

Climate change and deforestation increase the vulnerability of Amazonian forests to post-fire grass invasion

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Abstract

Aim: We aimed to evaluate the vulnerability of the Amazon forest to post-fire grass invasion under present and future climate scenarios.

Location: Amazon Basin.

Time period: 1981–2017 and 2070–2099.

Major taxa studied: Plants.

Methods: We combined a fire–ecosystem model with remote sensing data and empirically-derived equations to evaluate the effects of a high-intensity fire (i.e., during an extreme drought) and logging in forest edges on tree canopy, and exotic grass cover under present and unmitigated climate change scenarios. We also contrasted simulated vegetation recovery time (as a function of climate variability) and current fire return intervals to identify areas in which fire–grass feedbacks could lock the system in a grass-dominated state.

Results: Under current climatic conditions, 14% of the Amazon was found to be vulnerable to post-fire grass invasion, with the south-eastern Amazon at the highest risk of invasion. We found that under unmitigated climate change, by the end of the century, 21% of the Amazon would be vulnerable to post-fire grass invasion. In 3% of the Amazon, fire return intervals are already shorter than the time required for grass exclusion by canopy recovery, implying a high risk of irreversible shifts to a fire-maintained degraded forest grassy state. The south-eastern region of the Amazon is currently at highest risk of irreversible degradation.

Main conclusions: Although resilience is evident in areas with low fire activity, increased fire frequency and intensity could push large Amazon forest areas towards a tipping point, causing transitions to states with low tree and high grass cover.

KEYWORDS

Amazon, climate change, grass–fire cycle, grass invasion, regime shifts, savanna–forest boundaries, tipping points

1 | INTRODUCTION

Tropical forests contain between one-half and two-thirds of the terrestrial global biodiversity and provide vital ecosystem services at

local, regional and global scales (Dixon et al., 1994; Foley et al., 2007; Marengo et al., 2018). However, these forests are undergoing widespread loss and fragmentation as a result of deforestation, climate change and fire (Esquivel-Muelbert et al., 2019; Hansen et al., 2013;

Silva et al., 2020). Changes in land cover impose the largest threat to tropical forests (Barlow et al., 2016), but remnant forest areas are also experiencing degradation, and tropical forests are especially sensitive to such changes, particularly fire (Barlow & Peres, 2008; Berenguer et al., 2021; Staver et al., 2019). Modelling (Van Nes et al., 2018), observational (Dantas et al., 2013, 2016; Hirota et al., 2011) and experimental (Silvério et al., 2013) studies suggest that a positive feedback between loss of canopy cover and fire could cause a shift from closed-canopy forest to a grass-dominated ecosystem state at the local scale upon the invasion of forests by grasses. In the Amazon, this process seems to be associated especially with high-intensity forest fires from a variety of land-management practices during exceptionally dry years, when fires can spread for hundreds of kilometres into the forest (Withey et al., 2018). However, the extent to which high-intensity fires can degrade large forest regions, such as the Amazon, is unclear. Although, structurally, these new grassy ecosystems can resemble savannas, they generally contain fewer species, and especially fewer (if any) endemic species, than ancient grassy ecosystems (Veldman et al., 2015; Veldman & Putz, 2011). Evidence suggests that the diversity typical of old-growth savannas can take centuries or even millennia to build up (Nerlekar & Veldman, 2020).

The probability of a forest-to-grassy ecosystem transition depends primarily on the ability of grasses, especially highly flammable invasive grass species, to colonize forested areas. Most of those grasses are shade intolerant, and studies suggest that, as long as dispersal or moisture is not limiting, these species are limited mostly by shade (Cardoso et al., 2018; Hoffmann et al., 2012; Silvério et al., 2013). Studies in both Africa and South America have identified a leaf area index (LAI) value of three as the critical canopy cover threshold below which shade-intolerant C_4 grasses can spread in the forest understorey (Cardoso et al., 2018; Hoffmann et al., 2012). Thus, any perturbation that reduces canopy cover below this level, such as fire or logging, creates suitable conditions for grass invasion and, possibly, the initiation of grass–fire feedback (Silvério et al., 2013). Grass invasion also depends on the ability of flammable grasses for dispersal to recently opened areas. The Amazon region has an ancient relationship with grasses, because these species have been present for millennia in the region (Kirschner & Hoorn, 2020). However, in upland forests, flammable grass abundance appears to be higher in degraded forests near pastures and roads (Macedo et al., 2012; Nepstad et al., 2008), because roads and vehicles are sources for invasive grass propagules into the forest interior over relatively long distances (Veldman & Putz, 2010, 2011). Although some short-term studies (<10 years) have found grass invasion up to 250 m from forest edges (Balch et al., 2015), it is unlikely that this reflects dispersal limitation alone, because evidence suggests that, over time, invasive grasses can be found up to 30 km from logging areas (Veldman & Putz, 2010).

Fire intensity is a fundamental aspect mediating the impacts of fires on forest canopy cover. Fire intensity determines tree mortality and biomass consumption in a fire event, and a single high-intensity fire can cause enormous damage to above-ground biomass in

tropical forests (Barlow et al., 2003; Brando et al., 2014). Fire intensity is largely controlled by climate, and its effects on litter fuel moisture and availability. By decreasing rainfall amounts and increasing temperatures (hence, increasing the availability of dry litter fuels), climate change is predicted to promote fires of higher intensities in some forest regions, as drought becomes more pronounced (e.g., the south-eastern portion of the Amazon Basin) (De Faria et al., 2017). This would amplify the effects of fire on canopy cover, potentially increasing the extent of forest areas subject to grass invasion. In addition to fire, logging within forest edges can also facilitate grass invasion. Evidence suggests that canopy cover can be reduced by 60% in areas within 3 km from a forest edge (Pereira et al., 2002; Wuyts et al., 2017). The combination of high-intensity fires and logging could substantially increase the extent of areas invaded by exotic grasses in the future.

Once grasses have invaded the forest understorey, both fire intensity and fire frequency might increase abruptly, because high cover of low-bulk-density grass fuels dramatically increases flammability (Hoffmann et al., 2011). To avoid being arrested in this 'fire trap' (Grady & Hoffman, 2012; Trauernicht et al., 2016), the forest must be sufficiently resilient; that is, it must recover canopy cover quickly enough to exclude shade-intolerant flammable grasses before the next fire (Hoffmann et al., 2012). Given that the growth rate of trees (at the regional scale) depends mainly on climate and moisture availability, the resilience of the forest is also dependent on how future climate will affect forest recovery rates in relationship to the length of fire intervals in different parts of the forest.

