Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire

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AUTHOR CONTRIBUTIONS

All authors on this work contributed data, conversation, and manuscript feedback. ACS synthesized and analyzed data, prepared figures and data products, and wrote the paper.

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Remotely sensed data are available freely online and RAINFOR plot-level tree size data are available at forestplots.net.

ABSTRACT

Understory fires represent an accelerating threat to Amazonian tropical forests and can, during drought, affect larger areas than deforestation itself. These fires kill trees at rates varying from < 10 to c. 90% depending on fire intensity, forest disturbance history, and tree functional traits. Here, we examine variation in bark thickness across the Amazon. Bark can protect trees from fires, but it is often assumed to be consistently thin across tropical forests. Here, we show that investment in bark varies, with thicker bark in dry forests and thinner in wetter forests. We also show that thinner bark translated into higher fire-driven tree mortality in wetter forests, with between 0.67 to 5.86 gigatons CO_2 lost in Amazon understory fires between 2001-2010. Trait-enabled global vegetation models that explicitly include variation in bark thickness are likely to improve the predictions of fire effects on carbon cycling in tropical forests.

KEYWORDS: carbon cycle, Amazonia, tree mortality, tropical forest, functional traits

SPANISH LANGUAGE ABSTRACT

En los bosques tropicales de la Amazonia, los incendios de sotobosque representan una amenaza que se está acelerando. Durante la sequía, pueden afectar un área mayor que la deforestación misma. Estos incendios pueden matan árboles a tasas que varían desde <10 hasta cerca de 90% dependiendo de la intensidad del fuego, la historia de perturbaciones forestales y los rasgos funcionales de los árboles. En este estudio, examinamos la variación en el grosor de la corteza en la Amazonía. La corteza puede proteger los árboles de los incendios, pero normalmente se supone que es uniformemente delgada en los bosques tropicales. Aquí, mostramos que el grosor de la corteza varía bastante, con una corteza más gruesa en los bosques secos y más delgada en los bosques húmedos. También, mostramos que cortezas más delgadas resultan en tasas de mortalidad más altas en bosques más húmedos. En total, estimamos que los incendios en el sotobosque de la Amazonía han añadido entre 0,67 y 5,86 gigatoneladas de CO_2 atmosférico entre 2001-2010. Los modelos globales de vegetación que predicen los efectos de los incendios sobre el reciclaje de carbono en los bosques tropicales deberían incluir explícitamente la variación en el grosor de la corteza.

PORTUGUESE LANGUAGE ABSTRACT

Os incêndios rasteiros de sub-bosque representam uma ameaça cada vez maior às florestas tropicais da Amazônia. Durante secas, eles podem afetar áreas maiores do que àquelas desmatadas. Esses incêndios matam árvores a taxas que variam de <10 a c. 90%, dependendo da intensidade do fogo, da história de distúrbios florestais e das características funcionais das árvores. Neste estudo, examinamos a variação na espessura da casca na Amazônia. A casca pode proteger árvores do fogo, mas geralmente é considerada uniformemente fina para diversas florestas tropicais. Aqui, mostramos que a espessura da casca varia, com cascas mais espessas ocorrendo em florestas secas e mais finas ocorrendo em florestas mais úmidas. Mostramos também que a casca mais fina resulta em taxas de mortalidade mais altas em florestas úmidas. No total, estimamos que os incêndios de sub-bosque adicionaram entre 0,67 e 5,86 gigatoneladas de CO_2 atmosférico entre 2001-2010. Os modelos globais de vegetação devem incluir explicitamente a variação na espessura da casca ao prever os efeitos do fogo no ciclo do carbono de florestas tropicais.

INTRODUCTION

Fire has emerged as a primary threat to tropical forests in the Amazon over the past three decades, in response to a combination of deforestation and increasing severity and frequency of droughts (Cochrane 2003; Chen *et al.* 2014). Throughout the 20th century, fires were largely restricted to areas experiencing deforestation or existing cleared areas for agricultural maintenance (Alencar *et al.* 2011), but fires can now spread readily through forests that have not been otherwise disturbed (Morton *et al.* 2013), dramatically increasing burned areas. Today, during major droughts (including 2005, 2007, 2010, and 2015-2016), forest understory fires affected larger areas in the Amazon basin than deforestation itself (Aragao *et al.* 2018) – in some years as much as 5x larger (Morton *et al.* 2013). This trend is projected to continue in coming decades, with a greater frequency of Amazon droughts in response to anthropogenic global change (Le Page *et al.* 2017). Predicting forest responses to fires is increasingly imperative.

However, our understanding of the short- and long-term ecological impact of tropical forest understory fires is poorly developed, which limits assessments of fire impacts on ecosystems and the global carbon cycle (van der Werf *et al.* 2009; Rappaport *et al.* 2018). One major source of uncertainty is the variability in rates of tree mortality across diverse forests in response to understory fires, with estimates ranging from <10% to c. 90% (Barlow *et al.* 2012). Fire intensity clearly impacts tree mortality (Barlow *et al.* 2012, Brando *et al*. 2014, Rappaport *et al*. 2018), but even so, diverse forests can react differently to similar fire intensity (Hoffmann *et al.* 2009; Barlow *et al.* 2012; Brando *et al.* 2019). Forest history likely explains some part of these differences (Barlow & Peres 2008), but underlying fire-related traits may also vary geographically – a contribution which has, to date, been overlooked in the humid tropical forest context where fires are increasing in prevalence.

Among fire-related functional traits, bark is the most amenable to widespread sampling (e.g., (Rosell 2016), and appears broadly to govern fire-driven mortality of tree stems (Harmon 1984). The corky outer bark protects trees from fires by insulating tree cambium and xylem (Michaletz *et al.* 2012; Rosell 2016; Pausas 2017), thereby reducing mortality from cambial necrosis or cavitation due to excessive heating. Reductions in stem mortality among trees with thicker bark have been extensively described in more flammable systems, like savannas (Trollope & Tainton 1986; Gignoux *et al.* 1997; Hoffmann *et al.* 2009; 2012), but variation in bark thickness can also determine size- and species-specific differences among trees in their susceptibility to fires even within tropical forests (Barlow *et al.* 2003; Hoffmann *et al.* 2009; Brando *et al.* 2011). However, while bark in savanna and other flammable systems has been the subject of large-scale synthesis (Dantas & Pausas 2013; Pellegrini *et al.* 2017), the extent and determinants of variation in bark thickness within humid tropical forests are not known, complicating efforts to predict carbon losses in the years following fires.

