The Susceptibility of Southeastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment

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The interaction between droughts and land-use fires threaten the carbon stocks, climate regulatory functions, and biodiversity of Amazon forests, particularly in the southeast, where deforestation and land-use ignitions are high. Repeated, severe, or combined fires and droughts result in tropical forest degradation via nonlinear dynamics and may lead to an alternate vegetation state. Here, we discuss the major insights from the longest (more than 10 years) and largest (150-hectare) experimental burn in Amazon forests. Despite initial forest resistance to low-intensity fires, repeated fire during drought killed the majority of trees, reduced canopy cover by half, and favored invasive grasses—but the persistence of this novel vegetation state is unknown. Forest edges, where drying, fire intensity and grass invasion are greatest, were most vulnerable. Crucial to advancing fire ecology in tropical forests, we need to scale these results to understand how flammability and resilience postfire varies across Amazon forest types.

Keywords: deforestation, fire ecology, prescribed fire, transitional Amazon forests, tropical forest degradation

Tropical forest fires threaten carbon stores, biodiversity, and human livelihoods and well-being. However, understanding the drivers and consequences of altered and novel fire regimes in tropical forest systems is a nascent science (Goldammer 1990, Nepstad et al. 1999, 2001, Cochrane 2003, 2009). In 1985, one of the first reconstructions of historical Amazon forest fires, conducted using charcoal records, suggested that Amazon fires happened every several centuries (Sanford et al. 1985). Recent fire frequencies in standing forests (Alencar et al. 2011, Morton et al. 2013), however, substantially exceed these historical patterns (Bush et al. 2008). Global images of our flammable planet (Roy et al. 2008) illustrate the marked bands of fire in the tropical forest biome that were unimaginable only decades ago—in southeast Asia, central Africa, and the Amazon. In a short time span, tropical fire science has gone from first documenting fire in humid tropical forests to understanding modern fire as an important and unprecedented agent of change. Through deforestation fires in the tropics, intentional burning by people has contributed nearly 20% of greenhouse-gas emissions since preindustrial times (Bowman et al. 2009).

In closed-canopy tropical forests, three general mechanisms drive broad-scale patterns of fire activity. First, ignitions are associated predominantly with deforestation and land management in tropical frontier zones. Natural lightning ignitions are rare, despite high lightning frequency (Christian et al. 2003). Second, fuel loads are expected to be substantial because of high biomass and productivity. At the high end of net primary production (NPP) and precipitation (PPT), the world's tropical forests are predicted to be fuel-abundant but climate-restricted fire systems (Krawchuk et al. 2009). Third, closed-canopy tropical forests are flammable only during a seasonal climate window, which is often exploited to initiate intentional fires to burn felled trees, manage pasture, or renew old fields. An exploration of pantropical drivers of fire suggests that active fires and burned areas are highest where intermediate levels of net primary production and precipitation occur (NPP, 500–1000 grams of carbon per square meter per year; PPT, 1000–2000 meters [m] per year, van der Werf et al. 2008). Across South America, including different biomes and land uses, annual sums of active fire detections (predominantly from land use) are associated with decreased precipitation (Aragão et al. 2008) and longer dry season length—conditions that can be predicted on the basis of sea surface temperature anomalies (Chen et al. 2011). Overall, the expectation is that dry season length limits fires in wetter systems, whereas a lack of

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fuels limit fires in drier ecosystems—where these two varying constraints dominate along the Amazon's northwest–southeast seasonal gradient is still unknown.

Intentional human uses of fire in the Amazon include diverse applications, such as deforestation fires to remove unwanted biomass, pasture fires to maintain forage grasses, and slash-and-burn agriculture (Schroeder et al. 2009). Moreover, the socioeconomic drivers that encourage fire use vary substantially among these different types of burning practices (Nepstad et al. 1999). In addition, accidental fires often escape into adjacent, intact or degraded forests (Balch et al. 2010). These forest understory wildfires can carry for weeks or months and burn extensive areas, particularly during dry years. In the drought of 1997–1998, for example, understory wildfires burned nearly 40,000 square kilometers (km^2; Alencar et al. 2006). From 1999 to 2010, more than 85,000 km^2 burned in the southern Amazon alone (Morton et al. 2013). In dry years, estimates of Amazon forests degraded by fire can exceed Brazil's annual deforestation estimates (INPE 2015) and can potentially reverse the carbon sink observed in intact Amazon forests (Davidson et al. 2012, Balch 2014, Gatti et al. 2014).

Observational studies have linked fire intensity directly to Amazon tree mortality, either through proxy char heights or heating of trunk boles (Uhl and Kauffman 1990, Barlow et al. 2003, Brando et al. 2012). Postfire mortality ranges from 36% to 64% for central Amazonian forests (dead stems divided by total live and dead stems at least 10 centimeter [cm] in diameter, for a review of field studies, see Barlow and Peres 2006), compared with 8% to 23% in forests located at the edge of the Amazon basin—for example, in Bolivia and the Brazilian states of Roraima and Mato Grosso (Pinard et al. 1999, Ivanauskas et al. 2003, Balch et al. 2011). South of this transitional forest edge, in the Brazilian savanna (or *cerrado*), postfire woody stem mortality declines to 5% to 19% (Hoffmann and Moreira 2002). The mechanisms that drive this variation in observed fire-related mortality across the Amazon forest and cerrado transition still remain unclear but likely reflect a combination of differences in fire regime (frequency and intensity) and plant sensitivity to fire.

An experimental burn in the southeast Amazon

In order to explore outstanding questions about the drivers of Amazon forest flammability and vulnerability, controlled experiments are essential. Experimental burns in Amazon forest systems (Kennard and Gholz 2001, Ray et al. 2005, Balch et al. 2008) are rare because they are difficult to conduct because of the complex permitting process and substantial logistics. Here, we discuss the insights from a decade-long burn experiment (150 hectares [ha]) in a southeast Amazon forest, where we tested the effects of an annual burn (B6, burned six times in 7 years) and triennial burn (B3, burned three times in 7 years), compared to an unburned control in 50-ha plots (figures 1 and 2a). The two fire regimes, an annual and triannual burn conducted near the end of the dry season, were designed to mimic the high fire frequency that can occur when fires associated with deforestation and land management practices escape into adjacent forests. These wildfires are generally slow-moving, low-intensity surface fires that move through the forest understory.