One forest region that might face the threat of shifting towards a grass-invaded system is the Amazon. This threat is driven, in part, by a recent sharp increase in fire frequency (from once every 500–1,000 years, before modern-day human colonization, to once every 5–10 years; Bush et al., 2008), owing to increasing sources of fire ignition, deforestation and climate change (Balch et al., 2015; Fearnside, 2013; Gutiérrez-Vélez et al., 2014). The prevailing view is that natural fires are very rare in the region and that the significant change in fire frequency is linked to the post-European colonization of the Americas, with climate playing a role in influencing the severity of these fires (Bush et al., 2008). As fire activity increases, the probability that a fire coincides with an extreme drought, producing high-intensity forest fires, also increases.

In this study, we combined remote sensing data, present climate and future projections, empirical equations and the ecosystem fire model CARLUC-Fire to simulate fire impacts on forest areas, the resulting vulnerability to grass invasion and the reversibility of this process. This model has already been used successfully to simulate fire behaviour in the Amazon (Brando et al., 2020; De Faria et al., 2017, 2021). We determined the vulnerability of the Amazon Basin to grass invasion by combining this model output (converted to post-fire canopy cover losses) with canopy cover losses attributable to logging and empirical equations relating forest canopy cover and the probability of grass invasion (from Silvério et al., 2013), in addition to exotic grass propagule dispersal limitation (using information on distance from roads). We also evaluated the reversibility of grass

invasion in relationship to present fire frequency by contrasting simulated vegetation recovery time (as a function of climate) and fire return intervals.

Using this framework, we addressed the following questions:

1. Are there large areas in the Amazon under threat of grass invasion and irreversible shifts to novel grass-dominated ecosystem states in response to fire?
2. Where in the Amazon are the most vulnerable areas found?
3. How will climate change and the expansion of the road network affect these patterns?

We hypothesized that the already drier climate and high logging rates in the south-eastern Amazon (Silva Junior et al., 2018) would result in the highest probability of grass invasion and ecosystem shifts in present conditions, especially near forest edges. Furthermore, this same region is predicted to experience increases in temperature and decreases in precipitation under climate change (Chen et al., 2011; De Faria et al., 2017; Phillips et al., 2009). Therefore, we hypothesized that grass invasion would greatly increase in the region under climate change, potentially undermining forest resilience to state shifts in some areas. We also hypothesized that projected expansions of the road network across the basin would contribute to grass invasion near to roads in the future.

2 | MATERIAL AND METHODS

2.1 | Study region

Our study focused on Amazonia *sensu stricto* in South America (Eva et al., 2005), which contains c. 5.5 million km² of tropical forest. Given that our main interest was in the effect of climate change and logging on forest remnant areas, we excluded deforested areas from the analyses. We also excluded wetland areas, because most of our assumptions and equations were derived from studies on upland Amazon forests, which have different patterns of structure and function compared with floodplain forests (Flores et al., 2017). Deforested areas were determined using deforestation maps from the annual Landsat-based Project for Monitoring Amazonian Deforestation (PRODES; INPE, 2017), and the wetland mask generated by Hess et al. (2015) was used to exclude floodplain forests.

2.2 | Summary of the analytical framework

To investigate forest resilience to post-fire grass invasion, under both current climate and unmitigated climate change, a framework combining remote sensing, fire-ecosystem modelling and empirically derived equations from a fire experiment study was developed. The methodological workflow used for this study is summarized in Figure 1.

2.2.1 | Model description

To simulate canopy cover losses in terms of LAI losses after a fire, we used the CARLUC-Fire model (De Faria et al., 2017). The model is a modified version of the carbon and land-use change dynamic carbon model, CARLUC (Hirsch et al., 2004). CARLUC is a process-based model of forest growth and the C cycle, driven by four monthly climatic variables: photosynthetically active radiation (PAR; in moles per square metre per month), vapour pressure deficit (VPD; in kilopascals), precipitation (in millimetres per month) and mean air temperature (in degrees Celsius), to estimate net primary productivity (NPP) and the relative changes in C-biomass stocks, in addition to litter, wood debris and humus accumulation (Hirsch et al., 2004). CARLUC-Fire is a modification of this model that combines the resulting litter biomass component with climatic conditions to simulate fire intensity (variable across the Amazon) under specified extreme drought conditions [i.e., a deficit of -40 mm in relationship to the mean maximum climatological water deficit (MCWD; defined below)], based on litter amount and moisture. Fire intensity (FI; in kilowatts per metre) measures the rate of energy released along the fire front and is strongly correlated with the above-ground impacts of fire.

The model was calibrated and evaluated for the southern Amazon using data from a large-scale fire experiment that prescribed experimental fires (from 2004 to 2010) in forest areas (Brando et al., 2014; De Faria et al., 2017). In the model, the intensity of a fire depends on the fire spread rate (FSR; in metres per minute) and the mass of fuel consumed by fire (*W*; in kilograms per square metre). Both FSR and *W* depend on litter moisture content (LMC; as a percentage), and *W* is also a function of load mass (Supporting Information Table S1; Figure S1). Fuel conditions and loads and, thus, fire intensity are influenced by climate, because the MCWD is set to -40 mm in relationship to the mean climatic condition of the grid cell, simulating drought conditions whose severity depends directly on climate. MCWD is defined as the annual cumulative difference between precipitation and mean regionwide evapotranspiration. We used a fixed value for evapotranspiration (100 mm/month) corresponding to the mean of the values observed in different seasons and locations in Amazon forests (Aragão et al., 2007; Zemp et al., 2017). In these conditions, fuel moisture declines with increasing temperature and VPD (Ray et al., 2005), while fuel amounts increase with water stress represented by MCWD (Supporting Information Equation S1).

The relationship between MCWD and changes in biomass (Phillips et al., 2009) was derived from the Amazon forest inventory network (RAINFOR). When the difference between MCWD and the time-series mean MCWD drops below -40 mm, leaf and branch shedding occurs as a linear function of MCWD, and part of the live carbon stocks is transferred to litter material. Increasing the fuel loads leads to increasing fire intensity. Given that fire intensity and damage to above-ground biomass are highly correlated in tropical forests (Brando et al., 2012, 2014), especially regarding fire-induced tree mortality (i.e., biomass turnover) in woody plants

