Drought impact on forest carbon dynamics and fluxes in Amazonia

Christopher E. Doughty[1]*, D. B. Metcalfe[2], C. A. J. Girardin[1], F. F. Amezquita[3], D. Galiano[3], W. Huaraca Huasco[3], J. E. Silva-Espejo[3], A. Araujo-Murakami[4], M. C. da Costa[5], W. Rocha[6], T.R. Feldpausch[7], A. L. M. Mendoza[3], A. C. L. da Costa[5], P. Meir[8, 9], O. L. Phillips[10], Y. Malhi[1]

[1]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, U.K.; [2]Department of Physical Geography and Ecosystem Science, Lund University Lund, Sweden; [3]Universidad Nacional San Antonio Abad del Cusco, Cusco, Perú; [4]Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia; [5]Universidade Federal do Pará, Belém, Pará, Brazil; [6]Amazon Environmental Research Institute (IPAM), Canarana, Mato Grosso, Brazil; [7]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, U.K.; [8] School of Geosciences, University of Edinburgh,UK; [9]Research School of Biology, Australian National University, Canberra, Australia; [10]School of Geography, University of Leeds, U.K.

*Corresponding author: chris.doughty@ouce.ox.ac.uk

Running title – Impact of drought on Amazonia

Key words: Drought, Amazon, GPP, NPP, tropical forests, allocation

Abstract – In 2005 and 2010, the Amazon basin experienced two strong droughts[1], driven by shifts in the tropical hydrological regime[2] possibly associated with global climate change[3] as predicted by some global models[3]. Tree mortality increased following the 2005 drought[4] and regional atmospheric inversion modelling showed basin-wide decreases in CO_2 uptake in 2010 compared to 2011[5]. But the response of tropical forest carbon cycling to these droughts is not fully understood and there has not been a detailed multi-site investigation *in situ*. Here we use several years of data from a network of 13 one hectare forest plots spread throughout South America, where each component of net primary production (NPP), autotrophic (R_a) and heterotrophic respiration (R_h) is measured separately, to develop a better mechanistic understanding of the impact of the 2010 drought on the Amazon forest. We find surprisingly that total NPP remained constant throughout the drought. However, towards the end of the drought, autotrophic respiration, especially in roots and stems, declined significantly compared to measurements in 2009 made in the absence of drought, with extended decreases in autotrophic respiration in the three driest plots. In the year following the drought, total NPP continued to remain constant but the allocation of carbon shifts towards canopy NPP and away from fine root NPP. Both leaf-level and plot-level measurements indicate that drought suppresses photosynthesis. Scaling these measurements to the entire Amazon basin using rainfall data, we estimate that drought suppressed Amazon-wide photosynthesis in 2010 by 0.38 Pg C (0.23 - 0.53 Pg C). Overall, we find that during episodic drought, instead of reducing total NPP trees prioritized growth by reducing autotrophic respiration. This suggests that trees reduce investment in tissue maintenance and defence, in line with eco-evolutionary theories which hypothesize that trees are competitively disadvantaged in the absence of growth[6]. We propose that weakened maintenance and defence investment may, in turn, cause the increase in tree mortality following drought observed at our plots.

How does drought affect tropical forests? This question has been studied in long-term experimental drought studies [7,8], long-term biomass plots that have tracked forest dynamics through drought events [4], and through remote sensing [9-11]. Increased mortality of trees using a large network of 1 ha plot censuses was observed following the 2005 Amazonian drought, turning the forest from an estimated net biomass carbon (C) sink of ≈0.71 Mg C ha^{-1} yr^{-1} [12] to a temporary net source of CO_2 to the atmosphere of twice this, with a total impact (i.e., committed source minus baseline sink) of 1.2-1.6 Pg C [4]. This increase in drought-induced tree mortality has also been seen in two multi-year experimentally droughted plots in Amazonia, dominated by a sustained increase in large tree mortality[7]. Remote sensing of canopy backscatter following the 2005 drought indicated that, in some parts of Amazonia, the drought caused a change in structure and water content associated with the forest upper canopy. This suggests a slow recovery (>4 y) of forest canopy structure after the severe drought in 2005[10].

Since future droughts in tropical regions may increase in frequency and severity[1-3], a better understanding of whether net CO_2 fluxes to the atmosphere from tropical forests increase or decrease during drought periods is urgently required. Drought could either suppress gross primary productivity (GPP), which would lead to an immediate reduction of CO_2 uptake, or it could reduce heterotrophic respiration thereby reducing the CO_2 source to the atmosphere, or both[13]. The Amazon basin in 2010 was drier than in 2011, but not warmer, enabling the separation of the influences of temperature and precipitation[5]. A recent atmospheric inversion study in the Amazon basin found that forests took up 0.25±0.14 Pg C less CO_2 in 2010 (the year of the drought) than 2011 after accounting for the effect of increased fires during the drought[5]. A previous study using isotopic techniques found a similar result, with the basin turning from a potential sink to a source following the dry El Niño year of 1997[14]. These results indicate that annual Amazon droughts apparently suppress photosynthesis more than respiration, but such a relative decrease has not been directly verified with on the ground measurements.

To be able to understand long term carbon storage in the tropics, top-down estimates of GPP and net respiration CO_2 fluxes to the atmosphere alone are insufficient. It is also important to understand how the products of photosynthesis are allocated between plant metabolism and biomass growth (net primary productivity, NPP) and how that growth is allocated amongst different organs of the tree[15]. Total autotrophic respiration plus total NPP should approximately equal total GPP over long (multi-year) timescales. However, over shorter timescales the two may differ as forests may store 'old' carbon in the form of non-structural carbohydrates (NSC), which may be abundant in tropical forests (~16 Mg C ha^{-1}, more than enough carbon to rebuild the entire leaf canopy)[16]. These

NSCs may function as a reserve that enables continuation of high rates of growth during periods of reduced carbon income from photosynthesis[16-18].

For several years, we have measured the main components of total NPP (including one to three month records of fine root, woody, and leaf flush NPP) and autotrophic respiration (including rhizosphere, stem wood, and canopy leaf respiration) at 13 one-hectare rainforest plots in three South American countries, covering contrasting climatic and soil conditions and also across a 2800m elevation range in the Andes (ED tables 1-3). Initial results from these measurements have been described in a series of companion papers [19-23] presenting complete mean annual sums and mean seasonal cycles of NPP and autotrophic respiration (R_a). This methodology has shown close agreement with independent eddy covariance data on seasonal and annual timescales (ED Figure 1 – slope is within the error of a one-to-one line - 3.0 ± 7.8% (95% confidence interval)) [24]. Here, we synthesize and further analyse these results to focus specifically on the basin-wide trends before, during and after the 2010 drought, constrained by concurrent measurements in a larger network measuring woody NPP and mortality[4] and inversion studies monitoring changes in atmospheric CO_2 concentrations[5]. Of the 13 plots, six experienced drought in 2010 (ED Figure 2). Of these six, three can be considered lowland humid forest more typical of Amazonia (based on species composition and maximum cumulative water deficit (MCWD)) and three are drier forests at the Amazon forests' southern margins.

