Drought–mortality relationships for tropical forests

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Summary

• The rich ecology of tropical forests is intimately tied to their moisture status. Multi-site syntheses can provide a macro-scale view of these linkages and their susceptibility to changing climates. Here, we report pan-tropical and regional-scale analyses of tree vulnerability to drought.

• We assembled available data on tropical forest tree stem mortality before, during, and after recent drought events, from 119 monitoring plots in 10 countries concentrated in Amazonia and Borneo.

• In most sites, larger trees are disproportionately at risk. At least within Amazonia, low wood density trees are also at greater risk of drought-associated mortality, independent of size. For comparable drought intensities, trees in Borneo are more vulnerable than trees in the Amazon. There is some evidence for lagged impacts of drought, with mortality rates remaining elevated 2 yr after the meteorological event is over.

• These findings indicate that repeated droughts would shift the functional composition of tropical forests toward smaller, denser-wooded trees. At very high drought intensities, the linear relationship between tree mortality and moisture stress apparently breaks down, suggesting the existence of moisture stress thresholds beyond which some tropical forests would suffer catastrophic tree mortality.

Introduction

Terrestrial life thrives where both warmth and water supply are greatest. In the wet lowland tropics, in particular, biodiversity, productivity and carbon stocks all tend to reach their greatest values (Gentry, 1988; Heywood, 1995; Malhi *et al.*, 2004). The question of how the world's richest ecosystems respond to moisture deficits (or 'drought') is therefore a central concern for ecologists. Because the terrestrial tropics may experience significant climate change, including more frequent and more extreme moisture deficits, in this century (e.g. Williams *et al.*, 2007), this is also an important question for society.

One important approach to determining drought sensitivity is by experiment, in which rainfall is partially excluded from a patch of forest over a period of several years (cf. Brando *et al.*, 2008; Meir *et al.*, 2009; Costa *et al.*, 2010). However, these are expensive, challenging projects, and so in total only two hectares have been droughted. The two experiments are located relatively close to one another in northeastern Amazonia in deep infertile soils, and so alone are insufficient to allow firm biome-wide conclusions to be drawn. Macro-ecological analysis that incorporates observations from numerous long-term monitoring sites across the tropics can therefore complement site-specific studies, although there are limits to the tree-level mechanistic insights such census data can give us because the tropical demographic data represent many thousands of trees. Our intention here therefore is to reveal the macro-ecological pattern and process in tree death, to inform ecophysiological work and provide some broad 'ground-truthing' context for vegetation modelling.

To date, the only large-scale observational evaluation of an actual tropical drought concerned the unusual 2005 episode in Amazonia, for which long-term plots were remeasured after the event and their biomass growth and mortality compared with earlier records (Phillips *et al.*, 2009). However, there are a large number of additional, local studies, in which drought impacts – and the lack thereof – are reported from various sites in the tropical forest biome. These reports concern El Niño-associated droughts, in some cases more intense than those any of the sites experienced in the 2005 Amazon drought, and spanning a wider range of climate types and biogeographical zones. While few of these studies report impacts on biomass and growth, they do report impacts on stem mortality. A key conclusion of our earlier study (Phillips *et al.*, 2009) was that most drought impact is mediated by mortality and not by growth processes, so by synthesizing the various local mortality reports we can hope to derive a more general view of tropical forest drought sensitivity. In the current study we attempted the first world-wide investigation of tropical drought impact, by starting with the tree-by-tree mortality outcomes from the 2005 Amazon event, which were generated by the pan-Amazon RAINFOR project (Red Amazonica de Inventarios Forestales) and which were not previously reported, and adding additional stem mortality results from all El Niño impact studies with tropical forest data suitable for such analysis. Where possible we also assessed regional patterns in stem mortality risk, and examined individual tree attributes – size and species wood density – which have been hypothesized to affect the sensitivity of tropical trees to constraints in moisture supply (e.g. Hacke *et al.*, 2001; Kitahashi *et al.*, 2008; Patiño *et al.*,

2009; Poorter *et al.*, 2010). Because larger trees may tend to have lower wood density (e.g. Sungpalee *et al.*, 2009) we also attempted to dissect out these candidate risk factors for drought-related mortality.

How moisture stress should be assessed and compared across sites is not immediately clear. Previously we showed that a simple measure of moisture stress (monthly cumulative water deficit (MCWD); Aragão *et al.*, 2007) is as effective a predictor of impacts on Amazon biomass as more sophisticated drought metrics that attempt to account for soil moisture-holding capacity and daily fluctuations in evapo-transpirative demand. Nevertheless, whether MCWD provides a satisfactory universal measure of tropical drought vulnerability is debateable. For example, the impacts of dry season moisture deficit might be modulated by longer-term climate factors. Thus it can be argued that an intense moisture deficit, beyond the local long-term mean, would have greatest ecological impact in forests which are normally very wet. In such events, genetic and ontogenetic drought adaptations would carry a severe selective penalty in reduced competitive vigour. However, the converse expectation is also plausible – an excess moisture deficit should have the greatest impacts in normally drier forests, because here there is a greater risk of crossing a biome threshold to savanna (or dry forest) climate and it is well established that biome boundaries represent the range limits of many tree species (e.g. Ratter *et al.*, 1997). We do not know which of these opposing sets of mechanisms should in practice be more important. If they are unimportant – or cancel each other out – MCWD may be sufficient, but otherwise a different approach may be more appropriate. We therefore assess tree mortality in relation both to MCWD and to another simple moisture index that accounts for mean annual rainfall. We refrain from accounting for soil water-holding capacity because across the published tropical tree plots soil assessments are incomplete and methodological standardization is patchy.

A further challenge is relating the demographic response to the drought. Firstly, as the demographic metrics (mortality and growth) are obtained in annual or supra-annual censuses, and drought is typically a sub-annual event, the 'drought interval' inevitably includes some nondrought period. This problem, discussed in detail by Lingenfelder & Newbery (2009), can affect the metrics computed. Secondly, how rapidly droughts actually kill trees is uncertain. Thus, if droughts mostly affect senescent or moribund trees we would expect post-drought mortality to subside below pre-drought levels, but if drought has a wide impact damaging many trees, then the full stand-level demographic impact of droughts may take years to play out. The literature provides contrasting reports of the immediacy, or otherwise, of drought-driven death – in some cases (e.g. Williamson *et al.*, 2000) mortality rapidly fell to pre-drought levels, but in others impacts apparently lagged behind the actual drought event (e.g. Lingenfelder & Newbery, 2009). In an extreme case from boreal Canada, a mortality peak lagged the drought by at least 3 yr (Hogg *et al.*, 2008). Where possible we have therefore assembled data for 'pre-drought', 'drought', and 'post-drought' intervals to try to assess whether tropical drought impacts do, or do not, lag the episode of moisture stress.

More generally, our approach attempts to review all relevant data to assess whether general trends emerge from long-term plot-monitoring efforts, both regionally and across the tropics. We therefore combine our Amazon 2005 data with observations of other droughts in Amazonia and elsewhere in the Americas, Borneo, and Africa. We ask a set of questions about the vulnerability of tropical forests to droughts, first for the best-sampled region (Amazonia), and then when data permit we repeat the analysis for the whole tropical data set and for Borneo, which is the next best-sampled region: does large tree size predict drought mortality risk?; does low wood density predict drought mortality risk?; how do tree mortality rates vary with moisture stress?; does long-term mean precipitation modulate the forest's response to short-term drought?; to what extent can we specify a biome-wide sensitivity, or are there regional differences?; do forest dynamics return to normal once the drought ends, or do higher mortality rates persist?