In 2004, the experimental forest block was established adjacent to a soybean field (formerly cattle pasture) on a privately owned farm just south of Querência, Mato Grosso, in the southeastern part of the Amazon basin (13 degrees, 4 minutes south; 52 degrees, 23 minutes west; figure 1). Intensive measurements before, during, and after the fire captured the fuel and microclimate drivers of fire behavior. Responses to fire in terms of tree mortality, forest structure, plant diversity, and early regeneration patterns were also measured (for details, see supplemental appendix S1). This forest system is at the moisture limit for Amazon closed-canopy forests (1770 millimeters [mm] per year from 2005 to 2011), with an intense dry season from May to September when monthly rainfall is typically less than 10 mm (Rocha et al. 2013). This forest is closed canopy (its leaf area index [LAI], is approximately 5 square meters of leaf area per square meter of ground area [m^2 per m^2]) but lower in stature (with a height of approximately 20 m), biomass (approximately 166 megagrams [Mg] per ha), and diversity (approximately 100 tree species) than more northern Amazon forests (Balch et al. 2008). This site lies at the transition between the cerrado and the more humid northern forests, is concurrent with an expanding agricultural frontier, and is highly threatened with conversion. Less than 25% of this transitional forest's original extent (400,000 km^2) is expected to remain by 2050 (Soares-Filho et al. 2006).

Over the course of the experiment, we witnessed three sequential phases: initial forest resistance to fire (indicated by low tree mortality in the burned plots, 0–3 years), subsequent forest fragility due to an extreme drought and fire event (illustrated by an abrupt increase in tree mortality in year 4), and postfire arrested recovery due to grass invasion along forest edges (after year 5). The most important results gained from this experiment are that (a) complex interactions between fuels and climate drive fire extent and intensity, (b) this transitional forest tolerates disturbance initially but not repeated or extreme coupled disturbances, (c) different fire frequencies elicit differing forest responses, (d) a diversity of plant species leads to high variability in fire-induced mortality rates, and (e) a transition to an alternate vegetation type dominated by grasses can occur along degraded forest edges following repeated burning. Each of these findings is discussed in detail below. Overall, our results provide insights into what may drive southeast Amazon forest flammability and vulnerability. The former refers to the likelihood that fire will spread in the forest understory, and the latter refers to the likelihood of tree death in response to fire damage.

Fuel and climate interactions control fire extent and intensity in seasonal tropical forests

In the southeastern Amazon, the length and severity of the annual dry season make this region highly vulnerable to

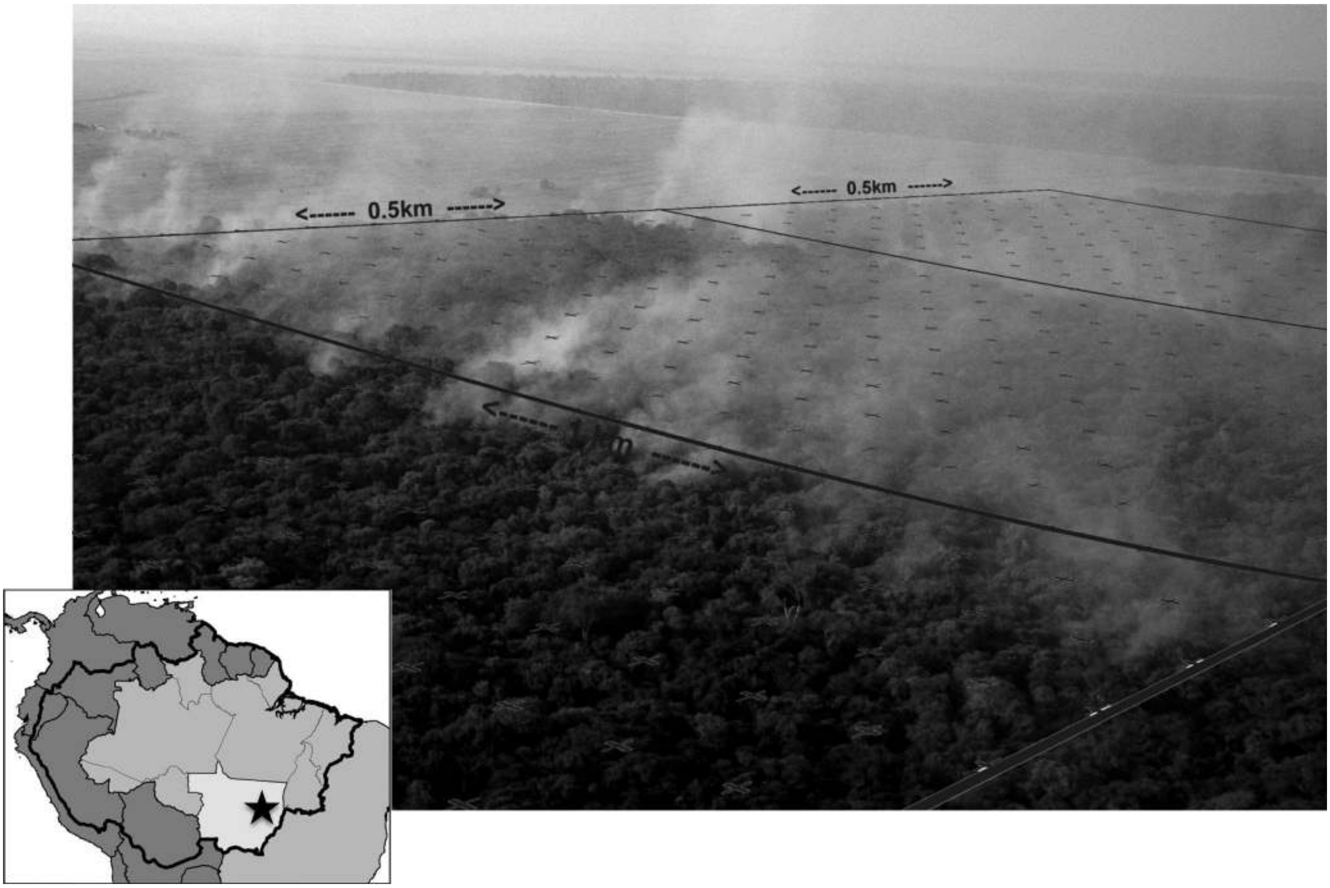

Figure 1. Aerial view of smoke from initial burn in two 50-hectare plots (the crosses indicate the sampling network); the inset shows the field site location in Mato Grosso state, in the Amazon Basin. Abbreviation: km, kilometers. Photograph: Paul Lefebvre.