Known relationships of bark thickness variation to fire history (Pausas 2017) and abiotic drivers (Richardson *et al.* 2015) allow us to generate informed expectations. The null expectation is that bark is consistently thin and variation therefore minimal. After all, the contemporary literature often assumes that today's fire return intervals in Amazonia are a historical anomaly (Cochrane 2003), such that fire protection may be unnecessary for tropical forest trees. However, the paleo-literature suggests that some Amazonian forests may historically have burned, at least with relatively low frequency in the drier south and east (Bush *et al.* 2008; Power *et al.* 2008). Moreover, within sites, bark thickness varies in tropical forests (Paine *et al*. 2010), and work in temperate forests has documented patterns of variation linked to rainfall (Richardson *et al.* 2015) and fire occurrence (Abatzoglou & Williams 2016). A more plausible alternative hypothesis might therefore be that variation in bark thickness across the Amazon is substantial, reflecting varying evolutionary pressures across the basin, especially from fire (Bond & Midgley 2001; Pausas *et al.* 2006; Pausas 2017) but also from other processes (Rosell 2016). From a more applied perspective, understanding the variability in bark thickness in humid tropical forests will be a key step towards improving spatially-explicit predictions of fire-driven tree mortality and the resulting carbon emissions.

Here, we evaluated the extent and degree of variation in bark thickness across Amazonian tropical forests, combining data from a total of 6,280 trees in forests in 13 plots (~ 1 ha each), in diverse regions across Amazonia (see Extended Data Figure 1, Extended Data Table 1), and evaluate variations with respect to climate (annual rainfall and maximum cumulative water deficit [MCWD]), yielding estimates of bark thickness across all Amazonian forests. We then combined these maps of bark thickness with published relationships between bark thickness and tree mortality (Hoffmann *et al.* 2009; Brando *et al.* 2011) to evaluate the potential contributions of bark thickness variation to estimates of tree mortality and biomass loss from understory fires in Amazon forests, evaluated against observed tree mortality and biomass loss synthesized from published studies.

MATERIALS AND METHODS

Functional Traits and Plot Level Size Class Distributions. We measured bark thickness at 13 sites located throughout the Amazon between 2000 and 2013 (see Figure S1). At each site, we sampled all trees in plots to total ~ 1 ha of area sampled at each site (see Table S1 for plot dimensions). Trees were identified to species at 12 sites (leveraging existing data) or morphospecies at one. At each tree, diameter was measured at breast height (1.3 m), bark was sampled with a corer at 2-4 points around the trunk of a tree, 0.35 m ± 0.05 m above the ground.

For comparison, where data were available, we also evaluated patterns of tree height and wood density across sites. Because tree height and wood density both contribute by definition to biomass (Chave *et al.* 2014), systematic variation in these traits can impact patterns of forest biomass (Quesada *et al.* 2012; Álvarez-Dávila *et al.* 2017), with downstream effects on estimates of biomass loss. Therefore, we examined these directly in order to control for their possible contributions to biomass loss estimates; they also provide a useful point of comparison for evaluating the magnitude of variation in bark thickness. Height was available at a subset of RAINFOR-associated sites (with height observations at a total of 6 sites), with height measurements following published RAINFOR protocols (Feldpausch *et al.* 2011). Wood density was extracted via the 'BIOMASS' R package from a freely available dataset published by Chave *et al*. (2014), with tree species, genus, or family as the lookup for extraction.

Rainfall Climatology and Fire. Annual rainfall and maximum climatological water deficit (MCWD) was calculated from data from the Tropical Rainfall Measuring Mission (Nicholson *et al.* 2003; Brando *et al.* 2014) from 1998 to 2012 at 0.25 degree resolution. Annual rainfall was calculated by summing monthly rainfall products, and averaging across years to determine mean annual rainfall.

MCWD was calculated starting from the first month of the year (south of the Equator = January; north of the Equator = July), when climatological water deficit was defined as 0. Each month, we subtract the theoretical water demand (evaporation plus transpiration) of a typical tropical forest (100 mm monthly rainfall) from the incoming rainfall and add it to the existing water deficit; if the result is > 0 (*i.e.*, there is excess rainfall), we reset the water deficit to 0. After the last month of the year, this yields the CWD for the year. MCWD is defined as the maximum of CWD across all years for each pixel (see also Aragão *et al.* 2007; Brando *et al.* 2010).

Fire occurrences were derived via two methods. First, we used the MODIS Active Fires Product (Giglio *et al.* 2016) at the 1 km scale; we used the Active Fires instead of the Burned Area product because the latter is considered somewhat more sensitive in detecting forest-understory fires that do not generate a typical ash or char reflectance values needed for burned area mapping. Pixels in which fires occurred were considered burned, but were then masked with tree cover from Hansen's Landsat-based tree cover estimates at a 1 km resolution (Hansen *et al.* 2013), to eliminate fires directly associated with deforestation from our predictions of fire-driven losses (a known limitation of the Active Fires product for estimating understory fire extent; (Morton *et al.* 2013). Each year, the burned area map was masked with all areas that experienced deforestation of at least 2% (that year or any previous year). A deforestation threshold of 2% is conservative, with the goal of eliminating direct deforestation fires and focusing instead on forest-understory fires. Overall, we see that fire extent has declined in MODIS Active Fire detections as deforestation has, suggesting some link, despite our efforts at masking. For this reason, we have also used an independently calibrated estimate of understory fire extent (Morton *et al.* 2013) (also using data from the MODIS satellite; referred to in figures as 'Morton'), which is even more conservative in removing deforestation-linked fires. Both fire distribution products detect increases in fire activity during droughts associated with climate anomalies, suggesting that this is a robust finding. However, given the moderate resolution of these satellite-based data products, both likely underestimate the true spatial coverage of wildfires in closed canopy forests. For both products, we re-aggregated burned area to yield an estimate at the resolution of rainfall and MCWD calculations.

Climatological data were produced, extracted at each site, and modeled to produce basin-wide estimates of bark thickness using the packages *sp*, *ncdf4*, and *raster* in R 3.2.2. Fire and tree cover data were managed in the same way.