Throughout the two year period of study, the eight non-drought plots showed steady NPP, R_a, and total plant carbon expenditure (PCE - the sum of NPP and R_a or the carbon expended by the autotrophic metabolism of the ecosystem; green line Figure 1). Total NPP was surprisingly invariant throughout the drought period at all of our plots (Figure 1c). Among the six drought-affected plots, there were differences between those in the dry lowlands (red lines, N=3) and those in the more humid areas (black lines, N=3). PCE in the humid lowland plots was constant at the start of the drought, but then both PCE and R_a decreased significantly ($P<0.05$ and $P<0.01$ respectively, paired T-test, N=3 plots) through early 2011 relative to the 2009 baseline. The humid plots recovered to the 2009 baseline within a few months after the drought but decreases in R_a at the three dry lowland plots persisted for a year after the 2010 drought (Figure 1b). This short-term decrease in R_a (dominated by changes in rhizosphere and stem respiration - ED figure 7) is in contrast to the results from multi-annual experimental drought where R_a increased (dominated by changes in leaf respiration)[19].

PCE should approximately equal total photosynthesis in an ecosystem over annual to multi-annual time scales, with any discrepancy between the two on shorter (monthly) timescales caused by changes in unmeasured carbon pools such as non-structural carbohydrate reserves. Therefore, a decrease in PCE must equal an equivalent decrease in GPP during a prior period. At our humid drought sites, PCE decreased by 1.90 ± 1.04 Mg C ha^{-1} yr^{-1} (95% C.I.) following the drought period compared to the 2009 baseline (yellow region of Figure 1a). *In situ* measurements of light saturated

maximum photosynthesis made at a subset of our plots indicate that photosynthesis did decrease significantly ($P<0.001$, T-test, N=20 trees) during the drought period compared to non-drought conditions, pointing to the drought as the cause of the drop in PCE (ED Figure 3). This measured decrease in photosynthesis is of a similar magnitude to modelled decreases in photosynthesis from drought in Eastern Amazonia[25]. We hypothesize that the asynchrony between the decrease in PCE and the start of the drought indicates that the forests relied on non-structural carbohydrate reserves to initially maintain constant growth and respiration during the drought period (ED Figure 4). Towards the middle of the drought period, R_a decreased in the rhizosphere and stems, while NPP and growth continued to remain relatively constant. Since autotrophic respiration consists of maintenance (non-growth) respiration and the respiratory costs associated with growth, this suggests that maintenance respiration must have declined. The decrease in R_a continued following the end of the drought period, potentially allowing the replenishment of the NSC stores once normal photosynthesis resumed (ED Figure 4). Drought reduced PCE by a larger amount in dry zone plots than in humid zone plots, with total PCE continuing to decline through 2011. The greater total decline in PCE is indicative of a larger percentage decrease in total photosynthesis during the drought at the drier plots, a plot-scale observation which matches our *in situ*, leaf level measurements (ED Figure 3). Our data show little change to net heterotrophic respiration in the humid plots (supplementary results and Figure 1d black line), and this suggests that the drought forest plots were first a net C source in 2010 due to suppressed photosynthesis, and then a net C sink in early 2011 as photosynthesis returned to normal, whilst R_a in the stems and rhizosphere remained slightly suppressed compared to previous periods (ED Figure 4 and 7).

There was strong seasonality in the components of NPP, with peaks in leaf growth generally anti-correlated with the peaks in woody growth. Hence variation in seasonal growth rates was driven more by shifts in allocation of NPP than by variation in its total magnitude[26]. NPP allocation in the non-droughted plots did not change significantly between 2009 and 2010 (Figure 2 green). In the droughted plots there were no significant shifts in allocation patterns during the drought period itself, but in the 6 months following the drought there was a significant shift in C allocation for both the humid and dry lowland plots following the drought period away from fine root growth ($P<0.01$, paired T-test, N=3) and towards canopy growth (a combination of LAI and litterfall – see methods - $P<0.05$, paired T-test, N=3) (Figure 2 red and black). Droughts typically increase leaf fall, a strategy thought to minimize drought-induced xylem embolisms, and can cause temperature-related leaf damage as evaporative cooling decreases[8]. Therefore, preferential allocation of carbon towards the canopy in the year following the drought is consistent with known physiological drought responses, and likely represents additional carbon required to replenish lost and damaged leaves and thereby rebuild photosynthetic capacity. The significant shift away from fine root growth was surprising since it has often been assumed that fine root growth might increase during a drought, but may simply be a reflection of the immediate priority of replacing lost canopy cover instead of a long

158 term shift away from root growth (for longer-term allocation patterns see ED Figure 5 and a
159 companion paper[26]).

160 Individual tree mortality rates approximately doubled at our droughted plots, showing a
161 marginally significant increase (P=0.06; paired 1-tailed T-test, N=5) from a long term mean of
162 1.6±0.6% (Tambopata, N=3) and 2.0 ± 0.4% (Kenia, N=2) to peaks of 3.6% (Tambopata) and 6.7%
163 (Kenia) following the drought (ED figure 6). Mortality remained relatively stable at the non-drought
164 plots. We tested mortality in a bigger subset of plots at Tambopata and Caxiuanã going back ~30
165 years at some plots (supplementary results) and found that biomass loss rates increased significantly
166 (P<0.05, Wilcoxon signed rank test) at Tambopata (drought, N=9) but not at Caxiuanã (no drought,
167 N=6). Committed carbon released due to mortality increased by ~1 and 3 fold in Kenia and
168 Tambopata respectively, compared to a 1.6 % yr^{-1} basin wide average (Figure 3e) [27]. Similar drought-
169 induced mortality was also seen across the wider basin following the 2005 drought[4]. The Bolivian
170 plots experienced more severe drought ($MCWD_{anom}$<-240 mm) and here, more trees died more
171 quickly than in the Peruvian plots which were less strongly droughted ($MCWD_{anom}$ = -51 mm). Our
172 data indicate that mortality rates peaked 1-2 years after the drought, consistent with the hypothesis
173 that trees were weakened during the drought from reduced maintenance but only succumbed later[19].

174 Plant carbon expenditure was significantly related (P<0.05, linear regression) and
175 autotrophic respiration was marginally significantly related (P=0.08, linear regression) to the anomaly
176 in MCWD for both annual sums (N=13 individual plots for 2009 minus 2010, PCE_{anom} =-1.0+0.011*
177 $MCWD_{anom}$, r^2 = 0.34, with a standard error on the slope of ±0.004, Figure 3a and b). The anomaly in
178 NPP, on the other hand, showed no significant relationship with the MCWD anomaly (Figure 3c,
179 P>0.10). We combine a TRMM (v7 years 1998-2012) based $MCWD_{anom}$ for each TRMM pixel in the
180 Amazon in 2010 and 2011 with the slope of the above equation (with an intercept of zero) to estimate
181 that mean net total photosynthesis decreased by 0.38 Pg C (0.23 - 0.53 Pg C) in 2010 compared to
182 2011, based on a mean South American tropical forested area of 6.77×10^6 km^2 (Figure 3d). For the
183 same period, an Amazonia-focussed atmospheric inversion modelling study estimated a decreased
184 flux of 0.25±0.14 Pg C in 2010 relative to 2011 from reduced photosynthesis, which is within our
185 error estimates[5].

