

QUANTIFYING THE IMPACTS OF WILDFIRES ON FOREST CARBON  
STOCKS AND CO<sub>2</sub> EMISSIONS ACROSS BRAZILIAN AMAZONIA



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## DECLARATION

I hereby declare that this work has been originally produced by myself for this thesis and it has not been submitted for the award of a higher degree to any other institution. Inputs from co-authors are acknowledged throughout

Camila Silva, Lancaster, September 2020

## **Author contribution**

For the developing the data chapters I had the contribution of various collaborators, including a team of researchers from British and Brazilian Research Institutes and Universities, local field supporters during field work, local community members, landowners and funding agencies (Lancaster University Faculty of Science and Technology, UKRI, NERC, CNPQ, FAPESP, IPAM, Embrapa).

## **Chapter 2**

L.E.O.C.A conceived the study. L.E.O.C.A., J.B. and L.O.A. designed the study. C.S., A.P.L., M.A.S. and B.C. processed the data. C.S. performed the analyses with support from L.E.O.C.A., F.E.S. and J.B., C.S., L.E.O.C.A., I.B., H.A.M.X., E.B., P.M.L.A.G., M.S., B.C., L.K. and A.P.L. carried out the FATE field data collection. C.S., L.E.O.C.A. and J.B. wrote the paper with contributions from all co-authors.

## **Chapter 3**

J.B. and C.S. conceived the study. C.S. and J.B. designed the study. C.S. processed the data. C.S. performed the analyses with support from J.B., L.E.O.C.A and P.Y. C.S., L.E.O.C.A., I.B., H.A.M.X., E.B., P.M.L.A.G., M.S., B.C., L.K. and A.P.L. carried out the FATE field data collection. C.S., J.B. and P.Y wrote the paper with contributions from all co-authors.

## **Chapter 4**

C.S., J.B. and L.E.O.C.A. conceived the study. C.S., J.B., L.E.O.C.A. and A.A. designed the study. C.S. and L.R. processed the data. C.S. performed the analyses with support from J.B., A.A., L.R and L.E.O.C.A. C.S wrote the chapter with the contributions from all co-authors.

*“One way to open your eyes is to ask yourself, What if I had never seen this before? What if I knew I would never see it again?”*

—Rachael Carson

*To the memory of my beloved dad, José Maria da Silva.*

**Dedication**

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## ABSTRACT

Drought-induced wildfires are an increasing threat to tropical forests. More frequent and intense droughts combined with increasing anthropogenic disturbances are converting previously fire-resistant humid forests into fire-prone ecosystems. Understanding the impacts of wildfires in tropical forests is critical to maintain the vital role of tropical forests in regulating climate and supporting human wellbeing. However, the long-term effects of wildfires on forest carbon stocks and emissions are still poorly understood. This thesis addresses this knowledge gap by investigating fire-induced changes across 63 Amazonian forest plots and quantifying associated carbon emissions. I first assessed long-term changes in biomass stocks and dynamics among tree functional groups (chapter 2), showing that a 25% reduction in carbon stocks persists for at least 30 years after wildfires. Losses outweighed carbon gains in the short-term (1-8 years), but although the carbon balance returned to baseline levels over the long-term carbon stocks had not recovered to pre-fire levels, even after 30 years. In chapter 3, I quantified year-to-year net CO<sub>2</sub> emissions from burned forests, based on changes in stem mortality, decomposition and vegetation growth. The models I proposed showed that following combustion emissions, a large pulse of carbon is released to the atmosphere through decomposition, peaking at c. 5 years after the fires, which was responsible for up to 73% of all fire-induced emissions over the 30-year period. Post-fire regrowth only offset 35% of all fire-induced carbon emissions. Finally, my spatio-temporal approach to scale-up immediate and long-term CO<sub>2</sub> emissions from wildfires in chapter 4 showed that the greatest combustion and decomposition emissions occur in forests with the highest biomass. Overall, this thesis demonstrates that the effects of fire on forest carbon stocks persist for many years and that environmental policies should focus on tackling wildfires in the humid tropics, especially where forests are hyper carbon-rich.

**Keywords:** humid tropical forests, Amazonia, carbon stocks, fire, tree mortality, post-fire regrowth, CO<sub>2</sub> emissions

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## RESUMO

Incêndios florestais associados a secas extremas representam uma ameaça crescente em florestas tropicais. Secas mais intensas e mais frequentes combinadas a distúrbios causados pela ação humana estão alterando florestas húmidas, uma vez resistentes ao fogo, em ecossistemas sujeitos a fogo. O entendimento dos impactos de incêndios descontrolados em florestas tropicais é fundamental para que seja mantido o papel vital dessas florestas em regular o clima e o sustento do bem-estar humano. Entretanto, os efeitos de longo-prazo desses incêndios nos estoques de carbono das florestas e as consequentes emissões são ainda pouco compreendidas. Essa tese aborda essa lacuna de conhecimento por meio da análise das mudanças oriundas do fogo em 63 parcelas em florestas da Amazônia e da quantificação das emissões de carbono associadas. Primeiramente eu avaliei as mudanças em longo-prazo nos estoques de biomassa e dinâmica ao longo de grupos funcionais arbóreos (Capítulo 2), mostrando a persistência de uma redução de 25% nos estoques de carbono por até 30 anos depois dos eventos de incêndios. As perdas de carbono extrapolaram os ganhos no curto-prazo (1-8 anos), e apesar do balanço do carbono ter retornado aos níveis da linha de base no longo-prazo os estoques de carbono não recuperaram os níveis anteriores ao distúrbio mesmo após 30 anos. No capítulo 3, eu quantifiquei ano a ano as emissões líquidas em florestas queimadas, com base nas mudanças em mortalidade de fustes, decomposição da madeira morta e regeneração da vegetação. Os modelos que propus mostraram que após as emissões por combustão há um pulso considerável de carbono liberado para atmosfera através da decomposição, atingindo um pico 5 anos após o evento do fogo, responsável por até 73% de todas as emissões por fogo ao longo de 30 anos. A regeneração após o fogo neutraliza apenas 35% de todas as emissões derivadas do fogo. Finalmente, minha abordagem espaço-temporal para extrapolar emissões de CO<sub>2</sub> imediatas e tardias derivadas de incêndios florestais descontrolados, no capítulo 4, mostrou que a maior parte das emissões por combustão e decomposição ocorrem em florestas com os maiores estoques de biomassa. De maneira geral, essa tese demonstra que os efeitos do fogo nos estoques de carbono persistem por muitos anos e que as políticas ambientais deveriam focar em combater os incêndios na região tropical húmida, especialmente em florestas com alto teor de carbono estocado.

**Palavras-chave:** florestas tropicais húmidas, Amazônia, estoques de carbono, fogo, mortalidade de árvores, regeneração pós-fogo, emissões de CO<sub>2</sub>