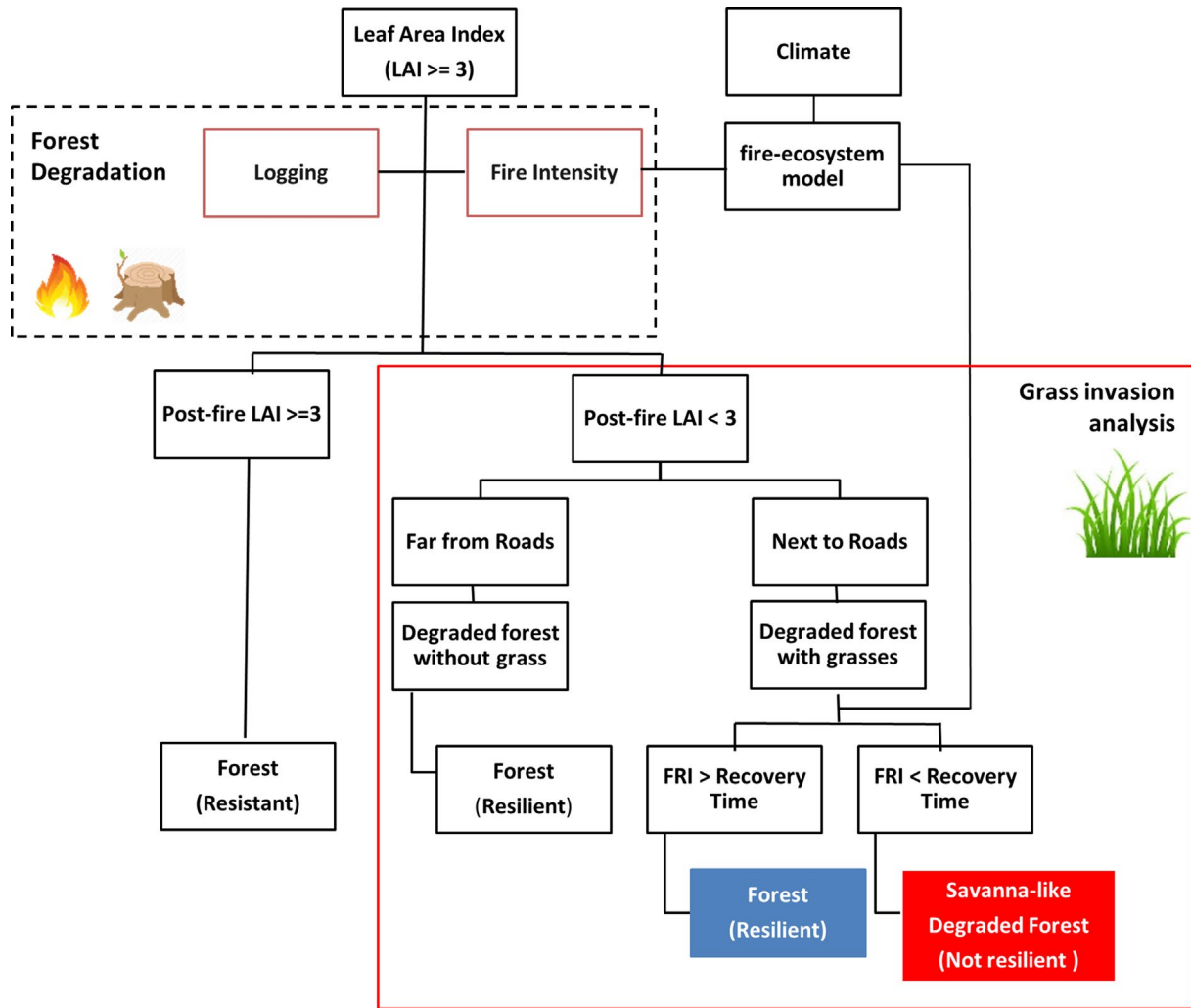


FIGURE 1 Diagram of the framework used in this study, combining remote sensing [MODIS LAI and fire return interval (FRI)] and the fire–ecosystem model CARLUC-Fire to map the risk of post-fire grass invasion across the Amazon. CARLUC-Fire is an ecosystem model that simulates how climate affects the intensity of extreme drought-related fires, under a given climate scenario in addition to forest recovery time to reach an Leaf Area Index (LAI) value of three

(Higgins et al., 2000), a high fire intensity implies larger canopy cover losses.

Based on fire experiments relating fire intensity and fire-induced biomass losses (Brando et al., 2014; De Faria et al., 2017), in which the relationship showed an adjusted R^2 of 0.98, CARLUC-Fire can be used to calculate the percentage of the above-ground biomass (AGB) that is lost as (Equation 1):

$$\text{Percentage loss of AGB} = \frac{1}{1 + \exp(2.45 - 0.002373 * FI)} \quad (1)$$

The percentage loss of AGB is provided by the model as leaf, branch and stem components. AGB leaf loss can be converted to LAI loss by multiplying it by a specific leaf area (the fresh area of a leaf divided by its total mass) value of $20 \text{ m}^2/\text{kg}$, following Hirsch et al. (2004). The LAI losses can then be subtracted from the initial (pre-fire) LAI.

2.2.2 | Grass invasion modelling and forest resilience assessment

To understand how a fire event could affect the probability of grass invasion, in present (1980–2017) and future conditions (2070–2099), we calculated post-fire LAI losses as a function of climatic conditions using the CARLUC-Fire model. This loss was then subtracted from the pre-fire LAI in present (observed MODIS LAI data) and future (simulated LAI data) climatic conditions (see details in Section 2.2.3). We then compared the results with and without imposing an additional loss of 60%, corresponding to logging in forest edge areas (based on literature information; Pereira et al., 2002) to simulate the additional effect of deforestation. The final LAI was used to calculate the probability of grass invasion using an empirical equation from fire experiments in southern Amazon sites. Areas that were far from roads (>30 km) were masked out to account for the dispersal limitation of exotic grass species (Veldman & Putz, 2010).

Finally, we evaluated the reversibility of grass invasion in relationship to present fire return intervals by comparing the pixel-level (3 km × 3 km) time required for an invaded forest pixel to recover an LAI value of three (empirically estimated as the value separating areas with high and low probabilities of grass invasion; Hoffmann et al., 2012) and compared this lag with pixel-level fire return intervals from a MODIS product (MDC64A1; Giglio et al., 2018). To simulate the forest canopy recovery time, we also used the CARLUC-Fire model.

2.3 | Pre-fire canopy cover

Although the CARLUC-Fire model can be used to simulate LAI based on climatic conditions, to minimize model uncertainties, we set the initial pre-fire LAI to 2010 estimates of the MODIS-derived LAI product (MCD15A2H; Myneni et al., 2015). Given that in future climate conditions the vegetation potential could change, we implemented a correction in the present LAI values in order to account for these potential differences. Specifically, for the future conditions, we added the pixel-level differences in productivity between present and future climates, as simulated by the CARLUC-Fire model, thereby accounting for potential changes in tree cover (LAI). The correction term was calculated by: (1) simulating present and future leaf biomass using the CARLUC model; (2) multiplying these values by SLA to obtain LAI; (3) calculating the difference between the estimated LAI for future and present conditions mediated by differences in plant productivity resulting from climate change; and (4) summing the difference to the MODIS product LAI values. This was targeted at improving the realism of our results in relationship to purely simulated LAI values. Although these remote sensing products generally do not capture understorey vegetation structure accurately, field data suggest that the LAI of the upper stratum is a fairly accurate predictor of the total LAI of a tropical forest stand (see Supporting Information Figure S2).

