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Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior

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Abstract

Large-scale wildfires are expected to accelerate forest dieback in Amazônia, but the fire vulnerability of tree species remains uncertain, in part due to the lack of studies relating fire-induced mortality to both fire behavior and plant traits. To address this gap, we established two sets of experiments in southern Amazonia. First, we tested which bark traits best predict heat transfer rates (R) through bark during experimental bole heating. Second, using data from a large-scale fire experiment, we tested the effects of tree wood density (WD), size, and estimated R (inverse of cambium insulation) on tree mortality after one to five fires. In the first experiment, bark thickness explained 82% of the variance in R, while the presence of water in the bark reduced the difference in temperature between the heat source and the vascular cambium, perhaps because of high latent heat of vaporization. This novel finding provides an important insight for improving mechanistic models of fire-induced cambium damage from tropical to temperate regions. In the second experiment, tree mortality increased with increasing fire intensity (i.e. as indicated by bark char height on tree boles), which was higher along the forest edge, during the 2007 drought, and when the fire return interval was 3 years instead of one. Contrary to other tropical studies, the relationship between mortality and fire intensity was strongest in the year following the fires, but continued for 3 years afterwards. Tree mortality was low ($\leq 20\%$) for thick-barked individuals (≥ 18 mm) subjected to medium-intensity fires, and significantly decreased as a function of increasing tree diameter, height and wood density. Hence, fire-induced tree mortality was influenced not only by cambium insulation but also by other traits that reduce the indirect effects of fire. These results can be used to improve assessments of fire vulnerability of tropical forests.

Keywords: Amazon, bark thickness, climate change, fire, forest dieback, generalized linear models, Newton's law of cooling, plant traits, tree mortality, wood density

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Introduction

The synergistic effects of droughts, forest degradation by logging, landscape fragmentation, and increased fire ignition have altered large areas of Amazon forests by reducing canopy density, live biomass, and fire resistance (Cochrane *et al.*, 1999; Nepstad *et al.*, 2001; Alencar *et al.*, 2004, 2006; Nepstad *et al.*, 2008; Aragão & Shimabukuro, 2010). If predictions of drier and warmer future climatic conditions hold true, even larger portions of Amazonia will soon be vulnerable to fire (Golding & Betts, 2008; Nepstad *et al.*, 2008); 16 of 23 climate models predict substantial reductions in precipitation by the mid 21st Century in eastern Amazonia due mostly to increased atmospheric CO_2 (Malhi *et al.*, 2008). While this change in climate is anticipated to have substantial effects on tropical forest dynamics (Barlow *et al.*, 2002; Nepstad *et al.*, 2008), by increasing the fire frequency and intensity, few data are available in the tropics to understand the vulnerability of forest tree species to fire nor the physiological and morphological characteristics that determine this vulnerability.

One important mechanism by which slow-moving, low-severity understory forest fires alter ecosystem processes (e.g. water, energy and carbon exchange with the atmosphere) is by killing trees (Pinard *et al.*, 1999; Barlow *et al.*, 2003a,b). Surface fires in closed canopy

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tropical wet and moist forests characteristically spread slowly through the understory and heat only the bases of tree stems. If heating is sufficient to kill cells in the vascular cambium around the entire circumference of a tree's bole, the tree is expected to die (Michaletz & Johnson, 2007), although that process may take several years (Barlow *et al.*, 2003b; Baker *et al.*, 2008; Barlow & Peres, 2008).

Two experimental tree bole-heating studies conducted in the Amazon (Uhl & Kauffman, 1990; Pinard & Huffman, 1997) documented the importance of bark thickness in insulating the vascular cambium; both studies showed that inner bark temperatures rose above lethal levels (e.g. 60 °C) in response to simulated fires (e.g. a burning rope tied around the tree bole), except for a few individuals with thick bark. Such observations, and others from temperate zone studies, were used as the basis for simple models in which bark thickness is the most important plant trait in avoiding fire-induced tree mortality (Dickinson & Johnson, 2001; VanderWeide & Hartnett, 2011). These models have been used to predict the generally high fire vulnerability of tropical forests (Uhl & Kauffman, 1990; Pinard & Huffman, 1997; Hoffmann & Adasme, 2009). In the one study that actually tested the bark thickness–tree mortality relationship (as opposed to heating–cambial damage relationships), Barlow *et al.* (2003a) found that 3 years after a fire, live trees in a burned forest in Eastern Amazonia had thicker bark (BT = 6.3 mm) than trees in a nearby unburned forest (BT = 5.5 mm). While studies that relate cambial insulation to fire-induced tree mortality provide a first approximation of fire vulnerability of Amazonian forests, the complex mechanisms influencing fire-induced tree mortality still remain poorly understood.

Plant traits other than bark thickness that reduce the impacts of fire on the physiology and structure of tree trunks may exert important influences on fire-induced tree mortality (Michaletz & Johnson, 2007). Trees wounded during surface fires, for instance, are susceptible to wood decay that can be slight or fatal depending on the capacity of the tree to compartmentalize the damage, which generally increases with wood density (Romero & Bolker, 2008). As trees grow larger, they also become less susceptible to indirect fire damage caused by falling trees and branches that were killed by the burns. Similarly, larger diameter trees are less likely to have their entire circumference heated during a fire (Gutsell & Johnson, 1996), and taller trees may disproportionally survive fires because their crowns are less likely to be damaged. Thus, large individuals may be more likely to survive surface fires than smaller trees even if bark thickness is the same. Exceptions to this pattern are probably large individuals with buttress, which tend to have thin bark and to accumulate fuel near the trunk (Barlow *et al.*, 2003a).

Knowledge of the mechanisms responsible for fire-induced tree morality is needed to predict the responses of tropical forests to global changes. Several coupled climate and dynamic global vegetation models (DGVM), for example, predict substantial alterations in the structure and functioning of forests in Amazonia due to climate change alone (Cramer *et al.*, 2001; Sitch *et al.*, 2008; Galbraith *et al.*, 2010). However, synergistic interactions between climate change and fire may drive this process further and more rapidly than currently predicted (Nepstad *et al.*, 2008). Unfortunately, few of the existing DGVM directly represent the effects of fire on the vegetation of the Amazon. To represent these effects accurately and therefore to improve predictions of forest changes in the region, a better understanding of the mechanisms associated with fire-induced tree mortality is needed.