fire, even in years of average rainfall. For example, the litter moisture content (LMC) and vapor pressure deficit (VPD, a measure of air dryness) of these forests are respectively well below and above (Balch et al. 2008) the thresholds defined for fire spread in Amazon forests (a VPD of more than 0.75 kilopascals [kPa] and an LMC of less than 23%; Ray et al. 2005). We therefore expected that climate would be the predominant driver of fire in transitional forests, rather than fuels. However, we observed that fuel quantity and availability played an important role in driving fire behavior during experimental burns. After two experimental burns, we demonstrated fuel limitation for the first time in tropical closed-canopy forests (Balch et al. 2008), suggesting that there may be a shift from climate limitation to fuel limitation on fire in disturbed southeast Amazon forests. Moreover, fine fuels (leaf litter and small woody fuels) played a strong role in determining fire spread and intensity. After two burns, experimentally doubling the amount of fine fuels quadrupled the area burned and doubled flame heights (one metric ton of leaf litter was collected outside the experimental area and distributed across nine subplots; Balch et al. 2008). Documenting this fuel limitation pointed to the importance of the time interval between disturbance events in determining the intensity of future fires. This result suggests that the return interval between fires must be long enough for fuels to buildup if these burns are to result in intense wildfires.

The most intense fires were observed during the 2007 drought, at the edge of the plot that burned every 3 years (i.e., forest–cropland edge). Fire intensity (kilowatts [kW] per m), or the energy output at the fireline front, was estimated on the basis of the fuel consumed, the fire-spread rate, and the heat of combustion (Alexander 1982). At the forest edge (0–100 m), fire intensity in B3 was more than double that observed in the forest interior during the drought, 819 kW per m versus 319 kW per m. Fire intensity during the first burn (a nondrought year) was just a faction of this, ranging from 20 kW per m to 74 kW per m from the interior to the edge (Brando et al. 2014). The high fire intensity in B3 during the drought was, in part, explained by an increase in litter and small woody fuels that either accumulated between burns, or resulted from drought-induced litterfall and branchfall (Brando et al. 2014). Notably, fire intensity in B6 was lower than in B3 during the drought (142 and 220 kW per m at the interior and edge, respectively), which

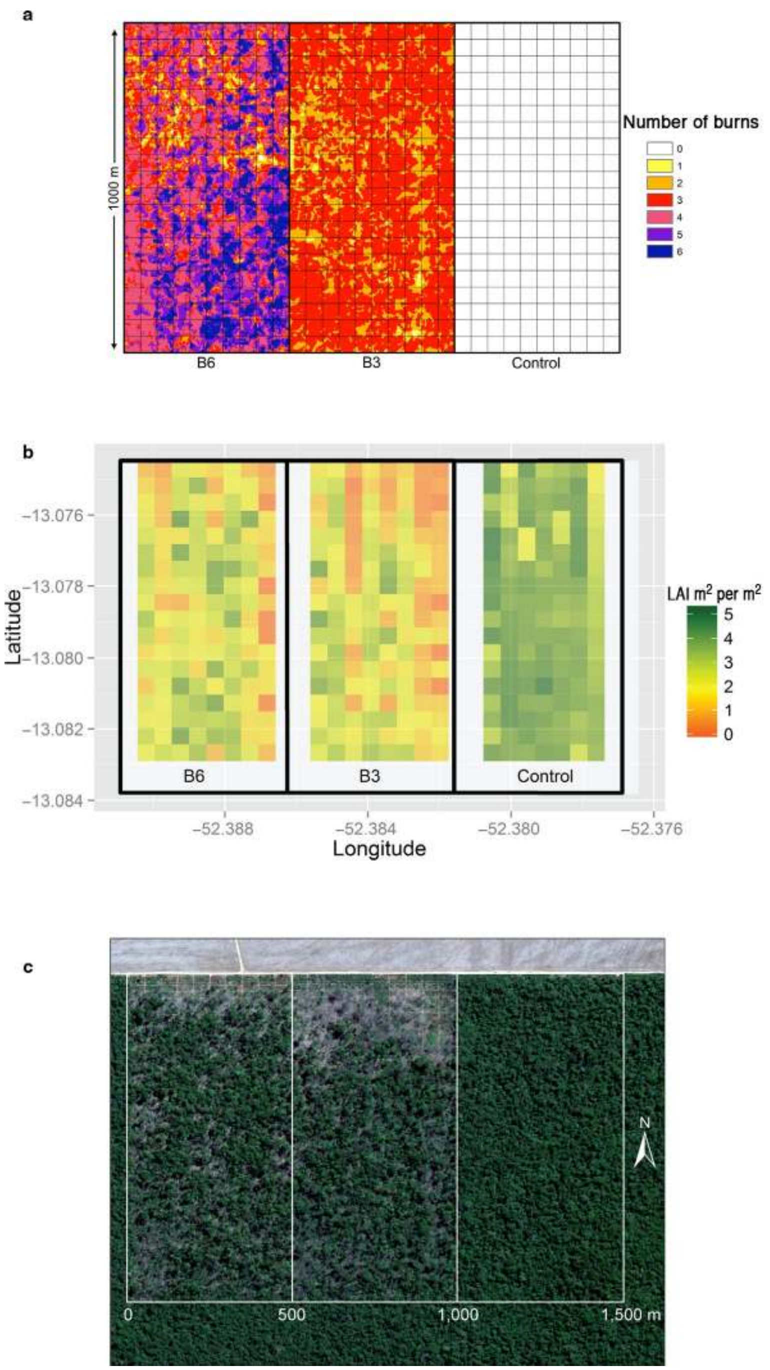

Figure 2. (a) Spatial heterogeneity in burn pattern across all six experimental fires (2004–2010), which was mapped in the month postfire on a 5 × 5–meter [m] scale on the basis of litter combustion and charred ground. Despite even application of firelines (10-km per plot per experimental burn) unburned islands remained within burned plots (light areas). Darker colored shading indicates areas within the plots that burned multiple times, because not every part of the plot burned equally during each fire treatment. From left to right the plots are B6 (burned in 2004, 2005, 2006, 2007, 2009, and 2010), B3 (burned in 2004, 2007, and 2010), and the control (unburned). (b) Canopy openness (the leaf area index [LAI], in square meters of leaf area per square meter [m^2 per m^2] of ground area) in 2012 across the plots. (c) Satellite image (2-m resolution) of the experimental forests in 2011 showing substantial loss of canopy cover along the burned edges. Satellite image: © 2011, DigitalGlobe; NextView License.

is because of both reduced litterfall and the continual reduction of fuels from the high frequency fire regime. These results point to the importance of accumulated fine fuels driving very intense wildfires during drought.