2.4 | Fire effects on forest canopy cover

To estimate the resulting canopy cover after a fire for present and future climatic conditions, we ran the fire component of the CARLUC-Fire model for two scenarios: one for current climate conditions and one for unmitigated predictions for climate change (2070–2099). For current conditions, we ran the model using mean climate conditions for 1980–2017, calculated using monthly series of temperature and vapour pressure from the Climatic Research Unit dataset (CRU TS; Harris et al., 2014) and precipitation (related to water stress, MCWD) from NASA's Tropical Rainfall Measurement Mission (TRMM, data product 3B43).

To adapt the biomass loss terms in CARLUC-Fire for the unmitigated climate change scenario, we used averaged air temperature (related to air dryness, VPD) and precipitation (related to water stress, MCWD) projections from all the 35 climate models

participating in the Coupled Model Intercomparison Project Phase 5 (CMIP5). Specifically, we used a scenario for 2070–2099 based on the Representative Concentration Pathway 8.5 (RCP8.5, representing an unmitigated climate change scenario). This scenario assumes a continued increase in greenhouse gas emissions, leading to increases in air temperature of c. 4–5 °C across the southern Amazon and reduced precipitation during the dry season (De Faria et al., 2017; Duffy et al., 2015; Phillips et al., 2009). The climatic variables were evaluated and bias corrected (correcting the projected/simulated output using the differences in the mean and variability between simulations and observations) with the observed data (CRU TS, v.3.22 and TRMM, product 3B43). The future VPD was derived from the variation in monthly air temperatures (ΔT between historical and future simulations) and used to model the future vapour saturation pressure (e_s) as a function of ΔT [$\Delta e_s(T) = 0.611 \exp(17.21\Delta T\Delta T + 237.3)$]; the vapour pressure was kept constant. Given that VPD is equal to vapour pressure (saturation) minus vapour pressure (air), an increase in vapour saturation pressure implies an increase in VPD.

2.5 | Logging impacts on forest canopy cover

In addition to the climate change-mediated effects of fire on LAI, we also analysed the impact of logging on canopy cover losses. Evidence suggests that logging occurs up to 2–3 km from the forest border and, alone, can reduce canopy cover by 10–60% (Pereira et al., 2002; Wuyts et al., 2017). To simulate the effects of logging on forest edges, we imposed an additional 60% LAI loss (a worst-case scenario) in the post-fire LAI in areas ≤ 3 km from the forest border. We also carried out a sensitivity analysis using the lower estimated loss percentage (10%). Deforestation areas were used to define forest borders. All paving and projected roads (for future scenarios) were also included as forest edges. Distances to edges were calculated using open software R (R Development Core Team, 2020) and QGIS (QGIS Development Team, 2017). Edge distances were not updated after applying fire-induced losses (i.e., degraded forests were still considered as remnant forest).

2.6 | Post-fire grass invasion analysis

In our approach, grass invasion is assumed to depend basically on two factors: light availability and dispersal limitation. We used an empirically derived equation (Supporting Information Equation S2; Figure S1) relating LAI and the probability of grass invasion from the study by Silvério et al. (2013) to evaluate grass invasion in each 3 km × 3 km pixel after fire- and logging-induced canopy cover losses. In addition to canopy cover, grass invasion also depends on the availability of grass propagule sources. To incorporate dispersal limitation of exotic grass species, we masked out areas that were far from roads (>30 km; Veldman & Putz, 2010) to make sure that only areas with sufficient exotic grass propagules were considered. We used the present road network (including unpaved roads

in the whole basin; Figure S3) for the analyses in present climatic conditions, and the projected future network [from Department of Transport Infrastructure (DNIT; <http://servicos.dnit.gov.br/vgeo/>)] for the analyses in future climatic conditions.

In the context of this study, we are considering invasion by any grass species, but especially exotic species, which are often perennial (D'Antonio et al., 2001; Silvério et al., 2013; Veldman & Putz, 2010; Zenni & Ziller, 2011). In general, perennial species have late germination and low seed production, but invasive species can invest substantial resources in reproduction and have high germination rates even when environmental resources are limited (Pysek & Richardson, 2008). Invasive species in the region include the African *Melinis minutiflora* (Zenni & Ziller, 2011), which was shown to produce over 2,000 seeds/m². Another important invasive species is *Urochloa decumbens* (Silvério et al., 2013). The seeds of both species are fire resistant and are often found distant from parent plants (Dairel & Fidelis, 2020; D'Antonio et al., 2001; Gorgone-Barbosa et al., 2016). Evidence suggests that *Urochloa decumbens* can show seed dormancy that is influenced by temperature variation (Dairel & Fidelis, 2020; Gorgone-Barbosa et al., 2016).

2.7 | Forest resilience analyses

To identify locations that might be under extreme threat of being trapped in a grass–fire feedback loop, we compared the time required for each pixel to recover a LAI value of three (thereby allowing for the exclusion of grasses) within the observed satellite-derived mean fire interval between 2003 and 2016. A LAI of three represents approximately the inflection point of the logistic model relating LAI and grass invasion probability (see Supporting Information Equation S2; Figure S4). At this point, small changes in LAI could quickly drive the system from one state (lightly invaded) to the other (substantially invaded; Supporting Information Figure S4). Given that the forest continues to lose tree cover during several months after a fire (Brando et al., 2019), it is very likely that a transition to a savanna-like state would occur if, immediately after a fire, LAI drops to three. Previous studies in moist savanna–forest regions of South America and Africa confirm this critical value (Cardoso et al., 2018; Hoffmann et al., 2012). Here, this threshold represents a probability of grass invasion of 30%.

The LAI recovery time was calculated as a function of our climate input variables using equations for forest productivity from the CARLUC model (Hirsch et al., 2004). These equations were calibrated for the Amazon and were shown to predict recovery 20 years after medium to severe disturbances, although the model does not explicitly consider resprouting (Hirsch et al., 2004; overall model parameter descriptions and error terms are shown in Supporting Information Table S2). Here, we assume that our high-intensity fires, alone and coupled with deforestation, represent medium to severe disturbances; therefore, we expect the model to perform well in simulating forest recovery after these events. We considered a forest area to be resilient when the time required

to achieve a LAI of three was shorter than or equal to the current mean fire interval of the area, and non-resilient otherwise. Fire return intervals per pixel (FRI) were calculated using MODIS Burned Area Product Collection 6 (MDC64A1; Giglio et al., 2018) and The Global Fire Atlas dataset (Andela et al., 2019). The FRI was calculated from the ignition frequency for a 13-year period (2003–2016) and was determined as the inverse of fire frequency. Based on observations for forests and savannas occurring in the same climate (Dantas et al., 2016), we reduced the mean fire interval by 50% in areas where LAI values drop below three after a fire and where a forest edge is near. We did not model changes in FRI resulting from climate change, because the relationship between fire probability and climate in South America is nonlinear (e.g., Lehmann et al., 2011; Bernardino et al., 2021) and, in the Amazon, it is greatly influenced by anthropogenic ignitions, generating much uncertainty in the exact location of fires. Moreover, we did not consider the effect of CO₂ fertilization on recovery rates because these effects are uncertain (Van der Sleen et al., 2015; Walker et al., 2020a) given the nutrient-limited nature of tropical soils (Ellsworth et al., 2017; Fleischer et al., 2019).