Above-Ground Biomass. At each site for which we collected tree size and bark thickness, we calculated biomass using the *BIOMASS* package (Chave *et al.* 2014) in R 3.2.2, based on species-, genus-, or (where necessary) family-level wood density and on plot location (as a proxy for tree height). To scale to basin-wide fire-driven biomass losses, we used a recently-published biomass map for forests that integrates remote-sensing with field-based biomass estimates from Avitabile and colleagues (2016). Biomass was also resampled to match the scale of the climatological data in R 3.2.2.

Effects of Bark Thickness on Mortality in Fires. Rates of mortality in fires were derived from two major studies examining forest tree mortality in fires (Hoffmann *et al.* 2009; Brando *et al.* 2011). The first considered the effects of bark thickness on stem mortality of forest trees in fires at the IBGE Reserve outside Brasilia by Hoffmann *et al* (Hoffmann *et al.* 2009). We constructed a linear model of tree mortality probability with respect to bark thickness (see Figure 2b) to model mortality of trees. As the model more representative of the range of forest understory fires (Figure 2a), we used this for most calculations in the main body of the paper. Second, we also used stem mortality from a fire experiment in the southern Amazon (at Tanguro) for a more detailed data source (see Brando *et al*. for a formal analysis of these data [2011]). Here, we considered mortality in the three years following a fire as fire-driven mortality, so this should be considered an estimate of short-term committed losses and not an estimate of instantaneous responses to a fire. Probability of mortality was modeled using a general linear model assuming an underlying binomial distribution (each tree survives or dies in/after a fire). Fires at Tanguro were mild during normal years and more intense during drought years (see Figure 2a), with major effects on tree mortality (see Figure 2b).

We modeled fire-driven mortality at each site using four different scenarios: 1) real trees, with measured diameters and bark thickness, 2) trees with measured diameters, with bark modelled according to the real community-wide bark allometric constant calculated at each site, 3) tree diameters drawn from an idealized diameter distribution calculated across all sites, and bark modelled according to the real bark allometric constant at each site, and 4) an idealized diameter distribution and bark modeled according to a bark allometric relationship modeled from climate at each site. In each scenario, we modeled the probability of mortality of each tree, from which we calculated proportional mortality and biomass losses.

Because mortality is a stochastic event (described by a deterministic rate), and because we propagated errors in bark allometry and diameter distribution estimates, we bootstrapped each scenario 100 times to calculate average probability of mortality and average biomass losses across sites. Scenarios reproduced qualitatively similar variation in tree mortality with respect to rainfall (see Figure S6). We followed the same method (scenario 4) to calculate mortality rates and biomass losses across the entire Amazon.

Comparisons with Observed Mortality and Biomass. Predictions were compared qualitatively and quantitatively with data from two meta-analyses of tree mortality in fires from across tropical forests by Hoffmann *et al* (2009) and Barlow *et al* (2012). The former included rainfall estimates but no locations, while the latter provided a map of study locations included in the synthesis (enabling comparison of rainfall vs. MCWD as drivers of forest tree stem mortality). Biomass loss estimates from Barlow *et al* (2012) were also used to directly estimate biomass losses (via a relationship between rainfall vs. biomass loss; see Figure 3B) for comparison with estimates generated via bark-mortality relationships.

RESULTS

Stem and region-level bark thickness varied substantially across the Amazon, constrained by a combination of tree size and climate. On individual stems, bark thickness varied from fractions of a millimeter to more than 4 cm of bark, and average bark thickness ranged from 0.5 mm to > 1 cm across plots. At each site, bark thickness increased with diameter at breast height (DBH; Figure S2), as expected (Hoffmann *et al.* 2003). This allometric relationship yields a constant for examining bark accumulation, controlling for tree size (α, where $bark = DBH^{\alpha}$). Bark accumulation varied with respect to climate (Figure 1a-b, S3), decreasing most predictably with rainfall ($R^2 = 0.62$, $df = 11$, $p = 0.0015$; Table S2), providing the first spatial estimate of bark investment across the Amazon (Figure 1c).

We next aimed to translate this variation in bark as a functional trait into predictions of tree mortality using published estimates linking bark thickness with tree stem mortality following tropical forest understory fires. These estimates are sparse in the literature, with forest work at only two sites, Amazon forests at Tanguro (Brando *et al.* 2011) and dense woodlands and riparian forests in the *cerrado* biome at the IBGE Reserve (Hoffmann *et al.* 2009). Stem mortality decreased with bark thickness and increased with increasing fire intensity (Barlow *et al.* 2012) (consistent with results from better-studied savanna systems [Williams *et al.* 1999]; Figure 2b). However, tropical forests where fires have been studied in detail (Tanguro and IBGE) have experienced relatively low-intensity fires compared to the documented range of fire intensities possible across the Amazon (Figure 2a).

In reality, stem mortality depends on actual bark thickness, not an allometric constant. Therefore, we also evaluated variations in realized tree bark thickness across sites that arose from variation in tree size across Amazonian forests. Whereas tree density increased markedly with rainfall (Figure S4), diameter class distributions showed no consistent trends (Figure S5). We also examined whether mortality estimates at each field site were sensitive to how we estimated bark thickness. Results were robust to all forms of bark thickness estimation (Figure S6), with no systematic biases introduced by general assumptions about size class distributions, although we note that local variations in tree size distributions might nonetheless change fire susceptibility depending on site history (Barlow & Peres 2008).

Thinner bark at high rainfall translated into consistently higher predicted mortality from understory fires (Figure 3a), which in turn translated into increasing biomass loss with rainfall (Figure 3b). We compared these predictions to observations of stem mortality rates from field observations across Amazonian forest fires (Hoffmann *et al.* 2009; Barlow *et al.* 2012), showing that stem mortality and biomass loss rates do actually increase with rainfall (Figure 3), even more strongly than our modeled estimates. Taken together, these patterns suggest that bark variability may indeed contribute to variability in the effects of fires on forests. Drier forests near the biogeographic limit of Amazonian forests – where, incidentally, most research on the relationship between bark and fire-driven mortality has focused – are substantially more resistant to fires than forests in the wetter core of the Amazon.