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# TABLE OF CONTENTS

<b>1</b>	<b>GENERAL INTRODUCTION .....</b>	<b>1</b>
1.1	TROPICAL FORESTS IN A HUMAN-DOMINATED WORLD .....	2
1.2	RECENT CHANGES IN TROPICAL FORESTS.....	3
1.2.1	<i>Deforestation and forest degradation .....</i>	<i>3</i>
1.3	FIRE IN TROPICAL FORESTS .....	6
1.3.1	<i>Ignition sources and wildfire types .....</i>	<i>7</i>
1.3.2	<i>Why do humid tropical forests burn?.....</i>	<i>8</i>
1.3.3	<i>Responses from humid tropical forests to fire.....</i>	<i>11</i>
1.3.4	<i>Wildfire impacts on carbon stocks and emissions.....</i>	<i>15</i>
1.4	STUDY SYSTEM – THE BRAZILIAN AMAZON .....	16
1.5	KNOWLEDGE GAPS, OBJECTIVES AND THESIS STRUCTURE.....	18
1.6	REFERENCES .....	20
<b>2</b>	<b>DROUGHT-INDUCED AMAZONIAN WILDFIRES INSTIGATE A DECADE-SCALE DISRUPTION OF FOREST CARBON DYNAMICS.....</b>	<b>28</b>
2.1	ABSTRACT .....	29
2.2	INTRODUCTION .....	30
2.3	MATERIALS AND METHODS.....	33
2.3.1	<i>Experimental design for field data collection .....</i>	<i>33</i>
2.3.2	<i>Field inventory and total aboveground biomass.....</i>	<i>35</i>
2.3.3	<i>Plot-level assessment of long-term effects of wildfires on forest biomass .....</i>	<i>36</i>
2.3.4	<i>Stem-level assessment of growth, recruitment and mortality.....</i>	<i>38</i>
2.4	RESULTS .....	39
2.4.1	<i>The long-term effects of wildfires on forest biomass at plot-level .....</i>	<i>39</i>
2.4.2	<i>Uncertainties .....</i>	<i>42</i>
2.4.3	<i>Mortality, recruitment and growth rates at stem-level .....</i>	<i>43</i>
2.5	DISCUSSION .....	46
2.5.1	<i>Post-fire changes in forest dynamics and consequences for the long-term recovery of biomass stocks 47</i>	
2.5.2	<i>Post-fire mortality among functional groups with high contribution to biomass stocks .....</i>	<i>48</i>
2.5.3	<i>Post-fire stem growth and recruitment.....</i>	<i>49</i>
2.5.4	<i>Prospects for forest recovery beyond the time-scale of our data.....</i>	<i>49</i>
2.5.5	<i>Post-fire forest recovery limitations and the future of tropical humid forests under the risk of wildfires 50</i>	
2.6	CONCLUSIONS.....	51
2.7	ACKNOWLEDGMENTS .....	51
2.8	SUPPLEMENTARY MATERIAL.....	52
2.9	REFERENCES .....	63
<b>3</b>	<b>ESTIMATING THE MULTI-DECADE CARBON DEFICIT OF BURNED AMAZONIAN FORESTS.....</b>	<b>67</b>
3.1	ABSTRACT .....	68
3.2	INTRODUCTION .....	69
3.3	METHODOLOGY .....	72
3.3.1	<i>Study region and field measurements.....</i>	<i>72</i>
3.3.2	<i>Estimating gross CO<sub>2</sub> emissions .....</i>	<i>73</i>
3.3.3	<i>Estimating CO<sub>2</sub> uptake by stem growth and recruitment.....</i>	<i>75</i>
3.3.4	<i>Net CO<sub>2</sub> emissions and the relative contribution of combustion .....</i>	<i>76</i>
3.4	RESULTS .....	77
3.4.1	<i>Temporal pattern of gross CO<sub>2</sub> emissions from fire-induced stem mortality and decomposition</i>	<i>77</i>

3.4.2	<i>Temporal pattern of gross CO<sub>2</sub> uptake due to post-fire recruitment and growth</i> .....	78
3.4.3	<i>Multi-decadal net CO<sub>2</sub> flux from burned forests: comparing the contribution of combustion and decomposition-related CO<sub>2</sub> emissions with post-fire CO<sub>2</sub> uptake</i> .....	79
3.5	DISCUSSION .....	81
3.5.1	<i>Improving emission estimates from Amazonian wildfires</i> .....	81
3.5.2	<i>The importance of avoiding further degradation in burned forests</i> .....	82
3.5.3	<i>Quantifiable uncertainties</i> .....	83
3.6	CONCLUSION.....	86
3.7	ACKNOWLEDGEMENTS .....	86
3.8	SUPPLEMENTARY MATERIAL.....	87
3.9	REFERENCES .....	92
<b>4</b>	<b>A NOVEL SPATIAL-TEMPORAL APPROACH TO ESTIMATE CO<sub>2</sub> EMISSIONS FROM AMAZONIAN FOREST FIRES</b> .....	<b>97</b>
4.1	ABSTRACT .....	98
4.2	1. INTRODUCTION .....	99
4.3	METHODS .....	101
4.3.1	<i>The spatio-temporal approach for quantifying the CO<sub>2</sub> fluxes of burned forests</i> .....	102
4.3.2	<i>Quantifying the total net emissions in an Amazonian landscape</i> .....	111
4.4	RESULTS .....	114
4.4.1	<i>Evaluating modelled emissions patterns over time and along a gradient of AGB stocks</i> .....	114
4.4.2	<i>Applying the burned forest emissions model to an Amazonian landscape</i> .....	116
4.5	DISCUSSION .....	118
4.5.1	<i>The implications of pre-fire AGB for net emissions</i> .....	119
4.5.2	<i>Caveats and knowledge gaps</i> .....	120
4.5.3	<i>Accounting for forest fire emissions in Brazil's climate policy</i> .....	122
4.6	CONCLUSION.....	123
4.7	ACKNOWLEDGEMENTS .....	123
4.8	REFERENCES .....	124
<b>5</b>	<b>GENERAL DISCUSSION</b> .....	<b>128</b>
5.1	<i>GENERAL DISCUSSION</i> .....	129
5.1.1	<i>Key findings</i> .....	129
5.1.2	<i>Implications of research findings to national conservation strategies and climate-change policies</i> 131	
5.1.3	<i>Future research priorities</i> .....	135
5.2	CONCLUSIONS.....	141
5.3	REFERENCES .....	141
5.4	APPENDIX – OTHER OUTCOMES.....	145

## LIST OF FIGURES

FIGURE 1.1	TYPES OF FOREST FIRES .....	8
FIGURE 1.2	POSITIVE FEEDBACKS CYCLE OF FLAMMABLE DISTURBED .....	10
FIGURE 1.3	EFFECTS OF UNDERSTORY WILDFIRES IN CENTRAL AMAZONIA.....	14
FIGURE 1.4	THE BRAZILIAN AMAZON AND THE ABOVEGROUND BIOMASS (AGB) .....	18
FIGURE 2.11	TREE INVENTORY PLOTS AND OVERLAP OF MAXIMUM CUMULATIVE WATER DEFICIT (MCWD).....	35

FIGURE 2.2 GAMM FITTED MODELS OF BURNED FORESTS PATHWAYS BY DEPENDENT VARIABLES .....	41
FIGURE 2.3 PROBABILITY DENSITY FUNCTION OF STEM MORTALITY AND STEM GROWTH .....	44
FIGURE 2.4 PROBABILITY DENSITY FUNCTION CLASSES OF STEM MORTALITY IN AND STEM GROWTH BY WOOD DENSITY .....	45
FIGURE 3.1 LOCATION OF OUR FOUR REGIONS .....	73
FIGURE 3.2 A) FITTED MODEL FOR PREDICTING FIRE-INDUCED NECROMASS PRODUCTION .....	78
FIGURE 3.3 FITTED MODEL FOR PREDICTING FIRE-INDUCED BIOMASS GROWTH .....	79
FIGURE 3.4 A) CO <sub>2</sub> FLUXES FROM WILDFIRES.....	81
FIGURE 4.0 MAIN STEPS OF THE DEVELOPMENT AND THE APPLICATION OF OUR SPATIO-TEMPORAL APPROACH FOR ESTIMATING CO <sub>2</sub> EMISSIONS FROM AMAZONIAN WILDFIRES.....	102
FIGURE 4.1 THE CHANGES IN FORESTS CARBON FLUXES AFTER WILDFIRES.....	104
FIGURE 4.2 THE RELATIONSHIP BETWEEN AGB AND NECROMASS COMPONENTS .....	106
FIGURE 4.3 A NON-LINEAR AND A LINEAR MODEL FOR QUANTIFYING INITIAL AGB LOSSES .....	107
FIGURE 4.4 THE ASYMPTOTIC MODEL USED FOR ESTIMATING FORESTS SUSCEPTIBILITY TO FIRE-INDUCED DELAYED MORTALITY OF FORESTS WITH <150 MG/HA .....	110
FIGURE 4.5 STUDY AREA IN THE SURROUNDINGS OF TAILÂNDIA, PA, EASTERN OF AMAZONIA REGION .....	112
FIGURE 4.6 THE PROCESSING FLOW OF THE SPATIAL DATA.....	114
FIGURE 4.7 OVER A PERIOD OF 30 YEARS SINCE FIRE AND ACROSS AGB STOCKS THE ESTIMATED A) ANNUAL GROSS EMISSIONS FROM DECOMPOSITION .....	116
FIGURE 4.8 ANNUAL BURNED AREA.....	117
FIGURE 4.9 LOW AGB AND HIGH AGB FORESTS RELATIVE CONTRIBUTION TO CUMULATIVE BURNED AREA .....	118
FIGURE 5.1 THE TRAJECTORIES OF INTACT NATURAL FORESTS SUBJECTED TO DEFORESTATION AND DEGRADATION IN AMAZONIA FROM 1995 TO 2017. ADAPTED FROM BULLOCK ET AL. 2020. ....	133
FIGURE S1 THE GENERAL ADDITIVE MIXED MODEL VALIDATION GRAPHS .....	61
FIGURE S2 PROBABILITY DENSITY FUNCTION OF STEM RECRUITMENT BY WOOD DENSITY CLASSES .....	61
FIGURE S3 LOESS FIT FOR PERCENT DIFFERENCE OF RECRUITMENT AND GROWTH IN RELATION TO UNBURNED FOREST. ....	62
FIGURE SM1 COMBUSTED NECROMASS THAT WOULD HAVE DECOMPOSED.....	88
FIGURE SM2 FIRE-INDUCED NECROMASS PRODUCTION .....	89
FIGURE SM3 RELATIVE CONTRIBUTION OF ESTIMATED PARAMETERS TO NECROMASS MODEL OUTPUT.....	91