186 Why would trees prioritize growth over maintenance or defence during and following a
187 drought? This strategy makes sense when viewed from an eco-evolutionary standpoint where any
188 decrease in growth of an individual tree puts that tree at a competitive disadvantage by increased risk
189 of loss of resources (light, water, or nutrients) to neighbours[6]. We hypothesize that this decrease in
190 maintenance and defence led to our plot-level increase in mortality. Thus, while such a drought-
191 induced strategy may reduce the mean per-tree performance in the forest via increased mortality, it is
192 still likely to be selected for on an individual basis given the evolutionary constraints proposed by

193 game theory [28]. In other words, this strategy increases mortality for a small proportion of trees
194 because most are locked in to growth competition with neighbours. Such unexpected carbon
195 allocation patterns have been theorized previously, but before now have lacked much empirical
196 support. For instance, trees may grow excess leaves not to improve carbon uptake but to shade out
197 competition[29] or they may over-allocate carbon to root growth in shallow soil systems in response to
198 competition[6].

199 Overall, our plot data indicate that drought suppressed total CO_2 uptake with little
200 reduction in growth and therefore, less carbon was available to the trees for defence and maintenance.
201 Reduced carbon would have also increased tree mortality from embolisms and cavitation because
202 non-structural carbohydrates (sugars) may be involved in sensing and reversing embolism[18]. The
203 debate over drought-induced tree mortality is often framed as being caused by either C starvation,
204 water cavitation, or biotic attack, but the three are often intertwined[30] because during drought there is
205 less C available to fend off all three threats. This insight and new mechanistic understanding can help
206 to improve predictions of the impact of future climate change on tropical forests.

207

Acknowledgements - This work is a product of the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk) and the RAINFOR and ABERG research consortia, and was funded by grants to YM and OP from the Gordon and Betty Moore Foundation to the Amazon Forest Inventory Network (RAINFOR) and the Andes Biodiversity and Ecosystems Research Group (ABERG), and grants from the UK Natural Environment Research Council (Grants NE/D01025X/1, NE/D014174/1, and NE/F002149/1, NE/J011002/1), the NERC AMAZONICA consortium grant (NE/F005776/1), the EU FP7 Amazalert (282664) GEOCARBON (283080) projects. Some data in this publication were provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors. We thank P. Brando and Tanguro partners for logistical support and advice. TRF is supported by a National Council for Scientific and Technological Development (CNPq, Brazil) award. PM is supported by an ARC fellowship award FT110100457; OLP is supported by an ERC Advanced Investigator Award and a Royal Society Wolfson Research Merit Award; YM is supported by an ERC Advanced Investigator Award and by the Jackson Foundation. CED acknowledges funding from the John Fell Fund.

Author contributions – CED, YM, and DBM designed and implemented the study. CED analysed the data. CED, CAJG, FFA, DG, WHH, JES, AA, MCC, ACLC, TF, AM, WR, and OP collected the data. CED wrote the paper with contributions from YM, OP, PM, and DBM.

Summary statement - Monthly averaged data for all our plots used to calculate the results are available in the supplementary material. Detailed plot descriptions for each plot are available in a series of companion papers ([19-23,32-33]). All raw data inputs are available upon request from the authors or from http://gem.tropicalforests.ox.ac.uk/.

References

1 Lewis, S. L., Brando, P. M., Phillips, O. L., van der Heijden, G. M. F. & Nepstad, D. The 2010 Amazon Drought. *Science* **331**, 554-554, doi:DOI 10.1126/science.1200807 (2011).

2 Gloor, M. *et al.* Intensification of the Amazon hydrological cycle over the last two decades,. *Geophys. Res. Lett* **40, doi:10.1002/grl.50377** (2013).

3 IPCC. Synthesis Report,Summary for Policymakers. *An Assessment of the Intergovernmental Panel on Climate Change* (2007).

4 Phillips, O. L. *et al.* Drought Sensitivity of the Amazon Rainforest. *Science* **323**, 1344-1347, doi:DOI 10.1126/science.1164033 (2009).

5 Gatti, L. V. *et al.* Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* **506**, 76-+, doi:Doi 10.1038/Nature12957 (2014).

6 Franklin, O. *et al.* Modeling carbon allocation in trees: a search for principles. *Tree Physiol* **32**, 648-666, doi:DOI 10.1093/treephys/tpr138 (2012).

7 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:DOI 10.1111/j.1469-8137.2010.03309.x (2010).

8 Nepstad, D. C. *et al.* The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *J Geophys Res-Atmos* **107**, doi:Artn 8085 Doi 10.1029/2001jd000360 (2002).

9 Xu, L. A. *et al.* Widespread decline in greenness of Amazonian vegetation due to the 2010 drought. *Geophys Res Lett* **38**, doi:Artn L07402 Doi 10.1029/2011gl046824 (2011).

10 Saatchi, S. *et al.* Persistent effects of a severe drought on Amazonian forest canopy. *P Natl Acad Sci USA* **110**, 565-570, doi:DOI 10.1073/pnas.1204651110 (2013).

11 Saleska, S. R., Didan, K., Huete, A. R. & da Rocha, H. R. Amazon forests green-up during 2005 drought. *Science* **318**, 612-612, doi:DOI 10.1126/science.1146663 (2007).

12 Phillips, O. L. *et al.* Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**, 439-442, doi:DOI 10.1126/science.282.5388.439 (1998).

13 Meir, P., Metcalfe, D. B., Costa, A. C. L. & Fisher, R. A. The fate of assimilated carbon during drought: impacts on respiration in Amazon rainforests. *Philos T R Soc B* **363**, 1849-1855, doi:DOI 10.1098/rstb.2007.0021 (2008).

14 Townsend, A. R., Asner, G. P., White, J. W. C. & Tans, P. P. Land use effects on atmospheric C-13 imply a sizable terrestrial CO2 sink in tropical latitudes. *Geophys Res Lett* **29**, doi:Artn 1426 Doi 10.1029/2001gl013454 (2002).

15 Malhi, Y., Doughty, C. & Galbraith, D. The allocation of ecosystem net primary productivity in tropical forests. *Philos T R Soc B* **366**, 3225-3245, doi:DOI 10.1098/rstb.2011.0062 (2011).

16 Wurth, M. K. R., Pelaez-Riedl, S., Wright, S. J. & Korner, C. Non-structural carbohydrate pools in a tropical forest. *Oecologia* **143**, 11-24, doi:DOI 10.1007/s00442-004-1773-2 (2005).

17 Dietze, M. C. *et al.* Nonstructural Carbon in Woody Plants. *Annu Rev Plant Biol* **65**, 667-687, doi:DOI 10.1146/annurev-arplant-050213-040054 (2014).

18 Sala, A., Woodruff, D. R. & Meinzer, F. C. Carbon dynamics in trees: feast or famine? *Tree Physiology* **32**, 764-775, doi:DOI 10.1093/treephys/tpr143 (2012).

19 da Costa, A. C. L. *et al.* Ecosystem respiration and net primary productivity after 8-10 years of experimental through-fall reduction in an eastern Amazon forest. *Plant Ecol Divers* **7**, 7-24, doi:Doi 10.1080/17550874.2013.798366 (2014).

20 Araujo-Murakami, A. *et al.* The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecol Divers* **7**, 55-69, doi:Doi 10.1080/17550874.2013.798364 (2014).