Materials and Methods

Collating biometric data

Methods for permanent plot fieldwork in Amazonia and data quality control in the pan-Amazon RAINFOR project (Red Amazonica de Inventarios Forestales) project are detailed elsewhere (Phillips *et al.*, 2004, 2008, 2009). Intercensus intervals average *c.* 5 yr, which is rather lengthy to expect to detect impacts of sub-annual scale droughts. For the purposes of this paper the analysis is restricted to measurement intervals shorter than 4 yr that included 2005 or any previous El Niño event. We were limited to 39 sites (119 plots) by the scarcity of frequently censused plots in the last century and difficulty in acquiring reliable precipitation data pre-1998. For occasional locations monitored over long periods and censused very frequently, we were able to assess the impact of two different droughts events well spaced in time. For these locations, we first assessed the impact of each drought separately by estimating mortality rates and MCWD for each interval compared with values of the preceding pre-drought interval. We then derived the among-drought mean values for each site. We maintain a database (Peacock *et al.*, 2007; López-Gonzalez *et al.*, 2009) in which we curate several hundred tree-by-tree long-term forest demographic data sets (http://www.forestplots.net). As these extend beyond Amazonia we also included four unpublished surveys from African and Bornean sites that

met RAINFOR standards and had appropriate high-resolution monitoring of drought periods.

To collate data for tropical droughts and for tree mortality, we surveyed the relevant literature. We included literature that published mortality rates for the same permanent plots through pre-drought and drought intervals and for which we were able to obtain climatological moisture deficit data for the same periods. We also included additional studies from Borneo where extreme droughts affected the forest in 1982–1983 and 1997–1998 – here some surveys were only carried out post-drought, but local pre-drought mortality rate estimates are available. The analyses presented here refer to our data set of lowland tropical wet, moist, and dry/moist transition forests on a broad range of strata (Table 1). We included data from plots that were located below 1000 m asl across the tropics. Forests growing in the most extreme soil conditions – white sands (typically arenosols) or frequently water-logged soils (typically histosols) – were excluded as the edaphic impact on local hydrology is likely to overwhelm climate fluctuations. Excessively freely draining white sands stunt tree growth and height (e.g. Anderson, 1981; Malhi *et al.*, 2004), while the topography and high organic content of histosols (Santiago *et al.*, 2005; Quesada *et al.*, 2010) imply exceptional capacity to store and supply moisture year-round. Otherwise, for Amazonia at least, the plots are representative of the wider landscapes in which they are found (Anderson *et al.*, 2009). In all, in addition to our Amazon data, suitable studies were available from Malaysian and Indonesian Borneo, Central America, the Atlantic Forest (Brazil), and central and eastern Africa (Leighton & Wirawan, 1986; Condit *et al.*, 1995, 2004; Nakagawa *et al.*, 2000; Williamson *et al.*, 2000; Laurance *et al.*, 2001; Aiba & Kitayama, 2002; Potts, 2003; Sist *et al.*, 2003; Gourlet-Fluery *et al.*, 2004; Newbery & Lingenfelder, 2004; Van Nieuwstadt & Sheil, 2005; Rolim *et al.*, 2005; Nepstad *et al.*, 2007; Brando *et al.*, 2008; Lewis *et al.*, 2009).

Collating meteorological data

For Amazon sites, three sources of meteorological data were used in order of priority: data collected adjacent to the plots; data collected from the closest meteorological station(s) within 50 km of the plot (accessed via Tutiempo (http://www.tutiempo.net) and Hidroweb (http://hidroweb.ana.gov.br/)); precipitation data measured by the Tropical Rainfall Measuring Mission (TRMM; 3B43 version 6) (North America Space Administration (NASA), 2008). TRMM monthly mean precipitation (mm h^{-1}) was available from 1998 to 2006 at 0.25° spatial resolution. For all other sites we used, in order of priority: the local monthly or dry season rainfall data presented in the papers themselves (typically these data were in tabular format but in a few cases (e.g. Linhares: Rolim *et al.*, 2005) we read these values off the published charts), and long-term rainfall values from the CRU 3TS data set (University of East Anglia Climate Research Unit (CRU), 2008).

Mortality analyses

Mortality rate estimates are potentially sensitive to the census interval over which they are calculated because different subpopulations have different turnover rates. To account for this, having estimated mortality rates for each interval by standard procedures (Sheil & May, 1996), we corrected to a standard interval of 1 yr by applying a generic census-interval correction procedure (Lewis *et al.*, 2004). Mortality rates based on census intervals that were already 1 yr or that were already census-interval corrected (one site: Danum Valley) were not corrected further. Site-specific corrections are theoretically preferable to the generic procedure we used, but any such correction would of course be complicated by the drought event which we hypothesize affects subpopulations differently, and in practice calculation of valid site-specific corrections is often limited by sample sizes of censuses and trees. Because the possible impact of varying census intervals is hard to quantify, we further explored the sensitivity of our findings to the census-interval effect by recalculating regional and global scale mortality–drought relationships based on the raw, noncorrected data.

For the mortality by tree size analyses, to maximize comparability with the available literature we examined simply whether canopy and emergent trees (defined as those with diameter ≥ 40 cm) had a more elevated probability of death than subcanopy and understory trees (< 40 cm diameter).

For mortality by wood density analyses, we only considered Amazon sites for which we have tree-by-tree census data and an extensive wood density database (Zanne *et al.*, 2009). We included all Amazon sites that were monitored in 2005 or in a previous El Niño event, and compared mean wood density of trees dying in the interval spanning the drought with the mean wood density of trees dying in the previous and subsequent moister periods. We applied selection criteria based on monitoring resolution. We considered all sites in which the drought event was captured by a census monitoring interval of < 4 yr. We excluded plots in which fewer than ten deaths were recorded in either the drought interval or the pre-drought period to reduce biases and errors as a result of under-sampling. A few plots captured both the 2005 drought and one or more previous El Niño droughts. In such cases we derived the mean wood density of all trees that died during the drought intervals. Any association of wood density with mortality could be confounded by tree size/mortality effects, so we recalculated the wood density/mortality association for small (< 40 cm diameter) and large trees.