3 | RESULTS

We found that 338,702 km², which is c. 6% of the total forest area in the Amazon (Figure 2a), has a high probability (i.e., >30%) of grass invasion after a fire under current climate (1980–2017). Under unmitigated climate change, this area increased to 526,358 km² by the end of the century (2070–2099), a 60% increase (Figure 2b). This area would amount to 10% of the Amazon and imply large changes in the frequency distribution of LAI owing to shifts in local forest LAI towards lower values (Figure 3). Climate change alone had a very subtle effect on forest productivity as simulated for future climatic conditions (Figure 3b); hence, the changes under climate change were explained mainly by changes in fire intensity, rather than vegetation productivity. In both present and future conditions, we found that the south-eastern part and, on a smaller scale, the south-western part of the Brazilian Amazon (Acre state) would be the most severely affected by high-intensity fires (Figure 2b).

Approximately 511,778 km² of the total forest area was up to 3 km from a forest edge (i.e., in human-influenced zones; Figure 2c). Most of these areas are located near roads in the south-eastern Amazon, particularly in the Xingu River headwaters and across the “arc of deforestation” in Brazil. Accounting for edge effects (logging) resulted in an increase in the areas at high risk of grass invasion by 240%, amounting to 809,849 km² in current conditions (c. 14% of the Amazon region; Figure 2c) and 1.15 million km², 21% of the region, in future conditions, when considering both increased fire intensity and edge effects (Figure 2d). In a more conservative scenario, in which canopy cover losses in edge areas were only 10% (instead of the assumed 60%, i.e., a worst-case scenario) areas at high risk of grass invasion would total 499,288 km² (an increase by 50%) and 689,154 km² in current and future conditions, respectively.

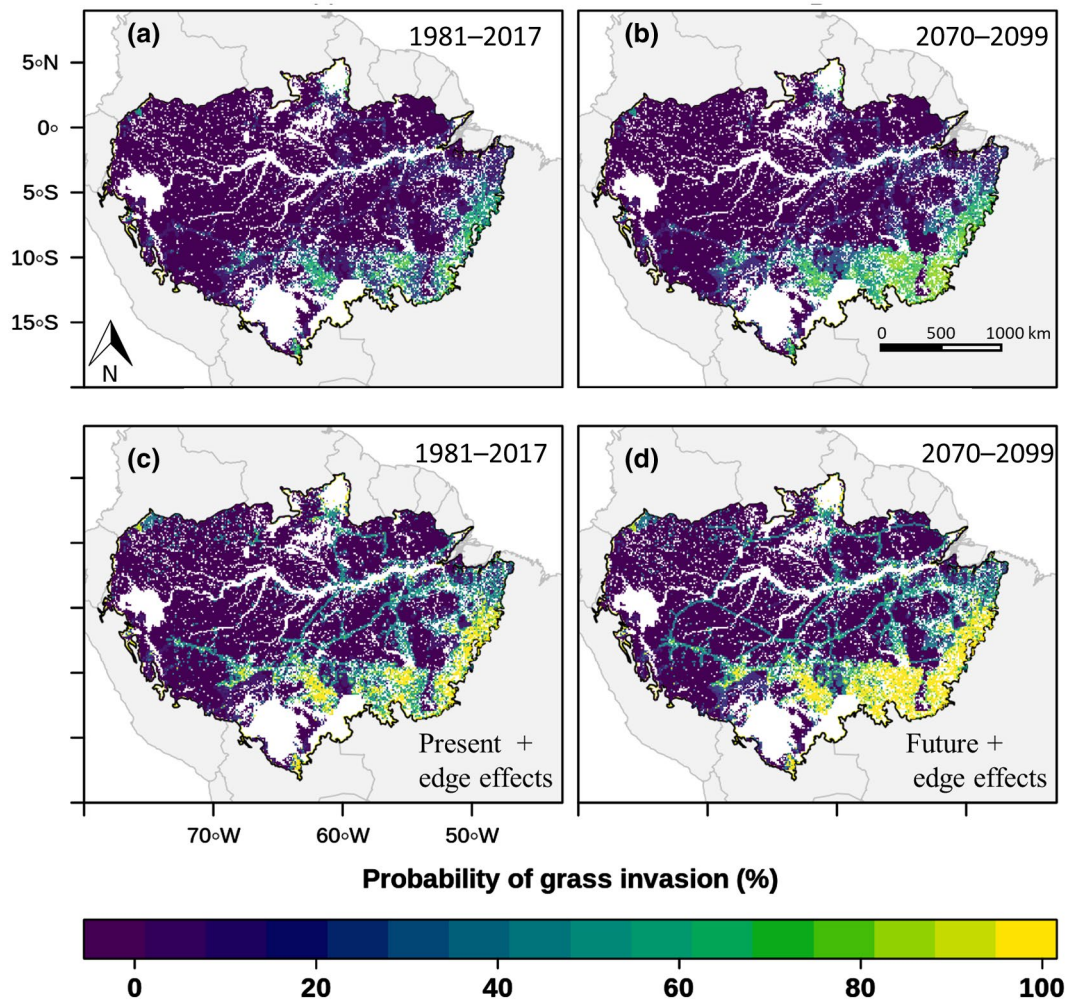


FIGURE 2 Probability of grass invasion (as a percentage) after fire across the Amazon as a function of climate (in present and predicted climate change conditions) and logging in forest edge areas. Grass invasion probability was calculated based on post-fire leaf area index (LAI) using empirically derived equations (see Materials and Methods) and distance from roads. Panels show the probability of grass invasion in (a,c) current conditions (1981–2017) and (b,d) projected climate change conditions (for 2070–2099), without (a,b) and with (c,d) edge effects from deforestation

The risk of a forest shift to an alternative grass-dominated state was considered to be especially high where the pixel-level FRI was already shorter than the pixel-level canopy recovery time. There were substantial spatial differences in simulated recovery time as a function of climate (post-fire time required to achieve an LAI of three). The southern and south-eastern parts of the Basin currently require the longest recovery times, with a mean of 4.6 years and median of 5.1 years (Supporting Information Figure S5). Mean FRIs in the Amazon were lowest in human-dominated areas, where FRI ranges from 1 to 10 years (Supporting Information Figure S6). Estimated increases in the frequency of fires owing to grass invasion would result in a fivefold increase in areas with low fire return interval (from 109,000 to 507,000 km²) as the mean FRI would drop from 5 to c. 2 years (Figure 4).