However, the response of fire to the interaction between fuels and patterns in the preceding longer-lead climate variables (several months to years prior), short-lead (several weeks prior), and immediate microclimate conditions (in the days or hours prior) during the burns are complex (figure 3). Key to understanding these dynamics is teasing out what controls fuel mass and what controls fuel moisture. Under the dry and hot conditions that occur during a drought, longer-lead climate variables (i.e., low soil moisture availability) first induce leaf shedding in order to reduce transpiration (Nepstad et al. 2002), making fine fuels the first fuel size class to increase. Furthermore, leaf shedding and tree mortality related to drought or prior disturbance decreases canopy cover, which increases understory dryness. Short-lead microclimate variables (i.e., VPD) then desiccate fuels in the days or hours prior to ignition, making more of the fuel bed available to burn and making ignition more likely. For example, VPD during the drought of 2007 was substantially higher in B3 (95% bootstrap confidence intervals [CI] = 3.2–3.6 kPa) and B6 (95% CI = 3.7–4.0 kPa) than in other years of the experiment (95% CI = 2.6–2.7 kPa; Brando et al. 2014). Under hot, dry conditions, fire spread rates and intensity increase as fires move quickly through dry or quickly drying fuels. In summary, a preceding disturbance (fire or drought) will increase fuel loads through leaf shedding and mortality, whereas very dry short-lead microclimate conditions will make more of the fuel bed available to burn.

One of the most surprising results we observed during our experimental fires was the nighttime continuation of firelines in the triennially burned plot during the severe drought in 2007. In all previous nondrought years, we witnessed that fires self-extinguished at night across burned plots because of

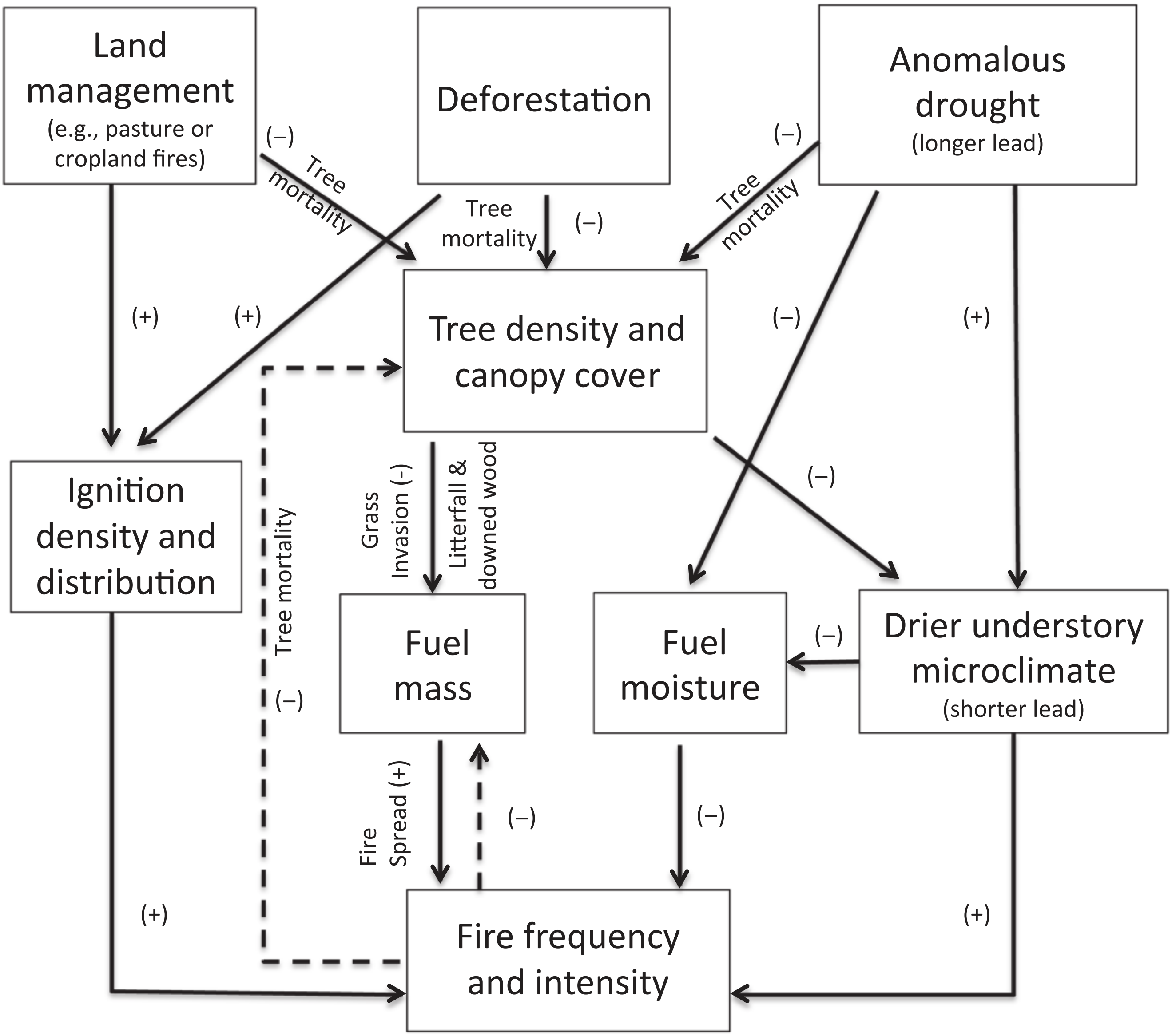

Figure 3. Major ignition, fuel, and climate drivers of understory forest flammability in the Amazon. Boxes indicate states, arrows indicate processes, and dashed lines indicate important system feedbacks. Positive and negative signs indicate the direction of the relationship (e.g., a drier understory microclimate will decrease fuel moisture).

increased air moisture. During the drought, we observed 145 m of active fireline in B3 that carried through the night into the following morning (approximately 12 hours after an initial 500 m of fireline was set). As nighttime VPD was similar across years, this result suggests that daytime drying of fuels to less than 23% litter moisture content (a threshold for fire spread in Amazon forests; Ray et al. 2005) can carry fires through the expected nighttime barrier to fire spread (e.g., higher humidity levels and lower temperatures at night). This observation provides a potential mechanism to explain how widespread forest fires can occur in Amazon forests.

Seasonal tropical forest trees are resistant to initial low-intensity fires but not repeated high-intensity fires

Overall, we observed initial resistance of trees and lianas to fire-induced damage and death, particularly of individuals with diameter at breast height (dbh) of at least 10 cm. However, with combined drought and repeated fire, we observed one of the highest tree and liana mortality rates documented in Amazon forests. Moreover, smaller stems and trees growing at the forest edge were the most vulnerable. In order to understand these patterns, we describe the tree mortality response and major predictors during drought and nondrought years.