To generate mortality vs drought intensity relationships, we first weighted plots to account for differential sampling effort. Our weighting procedure follows that detailed in Phillips *et al.* (2009) in accounting for both plot area and

Table 1 Locations and properties of monitored forests (see text for details of site selection)

Forest	Country	Site name	Site/plot code	Source	Drought	No. of plots	Area (ha)	Total time (yr)	Pre-drought time (yr)[1]	Drought time (yr)[2]	Weighting[3]
Africa	Cameroon	Dja National Park	DJK-01 to 06	This paper and Lewis *et al.* (2009)	2006	6	6.0	2.0	1.0	1.0	2.02
Africa	Tanzania	Udagaji	UDJ-01-02	This paper and Lewis *et al.* (2009)	1997–98	2	0.5	8.1	6.1	2.0	2.26
Atlantic Forest	Brazil	Linhares, Espirito Santo	Linhares	Rolim *et al.* (2005)	1987–88, 97–98	5	2.5	20.0	14.0	6.0	4.10
Borneo	Indonesia	Mentoko, East Kalimantan	Mentoko	Leighton & Wirawan (1986)	1982–83	3	0.6	5.0	1.0	1.3	0.84
Borneo	Indonesia	STREK-RKL4-1, 4-10, East Kalimantan	STREK	Sist *et al.* (2003)	1997–98	2	8.0	7.2	5.6	1.6	3.37
Borneo	Indonesia	STREK-RKL4-4, East Kalimantan	STREK	Sist *et al.* (2003)	1997–98	1	4.0	7.8	5.7	2.1	2.97
Borneo	Indonesia	Sungai Wain, East Kalimantan	Sungai Wain	Van Nieuwstadt & Sheil (2005)	1997–98	9	3.6	0.9	1.0	0.9	1.53
Borneo	Indonesia	Wartonokadri, East Kalimantan	Wartonokadri	Van Nieuwstadt & Sheil (2005)	1997–98	5	1.0	0.9	1.0	0.9	1.00
Borneo	Malaysia	Danum Valley, Sabah	Danum Valley	Newbery & Lingenfelder (2004)	1997–98	2	2.6	12.6	10.0	2.6	3.53
Borneo	Malaysia	Kinabalu lowland forest, Sabah	Kinabalu	Aiba & Kitayama (2002)	1997–98	2	2.0	4.0	2.0	2.0	1.41
Borneo	Malaysia	Lambir Hills, Sarawak	Lambir Hills	Nakagawa *et al.* (2000)	1997–98	1	8.0	4.8	3.9	0.9	2.53
Borneo	Malaysia	Lambir Hills, Sarawak	Lambir Hills	Potts (2003)	1997–98	3	2.1	5.0	4.0	1.0	3.62
Central America	Panama	Barro Colorado Island	Barro Colorado Island	Condit *et al.* (1995)	1982–83	1	50.0	8.0	5.0	3.0	4.92
Central America	Panama	Cocoli	Cocoli	Condit *et al.* (2004)	1997–98	1	4.0	4.0	3.0	1.0	2.32
Amazon, experimental	Brazil	Caxiuana Drought Experiment	Caxiuana	This paper and Costa *et al.*, 2010	Expt II	3	2.6	6.1	6.1	7.0	2.86
Amazon, experimental	Brazil	Tapajos Drought Experiment	Tapajos	Nepstad *et al.* (2007); Brando *et al.* (2008)	Expt I	1	1.0	3.2	3.2	3.2	1.79
Amazon	Bolivia	BEEM	BEE-01,05	This paper and unpublished	2005	2	2.0	4.6	2.8	1.8	1.93
Amazon	Bolivia	Sacta	SCT-01,06	This paper and unpublished	2005	2	2.0	4.7	1.2	2.6	1.36
Amazon	Brazil	BIONTE	BNT-01,02,03	This paper and unpublished	1987–88, 97–98, 2005	3	3.0	24.7	18.0	6.5	4.68
Amazon	Brazil	Caxiuana: TEAM	TEC-01	This paper and unpublished	2005	1	1.0	4.0	2.0	2.0	1.41
Amazon	Brazil	Caxiuana: TEAM	TEC-02,03,04,06	This paper and unpublished	2005	4	3.0	3.6	2.0	1.7	1.84
Amazon	Brazil	Caxiuana: terra preta	CAX-08	This paper and unpublished	2005	1	1.0	2.6	1.6	1.0	1.26
Amazon	Brazil	Dois Irmaos	DOI-01,02	This paper and unpublished	2005	2	2.0	14.4	8.2	6.2	3.12
Amazon	Brazil	Manaus: TEAM	TEM-03,04,05,06	This paper and unpublished	2005	4	4.0	1.9	1.0	0.8	1.61
Amazon	Brazil	Porongaba	POR-01,02	This paper and unpublished	2005	2	2.0	7.1	4.1	3.0	2.30
Amazon	Brazil	Projeto Dinamica Biologica de Fragmentos Florestais	BDF	Williamson *et al.* (2000); Laurance *et al.* (2001)	1997–98	12	12.0	14.1	12.7	1.4	4.85

Table 1 (*Continued*)

Forest	Country	Site name	Site/plot code	Source	Drought	No. of plots	Area (ha)	Total time (yr)	Pre-drought time (yr)[1]	Drought time (yr)[2]	Weighting[3]
Amazon	Brazil	Tapajos	TAP-80	Brando *et al.* (2008)	2005	1	1.0	6.0	5.0	1.0	2.24
Amazon	Colombia	Agua Pudre	AGP-01,02	This paper and unpublished	2005	2	2.0	14.2	12.2	2.0	3.75
Amazon	Colombia	Lorena	LOR-01,02	This paper and unpublished	2005	2	2.0	13.6	11.6	2.0	3.67
Amazon	French Guiana	Paracou	PAR-01 to -11	This paper and Gourlet-Fluery *et al.* (2004)	2005	10	4.9	3.8	2.0	1.8	3.37
Amazon	Peru	Allpahuayo	ALP-11,12,21,22	This paper and unpublished	2005	2	1.7	10.0	9.0	1.0	3.19
Amazon	Peru	Cuzco Amazonico	CUZ-01,02,03,04	This paper and unpublished	2005	4	4.0	7.9	5.0	2.9	2.82
Amazon	Peru	Sucusari	SUC-01,02	This paper and unpublished	2005	2	2.0	10.0	9.0	1.0	3.26
Amazon	Peru	Sucusari	SUC-03,04	This paper and unpublished	2005	2	2.0	5.0	4.1	0.9	2.28
Amazon	Peru	Tambopata	TAM-01,02,05,06,07	This paper and unpublished	1997–98, 2005	5	5.0	14.8	8.2	6.7	3.57
Amazon	Peru	Tambopata	TAM-08	This paper and unpublished	2005	1	1.0	4.4	2.2	2.2	1.48
Amazon	Venezuela	El Dorado	ELD-01,02,03,04	This paper and unpublished	1987–88	4	1.0	16.5	14.7	1.7	3.84
Amazon	Venezuela	Rio Grande	RIO-01,02	This paper and unpublished	1982–83	2	0.5	11.4	9.1	2.3	2.80
Amazon	Venezuela	San Carlos de Rio Negro	SCR-04D, SCR-05D	This paper and unpublished	2005	2	2.0	30.7	28.7	2.0	5.62

[1]'Pre-drought time', total length of the census intervals pre-dating the drought.
[2]'Drought time', total length of the census intervals containing the drought event. In cases with multiple droughts and multiple censuses the total time is used.
[3]Weighted proportional to: the cube root of area + the square root of pre-drought time – 1. See Phillips *et al.* (2009) for further details.

monitoring period, except that for a few plots in the literature the area monitored changed through time and so for these plots we calculated weights for both plot areas and took the mean. Weighting also accounted for the length of the pre-drought interval. We decided against weighting the length of the drought monitoring interval because the null hypothesis being tested is always that a one-off drought event shorter than the monitoring interval affects mortality.

Finally, for sites with distinct 'pre-drought', 'drought', and 'post-drought' intervals we explored the pattern of mortality rates across the three intervals and the extent to which drought effects might persist. Thus, we tested whether in the drought interval mortality was significantly boosted with respect to the pre-drought interval, whether the post-drought mortality declined significantly from drought interval levels, and whether the post-drought mortality was still elevated with respect to pre-drought levels.