Non-resilient areas, where recovery time exceeds fire return interval, could emerge in 102,092 km² under the current climate (Figure 5a) and in about five times this area in the future (562,736 km²), considering the present FRI (Figure 5b). This implies

that c. 10% of the forest in the Amazon Basin might be at risk of a regime shift to a low tree cover state by the end of the 21st century if burned.

4 | DISCUSSION

We estimated that 6% of the Amazon is currently vulnerable to grass invasion in the event that a high-intensity fire occurs, and that this percentage would increase to 10% by the end of the century under unmitigated climate change. The predicted increase in vulnerability to grass invasion is mostly attributable to drier and hotter future climates, promoting higher-intensity forest fires during drought years and causing greater post-fire losses of canopy cover. These results suggest that, by creating opportunities for grass–fire feedback to take over the control of ecosystem dynamics, isolated forest fires can play a key role in triggering shifts between alternative biome states in the present and, especially, in

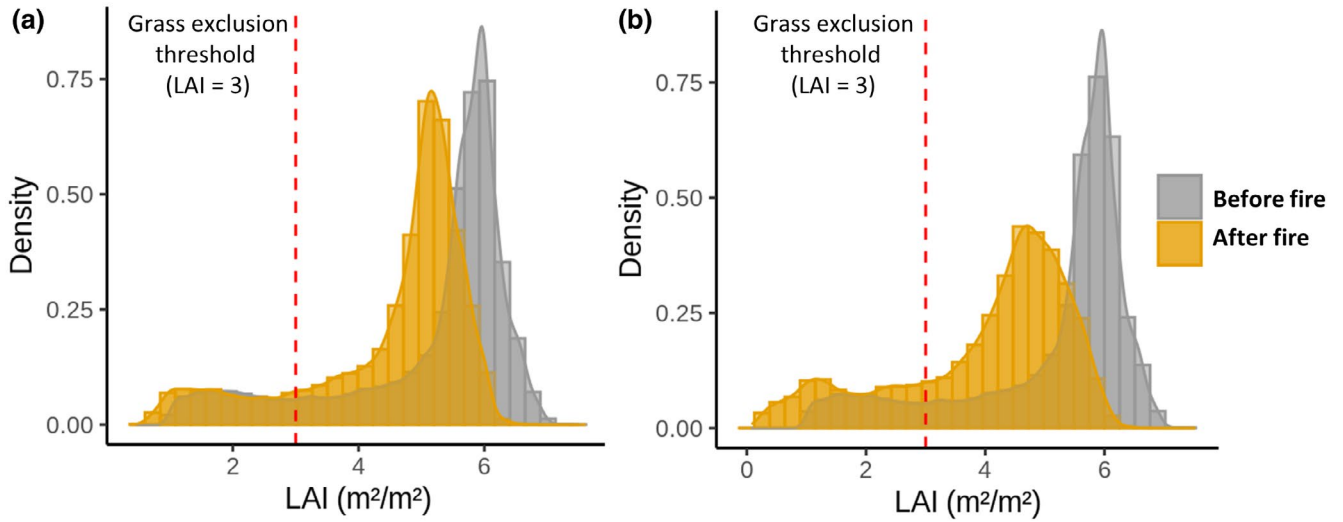


FIGURE 3 Density distributions of leaf area index (LAI) before and after a fire for the Amazon region under (a) current and (b) future climate scenarios. Red dashed lines indicate the grass exclusion threshold (LAI = 3), above which the forest has sufficient canopy cover to prevent the invasion of shade-intolerant grasses

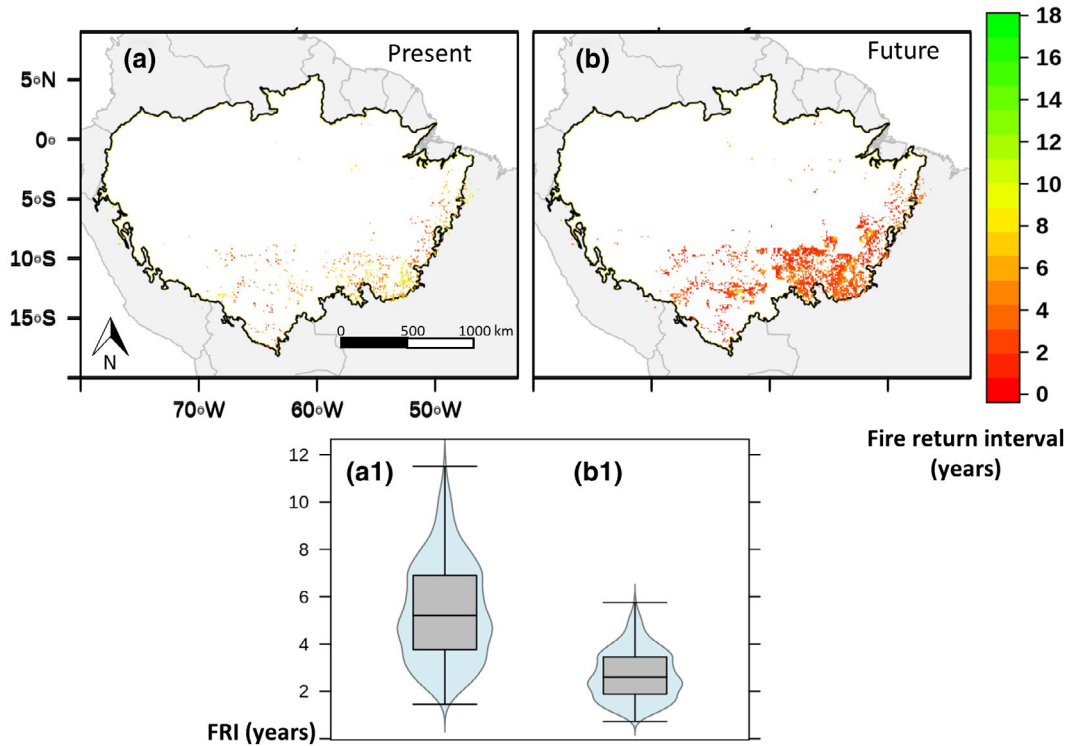


FIGURE 4 Fire return interval (FRI) before (observed) and after (predicted) grass invasion. FRI is defined as the mean number of years between two successive fire events. For present (a; 2003–2016) and future (b; 2070–2099) climates, predictions consider potential increases in fire frequency owing to grass–fire feedback. (a1, b1) The violin plots summarize FRI distributions. The width of each violin is a kernel density function

the future. The direct effect of logging is analogous. We found that 9% of the forest patches in the Amazon were located ≤ 3 km from an edge, most of which was concentrated in the south-eastern region. Edge effects resulting from deforestation were predicted to increase the area affected by grass invasion from 338,702 to