We conducted two sets of related experiments to identify the tree traits that are associated with fire survival. In the first experiment, we determined which bark traits best represent heat transfer rates through bark (R in units of °C s^{-1}) during experimental bole heating. We used a variation of the exact solution of Newton's Law of cooling to calculate R (see Appendix S1 for details), a measure of the rate at which conductive and convective heat is transferred through bark (the reciprocal of cambium insulation). Using that equation and thus a new approach to the study of fire-induced cambial damage (Appendix S1), we tested the following predictions: (i) as bark thickness (BT) increases, R decreases exponentially; (ii) as bark moisture content (BMC) increases, R also increases due to water's high thermal conductivity and despite its high heat capacity; (iii) as bark density increases, R decreases due to the inverse relationship between density and thermal diffusivity (see Appendix S1); and, (iv) BT is the most important bark trait in preventing the cambium temperature from rising to lethal levels.

To assess how bark and wood characteristics influence fire-induced tree mortality, we used 6 years of data from a large-scale fire experiment in the southern Amazon (Fig. 1). Specifically, we used an estimated value of R (derived from the heating experiment and referred to as $\hat{R}$), wood density, tree height, and stem diameter at breast height (dbh) to test the predictions that: (i) increasing tree dbh and height decrease the likelihood of fire-induced tree mortality, because larger and taller individuals both tend to have thicker bark and other traits that reduce the indirect effects of fire (e.g. taller and larger stems are less likely to be damaged by neighboring tree and branch fall); (ii)

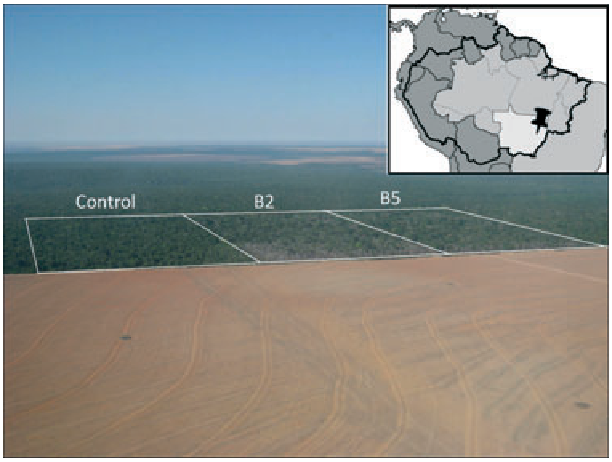

Fig. 1 Aerial view of the fire experiment (September 2008) and its location (top right of the figure).

decreasing $\hat{R}$ (i.e. increasing cambium insulation) increases the likelihood of tree survival more than other plant traits. We also evaluated the effect of fire exposure on tree mortality, testing the hypothesis that (iii) fire-related mortality within the first postfire year increases as a function of char height, which is an indicator of local fire intensity.

Methods

Study site and general approach

This study was conducted in a transitional forest in the southern part of the Amazon Basin (13°04′S, 52°23′; Fig. 1) where average annual precipitation is 1800 mm and the dry season extends from May to September (Balch *et al.*, 2008). To evaluate how different bark traits influence the likelihood of fire-induced tree mortality, we conducted a series of field experiments. First, we heated the air adjacent to the outer bark of trees with a propane torch to relate heat transfer rates (*R*) to bark traits. Second, we developed a predictive model of bark thickness as a function of tree dbh for the 24 most common species. Third, based on predicted bark thickness, we estimated *R* (referred to as $\hat{R}$) for each tree ($\geq$10 cm dbh) in experimental plots subjected to different fire frequencies. Fourth, we tested several statistical models of mortality as a function of $\hat{R}$ for trees in two 50 ha plots that were burned either twice (B2) or five times (B5) between 2004 and 2010. Finally, we compared the importance of $\hat{R}$ with other plant traits in avoiding fire-induced mortality.

Modeling cambium insulation

During the 2008 dry season, cambium vulnerability to fire-induced damage was estimated as the rate of change in cambium temperature (CT) as a function of the air temperature adjacent to the outer bark that was heated using a torch. We first removed a 5 × 5 cm sample of bark at 25 cm above the ground from each of 87 randomly sampled individuals 10–121 cm dbh that represented 18 species. These samples were taken to the laboratory for measurements of BT, density (ρ_b), and moisture content (BMC) following the procedures in Uhl & Kauffman (1990). From BMC and ρ_b, we derived estimates of bark thermal diffusivity (α) using linear regression models developed by Martin (1963) for *Pinus* spp. trees [see Dickinson & Johnson (2001) for more details].

Immediately following bark removal, a thermocouple was inserted between the inner bark and xylem (i.e. into the vascular cambium) and a second thermocouple was placed on the surface of the outer bark. The air adjacent to the outer bark of each tree was then heated using an industrial propane torch with a metal plate in front of the flame to prevent direct thermocouple or bark contact. Temperatures in the vascular cambium (CT) and in the air adjacent to the outer bark were recorded every 10 s for 13 min, which allowed detection of changes in cambium temperatures even for individuals with very thick bark. Using an asymptotic regression model [Eqn (1)], we estimated the rate of heat transfer [the parameter *R* in Eqn (1)] as a function of cumulative air temperature (CTF) at the outer bark, which integrates the colinear variables of time and air temperature adjacent to the outer bark into a single variable:

$$\mathrm{CT} = \mathrm{Asymptote} + (\mathrm{CT_i} - \mathrm{Asymptote})e^{\mathrm{CTF}e^{R}}. \qquad (1)$$

The main strength of this equation is that it relates cambium temperature to the initial cambium temperature ($\mathrm{CT_i}$) and fire intensity (CTF). Thus, with this equation we can also separate the rates of change in cambium temperature due to heat transfer rates (*R*) from the differential in temperature between the fire and the cambium. In other studies (Uhl & Kauffman, 1990; Pinard & Huffman, 1997), heat transfer rates were inferred via regressions between peak cambium temperature and bark traits, thus ignoring effect of initial cambium temperature – which ranged in this study between 16 and 28 °C. Once an estimate of *R* was attained via the above equation, we used linear regression to identify the bark traits which best predicted *R*. We compared models with the explanatory variables BT, BMC, ρ_b and α using Akaike's Information Criterion [AIC, Burnham & Anderson (2002)]. Once the best model relating *R* and bark traits was selected, it was used to predict *R* for every tree in the fire plots (referred to as $\hat{R}$).