During the first 3 years of the experiment we documented low mortality rates in response to a single (in B3) and three low-intensity annual burns (in B6). After 3 years, mortality of trees and lianas at least 10 cm dbh in B3 (4.8% per year) and B6 (5.7% per year) significantly exceeded mortality in the control plot (3.1% per year). Although mortality rates in B3 and B6 for the first 3 years were 1.5 and 1.8 times greater than in the control plot, these mortality rates (4.8% and 5.7% per year) were substantially lower than those reported from more humid Amazonian forests, which ranged from 36% to 64% in the central Amazon (Barlow and Peres 2006). This result suggests that this seasonally dry forest may be more resistant to fire than wetter Amazon forests. Notably, we also found that respiration, biomass production and allocation were similar between the control and the B6 plot (only a 14% and 5% decline in NPP and autotrophic respiration, respectively, in B6; Rocha et al. 2013), suggesting that productivity and carbon cycling in these forests were not greatly affected by the annual burning regime.

Although larger stems were fairly resistant to the initial burns, stems less than 10 cm dbh were highly vulnerable to fire-induced mortality (Balch et al. 2011). This inverse relationship between tree size and sensitivity to fire is consistent with other tropical studies (Cochrane and Schulze 1999, Pinard et al. 1999, Barlow et al. 2003a, Slik and Eichhorn 2003, van Nieuwstadt and Sheil 2005). In contrast, drought-induced mortality tends to increase with tree size (Condit et al. 1995, Nepstad et al. 2007). This may provide a partial explanation as to why our observed nondrought year mortality rates in the burned plots were so much lower than other studies, most of which were capturing the severe mortality response after *both* drought and fire, which likely includes death of *both* large and small stems.

In contrast to the very low mortality rates measured during the first 3 years of burning, the fourth and second fire event (in B6 and B3, respectively) during the drought of 2007 resulted in high fire intensities (see above) and consequently very high mortality. Mortality at the forest interior in the year following the major 2007 drought was 39% (± 5%, se, standard error) in B3, and 23% (± 2% se) in B6, compared with 7% (± 1% se) in the control (for stems of at least 10 cm dbh; Brando et al. 2014). High fire intensity was likely the combined result of increased fuel loads (particularly of smaller fuel size classes) and extremely dry, hot weather (Brando et al. 2014).

The single most important predictor of heat transfer to the cambium was bark thickness (Brando et al. 2012), explaining why smaller stems and species with thinner bark are more vulnerable to fire damage and death in our experimental forest. The relationship between tree death and bark thickness is consistent with other Amazon fire studies (Uhl and Kauffman 1990, Pinard and Huffman 1997). However, one notable discovery from our study was the importance of bark water content in buffering the cambium from extremely high temperatures because of water's capacity to dissipate heat through vaporization (Brando et al. 2012). As drought also influences trunk water storage, and likely bark water content, this may represent an important additional factor that exacerbates or inhibits fire damage. Furthermore, tree diameter, height, and wood density were secondary, but also significant predictors of fire-induced tree mortality (Brando et al. 2012), suggesting that plant characteristics besides bark thickness are also important in limiting fire damage and associated tree mortality. For example, it has been shown in Bolivia that tree species with the ability to compartmentalize wounds after stem damage tend to have higher wood density (Romero and Bolker 2008), which we have shown to be an important trait influencing tree survival postfire.

There is a detectable decrease in tree mortality that follows the wet–dry gradient from central to southeastern Amazonia (Barlow and Peres 2006), perhaps suggesting that historical fire frequencies are higher and that therefore fire-related adaptations may have evolved in species closer to the savanna boundary (Hoffmann et al. 2012). Given the northwest–southeast wet–dry gradient (Sombroek 2001) and west–east increasing wood density gradient (Baker et al. 2004), we hypothesize that across the Amazon basin there is likely an accompanying flammability and fire vulnerability gradient. We expect that a longer fire season in the southeast will make the forests more flammable for greater periods of time, whereas western Amazon forests may be more vulnerable to fire damage given their lower wood density and likely reduced ability to close wounds postfire. Currently, several confounding factors make it difficult to compare observed mortality rates after wildfires across Amazon sites. These factors include varying climate conditions that influence fire intensities, data collected at different time intervals postfire, and the interpretation of data sets lacking appropriate controls. Furthermore, there are notable differences in how mortality is designated (e.g., stem death, which is the death of an individual stem (this study), or "topkill," which is death of all aboveground plant tissue, including sprouts), and how mortality is quantified (cumulative percent versus annualized mortality rates).

Different fire frequencies elicit differing forest responses

Generally, fire intensities and burned areas were greater with a triennial rather than annual fire return interval. We were able to document negative and positive feedbacks in the same forest, where fire can either decrease or increase the likelihood and intensity of future fire depending on the disturbance return interval. A negative fire feedback, in which frequent fire leads to less intense future experimental fires, occurred in B6 because frequent fires reduced litterfall rates overall and removed fine fuels faster than they were replaced or surpassed (Balch et al. 2008). A positive fire feedback occurred when the time interval between fire events allowed for higher fuel accumulation from previous fire disturbance or when concurrent drought increased available fuels—that then caused more intense fires (Brando et al. 2014).

These two experimental fire frequencies, a very high and moderate return interval, elicited different responses in tree mortality, canopy cover, and regeneration patterns. Initially, tree mortality after three annual burns in B6 was only 16% greater than in the plot that burned once in the same period (4.8% per year versus 5.7% per year for stems of at least 10 cm dbh), and mortality was mostly limited to trees less than 20 cm dbh (Balch et al. 2011). However, after the 2007 drought-influenced burns, tree mortality rates quadrupled in the B3 plot and doubled in B6, resulting from high mortality even in large size classes (Brando et al. 2014). A similar pattern was observed in LAI, where canopy cover was greater in B3 until it burned for a second time in 2007 (Brando et al. 2014); by 2012, the average LAI was 1.9 m^2 per m^2 (standard deviation [SD] = 1.0) in B3, 2.2 m^2 per m^2 (SD = 1.0) in B6, and 3.9 m^2 per m^2 (SD = 0.7) in the control (figure 2b). For the smallest size class (seedlings), fire intensity was not as important as frequency of burning. Increased mortality and decreased regeneration of seedlings led to a 63% and 85% reduction in stem density (less than 1 cm dbh) in B3 and B6, after two and five burns over 6 years, respectively (Balch et al. 2013). By 2010, seedling density was 7.3 (SD = 1.1), 4.0 (SD = 0.6) and 1.2 (SD = 0.3) per m^2 in the control, B3 and B6 plots, respectively. Primarily because of this decline in seedlings, the proportion of regeneration by sprouting increased two- and fourfold in B3 and B6, compared to the control (Balch et al. 2013). In summary, larger stems were most vulnerable to high-intensity fires, whereas smaller stems were vulnerable to any fire intensity, making repeated fires more important than the intensity of any individual fire.