FIGURE SM4 RELATIVE CONTRIBUTION OF ESTIMATED PARAMETERS TO GROWTH MODEL OUTPUT .....	92
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## LIST OF TABLES

TABLE 2.1 MEAN DIFFERENCE IN % ( $\pm$ SE) BETWEEN EACH BURNED PLOT AND UNBURNED MEAN.....	40
TABLE 2.2 GAMM MODELS OUTPUT BY FIXED TERM FOR INTERCEPT AND THE SMOOTH TERM YSLF.....	42
TABLE S1 DESCRIPTION OF PERMANENT SAMPLE PLOTS BY REGION	53
TABLE S2 SUMMARY OF MEAN VALUES OF TAGB STOCK AND DYNAMICS PARAMETERS .....	54
TABLE S3 SUMMARY OF LOESS MODEL'S PARAMETERS .....	58
TABLE SM1 SUMMARY OF PERMANENT PLOTS LOCATED IN BURNED (BF) AND UNDISTURBED (UF) PRIMARY FORESTS	87
TABLE SM2 OUTPUT SUMMARY OF ESTIMATED PARAMETERS IN NON-LINEAR LEAST SQUARE REGRESSION MODELS .....	90
TABLE SM 3 BOOTSTRAP STATISTICS FOR MODELS ESTIMATE PARAMETERS.....	91

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# CHAPTER 1

## 1 GENERAL INTRODUCTION



## 1.1 TROPICAL FORESTS IN A HUMAN-DOMINATED WORLD

Tropical forests include a diverse range of humid and dry forest types between the tropics of Cancer and Capricorn. Over 90% of tropical forests are confined to the Amazon Basin, Congo Basin and Southeast Asia (FAO, 2020). They stand out globally as an exceptional reservoir of biodiversity and carbon. Covering only c. 10% of Earth's surface, tropical forests store 25% of the terrestrial carbon and contribute to 33% of global net primary productivity (Bonan, 2008). Their role in the global carbon cycle is largely based on the exchange of CO<sub>2</sub> (uptake and emissions) between forests and atmosphere, and about two thirds of the global carbon sink in established forests biomass is due to the permanence of intact tropical forests (Pan *et al.*, 2011).

These highly productive ecosystems provide habitat for one half of the world's terrestrial species (Dirzo & Raven, 2003) and multiple benefits to mankind, commonly referred to as 'ecosystems services'. Briefly, tropical forests help regulate climate by absorbing and storing carbon and thus controlling local temperatures, provide freshwater by recycling rainfall, mitigate natural disasters by reducing erosion and controlling flooding, improve food security by providing goods and services such as pollination and pest control, aid human health by providing traditional medicines and preventing infectious diseases, and deliver cultural services which have non-material benefits, including aesthetic inspiration and cultural identity (Brandon, 2014; Carrasco *et al.*, 2014). The conservation of tropical forests is thus not only essential for the persistence of millions of species but also for the maintenance of human well-being.

Contemporary and large-scale anthropogenic pressures threaten the health of tropical forest ecosystems (Laurance *et al.*, 2012; Malhi *et al.*, 2014; Ganivet, 2020). This is associated with the recent human-dominated period marked by accelerated industrial and transportation growth, the Anthropocene – a new geological epoch with the greatest human influence on Earth

systems functioning (Crutzen, 2002; Steffen *et al.*, 2007). The extent of human-induced changes in tropical forests is substantial, and even the most remote areas of forests are affected (Malhi *et al.*, 2014). Agriculture is the major driving force, replacing tropical forests across the world and accounting for 80% of all deforestation-driven activities (Hosonuma *et al.*, 2012). Degradation activities, although less evident, are also extensive (e.g. Bullock *et al.*, 2020) and have pervasive effects on tropical forest biota (Barlow & Peres, 2008; Aoyagi *et al.*, 2013) and climate (Pearson *et al.*, 2017). With the expected growth of urban populations (Defries *et al.*, 2010), climate change (Bonan, 2008), and current unbalanced systems where exploitation outweigh the conservation of natural resources (Foley *et al.*, 2005), the future of tropical forests in the Anthropocene is very uncertain.

## 1.2 RECENT CHANGES IN TROPICAL FORESTS

### 1.2.1 *Deforestation and forest degradation*

Deforestation, defined as forest clearance by the complete removal of vegetation, is prevalent across the tropics. Deforestation has increased significantly since the 1990s (Hansen *et al.*, 2013; Kim *et al.*, 2015) and from 2000 to 2012, it is estimated that 91,400 km<sup>2</sup> of forests were cleared per year (Hansen *et al.*, 2013). Some of the deforested areas are left to regrow, these so-called secondary forests recover carbon stocks at varying rates (Poorter *et al.*, 2016a; Suarez *et al.*, 2019), even within the same ecosystem (Elias *et al.* 2019), and exhibit greatly reduced biodiversity values (Gibson *et al.*, 2011). The forces driving the conversion of forests vary in their relative importance across the tropics (Houghton, 2012; FAO, 2020). For example, contrary to Africa and Asia where subsistence agriculture is the strongest driver of deforestation, in South America large-scale commercial agriculture is the main cause of deforestation (Houghton, 2012). The trends in forest conversion also vary by region and over time — for example, deforestation declined substantially in the Brazilian Amazon from 2004–2012 and increased up to 2020 (PRODES, 2020), while in other Amazonian countries, large

forest clearings have declined over time but small clearings increased (Kalamandeen *et al.*, 2018). As deforestation increases, what used to be large continuous forests patches become fragmented, creating many smaller isolated patches. Fragmentation result in loss of biodiversity, decrease in forest biomass and changes in nutrient cycling, with greatest effects in the smallest and most isolated fragments (Haddad *et al.*, 2015). The formation of forest edges has adverse effects, such as increased tree mortality and susceptibility to fire (Laurance *et al.*, 2011; Numata *et al.*, 2011). Finally, deforestation is a climate change force: it alters rainfall patterns (Spracklen *et al.*, 2012a) and temperature (Senior *et al.*, 2017), and increases atmospheric CO<sub>2</sub> concentrations (Malhi & Grace, 2000)

While deforestation is relatively easy to track in space and time, and has impacts that are increasingly well understood, there is growing recognition that degradation can be just as important. Forest degradation is defined as “changes in forest condition (often due to logging, drought, fire and fragmentation) that result in the reduction of the capacity of a forest to provide goods and services” (Parrotta *et al.*, 2012). Degradation types also vary across continents. For example, in South America uncontrolled fires are a more prominent driver of degradation than in Africa and Asia, where logging is considered more important (Hosonuma *et al.*, 2012). Until 2012, over 1,43 MKm<sup>2</sup> of forest were degraded in the tropics (Tyukavina *et al.*, 2016). In fact, forest degradation has even surpassed deforestation in some countries (Matricardi *et al.*, 2020). Because degradation is more difficult to detect and monitor, the actual loss of ecosystem functioning from degradation tends to be underestimated (Nepstad *et al.*, 1999).