Estimating bark thickness

Bark thickness could not be determined for all monitored trees in the experimental area because many trees were already dead when we conducted this study. Thus, we developed predictive models of BT for the 24 most common species (Fig. 2), which accounted for almost 85% of the total importance value index (IVI; Balch *et al.*, 2008). Specifically, we measured dbh and BT of 1000 individuals in an adjacent area to the fire experiment and related these two variables using species-specific linear models (Fig. 3). From BT, we then estimated a value for *R* for each monitored individual of the 24 focal species in the fire experiment area (*N* = 3752).

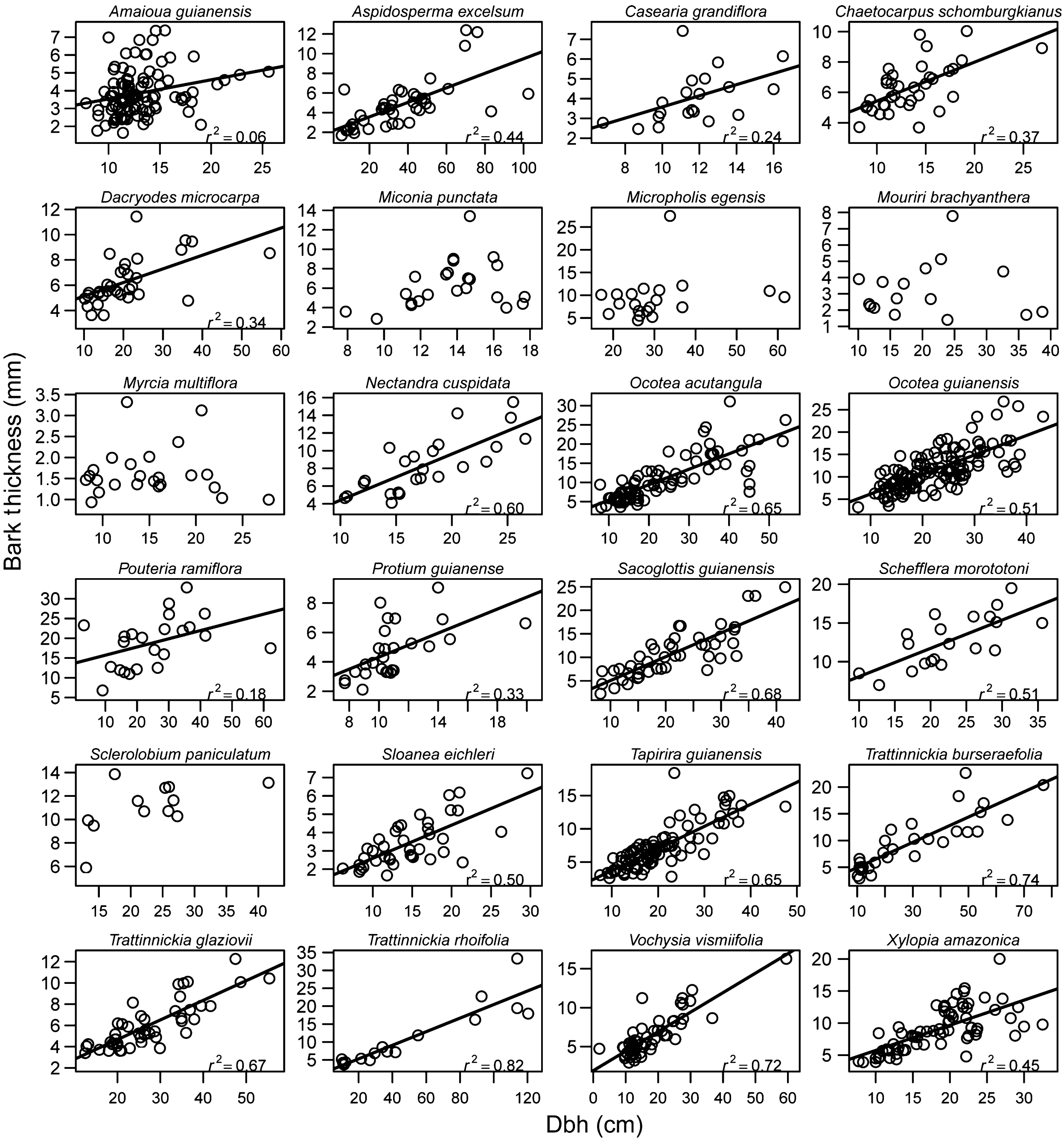

Fig. 2 Relationships between dbh and bark thickness (BT); when there was no relationship for a given species, predicted BT was based on the intercept of the model.

Linking tree mortality with cambium insulation (inverse of $\hat{\mathrm{R}}$*)*

Data from the fire experiment were used to assess probabilities of fire-induced tree mortality as a function of $\hat{R}$. In this experiment (Figs 1 and 3), three 50 ha plots were established in 2004 in Mato Grosso, Brazil (Balch *et al.*, 2008): a control with no signs of recent fires; a plot that was experimentally burned twice (2004 and 2007; plot B2); and a plot that was experimentally burned five times from 2004 to 2009 (plot B5). Within each of these plots, we conducted yearly mortality censuses for trees 10–20 cm dbh in six transects of 10 m × 500 m; for trees 20–40 cm dbh we used six transects of 20 m × 500 m per plot. All trees with dbh ≥40 cm were assessed annually for mortality in the entire 50 ha plots. In total, 6570 individuals of 97 tree species were sampled for