Climate and climate–mortality analyses

As discussed earlier, selecting an appropriate index of tropical forest droughting is challenging. As we lack high-resolution meteorological and soil data for many sites we restrict ourselves to simple moisture deficit metrics based on monthly rainfall which previously performed well (Phillips *et al.*, 2009), and in general we follow the procedures established in Phillips *et al.* (2009) for defining the 'pre-drought' and 'drought' intervals and estimating moisture status in those periods. However, the present analysis includes a wider climatological range of sites in terms of mean annual precipitation (MAP) and now includes such strong droughts that if repeated year-on-year some would decidedly move the precipitation regime away from a humid forest environment. We therefore used two rainfall-based moisture metrics.

Firstly, we assumed a mean loss rate via evapotranspiration (3.33 mm d^{-1}), based on empirical measurements and modelled estimates showing that a moist Amazon canopy transpires *c.* 100 mm each month in the dry season (Fisher *et al.*, 2009; Shuttleworth, 1989). While simplistic, this approach has precedent among both the observational and modelling communities (e.g. Sombroek, 1966; Cox *et al.*, 2004; Aragão *et al.*, 2007; Malhi *et al.*, 2009), and has the advantage of being compatible with TRMM satellite-derived monthly estimates of rainfall. We cumulated monthly water deficits over the dry period and estimated the maximum monthly cumulative water deficit (MCWD) in each year, as in Phillips *et al.* (2009). Secondly, we developed a simple index to account for the possible impacts of the mean annual precipitation (MAP) of the site on modulating the ecological response to a given dry season deficit: MCWD/MAP × 100%. For both metrics, the maximum deficit values experienced by each location were compared with the mean annual maximum deficits reached in the

pre-drought monitoring period. This difference provides the predictor variable for our statistical modelling of stem mortality impacts.

The biomass impact of the 2005 Amazon drought followed an approximately linear relationship with relative drought intensity (Phillips *et al.*, 2009). However, there is no *a priori* reason to expect such a linear relationship to be universally true, and the current data set includes a number of sites that were droughted more severely than any we reported before. We anticipated that forests might be resilient to modest droughts but that the tree mortality response could increase rapidly once a certain moisture stress threshold is passed. We therefore adopted a curve-fitting procedure, examining best fits for linear, log-linear, exponential, and two- and three-factor polynomial fits. Similarly, the impact of a drought on tree mortality may be expressed in different ways. We report analyses both in terms of absolute increase in mortality rate, and in terms of relative increase to account for the great variability in background mortality rates.

The various analytical combinations required that we developed multiple models. We initially considered 48 statistical models (based on 3 (data sets: Amazon, all tropical data, Borneo) × 2 (mortality metrics) × 2 (drought metrics) × 4 (linear and various nonlinear curve families)). To assess the impacts of different data subsets, an additional 16 models were considered for Amazonia – excluding the experimental droughts – and a further 48 for the whole tropics, Amazonia, and Borneo in which the analyses were rerun without census-interval correction to assess the sensitivity to our census-interval correction procedure (Supporting Information Tables S3, S4). We then selected the best models for each of the data set/mortality/drought combinations on the basis of adjusted R^2 and Akaike's information criterion (AIC) statistics, and computed 95% bootstrapped confidence intervals based on 1000 bootstrap samples for the lines of best fit. For polynomial models we fitted all possible two- and three-factor models and only selected a model with cubic terms when it had both a lower AIC than all other models (except the exponential model) and a greater R^2 than any other model. We used these outcomes to help address our questions about the sensitivity of tree mortality to moisture stress.

Results

Our data set includes 76 plots from Amazonia and 43 from the rest of the humid, lowland tropics. In total, 160 hectares were monitored before and through drought periods, for a total of 330 yr (Table 1).

Are small or big tropical trees more drought sensitive?

Across our whole data set, big trees (typically defined as those ≥ 30 or ≥ 40 cm diameter) were more vulnerable to drought than smaller trees (≤ 30 or ≤ 40 cm diameter). Of the 33 studies that reported size-specific mortality rates, 23 showed large trees suffering a greater relative increase, six failed to detect a size-related effect, and four found a greater drought elevated mortality risk in small trees than in large trees. The overall tally indicates a clear effect ($P < 0.001$, sign test). Among 18 droughted Amazon mortality studies, 12 reported that large trees suffered a greater relative increase in mortality, three found no size-related effect, and three indicated that mortality was increased for small trees more than for large trees ($P < 0.05$, sign test). Among the nine Bornean plot mortality studies, including published research and that newly reported here, eight reported that large trees suffered a greater relative increase, and one reported no clear pattern ($P < 0.01$, sign test). Among the five remaining sites in Africa, Central America, and the Brazilian Atlantic forest, three reported especially elevated mortality for large trees, and two no size effect. Overall, the effect was weakest in Amazonia, where the drying was least severe, but the tally across all droughted tropical forests and the consistent pattern within and across regions points to the generally greater vulnerability of large trees in tropical droughts.

To examine tree size effects more generally, we also tested whether the proportional increase in stand *biomass* loss rates in tropical droughts was significantly greater than the proportional increase in loss rates for all *stems* ≥ 10 cm diameter, for all droughted sites with available data for both metrics. For both biomass and stem mortality we computed census-interval corrected rates in the drought and pre-drought period, and derived the proportional increase for each during the drought period as compared with the pre-drought period. We then plotted the *difference* between the proportional increase in biomass mortality and the proportional increase in stem mortality, against the proportional increase in stem mortality (Fig. 1; note that the null expectation here is that the difference should average zero and thus the line should be flat). The distribution was positively skewed for drought periods (median = 53% difference in relative biomass and stem mortality rates; $P < 0.01$, Wilcoxon signed rank test), and only in three of 19 cases did biomass mortality rates increase less than stem mortality rates. Note also the marginally significant positive correlation, indicating that the relative impact on larger trees may itself become disproportionately greater in more severe droughts ($P = 0.054$, nonparametric Spearman's rank correlation coefficients). We conclude that tree size is a widespread risk factor for trees in tropical droughts.

Are light-wooded tropical trees more vulnerable to drought?

Mean wood density of Amazon trees dying in drought periods was assessed for 27 plots, including the 2005 drought

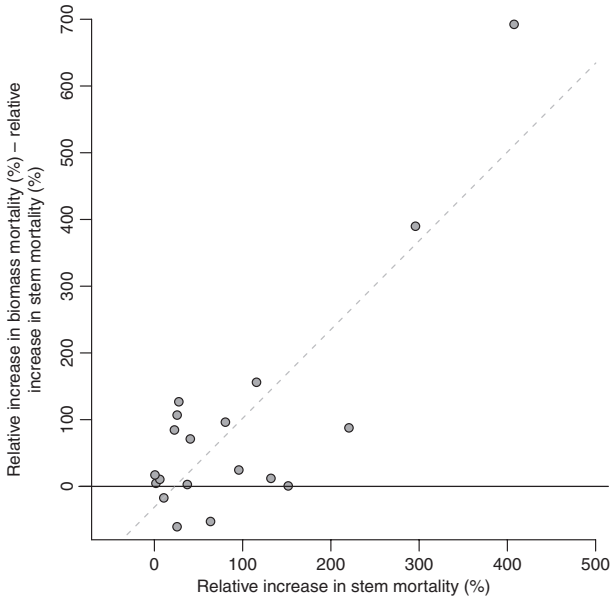

Fig. 1 The differential impact of drought on tree biomass vs tree stems. The difference between the proportional increase in biomass mortality and the proportional increase in stem mortality is plotted against the proportional increase in stem mortality. Thus the *y* and *x* axes are not independent, and the effect is to make the analysis conservative (other things being equal, computationally as *x* increases the *y* value will decrease). For both biomass and stem mortality we derived census-interval corrected rates in the drought and pre-drought periods, and the proportional increase for each during the drought period as compared with the pre-drought period. Results differ significantly from the null expectation of zero (the bold line), and the difference itself appears to become bigger in sites with greater stem mortality (dotted line). The figure contains data from all continents, but even for Amazon sites alone biomass mortality change is significantly greater than stem mortality change; we did not use the Amazon data from the Amazon dry-down experiments because we did not have biomass mortality data available. See text for further details and statistical results.