Plant biodiversity translates to high species variability in response to fire

Given the diversity of plant species in Amazon forests, we expect that there will also be a diversity of responses to fire. Our experimental work demonstrates there is, in fact, high interspecific variation in fire-related mortality (Balch et al. 2011). There are a suite of plant traits that reduce fire damage (bark thickness, tree size, height, and wood density), and an additional suite that confer an advantage in postfire recovery (sprouting capacity, wound closure rates, and chemical compounds that prevent secondary damage from rot or insects). Understanding how plant traits vary across tropical forest species will shed light on resistance and vulnerability to fire. Bark thickness, the trait that most strongly controls heat transfer and therefore relates to reduction of fire damage, varies substantially across the most common tree species at our site, ranging from 0.5 cm to 3.7 cm (Brando et al. 2012). Furthermore, average tree diameter, canopy height, and wood density vary across species, which are also important predictors of fire-induced mortality (Brando et al. 2012). We observed high variability in fire-induced mortality across tree and liana species. Species-specific, annualized mortality rates varied between 0% to 26% per year in the plot that burned once, and 1% to 23% year per in the plot that burned three times in 3 years (Balch et al. 2011). Furthermore, regeneration capacity and mode (i.e., from seed or coppicing) after burns was also different across species; some plant species exhibited obligate seeding, whereas others predominantly reproduced vegetatively via sprouting (Balch et al. 2013).

To illustrate the different response to fire across species, we describe the bark thickness (from Brando et al. 2012) and regeneration mode (from Balch et al. 2013) of three different plant species with high, moderate, and low mortality rates (from Balch et al. 2011). After 3 years, *Protium guianense* (Burseraceae)—a thin barked, subcanopy tree (8 mm bark thickness for a 20-cm-dbh stem)—exhibited the highest fire-induced mortality rates of any species, which were 26% and 23% per year, in B3 and B6, respectively. After two and five burns in each plot, this species reproduced predominantly via seed; less than 10% of regenerating stems came from sprouts across the control and burned plots by 2010. A common canopy tree, *Ocotea guianensis* (Lauraceae), had moderate mortality rates 3 years after the experiment started (8% and 11% per year in B3 and B6), thin bark (9 mm for a 20-cm-dbh tree), and reproduced predominantly via sprouting (almost 70% of regenerating stems were from sprouts in B6). One of the lowest mortality rates was observed for *Pouteria ramiflora* (Sapotaceae), which after 3 years exhibited 2% and 3% per year mortality rates in the burned plots. This species—a canopy emergent that is also found in the cerrado—has thick bark (18 mm for a 20-cm-dbh tree) and appears to reproduce predominantly via seed (less than 10% of regenerating stems came from sprouts). As these examples demonstrate, there are important differences in resistance (e.g., bark thickness) and regenerative capacities across species, which may result in changes in community composition as fires become more frequent.

Not only was there variability in the response to fire among the native tree species, but pasture grasses present in the burned plots also differed in their response (Silvério et al. 2013). Grasses invaded up to 250 m into the forest in both fire regimes 6 years after the experiment started, but the patterns and species composition differed between the burned plots (Silvério et al. 2013). Up to 100 m from the edge of both burned plots grasses dominated at least 50% of the area (Silvério et al. 2013). Notably, intermediate disturbance (B3) led to a community of grasses in which no grass species was dominant, whereas annual burning (B6) led to dominance by one species, *Aristida longifolia*—the only shade-tolerant C3 grass present in our inventory (Silvério et al. 2013). This suggests that different fire frequencies also select for different grass communities in this anthropogenic landscape.

Degraded forest edges are most vulnerable to fire-induced forest dieback

Forest edges are the degraded forests adjacent to different land uses—how they were created, whether plowed, burned, or cut, will leave different legacies of fuels and alterations to canopy structure that influence fire behavior. Generally, at tropical forest edges dry climatic conditions are exacerbated (Laurance et al. 2002), fuel levels are higher, fire sources are

Figure 4. Flame heights fueled by leaf litter at the forest interior during the initial experimental burns (left), and at the end of the experiment at the forest edge with primarily grass-fueled fires (right). Photographs: Jennifer K. Balch.

prevalent (Cochrane and Laurance 2002), and propagules of native savanna or invasive grass species are present (Veldman et al. 2009, Veldman and Putz 2011)—setting the stage for initiation of a novel grass-fire cycle (D'Antonio and Vitousek 1992). Overall, we found that canopy cover was lower, microclimate drier, and consequently fires were more intense (i.e., higher flame heights) at the forest edge (0–100 m) than at the forest interior (100–1000 m; figures 4 and 5). This led to subsequently higher tree mortality and greater likelihood of grass invasion at the forest edge (figures 5 and 2c). However, note an unexpected effect of leaf cutter ants (*Atta* spp) on fire behavior during the first burns (box 1). With several repeated burns, we also documented that edge-like conditions (drier microclimate, higher mortality levels, and pioneer or grass species) were observed further and further into the forest interior as the experiment progressed.

The pattern of grass invasion also yields some important insights. Initially, we observed that the C3 native grass, *Aristida longifolia,* invaded under a degraded, but still shady understory and then facilitated future fire and further grass invasion. This grass was also the only grass present in the control plot border (up to 5 m into the forest). C4 grass expansion and dominance occurred after repeated fires as cumulative tree mortality increased and canopy cover decreased (Silvério et al. 2013). A novel grassland state was initiated by frequent fire and dominated the forest edge up to 100 m into the forest after 8 years (Silvério et al. 2013). This new state consisted of native cerrado and exotic grass species associated with pastures. Canopy cover (indicated by LAI) was a strong predictor of grass establishment after experimental seed sowing (Silvério et al. 2013). Moreover, there is some evidence that nitrogen may be limiting to forest species' regeneration under high frequency burning regimes: in annually burned sub-plots where herbivores were excluded, tree and liana recruitment actually increased by 14% with nitrogen additions, and recruit diversity increased up to 50% when nitrogen was added (Massad et al. 2013). An open canopy and lower nitrogen availability may favor grasses and therefore yield establishment of this novel grass-fire cycle.