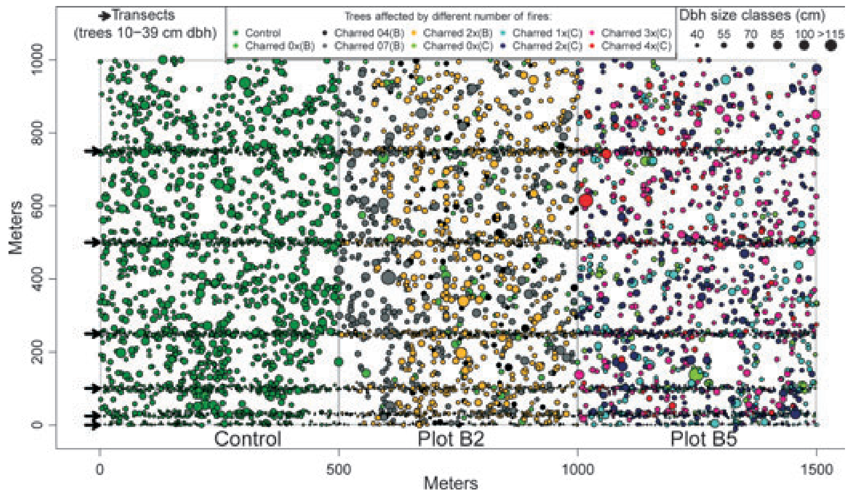

Fig. 3 Spatial locations of sampled trees in three 50 ha plots: control; plot B2 (burned in 2004 and 2007); and, plot B5 (burned yearly between 2004 and 2009, except for 2008). Each color represents the number of times a given tree was charred. The size of symbols represents the dbh of each tree. Only trees ≥ 40 cm dbh were censused across the entire 150 ha. Trees <40 cm in dbh were sampled along six transects (black arrows) that had two widths: one for trees with dbh between 10.0 and 20 cm and another one for trees with dbh between 20.0 and 40 cm (see Methods). Note that transects are not equally spaced to capture forest edge effects.

dbh (see Fig. 3); heights were measured for a subset of 4071 of these trees. Wood density data were derived from the literature for 87 species (Chave *et al*., 2006). Note that our first inventory was conducted prior to the first fires and that all fires were conducted during the peak of the dry season (August–September of each year).

Given that both the height and frequency of charring varied within plots (Balch *et al*., 2008; Balch *et al*., 2011), we grouped individual trees into the following categories: (1) never charred and located in the control plot (Control) or in plots B2 and B5 (C0x-B2-B5); (2) charred once and located either in plot B2 (C1x-B2) or in plot B5 (C1x-B5); (3) charred twice and located either in plot B2 (C2x-B2) or in plot B5(C2x-B5); and (4) charred three or more times and located in plot B5 (C3x-B5). For those in group (3) from above, note that because only trees that survived the first fire are included in this group, mortality could only occur after 2007 for trees charred twice in B2 and after 2006 for trees charred twice in B5.

Tree mortality and cambium insulation

To evaluate the probability of tree mortality as a function of $\hat{R}$ (and therefore assess the importance of $\hat{R}$ in avoiding fire-induced mortality), we compared logistic regression mixed models of mortality with the following covariates: (i) plot type (control, B2 and B5); (ii) treatment (number of times a tree was charred); (iii) fire severity, represented by char height lagged by one, two, three, and four years since the burns; (iv) tree resistance to fire, represented by $\hat{R}$ (derived from BT); (v) time (categorical for each year between 2004 and 2010); and (vi) distance from the forest edge. In addition to these fixed effects, the logistic models included crossed random effects of species and time. To avoid the effects of time-since-fire in evaluating fire-induced tree mortality (e.g. due to the longer observation period, a tree burned in 2004 was more likely to die than a tree burned in 2009), we evaluated mortality at a yearly basis but lagged char height by 1, 2, 3, and 4 years since the burn.

To assess the influences of spatial autocorrelation on the statistical models, we compared parameter estimates from the models with and without a spatial error structure [*glmer* function in R statistical software, Bates & Maechler (2009); and *glmmPQL*, Venables & Ripley (2002)]. As including the spatial structure did not change the results, we present only the estimates derived from the *glmer* function (Bolker *et al*., 2009).

Given that $\hat{R}$ was estimated from tree dbh, its association with mortality could simply be due to a demographic effect in which smaller individuals (with high $\hat{R}$) die at higher rates than larger individuals (with low $\hat{R}$), even in the absence of fire. To account for this potential demographic effect in models, the influence of $\hat{R}$ on mortality was evaluated based on the interaction between the fire treatment and $\hat{R}$ relative to its interaction with the control. Therefore, if that interaction did not differ for the control vs. the fire treatments, *R* was considered to have no effect on fire-induced tree mortality. The general patterns of mortality among treatments from 2004 to 2010 were evaluated based on parameters of the best model (Table 1).

Other correlates of fire-induced tree mortality

To compare the influence of $\hat{R}$, plant size (height and dbh), and wood density on tree mortality, we developed one generalized linear mixed models for each plant trait, given that these variables were multi-collinear and had different sample sizes (e.g. tree height, dbh, BT and wood density were measured for different group of trees). Each model had the same structure as described for *Model I* (Table 1), but included as a covariate either $\hat{R}$, tree height, dbh or wood density. Thus, the

Table 1 Logistic models of mortality, degrees of freedom, Akaike Information Criteria (AIC), and delta AIC (i.e. AIC of model I minus AIC from all the other models)

Model	df	ΔAIC
Model I: lagged char height + treat*(edge + $\hat{R}$ + years)	62	0
Model II: lagged char height + plots*(edge + $\hat{R}$ + years)	46	342
Model III: lagged char height + years + plots*(edge + $\hat{R}$)	32	575

Asterisk (*) indicates that main effects as well as interactions are included in the model: e.g. A*B denotes the main effects of A and B and their interaction.

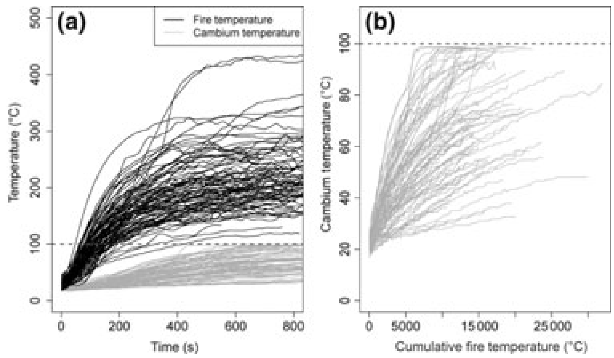

Fig. 4 Overall results from the bark heating experiment (87 individuals): (a) air temperature adjacent to the outer bark heated by a propane torch (black lines – above 100 °C; each line represents one individual) and cambium temperature (gray lines – below 100 °C; each line represents one individual) as a function of time; (b) cambium temperature as a function of cumulative air temperature adjacent to the outer bark (CTF). The dashed red lines in both figures represent 100 °C.

relative importance of a given variable in preventing fire-induced mortality was based on the estimate of the interaction between the fire treatments and each plant trait. All covariates were standardized (Gelman & Hill, 2007), making it possible to compare those estimates (i.e. interactions between fire treatments and plant traits) across models. Note that parameter estimates associated with $\hat{R}$ are presented in absolute terms (i.e. multiplied by −1) to facilitate comparison with the estimates from the other models. The potential effects of spatial autocorrelation were evaluated for all models but did not change the results (see section above on Modeling Mortality).