and previous El Niño events (Table S1). On a per-stem basis, the mean plot-level wood density of dead trees was lower in drought intervals than in nondrought intervals, but only marginally so (mean (SE) difference = 3.7 (1.7)%, $P < 0.05$, $t = 2.2$, and 0.017 (0.008) g cm^{-3}, $P < 0.05$, $t = 2.1$, paired *t*-tests). The effect persisted when biomass was taken into account by weighting the contribution of each dead tree by its biomass: mean plot-level biomass-weighted wood density of dead trees was 4.8 (2.2)% lower in drought intervals than in nondrought intervals ($P < 0.05$, $t = 2.2$), and 0.023 (0.011) g cm^{-3} lower ($P < 0.05$, $t = 2.1$, paired *t*-tests), consistent with an earlier analysis in Phillips *et al.* (2009) of an overlapping, smaller data set. Dry periods do indeed select for denser-wooded trees but the effect is weak.

We repeated the analysis for smaller (< 40 cm diameter) and larger (> 40 cm diameter) dead trees in Amazon droughts. For the larger trees the sample sizes were too small to assess whether wood density was a risk factor in drought periods, but for the smaller trees it was again significantly so (mean (SE) difference = 4.0 (1.8)%, $P < 0.05$, $t = 2.2$, and 0.019 (0.009) g cm^{-3}, $P < 0.05$, $t = 2.2$, and for biomass-weighted wood density 4.1 (1.8)%, $P < 0.05$, $t = 2.3$, and 0.019 (0.009) g cm^{-3}, $P < 0.05$, $t = 2.2$). Therefore, the overall pattern of slightly greater risk to low-density trees is not confounded by a separate effect of lower wood density trees in the canopy and emergent layers being killed by drought.

How do tree mortality rates vary with moisture stress?

As expected, the stem mortality of tropical trees increased with the intensity of dry season moisture stress experienced relative to that in the pre-drought interval (Table 2, Figs 2–4). For the whole data set the shape of the relationship was nonlinear: mortality rates tended to increase disproportionately at higher levels of moisture stress. These results represent biome-wide sensitivity to drought, but it is important to note that the low end of the relationship is dominated by Amazonia and the high end by Borneo. We return to this point below.

We repeated the same analyses using the mortality data without any census-interval correction, but this made little material difference (cf. Table 2 with Table S3, and Figs 2, 3, 4 with Figs S1, S2, S3).

Does long-term mean precipitation modulate the forest's response to short-term drought?

The drought metric that accounts for annual rainfall resulted in a slightly improved fit compared with the simpler delta-MCWD metric for most models (Table 2). This was shown by a tendency both for higher R^2 values and for lower AIC values when comparable models were evaluated for all data sets, except for the 'all data' compilation. The improvement that accounting for annual mean precipitation provided suggests that trees in those forests that are normally wettest may be less vulnerable to greater dry season deficits than normal. Conversely, the drier the long-term climate regime, the greater the impact of a given increase in MCWD. Again, when data were not census-interval corrected the analytical results were very similar to those with census-interval corrections.

Does drought vulnerability differ in Amazonia from that in other forests, or can we specify a biome-wide sensitivity?

For Amazonia, the stem mortality relationship to drought can be fitted to a range of model forms (Figs 2, S4). Note that the range of drought intensities recorded here is relatively small, and that the sensitivity of biomass mortality to drought in 2005 was strongly linear (Phillips *et al.*, 2009).

Table 2 Model fits for tropical tree mortality response to moisture deficits

Amazon (ΔMCWD)	R^2 adj	AIC	All data (ΔMCWD)	R^2 adj	AIC	Borneo (ΔMCWD)	R^2 adj	AIC
Change in mortality rate			Change in mortality rate			Change in mortality rate		
Linear	0.573	58.2	Linear	0.669	169.6	Linear	0.854	43.6
Log	0.536	60.3	Log	0.342	196.3	Log	0.759	48.1
Exponential	0.525	20.3	Exponential	0.717	33.0	Exponential	0.923	1.2
Polynomial $(x - x^2 + x^3)$*, Fig. 2a	**0.639**	**55.8**	**Polynomial $(x - x^2 + x^3)$*, Fig. 3a**	**0.910**	**120.8**	**Polynomial $(x - x^2 + x^3)$, Fig. 4a**	**0.942**	**36.1**
Proportional change in mortality rate			Proportional change in mortality rate			Proportional change in mortality rate		
Linear, Fig. 2b	**0.745**	**248.5**	Linear	0.620	499.8	Linear	0.765	122.7
Log	0.621	258.4	Log	0.319	522.5	Log	0.692	125.2
Exponential	0.437	74.1	Exponential	0.491	115.9	Exponential	0.778	16.1
Polynomial $(x - x^2 + x^3)$	0.748	249.9	**Polynomial $(x - x^2 + x^3)$*, Fig. 3b**	**0.853**	**464.7**	**Polynomial $(x - x^2 + x^3)$, Fig. 4b**	**0.912**	**114.9**

Amazon (ΔMCWD/annual rainfall)	R^2 adj	AIC	All data (ΔMCWD/annual rainfall)	R^2 adj	AIC	Borneo (ΔMCWD/annual rainfall)	R^2 adj	AIC
Change in mortality rate			Change in mortality rate			Change in mortality rate		
Linear	0.675	51.4	Linear	0.784	152.9	**Linear**, Fig. 4c	**0.966**	**30.5**
Log	0.633	54.5	Log	0.482	187.0	Log	0.908	39.4
Exponential	0.584	17.0	Exponential	0.728	31.4	Exponential	0.854	6.9
Polynomial $(x - x^2 + x^3)$*, Fig. 2c	**0.702**	**51.0**	**Polynomial $(x + x^3)$*, Fig. 3c**	**0.865**	**135.5**	Polynomial $(x - x^3)$	0.961	32.3
Proportional change in mortality rate			Proportional change in mortality rate			Proportional change in mortality rate		
Linear, Fig. 2d	**0.763**	**246.7**	Linear	0.745	484.2	Linear	0.919	113.2
Log	0.710	251.7	Log	0.457	513.7	Log	0.846	118.9
Exponential	0.448	73.5	Exponential	0.471	117.4	Exponential	0.697	18.8
Polynomial $(x - x^3)$	0.759	248.0	**Polynomial $(x + x^3)$*, Fig. 3d**	**0.849**	**464.6**	**Polynomial $(x - x^2 + x^3)$, Fig. 4d**	**0.960**	**107.9**

Data sets vary by region, tree mortality change metric, and moisture deficit change metric. Best-fit models are highlighted in bold and are displayed graphically in Figs 2, 3 and 4. AIC values of exponential models are not directly comparable to those of the other models as the *y*-variable is on a different scale ($\log_e(y)$). For polynomial models we fitted all possible two- and three-factor models and only selected a model with cubic terms when it had a lower AIC than all other models (except the exponential model), *and* a greater R^2 than any other model. An asterisk indicates where all polynomial terms are also significant.
MCWD, monthly cumulative water deficit; AIC, Akaike's Information Criterion.

