are included in the calculation of the mean, varying from 25 plots in 1983 (light grey) to a maximum of 204 plots in 2003 (dark grey). The uncertainty and variation is greater in the early part of the record due to relatively low sample size (see Extended Data Fig. 5)

Figure 2. Annual change in net above-ground biomass change, productivity and mortality for individual sites. The lines in the left panels show the long-term rate of change for 117 plots (or 87 units), estimated using linear regressions weighted by census-interval length and for display purposes centred around zero. This analysis includes only plots that were monitored for at least 10 years and contained three or more census intervals with at least one in the 1990s and one in 2000s. Red lines indicate long-term trends that negatively impact biomass stocks (e.g., decreasing net change, increasing losses) and green lines indicate trends that positively affect biomass stocks (e.g., increasing productivity). Bold black lines indicate the mean slope across all plots and CI (2.5-97.5 percentiles). Insets on the left panels show the frequency distribution of the slopes, with the mean slope and p-value for t-test of difference from no slope. The maps show the location of the sites, and colour and arrow length indicate the sign and magnitude of the slope, with adjacent plots joined into a single site for display purposes.

Figure 3. Relationships between annual net change in biomass of individual plots and their annual change in (a) basal area, (b) stem numbers per hectare, and (c) wood density. The mean values of the rates of changes are given in each panel along with the R-squared of the relationship with annual net biomass change. Number of plots included is 234 (i.e., those with data on change in basal area, stem numbers and wood density).

Extended Data Figure 1. Map showing locations of plots included in this study. The three-letter codes refer to plot codes (see Extended Data Table 1). Adjacent plots (<50 km apart) are shown as one for display purposes. Size of the dots corresponds to the relative sampling effort at that location which is calculated as the square root of plot size times census length. The grey area shows the cover of all open and closed, evergreen and deciduous forests for tropical South America, according to Global Land Cover map 2000.

Extended Data Figure 2. Scatterplot of mid-interval date against (a) net AGB change (b) AGB productivity and (c) AGB loss due to mortality for all data points and plots used in this analysis. Points indicate the mid-census interval date, while horizontal error-bars indicate the start and end date for each census-interval. To illustrate variation in net AGB change over time within individual plots, examples of time series for three individual plots are show as lines.

Extended Data Figure 3. Time trends of subsets of net above-ground biomass change, above-ground woody productivity and mortality rates for plots that were continuously monitored for the periods 1990-2011, 1995-2011 and 2000-2011 (top panels). Locations for the set of plots included in the analysis for the different periods are show in the maps in lower panels. Sample sizes (n), slopes of the long-term linear trends (sl) and p-levels (p) are shown in top panels.

Extended Data Figure 4. Mean number of plots (red lines), mean interval census length (black lines) and mean area (blue lines) of all plots. Note that the increased sampling in 2002 to 2004 is largely due to the short-term addition of 72 plots from one site (Ducke, north of Manaus), but this has no discernible effect on averaged biomass dynamics (cf. Fig. 1).

Extended data Figure 5. (a) Mean net biomass change on a per live stem basis (i.e., net biomass change/ stem), (b) mean growth gains per live tree (i.e., mean biomass accumulation of individual trees), and (c) mean mortality losses per dying tree (i.e., the mean biomass of dying trees). Analyses are based on 234 plots, excluding published studies without available stem-by-stem data.

Extended Data Figure 6. Rates of change in number of stems plus annualized fluxes of stems bigger than 10 cm in diameter. (a) Mean net change in number of stems, and (b) number of recruits, and (b) and number of dying trees. Analyses are based on 234 plots, excluding published studies without available stem-by-stem data.

Extended Data Figure 7. (a) Mean net basal area change, (b) mean basal area productivity, and (c) mean basal area mortality. Analyses are based on 234 plots, excluding published studies without available basal-area data.

Extended Data Figure 8. Scatterplots of (a) the slope of AGB mortality of individual plots against the slope of AGB productivity of plots, (b) the slope of AGB loss due to mortality of individual plots against the mean AGB productivity of plots, and (c) the slope of AGB productivity of individual plots against the mean AGB loss due to mortality of plots. The set of plots used in this analysis (117 plots, 87 units) includes only those that had at least 10 years of data and at least three census intervals (i.e., same criteria as plots shown in Figure 2).

Extended Data Figure 9. Scatterplots of (a) net AGB change or (c) AGB loss due to mortality of

individual plots against the total monitoring length of plots, and (b) the *slope* of net AGB change or (d) *slope* of AGB mortality of individual plots against the total monitoring length of plots. None of the relationships are significant (p>0.05). Note that the plots (117 plots, 87 units) used in the panels (b) and (d) are only those that had at least 10 years of data and at least three census intervals (i.e., same criteria as plots shown in Figure 2).

Extended Data Figure 10. Modelled estimates of the effects of linearly increasing mortality on necromass stocks (top panel), and soil organic-matter stocks (middle panel). The final panel shows the estimated fluxes of carbon from the forest to the atmosphere in three scenarios, (1) assuming constant mortality rate and a lag in decomposition of dead-tree biomass (green line), (2) assuming an increasing mortality rate similar to the observed trend (Fig. 1c) and a lag in decomposition as modelled (black line), and (3) with increasing mortality but with all dead-tree biomass instantly respired (red line).