Results

Cambium insulation

Although cambium temperatures (CT) were expected to steadily increase until they reached asymptotes of the torch temperature (i.e. temperature adjacent to the outer bark), they never exceeded 100 °C presumably because heat from the fire was absorbed in the process of boiling water (i.e. latent heat of vaporization, Fig. 4). Consequently, the presence of moisture in the bark not only prevented CT from rising above 100 °C, it also reduced the gradient in temperature between the air adjacent to the outer bark and the cambium. If the air adjacent to the outer bark were heated to 400 °C for 10 min, for instance, it might be expected to have created a difference in temperature with the vascular cambium of 400 °C minus the initial cambium temperature (CT_i). The presence of water in the bark, however, constrained this difference to only 100 °C minus CT_i. Despite the constraint imposed by water, R increased with increasing BMC (Fig. 5; R^2: 13%). Bark thickness was the best single predictor of R; heat transfer rates through the bark decreased exponentially as bark thickened (R^2: 82%; Fig. 5). The predictive model of R that included ρb, BMC, BT as covariates was only 1.2 AIC units lower than the model that included BT as a single covariate (Table 2).

Tree mortality and fire behavior

Tree mortality was more influenced by the number of fires to which each individual tree was exposed than by the plot in which it was located. Logistic models with the number of times each tree was charred as a covariate (instead of information on whether or not the plots were burned) had the lowest AIC values (Table 1), suggesting that mortality was variable within plots and associated with the number of times each tree was directly exposed to fire. Mortality rates also varied substantially among the treatments over time (interaction: treatment × time) and from the forest edge (higher mortality) to the plot interior (lower mortality; interaction: treatment × distance from the edge; Appendix S2).

From 2004 to 2006, the experimental fires had no detectable influences on mortality of trees charred once in plot B2 (only in 2004) and only a modest (but detectable) influence on mortality of trees charred twice in plot B5 (Fig. 6; Appendix S2). Trees charred once (either in 2004, 2005 or 2006) in B5, in contrast, were more likely to die than trees in the control, indicating substantial effects of the initial fire on mortality in plot B5, which was burned three times between 2004 and 2006. Within the year following the 2007 fires, mortality was exceptionally high for all treatments, but particularly for trees charred twice in plot B2, indicating that: (i) fires were more intense in 2007 than in other years and (ii) fire severity in plot B2 in 2007 was higher than

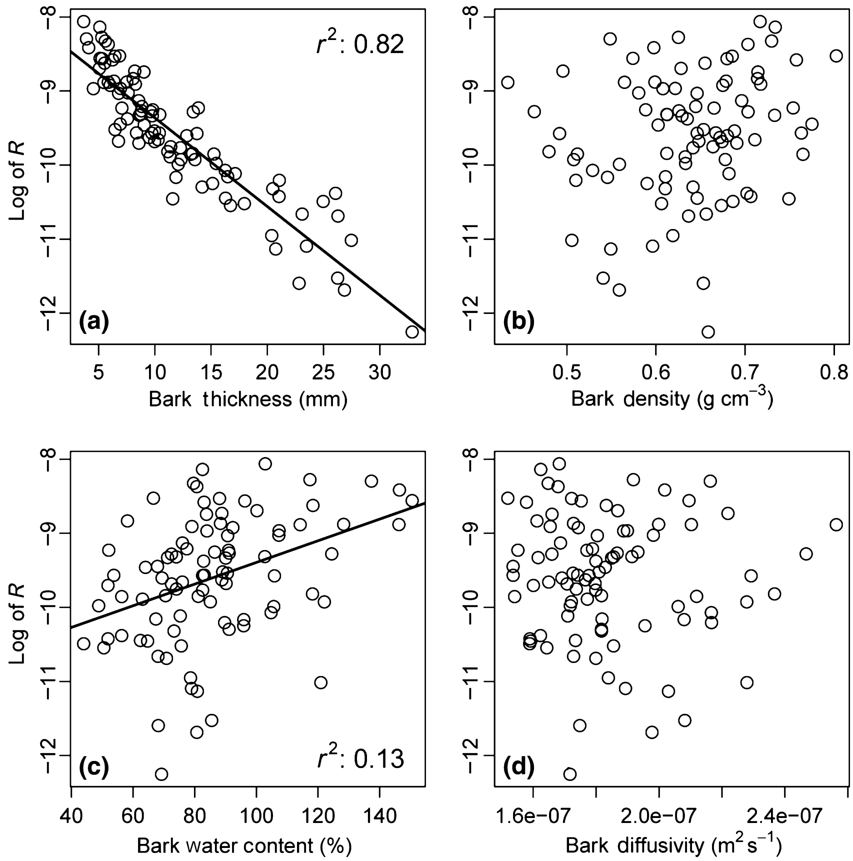

Fig. 5 Relationships between rates of change in cumulative heating (R) and (a) bark thickness, (b) bark density, (c) bark moisture content, and (d) bark thermal diffusivity.

Table 2 Model comparisons for heat transfer rates (R) using corrected Akaike Information Criteria (AICc). Also reported are the number of parameters (K), the adjusted R^2, and the AICc weight for each model

Models	K	Adj. R^2	ΔAICc	Weight
BT + ρb + BMC	5	0.83	0.0	0.44
BT	3	0.83	1.2	0.24
BT + ρb	4	0.83	2.5	0.13
BT + BMC	4	0.83	2.8	0.11
BT + α	4	0.83	3.3	0.086
ρb + BMC	4	0.40	115.0	0.00
BMC	3	0.13	146.5	0.00
Pb	3	0.03	156.7	0.00
A	3	−0.01	160.4	0.00

BT, bark thickness; ρb, wood density; BMC, moisture content; α, bark diffusivity.

in B5 (see Appendices S2 and S3). In the following years, from 2008 to 2010, mortality was significantly and substantially lower compared to 2007, but only in plot B5 did mortality fall below mortality in the control plot. Trees that were never charred but that grew in burned plots suffered higher mortality rates compared to the control between 2004 and 2007, and lower probabilities between 2008 and 2010.