There were too few non-Amazon data to specify a specific mortality–drought relationship for any other region except Borneo. The Borneo fit, albeit based on fewer plots, is very strong which may reflect the fact that the data cover a much wider range of droughting intensities. While linear fits are good, there is some evidence for nonlinearity – AICs are optimal for models with a cubic term. That Borneo forests are more drought-sensitive than Amazon forests is suggested by the displacement of the Borneo lines of best fit above the Amazon lines of best fit across most of the droughting range (Fig. 4). At the point of maximum Amazon droughting recorded in 2005 in our plots (5.3% drought index, and 118.3 mm MCWD), the Amazon mortality–drought relationship lies significantly below the Borneo one: the median expected mortality values at these drought values based on regression equations for 1000 bootstrapped Amazon data sets are lower than the equivalent values for 1000 bootstrapped Borneo regression equations ($P < 0.001$, Wilcoxon rank sum test).

Do forest dynamics return to normal once drought ends, or do higher mortality rates persist?

Mortality rates were compared within all sites with distinct 'pre-drought', 'drought' and 'post-drought' intervals (Fig. 5). Droughts are short – typically 3–6-month intervals – and much shorter than the drought measurement intervals which averaged 28 months. As a result, on average the mid-point of the 'drought interval' fell 1 month before the actual moisture deficit began, and the maximum water deficit was reached 9 months before the drought measurement interval ended. The 'post-drought' interval lasted on average for a further 26 months, so that across all sites its mean mid-point fell approx. $9 + 26/2 = 22$ months after the

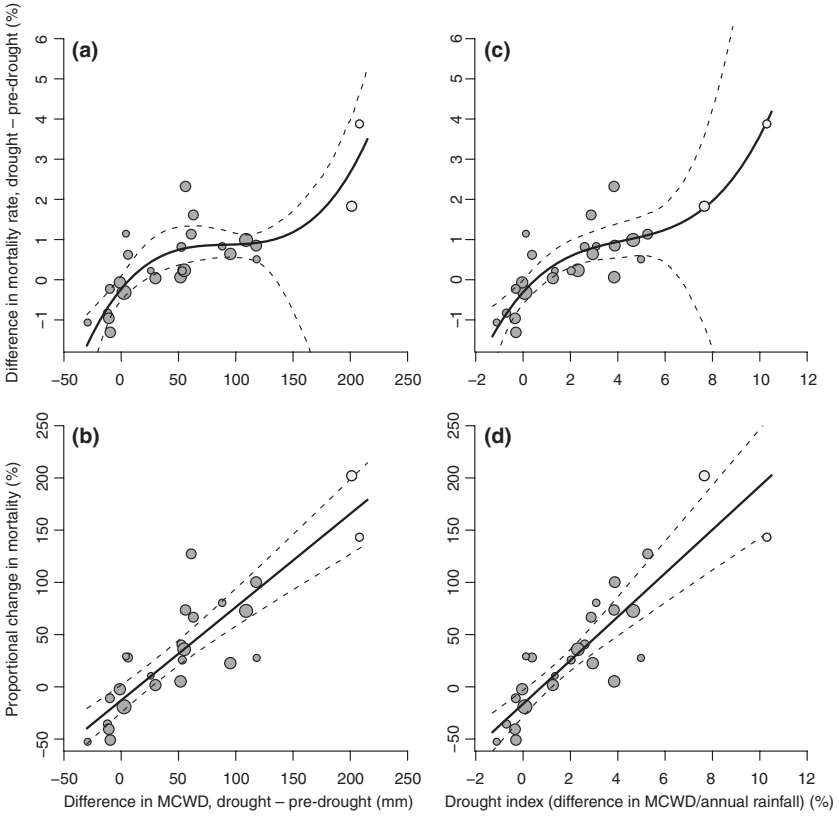

Fig. 2 Mortality sensitivity to drought for Amazonia. Dark grey symbols, natural droughts; light grey symbols, experimental droughts in eastern Amazonia. The best-fit models for each drought index and mortality rate metric are displayed, showing 95% bootstrapped confidence intervals. Weighting was based on plot size and monitoring interval (weights are proportional to symbol area). MCWD, monthly cumulative water deficit.

climatological drought ended. For these sites, drought interval mortality was, as expected, boosted with respect to the pre-drought interval ($P < 0.001$, $t = 4.66$, one-tailed paired t-test). We also found that the post-drought mortality declined markedly from drought interval levels ($P < 0.05$, $t = 2.32$), showing that most mortality effects of tropical droughts are felt within 9 months of the drought. However, the hypothesis that post-drought mortality rates fell back to or below pre-drought levels was rejected ($P < 0.05$, $t = 2.03$), suggesting that some lagged impact of drought may persist for 2 yr after tropical forest droughts end.

Discussion

Under normal conditions, tropical tree size is strongly correlated with competitive success, whether measured in terms of growth or in terms of reproduction (Phillips, 1993; Keeling *et al.*, 2008), but we find that in tropical drought conditions large size also confers a strong penalty. Size-related mortality risk is a widespread feature of tropical forest droughts: bigger trees are at greater risk of drought-induced death than smaller trees, and tropical droughts enhance biomass mortality rates more than they enhance stem mortality rates (Fig. 1). This is evident in Amazonia, and especially so in Borneo, where droughting was more severe, and, within the constraints of low data availability, appears also to be a general feature of other tropical forests. This contrasts with drought-related mortality in North America, where smaller trees were most at risk (van Mantgem *et al.*, 2009). The greater sensitivity of the largest trees in tropical forests is presumably a factor driving the biomass–drought relationship for Amazonia (Phillips *et al.*, 2009), and may be the mechanism that sets the ultimate limit on the stand-level forest biomass of tropical forests (Stegen *et al.*, 2010). It also means that there can be substantial biomass carbon loss even from short-lived tropical droughts that may not kill many trees on a stem number basis.