809,849 km² in present conditions and from 526,358 to 1.15 million km² in future conditions, totalling 14 and 21% of the region, respectively. Therefore, even if the Amazon experiences no land cover type conversions until the end of the century, we should expect isolated drought fire events under climate change coupled

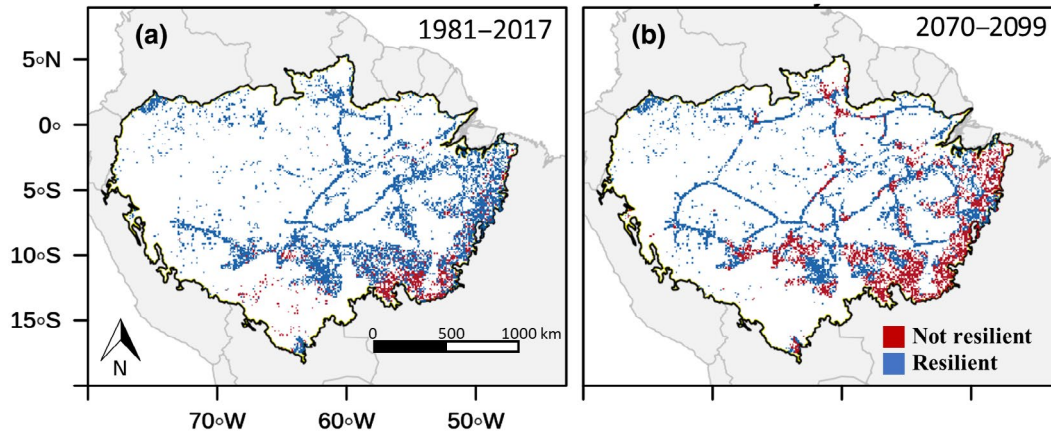


FIGURE 5 Resilient and non-resilient forest areas under (a) current and (b) unmitigated climate change conditions. Resilience is based on the difference between the fire return interval (FRI) and forest recovery time, either allowing or not allowing grass exclusion within a fire window. A site is considered resilient (blue) when the time required for the forest to recover a leaf area index of three and exclude shade-intolerant grasses is shorter than the FRI, and not resilient (red) otherwise

with logging to increase grass invasion in the region greatly, especially in the south-eastern Amazon.

Currently, most fires in the Amazon have an anthropogenic origin, resulting from slash and burn of forest resources (Nepstad et al., 2001), logging and deforestation (Barlow et al., 2020), because canopy cover usually buffers the vegetation against natural fires generated by lightning (Newberry et al., 2020). Accordingly, our results suggest that fire frequency is higher with more intensified land use. By reducing canopy cover below a LAI of three in areas near roads, not only would grasses be likely to invade, qualitatively changing the fuel type towards more flammable ones, but also forest understorey conditions would become drier (Hoffmann et al., 2012). Both factors would greatly increase ecosystem flammability. As a result, these areas could transit from human-driven fires to endogenous grass-fuelled fire regimes, characterized by a much higher frequency and intensity. For instance, in savanna-dominated landscapes with climate similar to those observed in drier Amazon areas (e.g., Silvério et al., 2013), the fire frequency in forest patches can be 10 times lower than in neighbouring grassy vegetation with the same climate (Dantas et al., 2013). A similar difference could be expected for forest-dominated landscapes. In fact, the higher (natural) fire frequency observed during the wet season, rather than the dry season, in these isolated moist savanna-forest landscapes suggests that long dry periods are not necessary for grass curing and endogenous high-frequency fire regimes to develop (Dantas et al., 2013; França et al., 2007).

Many locations with high vulnerability to grass invasion already experience recurrent fires. These include areas that we predicted to require the longest recovery periods, often over 5 years. This pattern results in an even higher probability that a subsequent grass-fuelled fire would occur before grass exclusion, driving even larger decreases in LAI and/or preventing recovery (Dantas et al., 2016; Hoffmann et al., 2012; Silvério et al., 2013). If fire frequency is not reduced in these areas, the chance that endogenous fire regimes would develop if a catastrophic fire occurred is considerable. These

highly vulnerable areas would occupy $\geq 10\%$ of the Amazon under unmitigated climate change, which amounts to c. 562,000 km² (562 million ha). Thus, in addition to climate change mitigation, intensive fire inhibition policies, especially in more vulnerable areas, could help to prevent irreversible shifts to grass-dominated biome states.

In both current and future climates, the areas with a high probability of post-fire grass invasion were shown to be concentrated in the south-eastern Amazon. This is consistent with previous empirical studies showing that grass invasion after fire already affects some of these areas (Balch et al., 2015; Veldman et al., 2009), which currently face the highest deforestation rates (Walker et al., 2020b). A recent study suggested that this region produces much of the rain supply for western and other Amazon forests through evapotranspiration (Staal et al., 2018). As a result, canopy cover losses and grass invasion in the south-eastern region could increase the frequency and severity of drought events; hence, the frequency of high-intensity forest fires regionally. This is especially alarming because studies suggest that a reduction in Amazon tree cover levels of 40% could represent the crossing of a regional-scale tipping point, with cascading effects on the central, southern and eastern Amazon (Lovejoy & Nobre, 2018; Nobre et al., 2016). Although our study did not include Amazonian wetlands, these areas are also considered to be highly vulnerable to state shifts (Flores et al., 2017).

An important strength of our modelling approach is the fact that model parameters have been specifically calibrated and validated based on data from upland Amazon forests, including the most important fire experiment in the region. Thus, we avoid potential biases related to extrapolation from other vegetation types and continents. This is especially important because the plant functional traits that regulate these processes differ greatly among and within biomes (e.g., see Bernardino et al., 2021; Dantas & Pausas, 2013, 2020). Moreover, our approach combined modelled and observed data, in addition to mechanistic and holistic approaches, in order to reduce the uncertainties related to modelling many interrelated variables, which also makes it parsimonious. Our model also includes the

effects of drought on forest structure, fuel loads and drying, which are key elements modulating the effects of forest fires (Cochrane et al., 1999; Balch et al., 2009; Brando et al., 2012; Meir et al., 2009; Nepstad et al., 2001). This process is not modelled by most dynamic global vegetation models (Powell, 2013; Trumbore et al., 2015). Finally, our approach explicitly incorporates dispersal limitation of grasses, a process that is often ignored when studying vegetation dynamics (e.g., Scheiter et al., 2013).