Mortality varied not only as a function of the number of times each tree was charred, but also as a function of char height (a proxy of flame height and thus fire intensity) for up to 3 years following the experimental fires. To quantify the importance of char height on time-lagged mortality, we varied char height by one standardized unit (equivalent to an increase in char height from 10 to 150 cm) and used the model estimates to predict mortality 1, 2, and 3 years after the fire, holding the other covariates in *Model I* constant at reference levels (Table 1). Such a simulated increase in char height caused a decrease in the probabilities of tree survival of 17%, 6% and 2% for the first, second and third year after the fire, respectively. As these results were consistent across treatments and highly significant, we conclude that fire-related mortality occurred mainly within the year following the fires. However, it is important to note that mortality 2 and 3 years after fires was still significantly different from zero (Appendix S2).

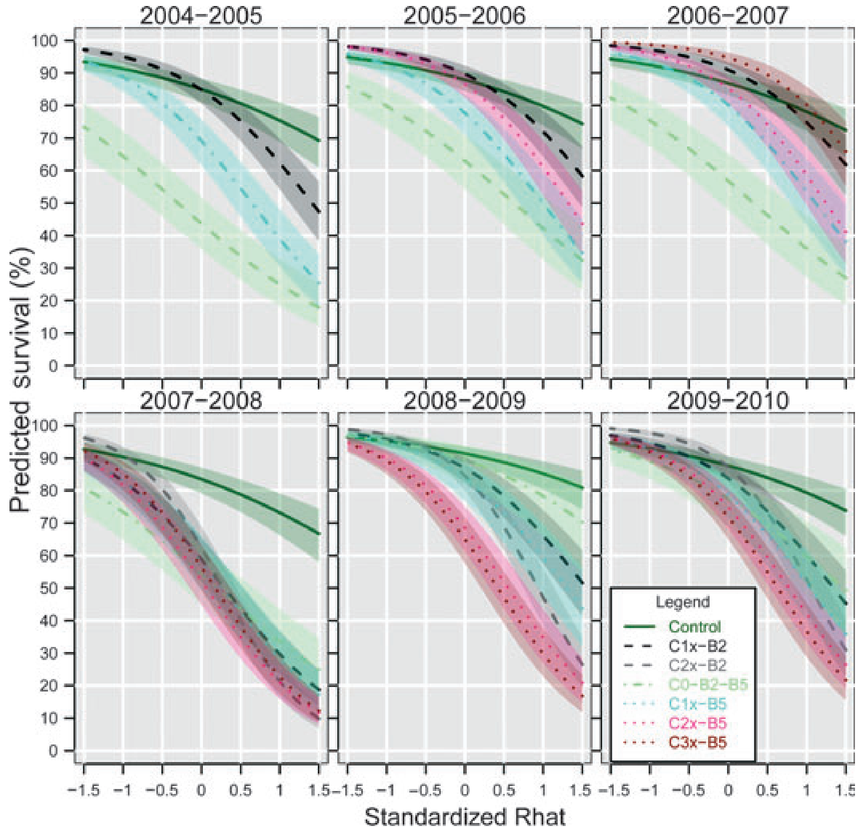

Fig. 6 Survival probabilities of trees ≥ 10 cm dbh as a function of $\hat{R}$ (inverse of cambium insulation derived from the heating experiment). Each panel represents the year of mortality census. Each color represents the number of times a given tree was charred in different treatments: Control, never charred; C1x-B2, charred once in plot B2; C2x-B2, charred twice in plot B2; C1x-B5, charred once in plot B5; C2x-B5, charred twice in plot B5; C3x-B5, charred three or more times in plot B5; and, C0x-B2-B5, never charred in plot B2 or B5. The *x*-axis represents the standardized rate of change ($\hat{R}$). In Appendix S2, we show the slopes and intercepts associated with this model.

Mortality and R *(inverse of cambium insulation)*

As cambium insulation decreased, tree mortality among charred trees increased at rates that were higher than those of trees in the control plot (Fig. 6). This result indicates that bark thickness had an important effect on fire-induced tree mortality. For example, a decrease of one standardized unit of $\hat{R}$ (equivalent to an increase in bark thickness from 5.6 to 16 mm) substantially increased the survival probability of trees charred once in plot B2 (28%), twice in plot B2 (40%), once in plot B5 (30%) and twice in plot B5 (35%). The greatest effects of $\hat{R}$ on mortality (and hence steepest absolute slopes relative to the control) were observed for trees charred (in order of decreasing importance) twice in plot B2, three times in plot B5, twice in plot B5, and once in plot B5 (Appendix S2). Thus, $\hat{R}$ was especially important for preventing fire-induced tree mortality for trees charred more than once. As expected, mortality rates of noncharred trees in the burned plots and trees in the control plot were not related to$\hat{R}$. The fact that mortality of uncharred trees was not related to cambium insulation provides confidence that uncharred trees were not directly affected by the fires. Finally, high mortality for small uncharred trees located in the experimental burned plots was observed, perhaps because they were more susceptible to damage from fire-induced falling of branches and trees.