We next calculated committed biomass-C fluxes across all Amazonian forests across years. The net result of incorporating variable bark into our predictions (from Figure 1) was a 57.6% increase over constant-bark estimates in the basin-wide understory fire-driven biomass loss, with estimates that more closely match biomass losses estimated directly from plot-level mortality observations (Fig. 4; plot-level estimates in Fig. 3a). Trends and variation are evident through time, with overall decreases in fire extent based on MODIS active fires, likely reflecting decreases in deforestation-associated fires during the study period, and dramatic increases in fire extent during drought years (*e.g.*, 2007 and 2010). Summing potential losses across years (see Fig. 4) yielded a total fire-driven aboveground biomass loss estimate ranging from 0.67 to 5.86 gigatons of CO_2 (0.18 to 1.60 gT C) to the atmosphere between 2001-2010.

DISCUSSION

Here, we find that tree investment in bark varies across Amazonian tropical forests, with thicker bark in dry forests and thinner in wetter forests. Combining these patterns with published relationships between bark thickness and tree mortality (Hoffmann *et al.* 2009; Brando *et al.* 2011) suggests that fire-driven tree mortality and biomass loss is greater in wet forests than in dry ones, which is also supported by our synthesis of observed post-fire tree mortality across the Amazon. Overall, thinner bark in wetter tropical forests may make these forests more sensitive to fire, which substantially changes estimates of fire impacts on the Amazon-wide carbon cycle. This fuller understanding of bark variability is likely to improve estimates of the fire-driven carbon cycle in tropical forests.

Variation in bark investment across tropical forests raises an intriguing question: Why are there thick-barked species in forests at all (Paine *et al.* 2010)? One possibility is that fire may have been historically widespread (if infrequent) in drier tropical forests, making thick bark advantageous. Certainly, the paleo-fire literature suggests that fires probably did occur in the Amazon before the modern era in drier Amazonian forests (Bush *et al.* 2008; Power *et al.* 2008) and much less so wetter ones (McMichael *et al.* 2012). Patterns of bark investment observed here are roughly consistent with this, suggesting that fire may have had some ecological and evolutionary importance at the margins of Amazonia. Another possibility is that the functionality of bark is not limited to withstanding fires, and that bark plays a role in drought tolerance (Rosell *et al.* 2013; Rosell 2016), nutrient and water storage (Richardson *et al.* 2015), and herbivore and disease defense (Richardson *et al.* 2015). Drought and water storage hypotheses are weakly supported by the current evidence. First, past work has shown that bark has limited function in mitigating drought susceptibility (Paine *et al.* 2010). Second, resource storage by bark is usually associated with inner bark (Pausas 2017), not the more insulating corky outer bark (Brando *et al.* 2011; Michaletz *et al.* 2012), such that future work should clearly differentiate between these two features. Anecdotally, most of the thick bark in this study was corky, although we did observe a few instances of extremely thick inner bark (see also Roth 1981); that bark was mostly corky is consistent with observations at Tanguro (included in this study) that bark thickness overall was more predictive of fire-protection than bark traits than bark moisture or density (Brando *et al.* 2011). However, the defense hypothesis argues that thin bark has evolved to resist pathogens at high rainfall (Richardson *et al*. 2015) where pathogen loads are heavy (Swinfield *et al*. 2012), consistent with and potentially contributing to patterns observed here. Mechanisms that lead to bark differences, particularly within forest system, merit further direct consideration.

Of course, important caveats apply, especially relating to the time scales of these patterns and processes. First of all, we have documented decreases in bark thickness only with respect to modern rainfall patterns, without considering any historical or paleo-rainfall distributions. Secondly, humans have been an important influence on the ecology of the Amazon basin for the past 16,000 years at least, perhaps filtering the composition of marginal Amazonian forests towards the species most tolerant of disturbances from fire (*e.g.*, Heckenberger *et al.* 2003). Although anthropogenic filtering cannot account for the existence of species with thick bark to begin with (*i.e.*, for standing variation in bark thickness), it may have strengthened existing patterns.

Whatever its evolutionary or ecological origins, patterns of bark investment across the Amazon suggest that fire-driven tree mortality should occur at higher rates in wet forests than in dry ones. These predictions are borne out in real mortality and biomass-loss estimates from understory fires (see Fig. 4), although, curiously, the observed response of mortality and biomass loss to rainfall was even stronger than our models predicted (Figure 3). There are a number of possible reasons that our models may underestimate high stem mortality rates in wet forests (see also Cochrane 1999; Barlow *et al.* 2012; Rappaport *et al.* 2018). One probable contributor is that we have only poorly represented the effects of fires that are intense (at least by tropical forest standards; Figure 2; Cochrane & Schulze 1999). This highlights a well-appreciated need for ways to quantify fire intensity, especially after fires have already occurred (see, *e.g.*, Rappaport et al., 2018), and for work across a broader range of forests and forest types.

Another possibility is that bark alone does not determine how trees respond to fire (Ryan & Williams 2011). For instance, hydraulic vulnerability may contribute to making the combination of drought and fire potent in killing tropical forest trees (Brando *et al.* 2014), if drought-induced water stress makes cavitation during fires more likely (Michaletz *et al.* 2012). Vulnerable hydraulic architecture – common in trees that have not experienced a history of drought or fire and perhaps also in taller forests – and root susceptibility to fires may both merit further examination as a contributor to fire-driven mortality of forest trees. Nonetheless, bark thickness clearly had major impacts on mortality and thus on biomass losses in understory fires.

An increased emphasis on plant functional responses to fire – via bark but also other traits – could further contribute to improving predictions of fire effects on tropical forests. For one, although fires often cause the mortality of the tree stem, they do not always kill the whole individual. Resprouting following fires (Hoffmann *et al.* 2009) can be widespread, and may dramatically speed forest community and biomass recovery following fires. Resprouting traits are understudied in tropical forests (Clarke *et al.* 2012), a critical gap if we are to understand the long-term implications of tropical understory fires for the carbon cycle. Conversely, repeated fires may slow post-fire forest succession. Changes in forest structure following an initial burn may predispose forests to additional fires (Barlow & Peres 2008), which in extreme cases can lead to grass invasion and eventual forest savannization (Silvério *et al.* 2013), although the generality of this runaway feedback is an issue of some debate (Cochrane 1999). Bark traits may make this more likely, since many of the smaller trees that grow back after fires have thinner bark, and these pioneers are often highly susceptible to subsequent fires (Barlow & Peres 2008).