Forest degradation can occur in multiple forms and at varying intensities, and the resulting effects interact and can be intensified by climate change. A growing number of studies report the impacts of forest degradation on biodiversity, such as shifts in fauna and flora species composition in logged and burned forests (Barlow & Peres, 2004; Bonnell *et al.*, 2011; Mayor *et al.*, 2015; França *et al.*, 2020), and consistent changes in forest structure and trees species

composition after fire (Barlow *et al.*, 2003a; Van Nieuwstadt & Sheil, 2005; Barlow & Peres, 2008) and drought-induced disturbances (Muelbert *et al.*, 2019, Phillips *et al.*, 2010). While logging, fires and fragmentation are drivers of forest degradation that are directly related to anthropogenic activities, climate change related drivers, such as changes in rainfall, increases in air temperature and changes in the patterns of extreme climatic events, which are indirectly related to human activity, can also lead to forest disturbances (Lewis *et al.*, 2009). Generally, human-related and climate-related forest degradation leads to a reduction of the substantial carbon stocks (Phillips *et al.*, 2010, Berenguer *et al.*, 2014, de Andrade *et al.*, 2017) and a weakening of the carbon sink potential of tropical forests (Brienen *et al.*, 2015, Hubau *et al.*, 2020). Recently, large swaths of intact tropical forests have shown sensitivity to climate change, with their carbon sink potential being reduced over time (Brienen *et al.*, 2015, Yang *et al.*, 2018, Hubau *et al.*, 2020). Although an increase in tree growth associated with CO<sub>2</sub> fertilization and increases in air temperature caused a peak in carbon uptake from intact tropical forests in the 1990s, in the last two decades, an asynchronous carbon sink saturation has been identified in intact Amazonian and African forests, as a result of increases in tree mortality (Hubau *et al.*, 2020). These recent findings suggest a directional change is occurring in intact forests, even without direct human interference.

In order to slow the rate of deforestation and degradation in tropical forests and reduce their consequences for the global carbon cycle, policy mechanisms such as REDD+ (Reducing Emissions from Deforestation and Degradation) have been established (UNFCCC, 2020). Additionally, 2021–2030 has been declared the United Nations Decade on Ecosystem Restoration, with the aim to halt and reverse ecosystem degradation (FAO, 2020). While these initiatives have been showing relative success in some regions, they are currently more challenging under recent climate change because forests become more susceptible to natural or anthropogenic disturbances (Malhi *et al.*, 2014; Brando *et al.*, 2019a)

### 1.3 FIRE IN TROPICAL FORESTS

In the last decade, large areas of tropical forest have been affected by wildfires, defined here as uncontrolled fires in vegetation (Page *et al.*, 2002) (Alencar *et al.*, 2006; Aragão & Shimabukuro, 2010). Over 200,000 Km<sup>2</sup> were affected by wildfires in Asia and South America during the 1997–1998 El Niño (Cochrane, 2003a). Furthermore, during the 2015–2016 El Niño, the strongest on record (Jimenez *et al.*, 2018), wildfires affected c. 40,000 Km<sup>2</sup> in Amazonia alone (Silva Junior *et al.*, 2019). Fires in tropical forests are not unprecedented (Sanford *et al.*, 1985), but in the past they were very scarce (Cochrane, 2003a; Bush *et al.*, 2008). For example, pre-Columbian records of localized and patchy charcoal in humid forests (Amazon basin) with low frequencies of burned tree phytoliths (silica found in plant tissues that persist after plant decaying) suggest occurrences of infrequent low-intensity fires probably with no influence on the forest canopy (Bush *et al.*, 2008; McMichael *et al.*, 2012a). As humid forests did not evolve with fire, these ecosystems are very sensitive to fire and are probably becoming the most vulnerable ecosystems to the recent fire-prone climate conditions (Jolly *et al.*, 2015a).

Fire is an evolutionary force shaping the distribution of global vegetation (Bond *et al.*, 2005; Bowman *et al.*, 2009; Staver *et al.*, 2011) but in recent times, humans have altered fire regimes world-wide, either increasing or decreasing their frequency and intensity beyond previous equilibria (Bond *et al.*, 2005; Krawchuk *et al.*, 2009; Archibald *et al.*, 2012; Andela *et al.*, 2017). Much of the knowledge about fire characteristics (e.g. intensity, severity and frequency) and its complex interactions with vegetation is based on fire-prone ecosystems (Bond & Keeley *et al.*, 2005). While in some fire-prone ecosystems, such as boreal forests and savannas, fire has been playing a key role in maintaining fire-dependant species by millions of years (Bond & Keeley, 2005; Bond *et al.*, 2005; Pivello, 2011), in tropical forests, where excessive moisture limits combustion, wildfire is not a natural feature and can cause substantial negative ecological

impacts (Cochrane, 2003a; Barlow & Peres, 2004). Yet, although I focus on tropical forest wildfires here, there are other types of fire, such as fires in natural and anthropogenic open lands (e.g. Barlow *et al.*, 2019). It is thus important to distinguish forest fires from other fire types (e.g. farming and deforestation fires).

### 1.3.1 *Ignition sources and wildfire types*

Human-originated ignition is the main way wildfires start in tropical forests, since lightning are commonly associated with heavy rainfall and rarely lead to wildfires (Cochrane, 2003a). Human fire-associated activities vary according to cultural and political aspects and infrastructure, but in general, fires are used to remove unwanted vegetation. For example, cattle ranchers burn pastures to remove weeds, smallholders use fires to practice swidden-agriculture, and fire is used to clear deforested land by burning felled trees after they were left to dry during the dry season (Figure 1.1E). These fires can accidentally escape and spread into adjacent forests (Figure 1.1D), and other times, wildfires can be started maliciously. Fires penetrate the forest interior through the edges, as these are drier and are usually invaded with flammable grasses (Silvério *et al.*, 2019). Forest wildfires can occur at low or high intensity – e.g. low-intensity wildfires (or understory fires) burn available fuel on the forest floor (Figure 1.1A), moving slowly for days or even months until they are extinguished by rain; and high-intensity wildfires (canopy or crown-fires) might occur in more open forests and usually advance from an understory fire (Figure 1B), reaching the forest canopy depending on the drought and wind conditions (Cochrane, 2003a). Distinguishing fire types and how they are triggered is fundamental for strategic action plans (Barlow *et al.*, 2019).