Other correlates of tree mortality

Overall, wood density and dbh had strong effects on mortality in the fire treatments (relative to the control); as values of these two covariates increased, the probability of fire-induced mortality decreased (Fig. 7 & Appendix S4). Furthermore, the highest deviations from the control were observed for charred rather than uncharred trees. The exception to this pattern was in models including dbh; an increase in dbh among noncharred trees in the burned plots increased the

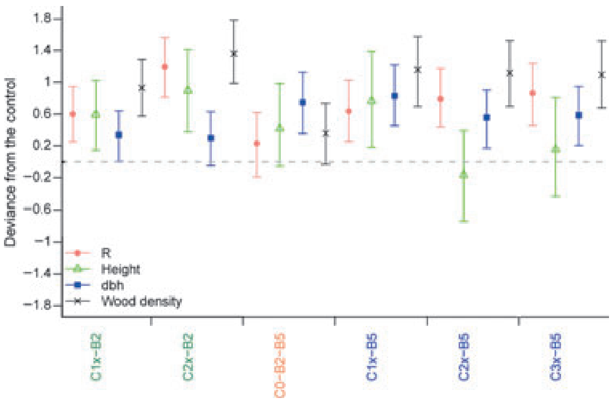

Fig. 7 Relative influence of $\hat{R}$, tree height, dbh and wood density on tree mortality for different fire treatments. On the *x*-axis, the plot B2 is represented by orange and B5 by blue. The influence of each variable on fire-induced mortality was inferred from the magnitude of the interactions between each plant trait and fire treatments, presented here the estimates on a logit scale. For example: an increase in the deviance in $\hat{R}$ causes a larger increase in mortality in the burned plots than in the control plot.

probability of mortality more than for trees in the control plot, probably because noncharred trees growing in the burned plots were affected by tree and branch fall, fire-induced damage to roots or canopy, and other potential secondary fire-related effects. Survival increased rapidly with tree height (Fig. 7) for trees charred once (plots B2 and B5) and twice (plot B5), but the slope of survival as a function of height was similar for trees in the control plot and trees charred twice and thrice (plot B5). In absolute terms, $\hat{R}$, dbh, and wood density played similar roles in reducing fire-induced tree mortality, while tree height was apparently less important.

Discussion

Cambium insulation

The rate of change in cambium temperature (a proxy for cambial insulation) is influenced by two distinct processes: (i) convective and conductive heat transfer rates (represented by *R*) and (ii) the difference in temperature between the cambium and the fire. Results from our externally applied heat experiment support the established idea that BT is the most important bark trait in reducing heat transfer rates (*R*) and an important trait in preventing fire-induced cambium damage (Uhl & Kauffman, 1990; Pinard & Huffman, 1997; Dickinson & Johnson, 2001; VanderWeide & Hartnett, 2011). In contrast, although *R* increased with increasing BMC, this relationship was weak and only marginally significant.

Whereas BT and, to a lesser extent, BMC influenced *R*, the presence of water in the bark reduced the differential in temperature between the cambium and the fire. The presence of water in the bark constrained bark temperatures to an asymptote at 100 °C, even when the temperature of the air adjacent to the outer bark was several times higher. This result suggests that theoretical models of fire-induced cambial damage that do not account for latent heat of vaporization (e.g. Mantgem & Schwartz, 2003) may overestimate the difference in temperature between the fire and the cambium and, in turn, underestimate the time before fire-induced cambial damage occurs. The importance of these results, however, will depend on the energy required for complete evaporation of bark moisture during a fire. In our bole-heating experiment, cambium temperatures never exceeded 100 °C, suggesting that bark water evaporation may indeed require substantial amounts of energy for that process to occur. It is still unclear, however, if bark water supplies would be depleted more rapidly through a natural fire, with a larger area of fire–bark contact. These relationships should be further evaluated with tree species from other ecosystems and over a wider range of fire temperatures and residence time, given that bark structural and physiological properties that influence latent heat of evaporation may be species specific. This is an important area of research that remains poorly understood.

Bark correlates with tree mortality

Although BT appears to be the most important tree trait for preventing fire-induced cambial damage, its importance in preventing fire-induced tree mortality is less well known, especially for tropical forests. To the best of our knowledge, the only study that has related BT and postfire mortality of Amazonian forest trees is that of Barlow *et al.* (2003a), who found that average bark thickness was greater in a once-burned than un-burned forest near Santarem 3 years following the 1998 fires. Based on these results, the authors suggested that the probability of tree survival increases with BT. We provide a comprehensive mechanistic analysis to show that $\hat{R}$ (and hence BT) is a good predictor of the likelihood of fire survival. Trees with bark $\geq$ 17 and 23 mm were fire-resistant (i.e. >75% probability of surviving) for low-to-medium (char height ranging between 34 and 50 cm) and medium-to-high severity (char height ranging between 50 and 180 cm) fires, respectively. Thus, we predict that trees representing only 6% of the basal area of this transitional forest are resistant to medium-to-high severity fires (Fig. 8). In contrast, trees with BT $\leq$ 5.0 mm were fire-sensitive (<25% probability of survivorship) in all fire regimes tested, comprising 17%

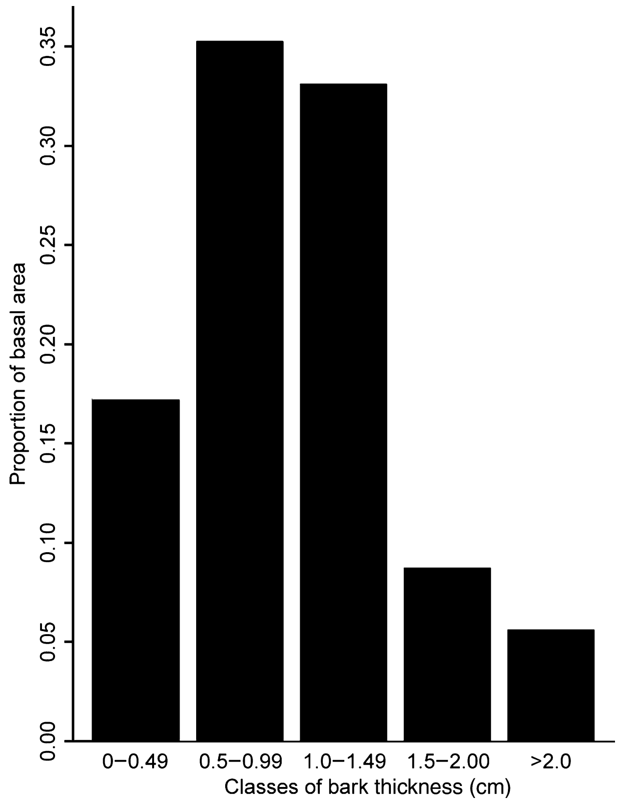

Fig. 8 The proportion of forest basal area occurring in each of five bark-thickness classes at Tanguro, Mato Grosso.

of the total basal area. The thresholds of fire resistance identified in this study are in the same range as that suggested by Pinard & Huffman (1997), who found that trees with BT $\geq$ 18 mm exhibited cambium peak temperatures lower than 60 °C during simulated fires, but these authors did not monitor subsequent mortality. As data on bark thickness become available for other forests of the Amazon, their fire vulnerability could be assessed using a similar approach to that used in this study.