21 Doughty, C. E. *et al.* The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil. *Plant Ecol Divers* **7**, 41-53, doi:Doi 10.1080/17550874.2013.798367 (2014).
22 Malhi, Y. *et al.* The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecol Divers* **7**, 85-105, doi:Doi 10.1080/17550874.2013.820805 (2014).
23 Rocha, W. *et al.* Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). *Plant Ecol Divers* **7**, 25-40, doi:Doi 10.1080/17550874.2013.798368 (2014).
24 Fenn, K., Malhi, Y., Morecroft, M., Lloyd, C. & Thomas, M. The carbon cycle of a maritime ancient temperate broadleaved woodland at seasonal and annual scales. *Ecosystems* (in press).
25 Fisher, R. A. *et al.* The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Global Change Biol* **13**, 2361-2378, doi:DOI 10.1111/j.1365-2486.2007.01417.x (2007).
26 Doughty, C. E. *et al.* Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought. *Ecology* **95**, 2192-2201 (2014).
27 Lewis, S. L. *et al.* Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos T Roy Soc B* **359**, 421-436, doi:DOI 10.1098/rstb.2003.1431 (2004).
28 King, D. A. A Model Analysis of the Influence of Root and Foliage Allocation on Forest Production and Competition between Trees. *Tree Physiol* **12**, 119-135 (1993).
29 Hikosaka, K. & Anten, N. P. R. An evolutionary game of leaf dynamics and its consequences for canopy structure. *Funct Ecol* **26**, 1024-1032, doi:DOI 10.1111/j.1365-2435.2012.02042.x (2012).
30 McDowell, N. G. *et al.* The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol Evol* **26**, 523-532, doi:DOI 10.1016/j.tree.2011.06.003 (2011).

315 **Figure legends**

316 **Figure 1** –**Impact of drought on carbon fluxes.** (a) Total plant carbon expenditure (PCE), (b) total
317 autotrophic respiration (R_a), (c) total net primary production (NPP), and (d) heterotrophic soil
318 respiration (R_h) by the forests for the three drought-affected forest plots in humid lowland zones (solid
319 black), in dry lowland zones (solid red), and the eight non-drought plots (solid green). Error bars
320 indicate the standard error of mean plot differences. For visual clarity we do not include all error
321 bars. Dashed lines show "normal" (2009; pre-drought) estimates smoothed with a span of 5months
322 during 2010 and 2011 for the lowland plots (black dashed) and the dry lowland plots (red dashed).
323 The vertical bar labelled "drought" represents the approximate period of the drought. The areas
324 highlighted in yellow represents the drought anomaly or the impact of the drought on total plant
325 carbon expenditure (numerically equivalent to GPP) and R_a.

326

327 **Figure 2** –**Impact of drought on carbon allocation**. (a) Total NPP, (b) mean carbon allocation to
328 canopy, (c) to wood, (d) to fine roots for non-drought lowland plots (green solid line; N=8), drought
329 plots in the humid lowlands (black solid lines; N=3), and drought plots in the dry lowlands (red
330 dashed lines; N=3). On the right (e-h) are the seasonally detrended anomaly data for each variable on
331 the left. All error bars are standard errors across plots. The vertical bar labelled "drought" represents
332 the approximate period of the drought. Significant change is determined with paired t-test comparing
333 six month periods during and following the drought to equivalent months in 2009 for all plots.

334

335 **Figure 3** – **Estimated impact of drought on the basin-wide flux of CO_2 -** The shifts in annual
336 fluxes in 2010 relative to 2009 for each individual plot for (a) plant carbon expenditure (PCE; equal to
337 GPP over longer time scales), (b) autotrophic respiration (R_a) and (c) total Net Primary Production
338 (NPP), plotted against the shift in maximum cumulative water deficit (MCWD) in 2010 relative to
339 2009. (d) Estimate of basin-wide anomaly in Gross Primary Production (2011 minus 2010; assumed
340 equal to PCE) based on the TRMM v7 calculated CWD anomaly (mm $month^{-1}$) and the slope of the
341 linear regression found in Figure 3a. We contrast 2010 to 2011 to compare with the atmospheric
342 inversion measurements collected during this period[5]. (e) Mortality rates as fraction of plot biomass
343 for Peruvian drought plots (grey line, N=3, error bars are s.e.), Bolivian drought plots (black line,
344 N=2), and no drought plots (red line, N=3). Mean Amazonian background tree mortality (no drought)
345 is shown as a black horizontal dashed line (from Lewis et al. 2004 Figure 3)[27] .

346

Methods – We measured total NPP and autotrophic respiration at 13 one ha plots (plots described individually below) throughout the Amazon basin through 2009-2010 (and 2009-2011 or 2009-2012 for droughted plots). A detailed description of each measurement is listed in ED Tables 1-3. Total measured NPP included canopy, woody, and fine root NPP. In our seasonal estimates of NPP we exclude several smaller components such as branchfall (although these data are shown in ED figure 6 and described in ED Tables 1-3), herbivory, coarse root, and small tree NPP (<10cm) that we have included in previous estimates of these sites. We calculate leaf flush by calculating the change in leaf area index, LAI (m^2 m^{-2}), multiplied by the mean specific leaf area, SLA (m^2 g^{-1}), and adding this to leaf litterfall following a procedure from Doughty and Goulden (2008)[31]. Total estimated autotrophic respiration consisted of rhizosphere respiration (i.e. respiration from roots, mycorrhizae and exudate-dependent soil microbes), woody respiration and canopy respiration. Each component was measured every 1-3 months, except for canopy respiration, which was measured only 1-2 times per plot at the leaf level but scaled to the canopy scale using monthly LAI partitioned in sun and shade components. Seasonal changes in autotrophic respiration during and following drought are due to monthly measured rhizosphere and woody respiration, not canopy respiration (ED Figure 7). Detailed information on the methodology and graphs showing data from each individual component are also available from a series of companion papers[19-23,32-33]. Each of these site papers includes a full spatial and scaling error analysis for each measurement so we do not include them here for brevity.

Photosynthesis - Leaf photosynthesis was measured in Bolivia in the peak of the drought (Nov 2010) and during a non-drought period (June 2011) on the same ~20 individual trees (12 different species from plot A and 17 species from plot B) in the plot using canopy top cut branches (immediately recut under water to restore hydraulic conductivity). These measurements are compared with leaf photosynthesis measurements in the Tapajos, Brazil on attached (not cut) canopy top leaves accessed via three walk up towers, to show that A_{sat} (light saturated photosynthesis) would not necessarily be expected to decrease during a typical dry season and the measurements were taken at the start of a typical dry season to near the end (ED Figure 3- methodological details in ED Tables 1-3).

Climate - We classified our drought sites according to cumulative water deficit (CWD) anomalies based on precipitation data collected from automatic weather stations at each of the plots (AWS) (Skye Instruments, Llandrindod, UK). Six of our 13 plots experienced drought in 2010 (negative CWD anomalies more than half the year) with a mean CWD anomaly of -107 mm in October and a mean MCWD of -135 mm , meaning that the driest month on average had a water deficit 135 mm greater than a normal year (ED Figure 2). This varied regionally with the highest MCWD in the Bolivian sites ($MCWD_{anom}$ = -240 mm) and the lowest in the lowland Peruvian sites ($MCWD_{anom}$ = -51 mm). We use Tropical Rainfall Monitoring Mission (TRMM) data from Jan 1998 to Dec 2012 (TRMM version 7) to calculate for each pixel the maximum monthly CWD anomaly (ED Figure 2). The basin wide median $MCWD_{anom}$ for 2010 for droughted tropical forest regions was 136 mm (excluding $MCWD_{anom} \geq 0$ mm). This implies that the mean of our droughted plots had equivalent moisture anomaly to the basin-wide "typical" Amazon drought for 2010 (ED Figure 2), but also that our plots did not experience the more severe drought seen by some regions of Amazonia.