Here, we provide the first evidence of substantial variation in bark investment across Amazonian forests. Thinner bark in wetter forests provides a convincing explanation for extremely high local tree mortality in understory fires, which improves our understanding of both carbon emissions and biodiversity losses. Together with improved models for fire behavior, a more comprehensive perspective on how plant functional traits (including bark thickness and resprouting) mediate ecosystem responses to global change will be critical to predicting the future of Amazonian forests and associated climate-carbon feedbacks, including fires (Cochrane 2003). In this study, aboveground biomass loss estimates based on varying bark thickness suggest that Amazon understory fires have added between 0.67 to 5.86 gigatons of CO_2 to the atmosphere between 2001-2010 (Fig. 4), without accounting for regrowth. Ignoring fire-related functional traits thus risks missing a major ecological influence on forest responses to fire, with consequences for predictions of tropical forest impacts on global carbon cycles.

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FIGURES

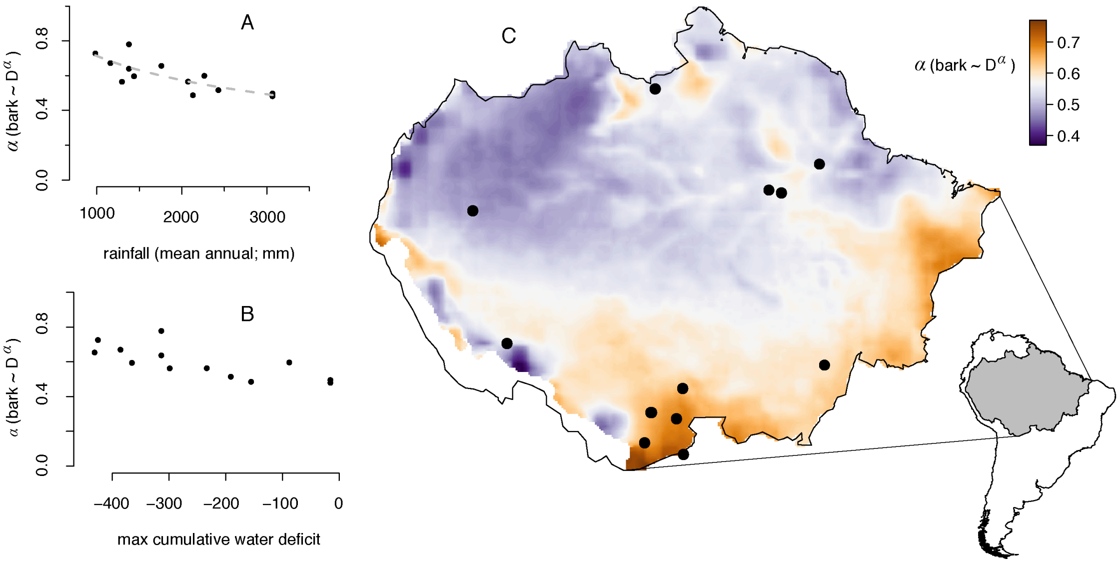

Figure 1. Response of community-wide bark thickness to rainfall (A) and maximum cumulative water deficit (B), and modeled bark thickness across the Amazon (C). Log-rainfall was the preferred explanatory variable (Table S2; $R^2 = 0.616$, $df = 11$, $p = 0.0015$). Higher values of α indicate that bark accumulates more quickly as tree diameter increases (*i.e.*, that bark is thicker). Thus, bark is thicker in lower-rainfall forests.

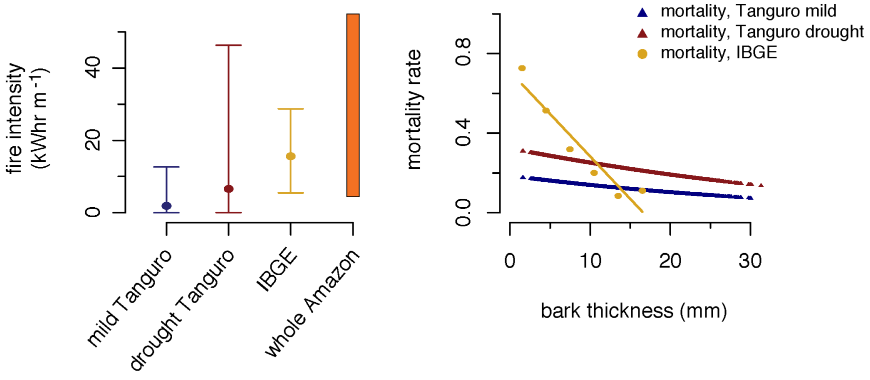

Figure 2. Fire intensity at Tanguro, the IBGE Reserve, and across the Amazon (A), and predicted mortality response to bark thickness from Tanguro and the IBGE Reserve (B). Fire intensities at Tanguro and IBGE were calculated from char height observations using equations given in [(Williams *et al.* 1998)]. At IBGE, the probability of tree mortality decreased with bark thickness ($R^2 = 0.909$, $df = 4$, $p = 0.0032$). At Tanguro, a model including bark thickness, year (as a proxy for fire intensity and drought stress), and the interaction between them was used to predict tree mortality (see Brando *et al.* (2014) for a formal analysis) and explained 16.2 % of variation in tree mortality. Tanguro data are drawn from Brando *et al.* (2011; 2014), IBGE data from Hoffmann *et al.* (2009), and whole-Amazon syntheses from Cochrane *et al.* (1999).