Tree size, wood density and tree mortality

Despite the generally strong relationship between tree mortality and BT, we observed only a weak relationship between tree mortality and cambium insulation for trees charred once in plot B2. Furthermore, two common thin-barked species (*Aspidosperma excelsum* and *Sloanea eischleri*) generally survived even when charred (Balch *et al*., 2011). These findings indicate that fire-induced tree mortality can also be modulated by plant traits other than cambium insulation. First, high wood density is associated with the capacity to compartmentalize wood decay (Romero & Bolker, 2008), which influences the likelihood of mortality. Wood density had a strong effect on postfire survival for some treatments. Increasing wood density by 0.8 g cm^{-3} predicts an increase in the probability of survivorship of 15% (from 48% to 63%) and 13% (48% to 61%) for trees charred once in plot B5 and noncharred trees in the burned plots, respectively. (An increase in one unit of wood density in the control increased the probability of survivorship by only 5%.). Thus, wood density is an important plant trait for predicting drought (Phillips *et al.*, 2009) and fire-induced tree mortality.

For both charred and uncharred trees in the burned plots, mortality decreased with increasing dbh. Whereas this relationship could result solely from the strong and positive relationship between BT and tree size, alternate (or concurrent) explanations are that large trees are less likely to be killed by other falling trees and that the likelihood of the entire circumference being exposed to cambium-killing temperatures decreases with bole size (Gutsell & Johnson, 1996). Although we could not fully isolate the individual effects of dbh and BT on mortality, small individuals were more likely to die in the burned than in the control plots even when there was no bark charring, suggesting that tree diameter (perhaps independently from BT) matters for surviving indirect fire-related effects (e.g. tree and branch fall). Tree height also led to decreases in fire-induced mortality, probably because during intense fires tall trees suffer less crown damage, but also because tree height is correlated with stem diameter and BT. While the presence of buttresses may increase the probability in mortality (Barlow *et al*., 2003a), we found that only 0.5% of the sampled trees had buttresses at this study site.

Forest resistance to fire

The minor effect of the 2004 fires alone on tree mortality (i.e. in the absence of subsequent fires) indicates that this forest is relatively resistant to nonrecurrent, low-intensity fires [as measured by fire-induced tree mortality of individuals $\geq$10 cm dbh; see Balch *et al.* (2011) for a discussion about smaller trees]. This resistance may result from long-term tree adaptations to cope with fire in the region. Although we are unaware of formal estimates of the fire return interval for transitional forests of Mato Grosso, even primary forests in this region are flammable during most dry seasons due to elevated vapor pressure deficits (Blate, 2005; Balch *et al*., 2008). Furthermore, given the presence of indigenous groups in the region who make use of fire as an ecosystem management tool (e.g. Heckenberger *et al*., 2003), these forests have been exposed to human-associated fire ignition for millennia. It is nevertheless apparent that during the experiment this tropical forest was severely altered, with substantially higher mortality in the burned plots than in the control.

The highest mortality occurred for trees with thin bark, low wood density, and small diameter that were located close to the forest edge and exposed to the higher intensity fires in 2007. However, it is still unclear whether this forest became more fire-resistant over time (because fire-sensitive trees were killed and surviving trees were released from competition) or became more fire-sensitive over time (because fire-wounded trees are more vulnerable to recurrent fires). Despite selection for fire-resistant individuals over time, mortality is expected to increase with recurrent fires. In this study, for example, tree death was substantially higher in the treatment B2 compared to the other treatments after the 2007 fires. As a result, surface fuel loads are expected to increase and canopy cover to decrease (Ray *et al.,* 2005), creating a system that is more flammable and prone to high-severity fires.

Predicted decreases in rainfall over portions of the tropics may cause extensive transformations in forest structure and functioning in the next 50 years, particularly in the eastern Amazon (Cox *et al*., 2000; Malhi *et al*., 2009). Synergistic effects of recurrent fires, forest degradation and forest fragmentation could certainly drive this process much more rapidly (Nepstad *et al*., 2008). In predicting the rate of forest loss due to recurrent fires, plant traits in addition to cambial insulation play important roles in determining fire-related death. The evidence that fire-related mortality occurs even when tree boles do not exhibit physical charring indicates that fires influence several processes at the stand level as previously shown for temperate forests (Agee, 1993). Examples of these processes include proximate fire-induced branch or tree fall, fire damage to roots or leaves, or various indirect processes triggered by fire (e.g. disease and drought-related death). These findings reinforce the notion that the fire vulnerability of tropical forest is related to plant traits that influence fire-induced mortality directly and indirectly. Knowledge of the relationship between mortality and other plants (presence of buttress, bark fissures, etc.) could further improve our ability to predict the fire vulnerability of tropical forests.

Conclusion

We draw four main conclusions from this study. First, mechanistic models of fire-induced cambial damage should consider not only variables that influence thermal conductivity (e.g. bark thickness), but also factors that influence the differential in temperature between the cambium and the fire (i.e. latent heat of vaporization). Second, bark thickness was a strong predictor of fire-induced tree mortality alone, but assessments of Amazonian forest vulnerability to fire would be improved by considering other plant traits, given that fire-induced tree mortality significantly decreased as a function of increasing tree diameter, height and wood density. Third, mortality censuses conducted in the year following a given fire captured most of the fire-induced tree mortality for this transitional forest, whereas in other tropical forests high mortality rates were detected for up to 3 (Barlow *et al*., 2003b) and 10 years postfire (Baker *et al*., 2008). Fourth, this transitional forest showed some resistance to a single surface fire during a year of average weather conditions but suffered high mortality rates when burned during a dry, hot year, especially when there was enough time for fuel accumulation and among individuals with thin bark, low wood density, and small diameter that were growing near the forest edge. This new understanding about forest vulnerability to fire in the southern Amazon should improve assessments of forest dieback.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Equations for heat transfer rates.
Appendix S2. Parameter estimates for Model I.
Appendix S3. Weather conditions and flame heights.
Appendix S4. Probability of fire-induced tree mortality as a function of tree size and wood density.

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