Statistics –All data were tested for normality and if they were normal, we did a two-tailed paired t-test using Sigmaplot (Systat Software inc., San Jose, Ca, USA). If normality was not passed, as with the mortality data, we used a Wilcoxon Signed Rank Test. We used a two-tailed test except for mortality where we expect the change to be in one direction and therefore used a one-tailed test. We calculated 95% confidence intervals by multiplying the standard error by 1.96.

Additional Mortality data - For the additional RAINFOR analyses for Tambopata and Caxiuanã, interval-by-interval loss rates in each plot were computed following standard RAINFOR field and ForestPlots.net data protocols (see for example Quesada et al. 2012 and Lopez-Gonzalez et al. 2011)[34-35] . At Caxiuanã, data were collected by the TEAM network whose protocols are closely based on RAINFOR models. These include multiple repeated diameter measurements of the same tree at 1.3m or above buttresses - allowing where necessary for point of measurement changes -, high-resolution botanical identifications of hundreds of tree species at each site, and the use of taxon-

specific wood density values, to derive from each individual tree ≥10cm diameter the stand-level values of biomass and biomass dynamics. We used a generalized region-specific height-diameter biomass allometry[36]. Because here the question is simply whether the 2010 drought coincided with mortality changes in each site, and not what the precise values of mortality were for individual intervals and plots, we did not attempt to account for the small effects of slightly varying census-interval lengths on wood production rates. Data were downloaded from ForestPlots.net in October 2014, and the TEAM database in April 2013.

Site descriptions of 13, one ha plots

Plots with drought in 2010

Kenia (N=2, 1 ha plots) - These plots were established and monitored on private property at the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (16.0158° S, 62.7301° W) from January 2009. The plots are 2 km apart, and are situated on inceptisols with relatively high fertility (high cation exchange capacity and phosphorus concentration) and low acidity compared with eastern Amazonian forests. The plots experienced almost identical climate and had sandy loam soil with 76% sand content. However, one plot was located on a shallow soil (< 1 m depth) over pre-Cambrian bedrock, leading to lower available water (we term this plot Kenia-B). The second plot was located on deeper soils in a slight topographic depression (henceforth termed Kenia-A). These differences in drainage and soil depth had an effect on forest composition at this ecotone, with Kenia-A hosting a more humid forest type typical of Amazonian forests and Kenia-B a drier forest type typical of *chiquitano* dry forests. For further details see Araujo-Murakami et al. 2014 [20].

Tanguro (N=2, 1 ha plots) - The study area is located on the Fazenda Tanguro (~80,000 ha) in Mato Grosso state, about 30 km north of southern boundary of the Amazon rainforest in Brazil (13.0765° S, 52.3858° W). The soil type at the site is a red-yellow alic dystrophic latosol (RADAM Brazil, 1974; Brazilian soil classification), a relatively infertile sandy ferralsol (FAO classification) or oxisol (Haplustox; U.S. Department of Agriculture classification scheme), the groundwater is at about 15 m depth, and no layers of soil prevent root penetration through the soil profile. These soils are amongst the least fertile in Amazonia and widespread across eastern Amazonia. The vegetation is closed canopy, old growth forest with a relatively low mean canopy height (20 m) and relatively low plant species diversity (97 species of trees and lianas greater than 10 cm DBH (diameter at 1.3 m stem height above the ground)) when compared with the wetter forests typical of the central Amazon. For further details see Rocha et al. 2014[23].

Tambopata (N=2, 1 ha plots) - The two study plots are located in the Tambopata reserve (TAM-05 12.837° S, 69.2937° W and TAM-06 12.828° S, 69.2690° W), in the Madre de Dios region of Peru. The geomorphology of the study region is based on old floodplains of the meandering Tambopata River. TAM-05 is situated on a Pleistocene terrace (< 100,000 years old). The soil at TAM-05 is a haplic cambisol (WRB taxonomy), and that at TAM-06 is a haplic alisol[37]. We incorporate mortality data from an additional nearby plot (TAM-09). No hardpan layers of soil prevent root penetration through the soil profile. For further details see Malhi et al. 2014[22].

We divide these six plots into three lowland plots (TAM-05, TAM-06, and Kenia-A - black lines figure 1 and 2) and three dry-lowland plots (2 Tanguro plots and Kenia-B - red lines figure 1 and 2). Distinction of dry-lowland plots is made by using mean MCWD for Tanguro and by species composition for Kenia-B with drier forest type species typical of *chiquitano* dry forests.

Plots with no drought in 2010

San Pedro (N=2, 1 ha plots) - The San Pedro site (13.0491°S, 71.5365°W) is located in the Kosñipata Valley, in the cultural buffer zone of the Parque Nacional del Manú, Cusco, Peru. The two plots at San Pedro lie very close to the transition between upper and pre-montane forest zones, which occurs in this valley at approximately 1500-2000 m. Although data on cloud cover frequency and cloud base elevation in the plots over the annual cycle are difficult to obtain, SP 1750 is immersed for longer periods than SP 1500 during the austral winter months. SP 1500 is estimated to be near the lower limit of the cloud base. For further details see Huasco et al. 2014 [33].

Wayqecha *(N=2, 1 ha plots)* - The Wayqecha (RAINFOR plot code WAY-01: 13.1751°S 71.5948°W) and Esperanza (RAINFOR plot code ESP-01) plots are high elevation cloud forest located in the cultural buffer zone of the Parque Nacional del Manú, Cusco, Peru at ~3000 meters elevation. The two plots lie a few hundred metres below the treeline transition to high elevation grasslands. For further details see Girardin et al. 2014 [32].

Caxiuanã-(CAX-08 and CAX-06) *(N=2, 1 ha plots)* – These plots are located in Caxiuanã National Forest Reserve, Pará in the eastern Brazilian Amazon. Terra Preta (1.8560° S, 51.4352° W)- The *terra preta* plot (plot code CAX-08 in the RAINFOR Amazon forest inventory network) was a late successional forest with a large proportion of fruit trees, on an isolated patch (< 2 ha) of fertile dark earth or *terra preta do Indio*. The original ferralsol soils became progressively enriched by the activities of local inhabitants between the years of 1280 to 1600AD[38]. The species composition of the *terra preta* plot was that of an old abandoned agroforestry system, with Brazil nut (*Bertholletia excelsa*), kapok (*Ceiba pentandra*) and also paleotropical tree crops including coffee (*Coffea*) and orange (*Citrus*). The water-side location of the *terra preta* plot results in a substantially different microclimate from that of the inland tower plot, with high solar radiation (the large cool water area of the bay suppresses cloud formation close to the bay) and higher temperatures. The *tower* plot (CAX-06) (1.7198 S, 51.4581 W) was a tall primary forest (35 m canopy height) situated on a clay-rich geric alumnic ferralsol (alumnic, hyperdistric, clayic), near an eddy covariance flux tower, with species composition typical of eastern Amazonia. For further details see Doughty et al. 2014[21].