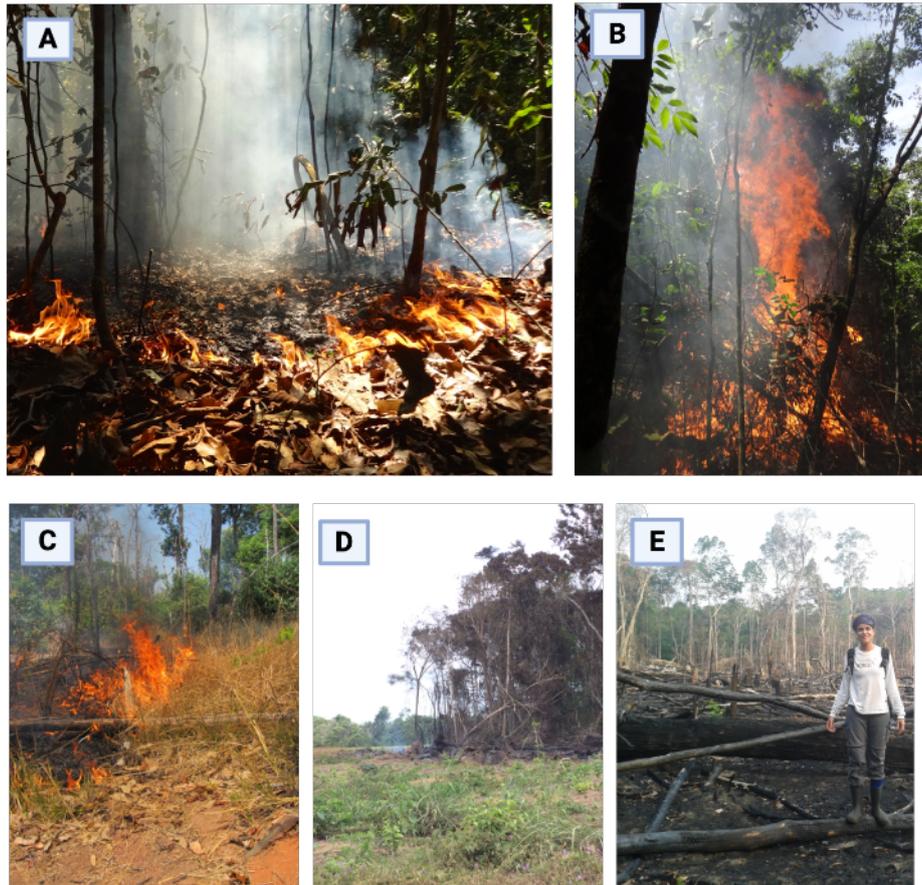


Figure 1.1 Types of forest fires; A) Low-intensity, understory wildfire in a closed-canopy forest in Mato Grosso; B) High-intensity wildfire burning the trunk of a tree and advancing to the forest canopy; C) wildfire in an open area burning dried grass close to a forest edge in Mato-Grosso; D) The frontier between a still-burning pasture and a completely burned forest edge in Para; E) a deforested area in Roraima — the felled trees on the ground were burned during the dry season of 2015. Photos taken during field work by Camila Silva, Filipe França, Haron Xaud and Paulo Brando.

### 1.3.2 *Why do humid tropical forests burn?*

Closed-canopy humid forests are generally fire-resistant, but extreme drought conditions can transform these forests into flammable systems (Cochrane *et al.*, 1999; Fearnside *et al.*, 1999; Brando *et al.*, 2014), and when this occurs, even a single man-made ignition is enough to cause forest wildfires. Extreme drought events are usually associated with El Niño in tropical regions

and are characterized by an anomalous reduction in rainfall, reaching up to 4 standard-deviation (Silva Junior *et al.*, 2019). During drought events, humid forests are subjected to water stress and become flammable. These flammable conditions occur when air in the forest understorey reaches high levels of dryness (vapor pressure deficit (VPD) > 0.75Kpa) and fuel moisture content is low (<23%) (Nepstad *et al.*, 1999; Ray *et al.*, 2010; Brando *et al.*, 2019a). Moreover, extreme drought conditions increase forest flammability by enhancing accumulation of fuel loads, i.e. by increasing leaf and branch fall (Nepstad *et al.*, 2004), and tree mortality (Phillips *et al.*, 2010; Rowland *et al.*, 2015).

Forest flammability is higher in human-modified forests as their canopies are more open, leading to drier and hotter understories. There is strong evidence for this from secondary forests, logged and/or burned forest, and forests edges (Uhl & Kauffman, 1990; Ray *et al.*, 2010; Silvério *et al.*, 2019). Some of these forests are also likely to have larger fuel loads on the ground, resulting from mortality inputs from a recent disturbance. For example, coarse woody debris (CWD) stocks in forests subjected to reduced impact and conventional logging in central Amazonia are one-and-a-half and four-fold those of undisturbed forests, respectively (Keller *et al.*, 2004). Forest edges, resulting from landscape fragmentation, are especially susceptible to fires due to their proximity to ignition sources, i.e. the agriculture lands, pastures and roads, and also because they are drier than the forest interior (Silva Junior. *et al.*, 2018). Once burned, previously undisturbed and human-modified forests become more susceptible to repeated fires (Barlow & Peres, 2008), as fuel is created by increased litterfall (Brando *et al.*, 2016a) creating a positive feedback of increasingly intense fires (Nepstad *et al.*, 2001) (Figure 1.2). In summary, fires in humid tropical forests are a result of multiple interactions between climatological drought, human-induced changes to forests, and the increase in ignition sources that accompanies deforestation, roads construction, and agriculture.

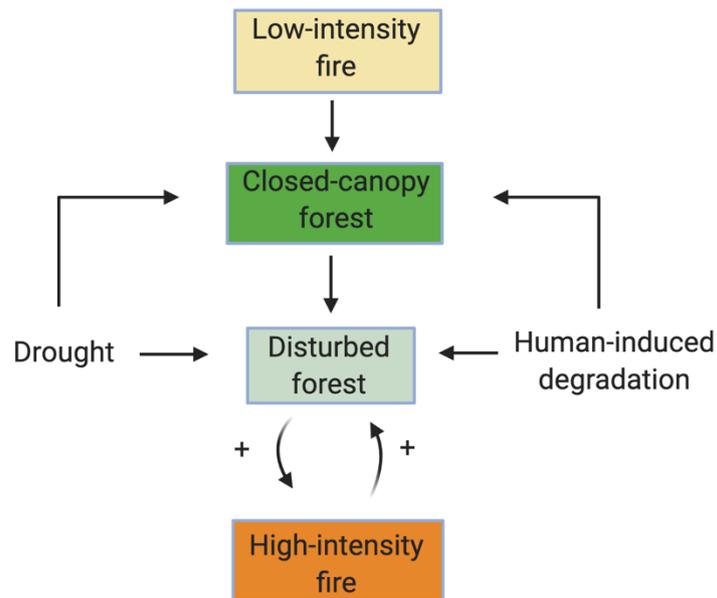


Figure 1.2 Positive feedbacks cycle of flammable disturbed forests and high-intensity wildfires. Closed-canopy forests are usually fire-resistant, but the combined effects of drought and human-induced degradation (e.g. logging, fragmentation), make these forests susceptible to low-intensity wildfires. Once disturbed, forests become more flammable with higher fuel stocks and drier understorey microclimate, creating conditions for high-intensity fires.

The 1982–1983, 1997–1998 and 2015–2016 El Niño droughts were the strongest recorded in the last four decades (Jimenez *et al.*, 2018), but the more moderate droughts of 2005 and 2010 also affected extensive forest areas in Amazonia (Aragão & Shimabukuro, 2010; Anderson *et al.*, 2018; Silva Junior *et al.*, 2019). The extent and intensity of these droughts varied regionally. For example, although 2005 and 2010 were in general less intense, in some regions they were more intense than any El Niño drought (Aragão *et al.* 2007, Lewis *et al.*, 2011, Aragão *et al.*, 2018a). These patterns are shown to be associated with regional changes in sea surface temperatures (Malhi *et al.*, 2014; Aragão *et al.*, 2018a). Worryingly, droughts are projected to increase in frequency and intensity in the tropics (Zelazowski *et al.*, 2011; Feng *et al.*, 2013; Malhi *et al.*, 2014). For example, in Amazonia, the mean interval of drought return declined

from 12 years in the last century, to six years in the first 16 years of this century (Marengo & Espinoza, 2016; Silva Junior *et al.*, 2019). Forest responses to droughts include increased mortality of large trees (Phillips *et al.*, 2010; Rowland *et al.*, 2015) and reductions in woody growth (Rifai *et al.*, 2018), which increases the available fuel for wildfires. Furthermore, drought-induced wildfires are expected to become more common in humid tropical forests (Krawchuk *et al.*, 2009; Le Page *et al.*, 2017). Although the total burned forest area has seen a reduction globally (Andela *et al.*, 2017), an increasing trend has been observed in closed-canopy forests (Hardesty *et al.*, 2005; Aragão & Shimabukuro, 2010; Aragão *et al.*, 2018a); forests that were historically fire-free regions.