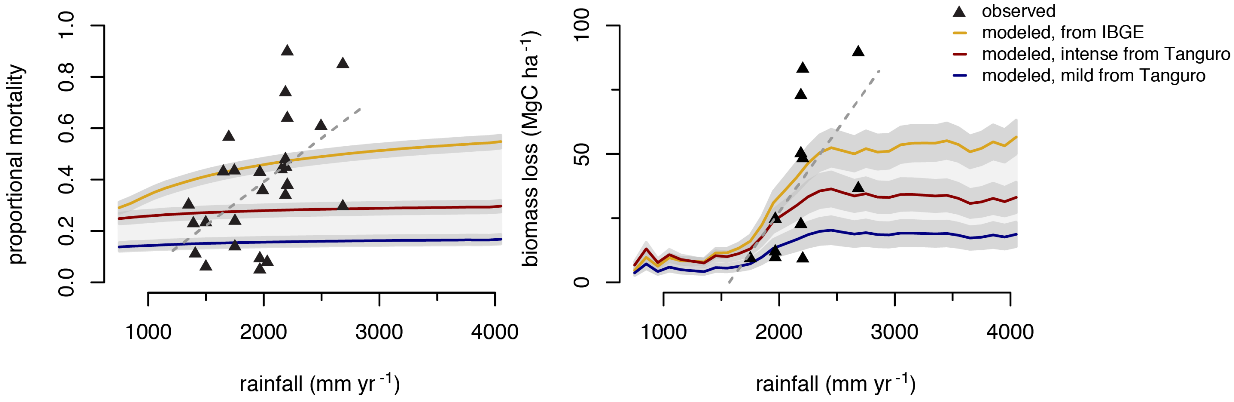

Figure 3. Modeled and observed fire-driven tree mortality (A) and biomass loss (B) in response to rainfall. Mortality (Hoffmann *et al.* 2009; Barlow *et al.* 2012) and biomass loss (Barlow *et al.* 2012) observations are drawn from published meta-analyses of field studies across the Amazon, and modeled fire-driven mortality is based on published relationships between tree bark and mortality at Tanguro in mild and intense fires (Brando *et al.* 2011) and at the IBGE reserve (Hoffmann *et al.* 2009). Observed fire-driven mortality rates increased with rainfall ($R^2 = 0.290$, $df = 24$, $p = 0.0045$) more strongly that modeled mortality did. So too did biomass losses ($R^2 =$

0.347, *df* = 10, *p* = 0.044). Note that in both cases, rainfall was a better predictor of observed mortality and biomass loss than MCWD ($R^2 = 0.121$, *df* = 15, *p* = 0.17 and $R^2 = 0.331$, *df* = 10, *p* = 0.05, respectively).

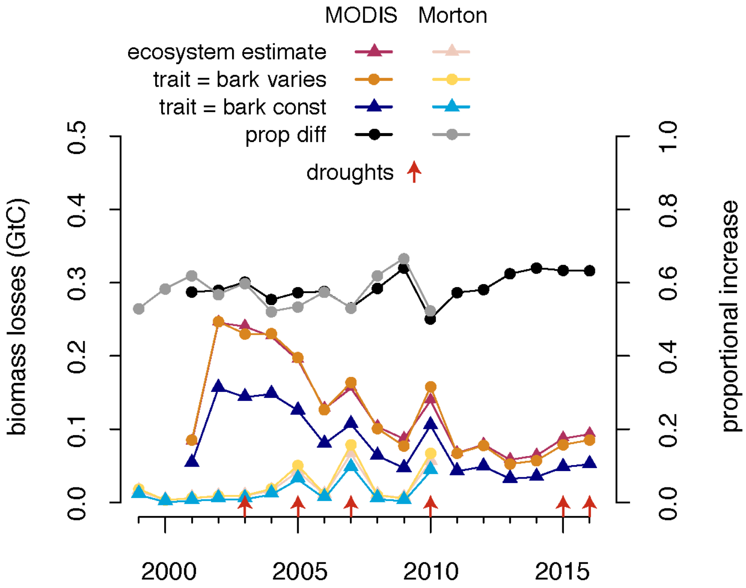

Figure 4. Predicted fire-driven losses of above-ground biomass (GtC) across all Amazonian forests, calculated from published estimates of biomass loss (Barlow *et al.* 2012) (magenta, pink) and modeled assuming constant bark thickness (navy, blue) vs. variable bark (orange, yellow) and a bark-mortality relationship from [(Hoffmann *et al.* 2009)]. For constant bark calculations, we assume bark equivalent to our four driest sites, near the southern edge of the Amazon. Fire extent was estimated directly from MODIS Active Fires data ('MODIS') (Giglio *et al.* 2016) and via independent MODIS-derived understory fire distributions ('Morton') (Morton *et al.* 2013). This reveals the effects of extrapolating current and future fire-driven losses from historical fire-driven losses in comparatively fire-tolerant forests. See Methods for detail. Including variations in bark thickness across the Amazon increases predicted fire-driven carbon losses by 57.6 ± 3.9% (see Table S2).

SUPPLEMENTARY FIGURES AND TABLES

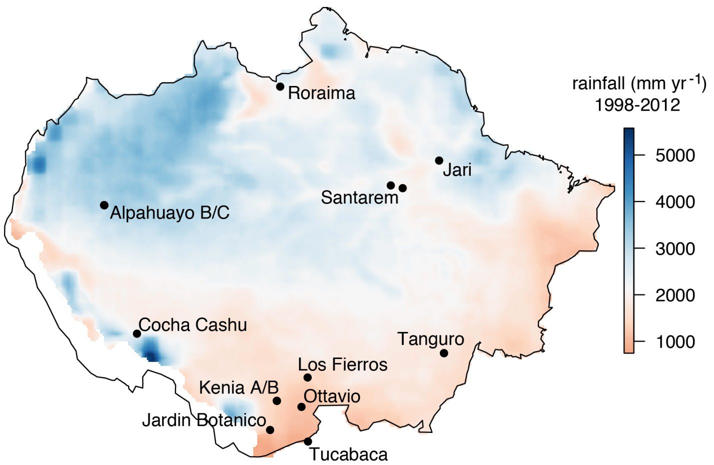

Figure S1. Mean annual rainfall and site locations and names across the Amazon.