At the same time, given that all models are wrong by definition (Box, 1976) and because it is difficult to incorporate all potential influencing local factors when working at this scale, there are some aspects that need to be considered when interpreting these results. For instance, it is assumed that the fire impacts in the vegetation are a function of fire intensity alone, as influenced by climatic variability. Yet, fire impacts are influenced by plant traits, such as bark thickness, which can vary in space and time across the Amazon (Staver et al., 2019). Therefore, we assumed that plant communities across the Amazon had similar bark thickness to that observed in our reference site in the southern Amazon (i.e., where the fire experiments were carried; Silvério et al., 2013). In Figure 6a, we show, using data from Staver et al. (2019), that relative bark thickness (proportion of bark in relationship to stem diameter) in the Amazon increases with fire intensity up to a threshold of 149 kW/m and then remains relatively stable around the value observed for our reference site (i.e., where the fire experiments were carried out; 0.60 mm/mm; Figure 6). Hence, we report in Figure 6b the difference in the relative bark thickness of each pixel and that of our reference site (limited to areas ≤ 30 km from a road, where grasses are assumed to be able to invade) and with fire intensity smaller than that threshold (range in which bark thickness increases with fire intensity). These results aim

to provide an overall idea of the location, magnitude and direction of potential biases in the estimation of grass invasion probability in our study.

We also assumed that the LAI values in the upper stratum (i.e., as captured by our remote sensing products) were representative of those on the ground; that is, that the dynamics of the regeneration stratum (i.e., whether trees resprout or not) are of little relevance at this scale. In support of this assumption, we used field data from Veenendaal et al. (2015; their fig. 3a) showing that the LAI of the total woody stratum (lower, medium and upper forest strata) at the stand level is very strongly related to that of the upper stratum ($R^2 = 0.96$; see Supporting Information Figure S2). This is likely to be especially true in the context of the present study, which simulates medium to severe disturbances, for which post-disturbance regeneration is fairly well predicted by the CARLUC-Fire model, although it does not consider resprouting explicitly (Hirsch et al., 2004). Our modelling also does not incorporate local factors, such as soil fertility or management history. However, with respect to the variation in soil fertility, a recent study suggests that soil fertility has little effect on tree–tree competition and plant growth across the Amazon (Rozendaal et al., 2020). Management history, in contrast, is likely to influence forest recovery rates by influencing the proportion of early versus late successional forest tree species (Elias et al., 2020; Héroult & Piponiot, 2018). There are also several geophysical feedbacks between fire and the environment that could affect the ability of vegetation to recover and that are not considered here (Archibald et al., 2018; Flores et al., 2020; Pellegrini et al., 2018). Although these aspects are weaknesses of our approach, one must consider that efforts to predict accurately the spatial variability in forest succession in the Amazon are at very early stages (e.g., see Norden et al., 2015).

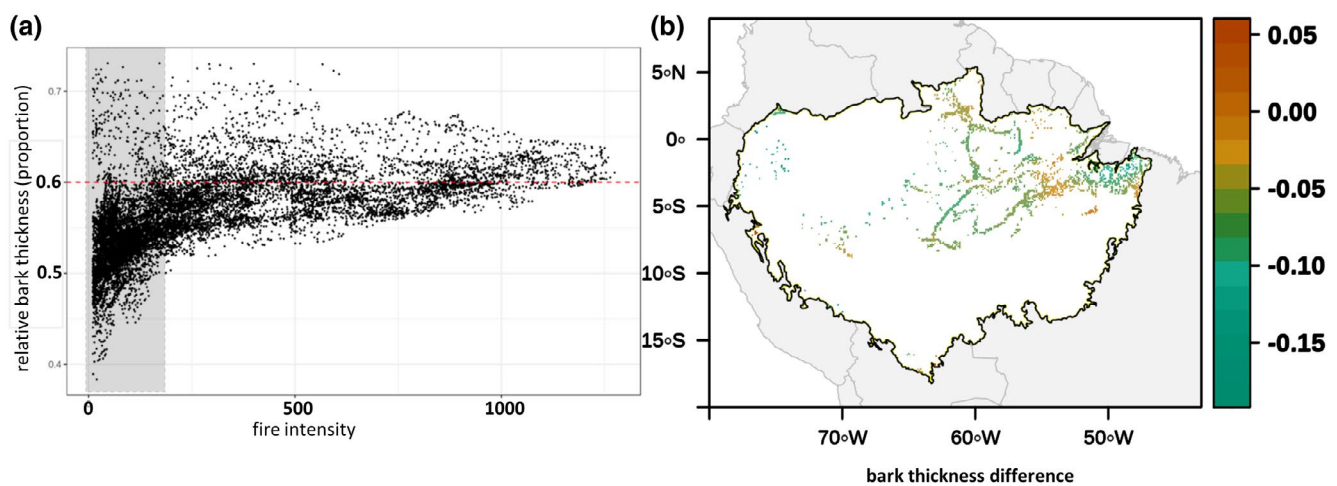


FIGURE 6 Uncertainties in the simulated fire effects associated with the variability in relative bark thickness (RBT; as a proportion of stem diameter) in the Amazon. (a) Relationship between RBT (from Staver et al., 2019) and fire intensity (from CARLUC-Fire) for 30,000 randomly selected points across the Amazon. The shaded rectangle indicates fire intensities at which bark thickness increases with fire intensity (breakpoint detected to be 149 kW/m using a sup (F) test (Hansen, 1997); $p < .001$). (b) Differences in RBT between the pixel mean value and that of the site for which CARLUC-Fire was calibrated (i.e., from the pixel that includes the experimental plots in the study by Silvério et al., 2013) for areas with fire intensity of <149 kW/m that fall <30 km from a road (where grasses can disperse). In (b), positive values indicate areas in which grass invasion might have been overestimated (and negative areas in which it could have been underestimated), owing to differences between bark thickness relative to the reference site

4.1 | Conclusion

In this study, we have shown that large parts of the Amazon, especially in the southern and south-eastern portions (but also scattered areas in other zones) are at high risk of post-fire grass invasion. Some of these areas already experience sufficiently frequent fires to cause a shift to a grass-dominated state, and these areas could increase dramatically in response to climate change, fragmentation and grass–fire feedbacks. Although resilience in canopy regeneration is evident in locations with low fire frequency, increased fire frequency could preclude the regeneration of forest cover and push these ecosystems towards a tipping point. If such a transition occurred in large areas, it would have major impacts for Amazonian biodiversity (Barlow & Peres, 2008) and for the ecosystem services provided by the forest. To avoid these negative impacts, two complementary strategies would be required. First, global action to limit greenhouse gas emissions is required in order to prevent severe climate change. Second, in order to limit anthropogenic fires, we recommend the creation of more protected areas, the implementation of effective monitoring systems, and that fire-free agricultural practices that do not use exotic grasses are encouraged, especially in the most vulnerable, south-eastern, part of the Basin.

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DATA AVAILABILITY STATEMENT

This study is based exclusively on open-source data. R code for climate analysis can be provided upon request.

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BIOSKETCH

Bruno L. De Faria (The research of the lead author) focuses on environmental modelling and working with feedbacks among climate, vegetation and fire. He is concerned with modelling risk analysis scenarios on the vulnerability of tropical forests to repeated drought and fire disturbances.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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