### 1.3.3 *Responses from humid tropical forests to fire*

The impacts of wildfires on humid tropical forests vary according to fire intensity and forest type. Closed-canopy forests are commonly affected by low-intensity understory wildfires, and these fires can be very damaging as they burn for long periods of time (Cochrane *et al.*, 1999) (Figure 1.3A). For example, tree mortality rates are higher than 40% even after low-intensity fires in Amazonia (Barlow & Peres, 2004) (Figure 1.3B). In Indonesia, wildfires killed 64% of trees in lowland rainforest during the 1998 El Niño (Van Nieuwstadt & Sheil, 2005). Rates of fire-induced tree mortality can be even higher in previously disturbed forests, which are more likely to experience high-intensity wildfires (Cochrane *et al.*, 1999, Brando *et al.*, 2019a). Repeatedly burned forests in Amazonia can lose more than 75% of their above-ground biomass (Cochrane *et al.*, 1999; Barlow & Peres, 2008). In floodplain forests, such as Amazonian flooded forests and the peat-swamp forests of Indonesia, wildfires can have a more pervasive effect, killing all trees (Siegert *et al.*, 2001; Flores *et al.*, 2016a). Peat swamps are susceptible as they have a characteristic thick layer of decomposing organic matter that, when dried, is a potent fuel that increases fire intensity (Brando *et al.*, 2019a). Flooded forests, during the dry season, are also particularly susceptible as the fires burn all of the roots that form a dense mat

on the forest floor (Flores et al 2016). In general, post-fire mortality rates in humid tropical forests are at least double that of those found in drier forests at the edges of the Amazon (Barlow & Peres, 2004).

The high rates of fire-induced tree mortality provide evidence of the sensitivity of humid tropical forest trees to fire, which is mainly associated with their thin bark, which gives little protection against heat damage (Barlow *et al.*, 2003b; Brando *et al.*, 2012a). As smaller trees tend to have thinner bark, those are the most susceptible to mortality when they burn (Barlow *et al.*, 2003b). Although large trees with thicker bark have been shown to survive the direct effect of fires (Balch *et al.*, 2011; Brando *et al.*, 2012a), an increased rate of mortality of such trees has been detected up to 3 years after the fires (Barlow *et al.*, 2003a) (Figure 1.3C). In general, it is expected that in drier climatic regions more trees have thicker bark and thus are more likely to survive wildfires (Pinard & Huffman, 1997; Pausas, 2015; Staver *et al.*, 2020). Regions with wetter climates are the most vulnerable as the majority of the trees have thin bark (Staver *et al.*, 2020), and tree size and bark thickness are shown to be the most important plant traits that determine survival (Barlow *et al.*, 2003b; Brando *et al.*, 2012a).

As humid tropical forests are very sensitive to fire, their recovery after a wildfire can be very slow. Some studies show that decreasing fire return-intervals in humid tropical forests change species composition and structure (Figure 1.3D) to such a degree that forest recovery to the original state will be impeded (Chapman *et al.*, 1999; Flores *et al.*, 2016b; Oliveras *et al.*, 2017). While succession in humid tropical forests is expected to be slow, taking centuries rather than decades to recover structure and diversity to pre-disturbance levels (Chapman *et al.*, 1999; Flores *et al.*, 2016b; Oliveras *et al.*, 2017), a suite of factors such as the loss of most old-growth primary forest species, the destruction of the seedbank, declines in animal populations that play a key role in dispersing seeds, and the climate sensitivity of pioneer vegetation, may slow this process even further (Barlow & Peres, 2008). Because frequently burned humid tropical forests

change drastically, the term ‘savanization’ is sometimes used to describe the fate of burned humid forests (Stark *et al.*, 2020). However, savannas are diverse and important ecosystems in their own right, and this term should not be used to describe a species-poor end point of degradation that lacks the woody species typical of savannas. The term ‘secondarization’ has been suggested instead, as the profound changes in structure and compositions make these forests more similar to young secondary regrowth (Barlow & Peres, 2008). However, burned forests are also distinct from secondary forests in their composition and their legal status; to avoid confusion over terminology it is probably more apt to call them ‘repeatedly burned forests’ or ‘heavily degraded forests’.

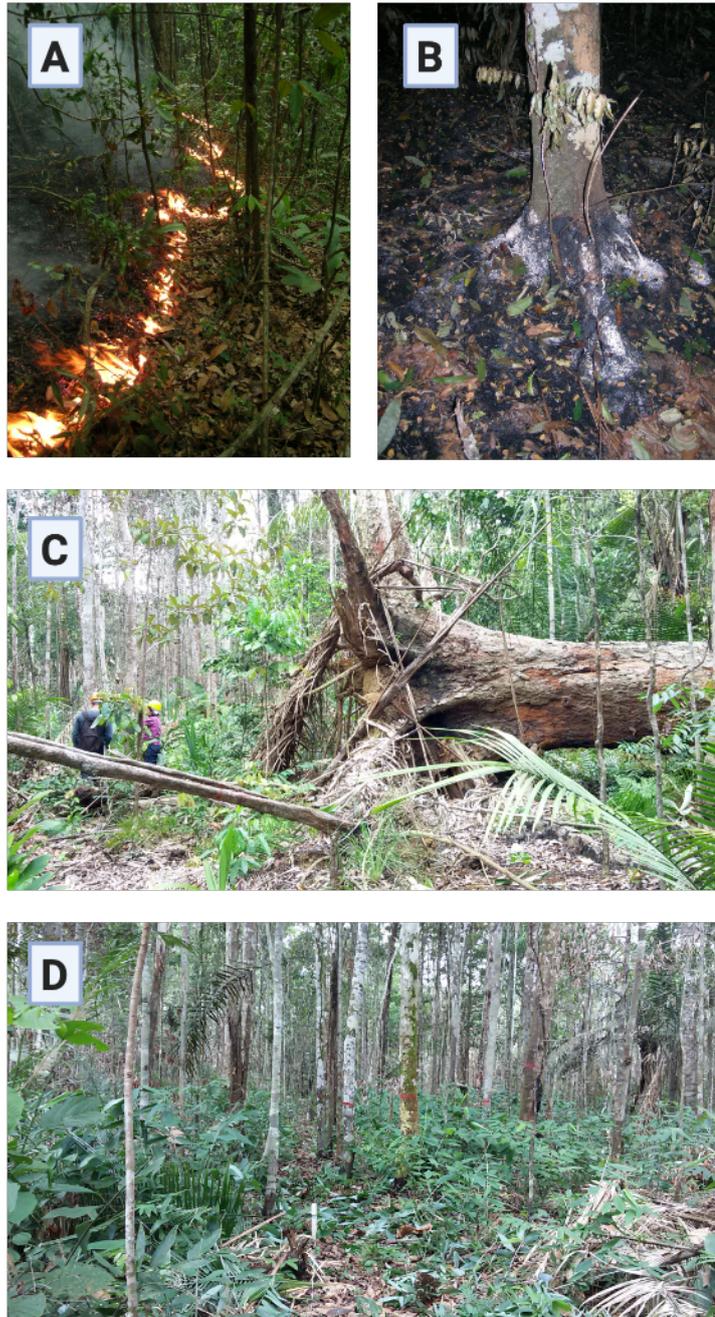


Figure 1.3 Effects of understory wildfires in central Amazonia, fire line in the understory of a closed-canopy forest in Pará state; B) the base of a small tree completely damaged by a long-lasting low-intensity wildfire ; C) a giant *Parkia pendula* tree, which died two years after low-intensity wildfires during the 2015–2016 El Niño in Amazonas state; D) a pioneer-dominated, reduced-biomass forest in regeneration three years after a wildfire. Photos were taken during field work by Jos Barlow and Aline Pontes-Lopes.

#### 1.3.4 *Wildfire impacts on carbon stocks and emissions*

Carbon emissions from wildfires in tropical forest are an important part of the global carbon cycle, as these forests store  $\sim 375$  Pg of Carbon (Avitabile *et al.*, 2016). It is estimated that burning emissions from deforestation in tropical forests contribute to  $326.16 \text{ Tg C y}^{-1}$ , which corresponds to 15% of all vegetation burning emissions from 1997-2016 (Van Der Werf *et al.*, 2017). Three main factors determine the carbon emissions from tropical humid forests: the extent of the forest area affected by fires, the fuel loads available for combustion, and the rates of fire-induced tree mortality (Withey *et al.*, 2018; Brando *et al.*, 2019b). The extent of the forest area affected by fires varies significantly across the tropics, and there are many uncertainties associated with satellite-derived estimates. Currently there are only two burned area datasets spanning the whole tropics, MCD64 (Giglio *et al.*, 2018) and FireCCI51 (Chuvieco *et al.*, 2018), and both are derived from the MODIS sensor aboard the Terra and Aqua satellites. Estimating burned area in closed-canopy tropical forests is challenging, because most fires are low-intensity understorey fires, which are difficult or impossible to detect with current thermal sensors (Anderson *et al.*, 2005). While the current burned area datasets are useful for estimating carbon emissions from open vegetation, emissions estimates for fire-affected closed-canopy forests likely have higher uncertainties associated with them (Alencar *et al.*, 2006).