Caxiuanã-(TFE-control) – *(N=1, 1 ha plots)* This control plot of an experimental drought study is approximately 2 km south of the tower plot mentioned above (1.7279°S, 51.468° W). It is a largely undisturbed *terra firme* forest, of the type widespread across eastern Amazonia. The study plot is located on highly weathered vetic acrisols typical of upland forests in the eastern Amazon, with a thick stony laterite layer at 3–4 m depth. The site elevation is 15 m above river level in the dry season and the water table has been occasionally observed at a soil depth of 10 m during the wet season. For further details see da Costa et al. 2014[19].

Extended Data results –

Heterotrophic respiration - Soil heterotrophic respiration showed no significant change during the drought period in the droughted *humid* lowland plots (Figure 1d black line, N=3) and no significant change with cumulative water deficit (CWD) anomaly ($P>0.05$). There was a slight suppression of R_H near the start of the drought, but this was compensated by a larger than normal increase in R_H later in the drought as some rains (although much lower than normal) arrived (Figure 1d black line). However, in contrast, the droughted *dry* lowland plots did show a large decrease in soil heterotrophic respiration at the start of the drought in comparison to 2009 (although only marginally significant $P<0.1$, N=3) (Figure 1d red line), but these regions are a geographically small part of the basin and their overall influence on basin wide fluxes is likely to be small. Mean temperatures were similar in 2010 and 2011 and therefore any change in heterotrophic flux was most likely to have been moisture driven (ED Figure 2). Dead wood respiration was initially suppressed during the dry season of the drought year but this was compensated by a large gain once the rains started, leading to no net annual change in dead wood respiration from the drought (ED figure 6). Branch fall did not increase during the drought and, in fact, slightly decreased, possibly because of lower wind speeds from reduced storm activity (ED figure 6). Our data show little net change to heterotrophic respiration, and therefore we estimate that the drought forest plots were first a net C source in 2010 due to suppressed photosynthesis, and then a net C sink in early 2011 as photosynthesis returned to normal but R_a remained slightly supressed compared to previous periods, an observation which is in line with a recent atmospheric inversion study of the Amazon basin[5].

Carbon Allocation shifts- In two of the plots (Kenia A and B), NPP allocation shifted towards roots in the second year after the drought, possibly to alleviate water stress for future droughts, or to increase nutrient uptake to track recovered carbon uptake (ED Figure 5 – NPP allocation patterns at this site are explored in detail in a companion paper[26]). However, allocation responses to drought vary strongly by site. For instance, in two lowland Peruvian plots that experienced milder drought, NPP

instead shifted back towards woody growth in the second year following the drought (ED Figure 5) while in two dry lowland Brazilian plots that experienced moderate drought, woody growth increased in the year following the drought at the expense of canopy and fine root growth (ED Figure 5). The two plots hardest hit by the drought ($MCWD_{anom}$ = -240 mm) showed a long term decrease in allocation of NPP towards wood even though total NPP remained constant (ED Figure 5). This indicates that care should be taken in the interpretation of tree growth and dendrochronology results as proxies for productivity following drought as they may be more influenced by shifting carbon allocation than by changes in total NPP. Our plots show no significant change in woody NPP growth rates during the drought although there is a small decline (Figure 2). Woody growth rates may actually decline, but our sample size of three is too small to capture the signal statistically.

Additional mortality results- To see if mortality increased more broadly in the regions surrounding our plots, we compared plots in the RAINFOR database near Tambopata (with drought according to our meteorological station data) to Caxiuanã (without drought in 2010). In Caxiuanã, we compared plots 1 to 6 (= TEC-01 to TEC-06 using the RAINFOR code) for pre-2010 mortality (starting in 2003) to mortality from a census in late 2010. In Tambopata, we compared plots TAM-01 to TAM-08 for pre-2010 mortality (mostly starting in 1983) to mortality from a census in mid-2011. For this dataset, we use a non-parametric Wilcoxon signed rank test and find significant increase in biomass mortality following the 2010 drought in the larger Tambopata dataset ($N = 9$, $p = 0.018$). We contrast this to Caxiuanã (a no drought site) where we also have high resolution met station data and find no significant change following 2010 ($N = 6$, $p > 0.05$).

Additional references

31 Doughty, C. E. & Goulden, M. L. Seasonal patterns of tropical forest leaf area index and CO2 exchange. *J Geophys Res-Biogeo* **113**, -, doi:Artn G00b06 Doi 10.1029/2007jg000590 (2008).

32 Girardin, C. A. J. *et al.* Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecol Divers* **7**, 107-123, doi:Doi 10.1080/17550874.2013.820222 (2014).

33 Huasco, W. H. *et al.* Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecol Divers* **7**, 125-142, doi:Doi 10.1080/17550874.2013.819042 (2014).

34 Quesada, C. A. *et al.* Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **9**, 2203-2246, doi:DOI 10.5194/bg-9-2203-2012 (2012).

35 Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M. & Phillips, O. L. ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *J Veg Sci* **22**, 610-613, doi:DOI 10.1111/j.1654-1103.2011.01312.x (2011).

36 Feldpausch, T. R. *et al.* Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* **9**, 3381-3403, doi:DOI 10.5194/bg-9-3381-2012 (2012).

37 Quesada, C. A. *et al.* Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* **8**, 1415-1440, doi:DOI 10.5194/bg-8-1415-2011 (2011).

38 Lehmann, J., Kern, D. C., Glaser, B. & Woods, W. I. *Amazonian Dark Earths: Origin, Properties, Management*. (Kluwer Academic Publishers, 2003).

39 Chave, J. *et al.* Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**, 87-99, doi:DOI 10.1007/s00442-005-0100-x (2005).

40 Doughty, C. E. An In Situ Leaf and Branch Warming Experiment in the Amazon. *Biotropica* **43**, 658-665, doi:DOI 10.1111/j.1744-7429.2010.00746.x (2011).

41 Martin, A. R. & Thomas, S. C. A Reassessment of Carbon Content in Tropical Trees. *Plos One* **6**, doi:ARTN e23533 DOI 10.1371/journal.pone.0023533 (2011).

42 Metcalfe, D. B. *et al.* Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *J Geophys Res-Biogeo* **112**, doi:Artn G04001 Doi 10.1029/2007jg000443 (2007).