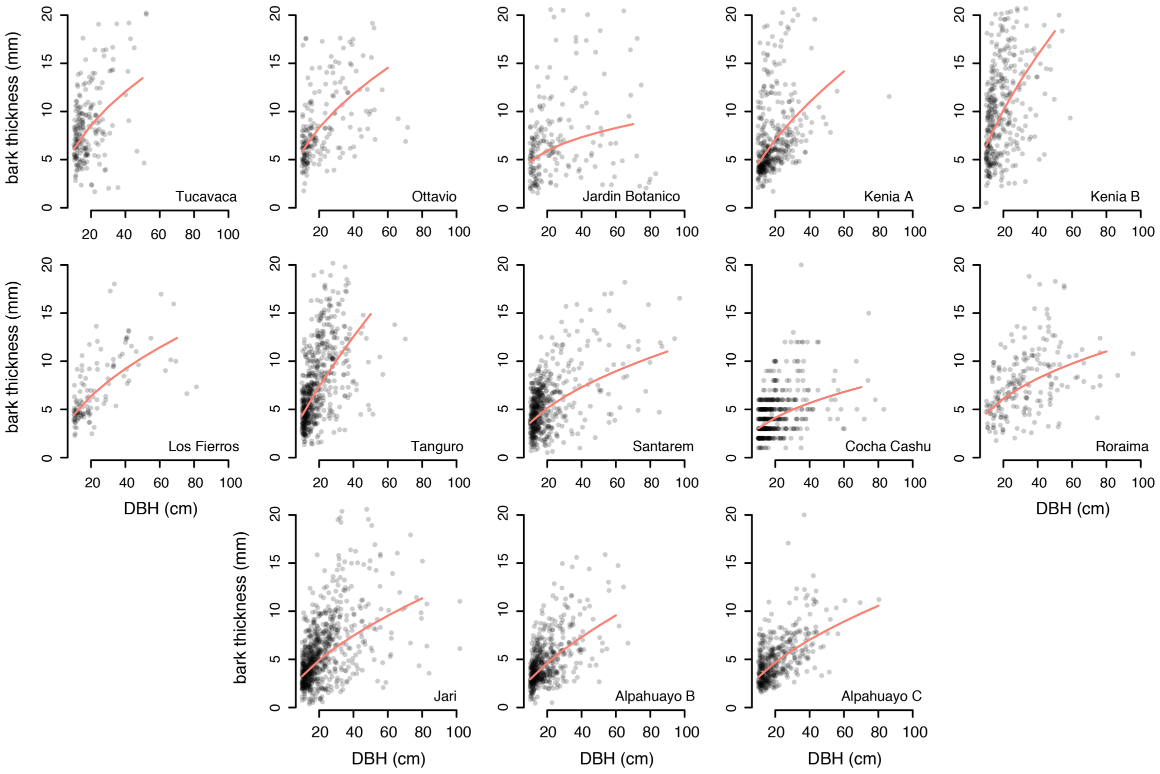

Figure S2. Bark allometries by site. Lines represent the best-fit relationship between diameter (DBH; cm) and bark thickness (mm) with a form given by $bark = DBH^{\alpha}$. Here, fits are shown to all trees at a site, but for formal analysis, allometric constants were calculated by species, and averaged weighted by species abundance at a site. Note that all plots have been truncated at 20 mm bark thickness and 100 cm DBH, focusing on the majority of data (89.4%) and avoiding sparse regions of morphological space.

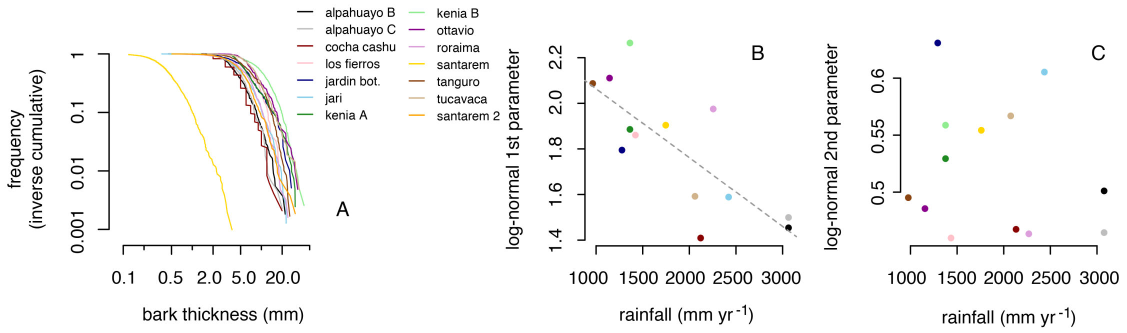

Figure S3. Inverse cumulative bark thickness distribution at each site (A), and response of the best-fit log-normal parameters at each site to rainfall (B-C). The first parameter of the log-normal distribution varied predictably with rainfall across sites ($R^2 = 0.592$, $df = 11$, $p = 0.0021$).

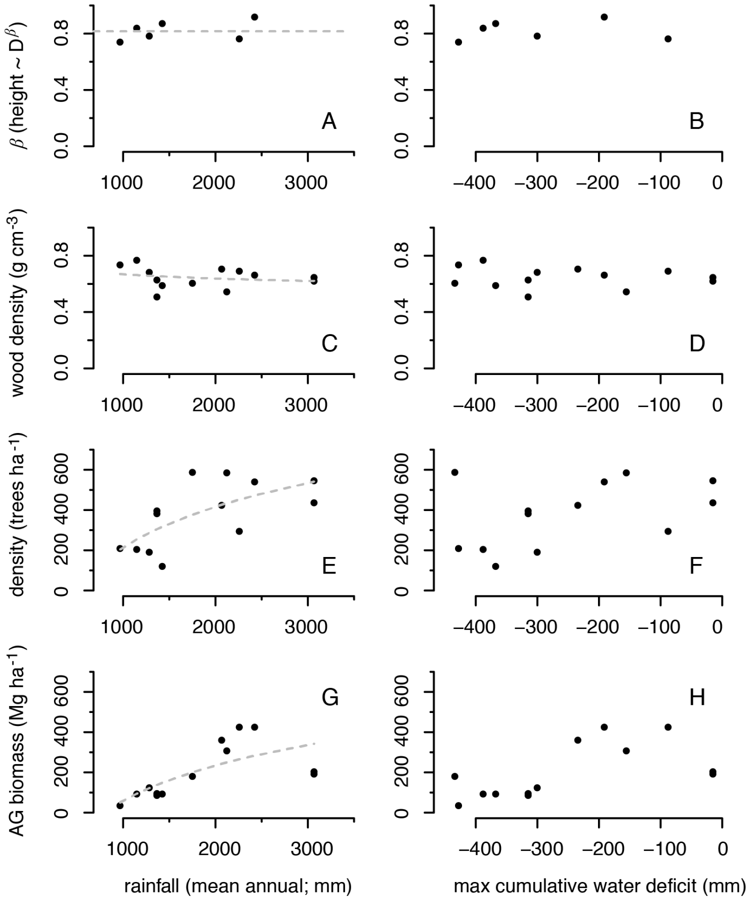

Figure S4. Response of height allometry (A-B), wood density (C-D), tree density (E-F), and above-ground biomass (G-H) at each site to rainfall and MCWD.