Fuel loads and tree mortality are also highly variable across regions. Combustion-induced emissions, which involve the instantaneous release of carbon to the atmosphere, are influenced by fuel loads and the combustion completeness of available fuels (Brando *et al.*, 2014). In Amazonia, for example, a wildfire event are estimated to consume 20 to 60 Mg C ha<sup>-1</sup> (Withey *et al.*, 2018; Brando *et al.*, 2019b; Silvério *et al.*, 2019). In Indonesia, it is estimated that the 1998 El Nino wildfires released 280 Mg C ha<sup>-1</sup> from the combustion of peat soils (Page *et al.*, 2002). Finally, it has been shown that tree mortality rates are higher for up to three years after

fires (Barlow *et al.*, 2003a; Osone *et al.*, 2016), with the largest trees taking the longest time to die (Barlow *et al.*, 2003a). As these large trees in humid forests store the largest fraction of aboveground carbon (Berenguer *et al.*, 2014), also contributing significantly to belowground carbon stock (~21% e.g. Saatchi *et al.*, 2011), their death and subsequent decomposition is important for the overall tropical forests carbon balance because this decomposition will release large amounts of carbon to the atmosphere, which is commonly referred to as ‘committed emissions’. Committed emissions have been estimated using general estimates for tree mortality or biomass loss. For example, Alencar *et al.* (2011) assumed a 10–50% fire-induced mortality rate for trees to estimate the carbon emissions from the wildfires during 1998 in the Amazon, while Anderson *et al.* (2015a) considered a 30% loss of biomass, but only within the first year following the 2010 wildfires in Mato Grosso.

#### 1.4 STUDY SYSTEM – THE BRAZILIAN AMAZON

The Amazon forest is the largest extant tropical forest in the world. A recent study showed that 11 of the remaining 17 mega-fragments of primary forests in the world are in the Amazon Basin (Hansen *et al.*, 2020). Amazonian forests store ~ 100 Pg C in live trees (Feldpausch *et al.*, 2012; Fauset *et al.*, 2015), and harbour ~25% of the Earth’s terrestrial species (Dirzo & Raven, 2003). The value of this biome to global, regional and local communities is immeasurable, and Brazil, which retains 64% of the biome in its territory, has a huge role in determining the preserving Amazonian ecosystems. The Brazilian Amazon covers an area of ~ 4M km<sup>2</sup> and the human population in the area is c. 20.3 million (IBGE, 2000), including c. 300 distinct indigenous groups (Aikhenvald, 2012), and many traditional peoples, such as the afro-descendants known as ‘Quilombolas’ and mixed-race known as ‘Caboclos’. The expansion of agriculture and cattle ranching led to increasing deforestation rates until 2005, after which rates decreased with the implementation of a policy to prevent and control deforestation (PPCDAM, 2004). Recently, forest degradation became a major threat. It is

estimated that up to 2014, the 308,311 km<sup>2</sup> that were deforested were surpassed by the 337,427 km<sup>2</sup> of forests that were degraded over the same time period, including logged, burned, edges and isolated fragments (Matricardi *et al.*, 2020). These figures do not include the megafires associated with the most recent droughts: in the last three decades the region was affected by four major drought events (1998, 2005, 2010 and 2015-2016) that led to extensive forest wildfires (Marengo & Espinoza, 2016; Jimenez *et al.*, 2018). Fire disturbance is a prevailing type of degradation in Brazilian Amazonian forests, as droughts are becoming more frequent in the region and large swaths of forest are already degraded (Aragão *et al.*, 2018).

The present project was carried out across the Brazilian Amazon (Figure 1.4). Data were collected in the states of Acre, Amazonas, Mato-Grosso, Roraima and Pará. These are five from the nine Brazilian states that comprise the Amazon biome. We focused on specific regions from each state where drought-induced wildfires have affected *terra-firme* forests. Although we focused on *terra-firme* forests, each region has a particular mosaic landscape composed of a variety of forest typologies. For example, bamboo-dominated forests are common in Acre, whereas lower biomass ‘transitional’ forests are common in Mato-Grosso and Roraima. Forest structure varies greatly across Amazonia, in both undisturbed and human-modified forests, and in this project, we tried to capture most of this variability. For Chapters 2 and 3 we focused on undisturbed forests affected by the occurrence of a single fire. In Chapter 4, we aggregated data sampled in undisturbed and human-modified forests affected by single and multiple fire events.

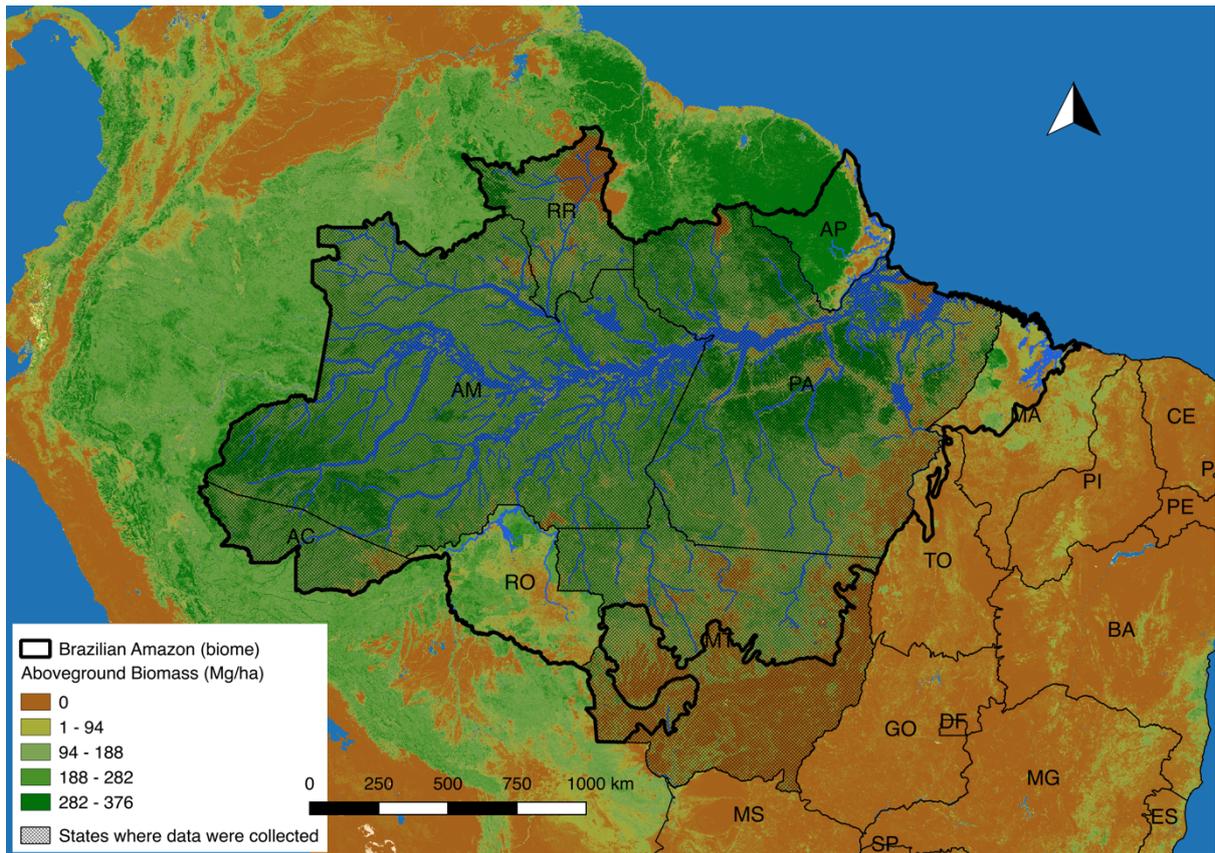


Figure 1.4 The Brazilian Amazon and the Aboveground Biomass (AGB) of the remaining vegetation for the year 2000 (AGB data from Avitabile *et al.* 2016). The current project is focused on burned terra-firme forests, with data collection carried out in the states of Acre (AC), Amazonas (AM), Mato-Grosso (MT), Para (PA), and Roraima (RR).