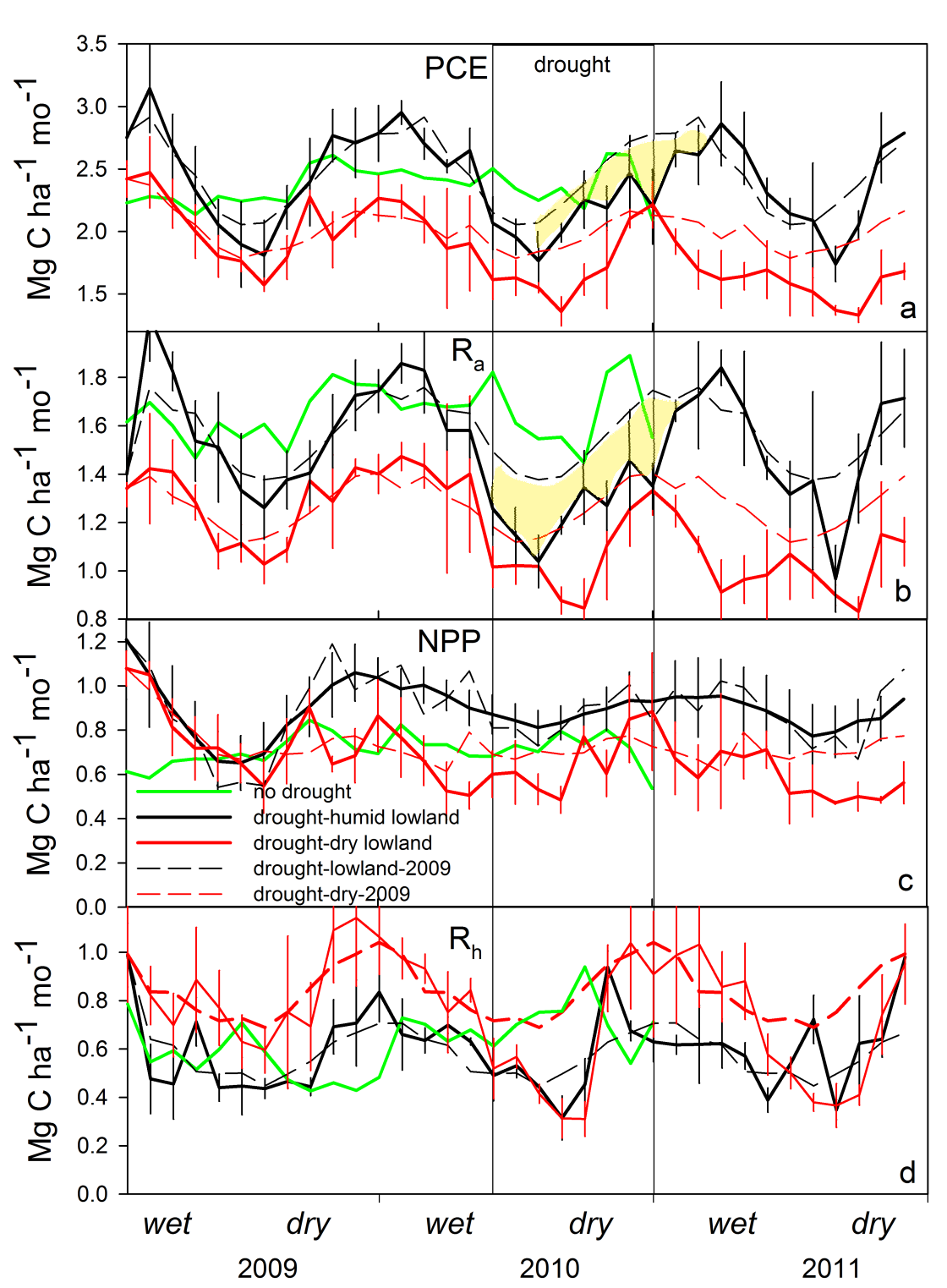
43 Malhi, Y. *et al.* Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *P Natl Acad Sci USA* **106**, 20610-20615, doi:DOI 10.1073/pnas.0804619106 (2009).

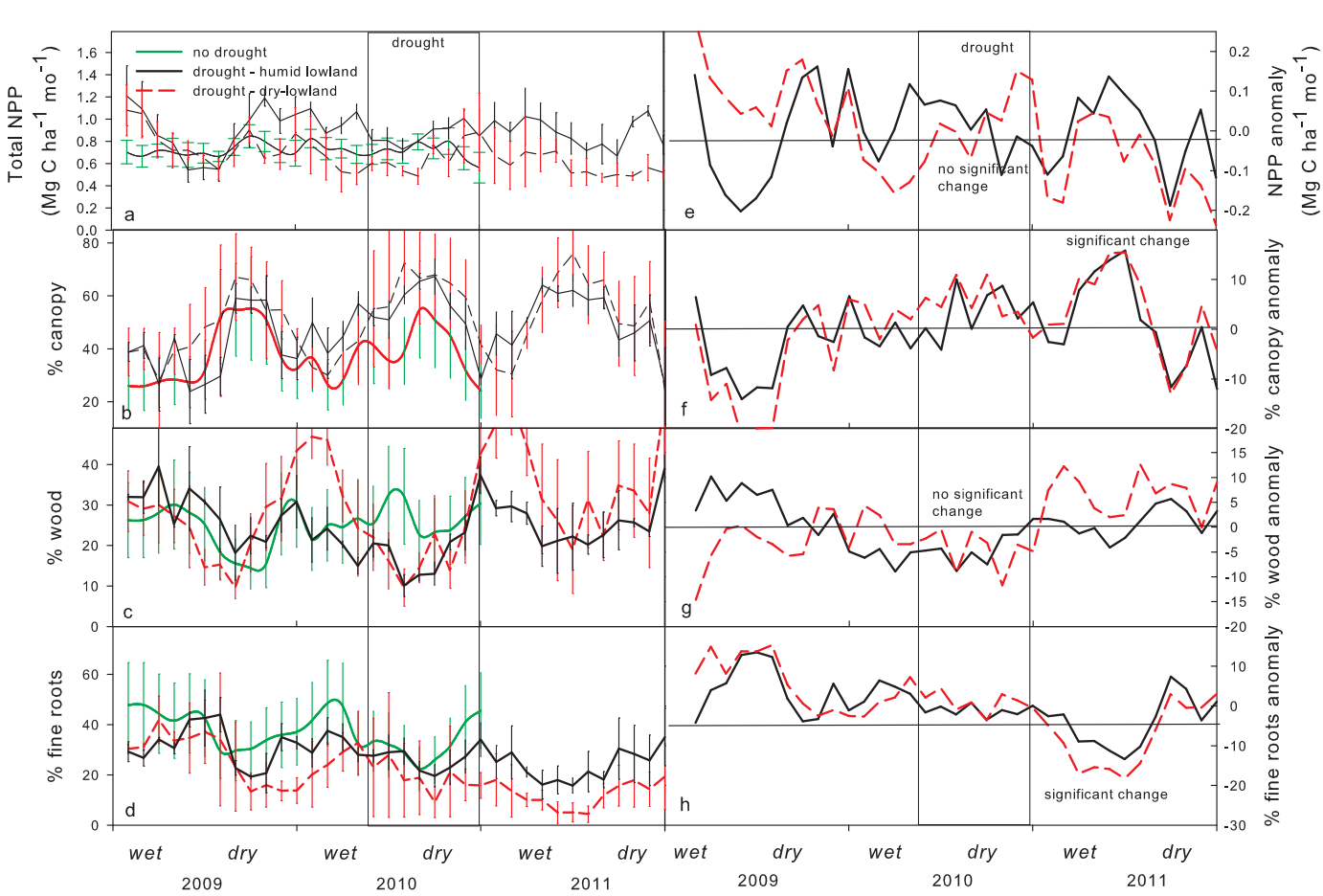
44 Chambers, J. Q. *et al.* Respiration from a tropical forest ecosystem: Partitioning of sources and low carbon use efficiency. *Ecol Appl* **14**, S72-S88 (2004).