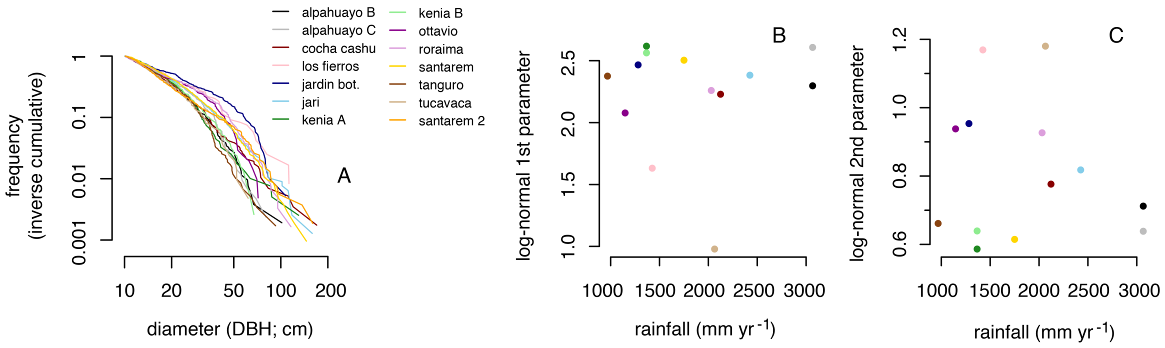

Figure S5. Inverse cumulative diameter distribution at each site (A), and response of the best-fit log-normal parameters at each site to rainfall (B-C).

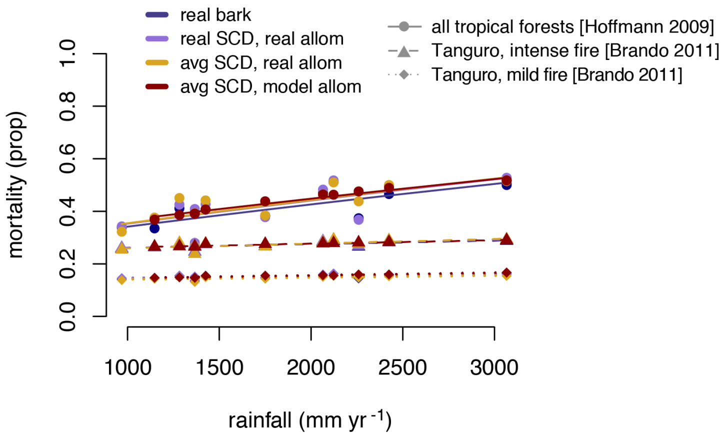

Figure S6. Fire-driven tree mortality response to rainfall, modeled using real bark measurements (blue), bark modeled on real diameter measurements and real bark allometric constants by site (purple), bark modeled on a stylized diameter distribution (see Figure S4) and real bark allometric constants by site (yellow), and bark modeled on a stylized diameter distribution and modelled bark allometric constants (see Figure 1) (red). Mortality was estimated using published relationships between bark and mortality from Tanguro (Brando *et al.* 2011) (triangle and diamonds for intense and mild fires, respectively) and from all tropical forests (Hoffmann *et al.* 2009) (circles).

Table S1. Sites and plot details.

Site	Plot dimensions	Total area sampled
Tucabaca	100 m × 100 m	1 ha
Ottavio	100 m × 100 m	1 ha
Jardin Botanico	100 m × 100 m	1 ha
Kenia A	100 m × 100 m	1 ha
Kenia B	100 m × 100 m	1 ha
Los Fierros	500 m × 20 m	1 ha
Tanguro	50 m × 50 m × 4	1 ha
Santarem†	50 m × 50 m × 5	1.25 ha
Cocha Cashu	100 m × 100 m	1 ha
Roraima	50 m × 50 m × 3	0.75 ha
Jari	10 m × 250 m × 6	1.5 ha
Alpahuayo B	100 m × 100 m	1 ha
Alpahuayo C	100 m × 100 m	1 ha

† At Santarem, species were identified only to morphospecies, so site-specific biomass was calculated for another nearby site, where taxonomic information was available, for use in analyses.

Table S2. Akaike information criterion model selection for bark allometry (α: bark = DBH$^{\alpha}$), height (β: height = DBH$^{\beta}$), and wood density (ρ) functional traits, and plot-level stem density (ha^{-1}) and above ground biomass (Mg ha^{-1}). The simplest model with ΔAIC < 2 was selected as the best, indicated in bold.

predictors	ΔAIC				
	bark (α)	height (β)	wood (ρ)	stem density (ha^{-1})	AG biomass (Mg ha^{-1})
~ log (mar) * mcwd	9.31	> 10	11.05	6.21	4.78
~ log (mar) + mcwd	3.92	> 10	6.85	1.18	6.04
~ mar * mcwd	9.11	> 10	11.84	5.60	0
~ mar + mcwd	4.39	> 10	7.44	2.73	8.40
~ log (mar)	***0***	8.65	2.83	***0***	***1.81***
~ mar	0.37	8.81	3.13	1.22	4.15
~ mcwd	1.83	9.96	3.26	5.14	4.92
~ 1	8.96	***0***	***0***	4.35	6.96

Table S3. Fire-driven carbon losses from Amazonian forests, calculated assuming constant bark thickness vs. variable bark. For constant bark calculations, we assume bark equivalent to our four driest sites, near the southern edge of the Amazon, where fires may have been historically frequent. This reveals the effects of extrapolating from comparatively fire-tolerant forests to the entire Amazon basin. Errors represent standard deviations.

fire extent estimate	mortality model	Total fire-driven biomass loss (GtC), constant bark	Total fire-driven biomass loss (GtC), variable bark	Percent change (%)
MODIS Active Fires	All forests[†]	0.16 ± 0.09	0.26 ± 0.14	57.6 ± 3.9
	Mild Tanguro[‡]	0 ± 0	0.11 ± 0.06	∞
	Intense Tanguro[‡]	0.097 ± 0.053	0.20 ± 0.11	1927.3 ± 14.3
MODIS-derived 'Morton'	All forests[†]	0.015 ± 0.017	0.024 ± 0.026	57.2 ± 0.047
	Mild Tanguro[‡]	0 ± 0	0.019 ± 0.021	∞
	Intense Tanguro[‡]	0.0010 ± 0.0011	0.010 ± 0.012	18.2 ± 0.16

[o] Morton *et al.* 2013

[†] (Hoffmann *et al.* 2009)

[‡] (Brando *et al.* 2011)

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