References

- 1 Ballantyne, A. P., Alden, C. B., Miller, J. B., Tans, P. P. & White, J. W. C. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* **488**, 70-72 (2012).
- 2 Le Quéré, C. *et al.* The global carbon budget 1959-2011. *Earth System Science Data* **5**, 165-185 (2013).
- 3 Pan, Y. *et al.* A Large and Persistent Carbon Sink in the World's Forests. *Science* 333, 988-993, doi:10.1126/science.1201609 (2011).
- 4 Phillips, O. L. *et al.* Drought Sensitivity of the Amazon Rainforest. *Science* **323**, 1344-1347, doi:10.1126/science.1164033 (2009).
- 5 Bugmann, H. & Bigler, C. Will the CO₂ fertilization effect in forests be offset by reduced tree longevity? *Oecologia* **165**, 533-544 (2011).
- 6 Huntingford, C. *et al.* Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nature Geoscience* (2013).
- 7 Booth, B. B. *et al.* High sensitivity of future global warming to land carbon cycle processes. *Environmental Research Letters* **7**, 024002 (2012).
- Feldpausch, T. R. *et al.* Tree height integrated into pantropical forest biomass estimates.
 Biogeosciences 9, 3381-3403, doi:10.5194/bg-9-3381-2012 (2012).
- 9 Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184-187 (2000).
- 10 Friend, A. D. *et al.* Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. *Proceedings of the National Academy of Sciences*, 201222477 (2013).
- 11 Fisher, J. I., Hurtt, G. C., Thomas, R. Q. & Chambers, J. Q. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol. Lett.* **11**, 554-563, doi:10.1111/j.1461-0248.2008.01169.x (2008).
- 12 Condit, R. Forest turnover, diversity, and CO₂. *Trends Ecol. Evol.* **12**, 249-250, doi:<u>http://dx.doi.org/10.1016/S0169-5347(97)01095-1</u> (1997).
- 13 Chambers, J. Q. *et al.* Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* **141**, 596-611, doi:10.1007/s00442-004-1676-2 (2004).
- 14 Van Breugel, M., Martínez-Ramos, M. & Bongers, F. Community dynamics during early secondary succession in Mexican tropical rain forests. *J. Trop. Ecol.* **22**, 663-674 (2006).
- 15 Gatti, L. *et al.* Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* **506**, 76-80 (2014).
- Clark, D. A., Clark, D. B. & Oberbauer, S. F. Field-quantified responses of tropical rainforest aboveground productivity to increasing CO₂ and climatic stress, 1997–2009. *Journal of Geophysical Research: Biogeosciences* 118, 783-794, doi:10.1002/jgrg.20067 (2013).

- Wang, X. *et al.* A two-fold increase of carbon cycle sensitivity to tropical temperature variations.*Nature* 506, 212-215 (2014).
- 18 Marengo, J. A., Tomasella, J., Alves, L. M., Soares, W. R. & Rodriguez, D. A. The drought of 2010 in the context of historical droughts in the Amazon region. *Geophys. Res. Lett.* 38, L12703, doi:10.1029/2011gl047436 (2011).
- 19 Jiménez Muñoz, J. C., Sobrino, J. A., Mattar, C. & Malhi, Y. Spatial and temporal patterns of the recent warming of the Amazon forest. *Journal of Geophysical Research: Atmospheres* (2013).
- 20 da Costa, A. C. L. *et al.* Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol.* **187**, 579-591, doi:10.1111/j.1469-8137.2010.03309.x (2010).
- 21 Nepstad, D. C., Tohver, I. M., Ray, D., Moutinho, P. & Cardinot, G. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* **88**, 2259-2269 (2007).
- 22 Ryan, M. G., Phillips, N. & Bond, B. J. The hydraulic limitation hypothesis revisited. *Plant, Cell Environ.* **29**, 367-381 (2006).
- 23 Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G. S. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* **73**, 915-924 (1985).
- Thomas, S. C. in *Size-and age-related changes in tree structure and function* (eds FC Meinzer, B Lachenbruch, & TE Dawson) Ch. 2. Age-related changes in tree growth and functional biology: the role of reproduction., 33-64 (Springer,, 2011).
- 25 Bigler, C. & Veblen, T. T. Increased early growth rates decrease longevities of conifers in subalpine forests. *Oikos* **118**, 1130-1138, doi:10.1111/j.1600-0706.2009.17592.x (2009).
- Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B. & Piovesan, G. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. *Global Change Biol.* 18, 960-972, doi:10.1111/j.1365-2486.2011.02617.x (2012).
- LaDeau, S. L. & Clark, J. S. Rising CO₂ levels and the fecundity of forest trees. *Science* 292, 95-98 (2001).
- Manusch, C., Bugmann, H., Heiri, C. & Wolf, A. Tree mortality in dynamic vegetation models A key feature for accurately simulating forest properties. *Ecol. Model.* 243, 101-111, doi:<u>http://dx.doi.org/10.1016/j.ecolmodel.2012.06.008</u> (2012).
- 29 Delbart, N. *et al.* Mortality as a key driver of the spatial distribution of aboveground biomass in Amazonian forest: results from a dynamic vegetation model. *Biogeosciences* 7, 3027-3039, doi:10.5194/bg-7-3027-2010 (2010).
- 30 Saleska, S. R. *et al.* Carbon in Amazon Forests: Unexpected Seasonal Fluxes and Disturbance-Induced Losses. *Science* **302**, 1554-1557, doi:10.1126/science.1091165 (2003).