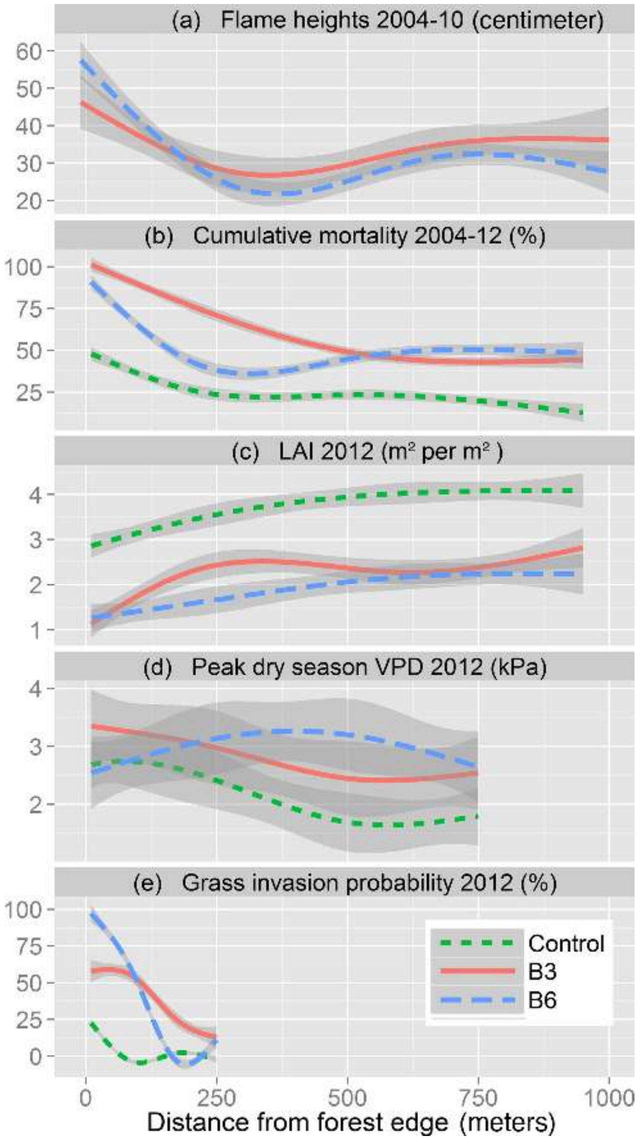

Figure 5. Fire intensity (approximated by flame heights), tree mortality, canopy cover, understory microclimate, and grass invasion likelihood across experimental plots as a function of distance from the forest edge (0 meters [m] is adjacent to agriculture; 1000 meters is the forest interior). (a) The average flame heights (in centimeters) across all experimental burns (2004–2010; Brando et al. 2014). (b) The cumulative tree and liana mortality (2004–2012; Balch et al. 2011 Brando et al. 2014). (c) The leaf area index (square meters of leaf area per square meter of ground area) in 2012. (d) The vapor pressure deficit in 2012 between 12:00–16:00, during peak dry season (July–September). (e) The probability of grass invasion in 2012 (grasses did not occur beyond 250 meters; Silvério et al. 2013).

High frequency fires, propagule availability, canopy openness, and perhaps nitrogen limitation facilitate grass establishment, which has substantial consequences for future flammability because grasses more than tripled fine fuel loads compared to forest litter (Silvério et al. 2013). Grass-dominated habitat only stores 16 Mg per ha of aboveground biomass, compared to the unburned control, which stores 166 Mg per ha (figure 6). Our results suggest that if ignitions are prevalent in the landscape, a novel grass-fire cycle may perpetuate this lower carbon state and prevent forest recovery (figure 3).

Conclusions

Overall, this experiment explored two fire regimes (an annual and triennial burn) in the southeast Amazon to determine what drives forest flammability and vulnerability (figure 2). Our results show that (a) complex interactions between fuels and climate drive fire spread, fire intensity, and area burned; (b) seasonal, closed-canopy Amazon forests can sustain initial fire disturbance but not repeated or coupled disturbances; (c) different fire regimes elicit differing forest responses; (d) postfire response varies with the diversity of plant species; and (e) a transition from forest to invasive grassland is already occurring along fire-degraded Amazon forest edges (box 2).

During a strong dry season, drivers of fire behavior are principally fuel mass and fuel moisture, and climate influences more the former whereas short-term weather influences more the latter. There are important interactions between fuel variables and microclimate conditions (figure 3) that experimental burns and highly detailed observations can tease apart. We documented that high-intensity fires can result from two pathways: (1) drought-induced fuels and a climate window to burn and (2) frequent, low-intensity fires that initiate a grass-fire cycle and make high fine fuel loads available to future intense fires (figure 4), which is not drought dependent. Our long-term research has therefore shown that documenting the rate of fuel inputs relative to fuel outputs is important to understanding what drives fire behavior in seasonally dry tropical forests under high frequency fire regimes.

Differing fire regimes elicited different forest responses, and this relates fundamentally to (a) decreasing fire intensity with extremely high fire frequency and (b) increasing vulnerability with decreasing tree stem size. For example, initial fires only killed stems less than 20 cm dbh, whereas extreme increases in mortality (including large stems) occurred during high intensity fires. Moreover, there was high variability in mortality across species, likely reflecting differences in traits that prevent fire damage (e.g., thick bark) or enable fast wound closure (e.g., higher wood density).

The future degradation of Amazon forests is likely to include a pathway mediated by fire dynamics at forest edges because of several combined factors (figure 5). First, grass propagules are present in nearby pastures. Second, fire ignitions are prevalent. Third, an annual dry season already exists to promote fires at forest edges, which may extend by a month because of deforestation-related declines in rainfall (Costa and Pires 2010). Moreover, over 8% of Mato Grosso's

Box 1. Tiny firefighters.