Severe droughts tend to kill trees standing (e.g. Slik, 2004), implying that they suffer a catastrophic physiological failure. That large trees should be at risk especially from the stronger droughts is consistent with predictions from theory that invokes hydraulic limitations as the dominant limit on tree height (e.g. Niklas & Spatz, 2004), and the general observation that hydraulic factors control foliar dieback in response to drought (e.g. Sperry *et al.*, 2002). While photosynthetic rates in emergent and canopy tropical trees typically decline in the afternoon as a result of stomatal closure, indicating that gross productivity is partially water limited (e.g. Kitahashi *et al.*, 2008), to our knowledge there have been no direct observations of cavitation killing large tropical trees in dry periods, perhaps because of the practical

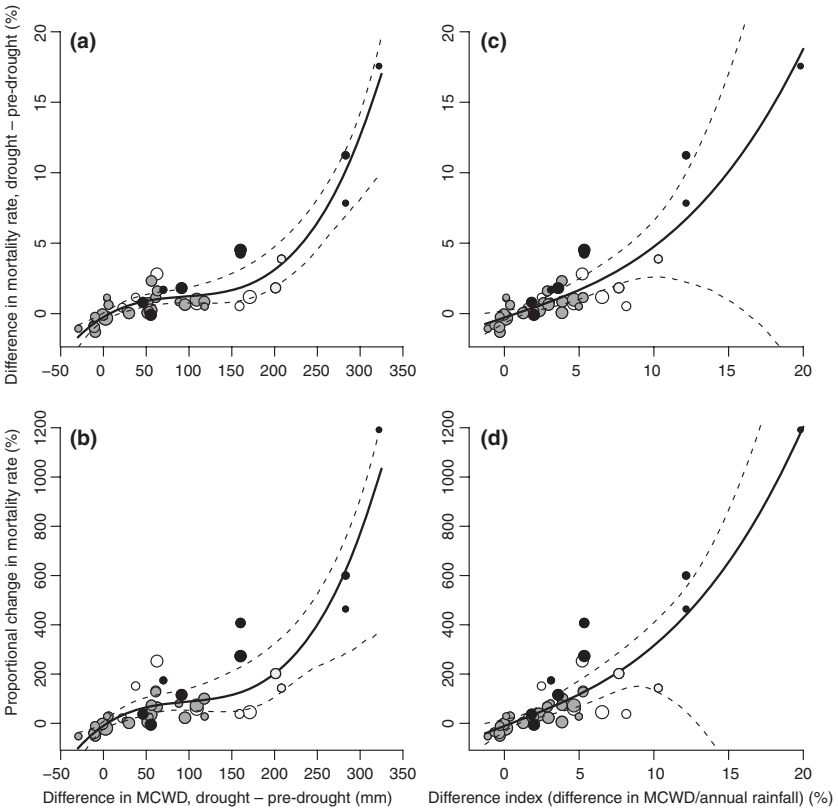

Fig. 3 Mortality sensitivity to drought for all lowland tropical forests with available data. Dark grey symbols, Amazonia; light grey symbols, experimental droughts in eastern Amazonia; black symbols, Borneo; white symbols, Africa, Central America and Atlantic Forest. The best-fit models for each drought index and mortality rate metric are displayed, showing 95% bootstrapped confidence intervals. Weighting was based on plot size and monitoring interval (weights are proportional to symbol area). MCWD, monthly cumulative water deficit.

difficulties involved, so whether hydraulic failure really is the dominant mechanism leading to drought-related mortality is not certain. Alternatively, the negative effects of extended moisture stress on carbon assimilation and storage in large trees may make them more vulnerable to disease, or to carbon starvation, as has been claimed for drought-related mortality in at least one subtropical site following extended severe drought (McDowell *et al.*, 2008).

Low wood density is also a predictor of drought mortality risk, albeit a rather weak one. Among trees smaller than 40 cm diameter, which represent 90% of dead trees, the same wood density effect is detectable. This shows that the additional drought mortality risk borne by large trees cannot be the driver of the overall wood density–drought mortality association. It also suggests that larger trees' vulnerability is not substantially attributable to their slightly lower wood densities, and may instead be a feature of their more exposed position in the canopy, leading to large evapotranspirative demand in dry periods. Wood density measures were lacking from the trees themselves, so we used species-level means to estimate wood density. This may have affected the apparent link with moisture deficit vulnerability – it has been shown that individual-level wood structural properties in Amazonia can diverge significantly from species means (Patiño *et al.,* 2009), with a significant site-level effect. Wood density has been shown by others to be associated with drought vulnerability (e.g. Tyree & Sperry, 1989; Hacke *et al.*, 2001; Poorter *et al.*, 2010), but the mechanism by which wood density may confer greater vulnerability to drought is still uncertain, as vessel width and especially pit pore width may vary substantially for a given wood density (e.g. Zanne & Falster, 2010), and any linkage to cavitation vulnerability may be mediated by variation in these traits rather than wood density *per se*.

Regardless of the drought metric used, the slope of the general relationship between stem mortality and drought is positive (Table 2, Figs 2, 3, 4). While the results are insensitive to assumptions about census-interval corrections (cf. Table S3, Figs S1–S3), the form does vary according to the geographic scope of analysis and the mortality and drought metrics used. In all four modelled fits for the entire data set, a two- or three-factor polynomial relationship clearly provides the best fit (Table 2, Fig. 3), suggesting nonlinearity in the response of tropical forests to strong droughts. This indicates that there might exist a threshold zone beyond which a very strong mortality response occurs, but the current data set is not yet sufficiently sampled across all regions to state this with confidence. In general, the non-Amazon data are more variable than the Amazon data. In particular, the high mortality rates reported from a few locations such as the Atlantic Forest (Rolim *et al.*, 2005) at apparently modest levels of drought are noteworthy. This

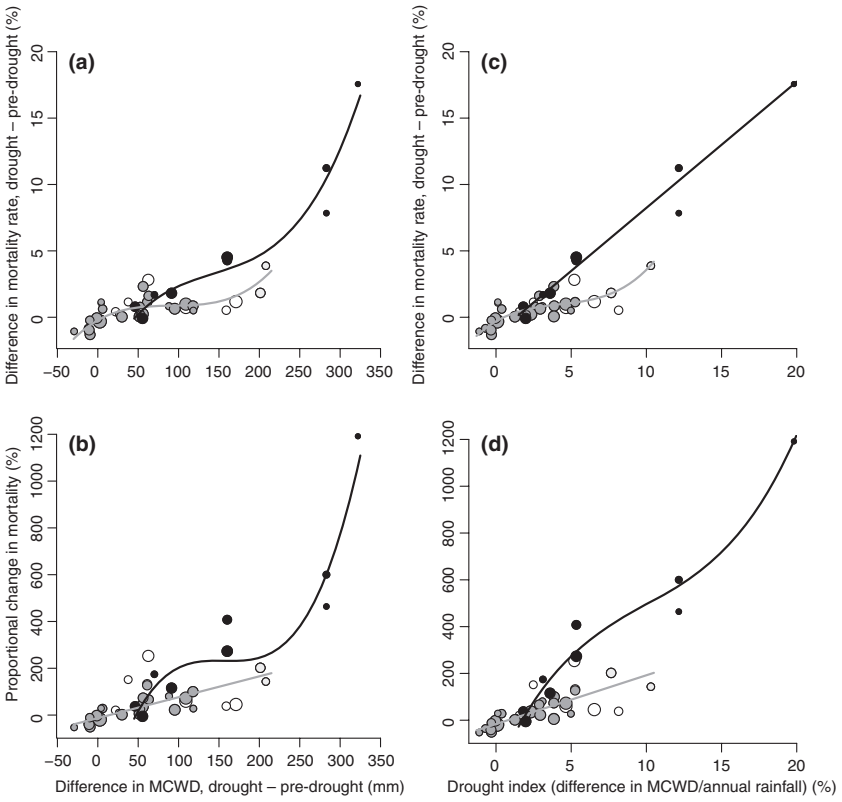

Fig. 4 Mortality sensitivity to drought for Bornean and Amazonian forests compared. The best-fit models for each region are displayed for each drought index and mortality rate metric. Weighting was based on plot size and monitoring interval (weights are proportional to symbol area). Black symbols, Borneo; dark grey, Amazonia; light grey, Amazon dry-down experiments; white, other tropical forests (Africa, Central America and Atlantic Forest). The Borneo fit is displaced significantly above the Amazon fit in all four panels. MCWD, monthly cumulative water deficit.