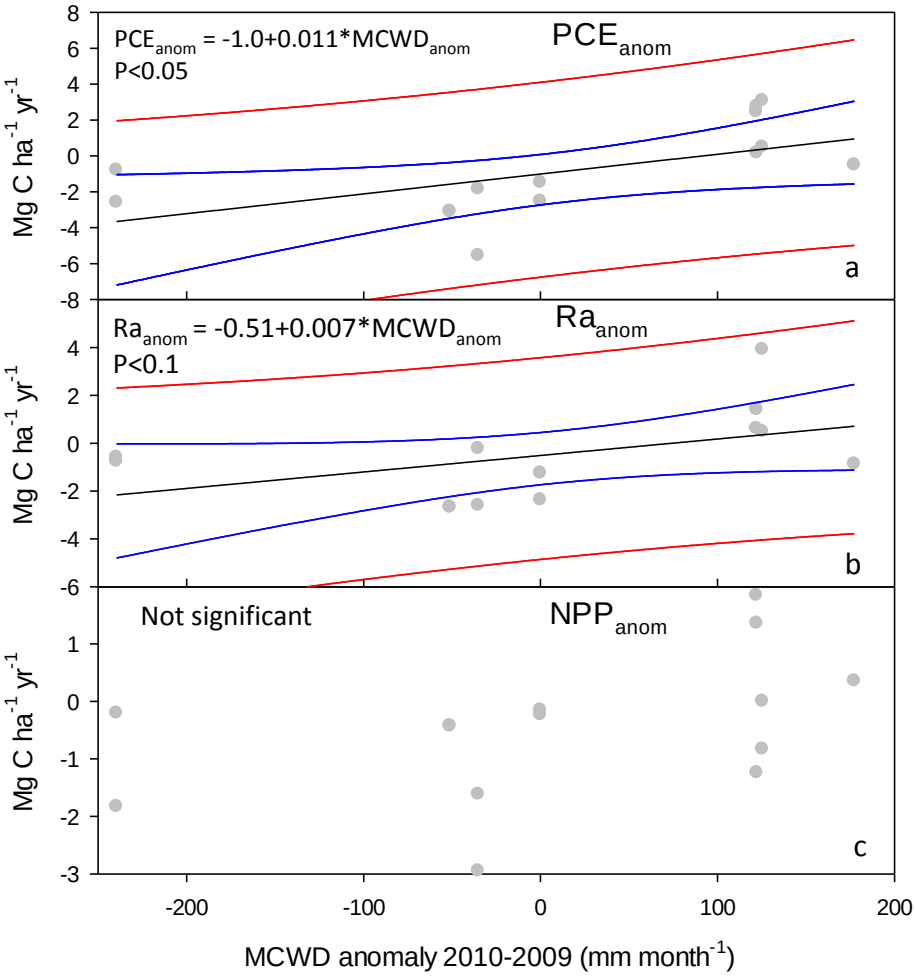
45 Malhi, Y. *et al.* Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *P Natl Acad Sci USA* **106**, 20610-20615, doi:DOI 10.1073/pnas.0804619106 (2009).

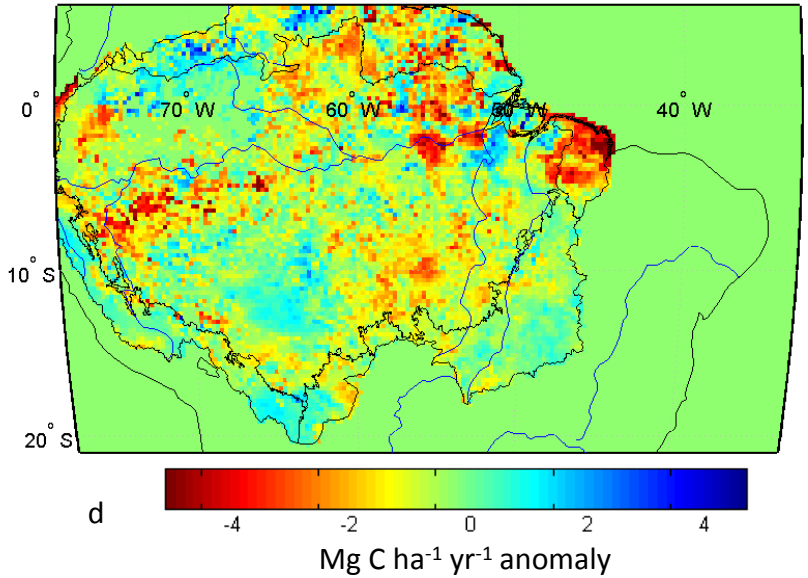
46 da Rocha, H. R. *et al.* Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecol Appl* **14**, S22-S32 (2004).

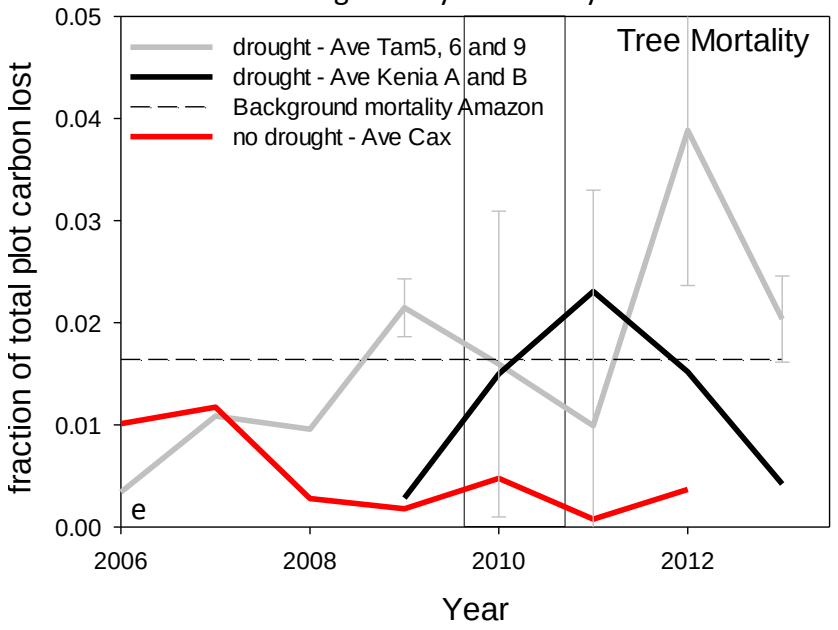
47 Brando, P. M. *et al.* Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *P Natl Acad Sci USA* **111**, 6347-6352, doi:DOI 10.1073/pnas.1305499111 (2014).


PCE
drought
a
R_a
b
NPP
c
R_h
d
Mg C ha^{-1} mo^{-1}
no drought
drought-humid lowland
drought-dry lowland
drought-lowland-2009
drought-dry-2009
wet
dry
wet
dry
wet
dry
2009
2010
2011


Total NPP (Mg C ha-1 mo-1)
no drought
drought - humid lowland
drought - dry-lowland
drought
a
% canopy
b
% wood
c
% fine roots
d
NPP anomaly (Mg C ha-1 mo-1)
drought
no significant change
e
significant change
f
% canopy anomaly
no significant change
g
% wood anomaly
significant change
h
% fine roots anomaly
wet
dry
2009
2010
2011


PCE_anom = -1.0+0.011*MCWD_anom
P<0.05
PCE_anom
a
Ra_anom = -0.51+0.007*MCWD_anom
P<0.1
Ra_anom
b
Not significant
NPP_anom
c
Mg C ha-1 yr-1
MCWD anomaly 2010-2009 (mm month-1)


0°
10° S
20° S
70° W
60° W
50° W
40° W
d
-4
-2
0
2
4
Mg C ha-1 yr-1 anomaly


drought - Ave Tam5, 6 and 9
drought - Ave Kenia A and B
Background mortality Amazon
no drought - Ave Cax
Tree Mortality
fraction of total plot carbon lost
e
Year