We observed an unexpected edge-fire interaction related to the presence of leaf-cutter ants in the genus *Atta* that prefer disturbed environments such as forest edges. These ants remove leaf litter and woody debris, which are potential fuels, in and around their nests and foraging trails—effectively creating a network of fire breaks. As a result, between 60%–90% of the unburned islands within burned plots (see spatial burn heterogeneity within experimental burn plots; figure 2) were within 30 m of ant nests, and burned area significantly increased with increasing distance to ant nests (Carvalho et al. 2012a). In addition, the number of ant nests declined with increasing distance from the forest edge, and, counter intuitively, burned area increased with increasing distance from the edge during the first few experimental burns (Carvalho et al. 2012a)—until grasses established and created a different fuel structure. Not only do these ants remove fuels, but plants that grow near their nests also benefit from higher nutrient availability, indicated by higher growth rates of a common tree species (*Amaioua guianensis*: Rubiaceae) near nests in the unburned forest (Saha et al. 2012). However, with an increase in leaf-cutter ant populations postfire, greater herbivory of seedlings and seed removal also occurred (Carvalho et al. 2012b). These findings at the forest edge provide new insights into fire ecology in Amazon environments and highlight the surprising importance of fine-scale phenomena in controlling larger-scale burn patterns, plant growth, and regeneration dynamics.

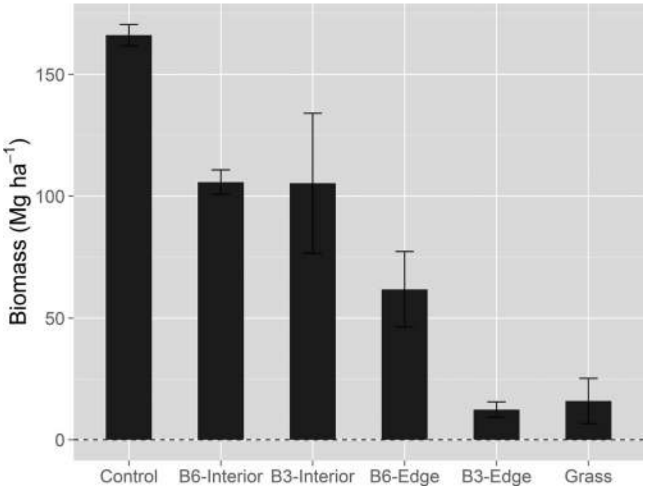

Figure 6. Aboveground biomass (in megagrams [Mg] per hectare [ha] Mg per ha) in the fire experiment in 2012 (trees at least 10 centimeters diameter at breast height and destructively sampled grass). The error bars represent the standard deviation. Estimates for woody biomass are given for forest edge (transects less than 200 meters [m]) and forest interior (transects 200–1000 meters). The control represents tree biomass for the entire unburned 50-ha plot. Grass biomass represents the mean for 14 samples of 1 square meters subplots, including Andropogon gayanus (*n *= 7) and Aristida longifolia (*n *= 7; see Silvério et al. 2013).

intact forests are currently within 100 m of an agricultural clearing (Brando et al. 2014). Fire-mediated degradation is already occurring along the lattice-like pattern of deforestation and land use, rather than as a gradual contraction of forests predicted by models of regional drying (Cox et al. 2004, Malhi et al. 2009). The relationship between edges and fire spread has been documented at large scales; for example, the amount of understory area that burned within 500 m of a deforestation event ranged from 25% to 46% during years with high deforestation rates (Morton et al. 2013).

Translating our experimental results to a basinwide perspective offers the following important insights. The decreasing dry-season length moving northwestward leads us to expect a different vulnerability to fire events—the climate window of opportunity for fire is generally shorter on an annual basis moving toward the northwest. Furthermore, not only does species diversity, and therefore trait variation, matter in determining overall forest response to increasing fire disturbance, but we also expect that the diversity of Amazon forest types (e.g., variation in canopy openness, canopy height, turnover rates, and wood density) will also translate to variation in resistance and vulnerability to fire damage and ensuing mortality.

The management implications are that fire-driven dieback will lead to a lower carbon state, where observed aboveground forest carbon stocks may be reduced by 90% with establishment of a degraded, novel grass state (figure 7). Managing forest fires in seasonally dry forests could be aided by using the nighttime barrier to fight fires, incorporation of firebreaks to prevent escaped fires, and protection of once- or twice-burned forests—which may lose their recovery potential after a third burn. Even though deforestation rates have declined by 80% since 2004 (INPE 2015), fire activity has not declined (Aragão and Shimabukuro 2010), suggesting that land-use practices are continuing to use fire as a tool (Balch et al. 2010). By 2050, under a warming climate and business-as-usual land-use scenarios, fire occurrence in Amazon forests may double (Silvestrini et al. 2011). Amazon fire could decrease, however, as extensive cattle pasture is replaced by more mechanized agriculture, which substantially reduces land management fires (Brando et al. 2013). Furthermore, because fire prevention is essential to protecting tropical forest carbon, REDD+ (the United Nations program Reduced Emissions from Deforestation and Degradation) may provide a mechanism to incorporate fire management into the costs of maintaining carbon in standing, intact

Box 2. Major findings from the experimental burn.

Rather than just dry, hot conditions driving fire in Amazon forests, interactions between fuels and climate are important.

Seasonal, closed-canopy Amazon forests can withstand initial fire disturbance, but not repeated or extreme concurrent disturbances.

Different fire frequencies (an annual and triennial burn) elicit nonlinear forest responses in plant mortality and ensuing changes in forest structure.

Postfire response varies with the diversity of plant species and therefore the diversity of plant traits the enable fire resistance or resilience.

A marked transition from forest to invasive grassland was observed at the forest edge under both fire frequencies in less than 10 years..

Figure 7. A nearby, intact forest adjacent to a pasture edge (top), and one of the experimental burned plots (B3) 10 years after the initial burn (bottom). Photographs: Jennifer K. Balch (top) and Paulo M. Brando (bottom).

Box 3. Outstanding research questions about the tolerance of Amazon forests to fire disturbance.

When and where does climate limitation on fire yield to fuel limitation along the Amazon's seasonality gradient?

How does fuel vary across Amazon forest types during drought and average precipitation years?

How do human ignitions vary by land use and annual or multiyear climate signals?

How does variability in Amazon tree traits within and across forest types relate to vulnerability to fire disturbance?

What are the fire frequency thresholds that limit forest tree regeneration and resprouting?

Which combinations of disturbance (e.g., fire, drought, wind, and insects) are the most lethal to trees?

What are the long-term consequences (more than 10 years) of increased fire frequency?

Does fire invoke a nitrogen or other nutrient limitation that affects the trajectory of post-fire recovery?
Will grasses persist or will forest species regenerate? Is fire necessary to perpetuate a novel grassland state?

forests (Nepstad et al. 2011, Barlow et al. 2012). An experimental network of sites is important to test major outstanding questions about what drives ecological thresholds to flammability and vulnerability across the Amazon basin (box 3). Coupled with remote sensing analyses, analysis of historical records, and modeling exercises, this experiment-based understanding will aid in refining predictions about the future of Amazon forests.

Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biv106/-/DC1*.

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