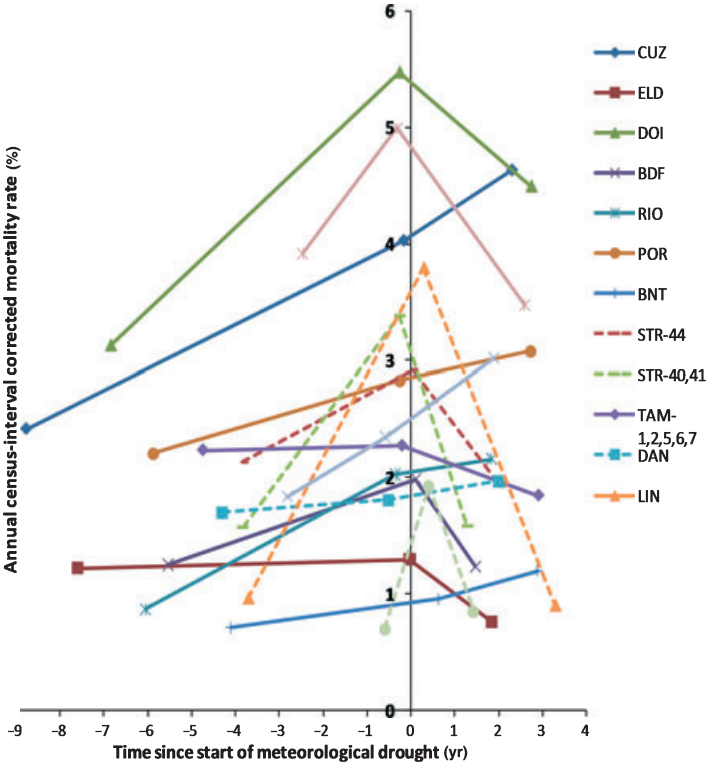

Fig. 5 Mortality rates for all tropical forest sites that have been monitored with at least one pre-drought interval, one drought interval, and one post-drought interval. Lines connect the mid-points of each period; lines are solid for Amazon sites and dashed for non-Amazon sites. For some sites there were multiple pre-drought census intervals available: in these cases the values displayed here are the composite time-weighted mean values of those mortality rates. See Table 1 for site/plot codes.

may be attributable to relatively low annual rainfall at these sites. Overall, the slightly improved fits to the drought index that accounts for annual rainfall suggest that the effects of a given quantity of moisture deficit are accentuated in lower-rainfall regimes. Transitional forests such as the Atlantic Forest site at Linhares may be more vulnerable because they include many moist forest taxa which are drought-sensitive at the edge of their range (cf. Engelbrecht *et al.*, 2007). Forests dominated by dry-adapted taxa could be expected to be more resistant, but unfortunately we are not aware of relevant data from mature dry forests, as long-term plots are very few in this biome.

Comparisons between Amazonia and Borneo are potentially instructive. While the nonlinearity in the pan-tropical graph is substantially driven by some highly impacted Borneo sites, even within Borneo nonlinear fits are optimal in three out of four graphs: for Borneo, at least, there is evidence for nonlinearity (Table 2). The Borneo lines of best fit are also displaced above those of the Amazon sites (Fig. 4), indicating that forests here react differently to a given level of drying. How then can we account for the apparent greater sensitivity of Bornean forests to drought? Identifying any single factor is difficult because of the many differences between the regions, but foremost amongst these is the climatology of drought itself. In much of Amazonia, periods of reduced moisture supply are predictable, annual occurrences, and 'droughts' occur when the dry season is particularly intense or lengthy. In large parts of Borneo, in contrast, moisture stress is unpredictable and supra-annual, being associated with occasional strong ENSO events (Walsh & Newbery, 1999). Here, trees may be evolutionarily selected to use stomatal control in the rare dry episodes rather than invest in potentially costly adaptations to their wood anatomy that are unnecessary in all but the most exceptional times. This is suggested by results from north Borneo, where trees from aseasonal yet occasionally drought-impacted forests were shown experimentally to be much more susceptible to cavitation than those growing in seasonally dry forests elsewhere (Tyree *et al.*, 1998).

Comparisons among sites and regions are also complicated by biogeographic and edaphic factors. Local variations in rooting depth and the ability of soils to supply water may be important, and could conceivably explain much site-to-site variation in drought sensitivity, but analysis of the impact of soil conditions on modifying drought responses is prevented by the difficulty in sampling sufficiently at all sites given locally heterogeneous rooting depth, particle size, and topography (cf. Phillips *et al.*, 2009 Supporting Online Material; Quesada *et al.*, 2010), and by the different methodologies used by research groups. Nonetheless, it is interesting to note that at the two Amazon drought experiments, at Tapajos and Caxiuana, the impact was rather similar and strong (Costa *et al.*, 2010). These sites are located in deep eastern Amazon soils with larger rooting depths than many Amazon soils (Quesada *et al.*, 2010), but their soils and ecology differ in some key characteristics (cf. Meir *et al.*, 2009 for discussion).

This study provides a complementary insight to that offered by an experimental approach, but also highlights some of the gaps in our understanding. A matter of substantial current and future scientific concern is the degree to which Amazon forests are susceptible to droughts, because of recent indications of some drying in southern Amazonia (e.g. Li *et al.*, 2008; Butt *et al.*, 2009), and some modelled expectations for longer, more severe dry seasons this century (e.g. Cox *et al.*, 2008). While analyses in the current paper suggest that they are less susceptible to drought than Bornean forests, there are several reasons why it would be wrong to conclude that Amazon forests have low drought sensitivity. Firstly, no tropical drought experiment has been attempted away from the lower Amazon region. We predict from first principles that a stronger tree mortality response would be observed if such an experiment were conducted in the shallow soils of western Amazonia. Secondly, this study highlights another large gap in experimental understanding – the droughts simulated for Amazon forests to date are apparently not as severe as those already experienced in other parts of the biome, so we have neither experimental nor observational data to tell us how forests here might respond to higher drought intensities. Thirdly, even at these rather low drought intensities we know that their sensitivity to drought in biomass terms is greater than the stem mortality–drought relationship implies (this is demonstrated, for example, by the greater sensitivity of large trees shown here, and the finding of large regional carbon losses reported in Phillips *et al.*, 2009), and we know that droughts can selectively kill specific kinds of plants (larger trees and lighter-wooded trees) so are capable of driving functional shifts. Finally, we show here that the mortality impact of drought in tropical forests may not be confined to the drought period *per se* but that some lethal effects can lag the actual drought by 2 yr or more. Our methods therefore probably underestimate total drought impact and so provide conservative estimates of the mortality sensitivity to drought.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Figs S1, S2, S3 Best-fit models for census-interval corrected data (S1, Amazon; S2, all tropical data; S3, Borneo).

Fig. S4 Best-fit models for Amazonia, excluding drought experiments.

Table S1 Amazon plot data with wood density of dead trees

Table S2 Mortality rates and drought metrics of monitored forests

Table S3 Model fits for mortality response to moisture deficit, using mortality data that had no census interval corrections

Table S4 Model fits for Amazon mortality response to moisture deficit, excluding drought experimental plots

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