### 1.5 KNOWLEDGE GAPS, OBJECTIVES AND THESIS STRUCTURE

Across the Brazilian Amazonia, most studies have focused on understanding impacts of wildfires in humid forests in the short-term (Cochrane *et al.*, 1999; Barlow and Peres, 2008; Brando *et al.*, 2014). While these studies have elucidated the magnitude of changes in carbon stocks and shifts in trees functional groups in the short-term after fires, we still lack knowledge about the long-term ecological consequences of wildfires in humid-forests non-adapted to fire. This is the first knowledge gap this thesis aims to address, since shifts in trees communities and a lag in the carbon losses caused by fire disturbances can impact the role of tropical forests in the global carbon cycle (Barlow and Peres, 2008, Van Nieuwstadt and Sheil, 2005, Brando

*et al.*, 2019b). The second knowledge gap this thesis addresses refer to the lack of estimates of post-fire carbon fluxes in humid forests at the annual basis. Most studies have focused on estimating immediate emissions from combustion or have estimated the committed emissions from trees mortality (Barlow *et al.*, 2003, Alencar *et al.*, 2006, Anderson *et al.*, 2015, Withey *et al.*, 2018, Aragão *et al.*, 2018), without quantifying the temporal dynamics of post-fire forest carbon fluxes. Finally, this thesis addresses a third knowledge gap – the lack of a method to scale-up forest fires emissions basin-wide over time. Although global fire emission models have attempted to estimate spatio-temporal emissions from vegetation across the humid-tropics (Van Der Werf *et al.*, 2017), they underestimate emissions from fires non-associated to deforestation (forest wildfires) by not considering long-term carbon deficit in burned forests.

This thesis focuses on understanding wildfire impacts on carbon stocks and the dynamics of Amazonian forests, as well as estimating wildfire-associated carbon emissions. This was addressed by the specific aims to:

- (i) Quantify the long-term changes in biomass, mortality, and wood productivity of burned forests over a period of 30 years and assess stem mortality and growth among functional groups; (Chapter 2 - Drought-induced Amazonian wildfires promote long-term disruption of forest carbon dynamics)
- (ii) Develop a statistical model based on measured changes in stem mortality, necromass decomposition and vegetation growth to quantify year-to-year net CO<sub>2</sub> emissions from burned forests; (Chapter 3 - Estimating the multi-decadal carbon deficit of burned Amazonian forests)
- (iii) Develop a spatial-temporal approach to scale-up immediate and long-term CO<sub>2</sub> emissions from wildfires. (Chapter 4 - A novel spatial-temporal approach to estimate CO<sub>2</sub> emissions from Amazonian forest fires)

This thesis presents three data chapters written for publication: Chapter 2 was published in *Philosophical Transactions of the Royal Society B*; Chapter 3 is in press in *Environmental Research Letters*; and I intend to submit Chapter 4 for review and publication (target journal is *Global Change Biology*). The thesis therefore comprises three stand-alone data chapters, with their aims and order reflecting the sequence of the work as it was carried out. Chapter 5 provides a summary of key findings of each chapter, the insights resulting from the connections among the outputs, and future research priorities. Supplementary information is given at the end of each chapter and an appendix at the end of the thesis contains other publications that have resulted from research to which I have contributed.

## 1.6 REFERENCES

- Aikhenvald AY (2012) *The Languages of the Amazon*. Oxford University Press, 1–560 pp.
- Alencar A, Nepstad D, Diaz MCV, Alencar A, Nepstad D, Diaz MCV (2006) Forest Understory Fire in the Brazilian Amazon in ENSO and Non-ENSO Years: Area Burned and Committed Carbon Emissions. *Earth Interactions*, **10**, 1–17.
- Alencar A, Asner GP, Knapp D, Zarin D (2011) Temporal variability of forest fires in eastern Amazonia. *Ecological Applications*, **21**, 2397–2412.
- Andela N, Morton DC, Giglio L et al. (2017) A human-driven decline in global burned area. *Science*, **356**, 1356–1362.
- Anderson LO, Aragão LEOC, Gloor M et al. (2015) Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought. *Global Biogeochemical Cycles*, 1739–1753.
- Anderson LO, Ribeiro Neto G, Cunha AP et al. (2018) Vulnerability of Amazonian forests to repeated droughts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**, 1–13.
- Aoyagi R, Imai N, Kitayama K (2013) Ecological significance of the patches dominated by pioneer trees for the regeneration of dipterocarps in a Bornean logged-over secondary forest. *Forest Ecology and Management*, **289**, 378–384.
- Aragão LEOC, Shimabukuro YE (2010) The incidence of fire in Amazonian forests with implications for REDD. *Science (New York, N.Y.)*, **328**, 1275–8.
- Aragão LEOC, Anderson LO, Fonseca MG et al. (2018) 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, **9**, 536.
- Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE (2007) Spatial patterns and fire response of recent Amazonian droughts. *Geophysical Research Letters*, **34**, L07701.

- Archibald S, Staver AC, Levin SA (2012) Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 847–852.
- Avitabile V, Herold M, Heuvelink GBM et al. (2016) An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology*, **22**, 1406–1420.
- Balch JK, Nepstad DC, Curran LM et al. (2011) Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management*, **261**, 68–77.
- Barlow J, Peres CA (2004) Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: Management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 367–380.
- Barlow J, Peres C a (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1787–1794.
- Barlow J, Peres CA, Lagan BO, Haugaasen T (2003a) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.
- Barlow J, Lagan BO, Peres CA (2003b) Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, **19**, 291–299.
- Barlow J, Berenguer E, Carmenta R, França F (2019) Clarifying Amazonia’s burning crisis. *Global Change Biology*, **00**, 1–3.
- Berenguer E, Ferreira J, Gardner TA et al. (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, **20**, 3713–3726.
- Bonan GB (2008) Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, **320**, 1444–1449.
- Bond WJ, Keeley JE (2005) Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–394.
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Bonnell TR, Reyna-Hurtado R, Chapman CA (2011) Post-logging recovery time is longer than expected in an East African tropical forest. *Forest Ecology and Management*, **261**, 855–864.
- Bowman DMJS, Balch JK, Artaxo P et al. (2009) Fire in the Earth System. *Science*, **324**, 481–485.
- Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Brando PM, Balch JK, Nepstad DC et al. (2014) Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 6347–52.
- Brando PM, Oliveria-Santos C, Rocha W, Cury R, Coe MT (2016) Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. *Global Change Biology*, **22**, 2516–2525.

- Brando PM, Paolucci L, Ummenhofer CC et al. (2019a) Droughts , Wildfires , and Forest Carbon Cycling : A Pantropical Synthesis. 555–581.
- Brando P., Soares-Filho B, Rodrigues L et al. (2019b) The gathering firestorm in southern Amazonia. *Science Advance in press.*, 1–10.
- Brandon K (2014) *Ecosystem Services from Tropical Forests: Review of Current Science*. Washington DC, 81 pp.
- Brienen RJW, Phillips OL, Feldpausch TR et al. (2015) Long-term decline of the Amazon carbon sink. *Nature*, **519**.
- Bullock EL, Woodcock CE, Souza C, Olofsson P (2020) Satellite-based estimates reveal widespread forest degradation in the Amazon. *Global Change Biology*, **26**, 2956–2969.
- Bush MB, Silman MR, McMichael C, Saatchi S (2008) Fire, climate change and biodiversity in Amazonia: A Late-Holocene perspective. In: *Philosophical Transactions of the Royal Society B: Biological Sciences*, Vol. 363, pp. 1795–1802. Royal Society.
- Carrasco LR, Nghiem TPL, Sunderland T, Koh LP (2014) Economic valuation of ecosystem services fails to capture biodiversity value of tropical forests. *Biological Conservation*, **178**, 163–170.
- Chapman CA, Chapman LJ, Kaufman L, Zanne AE (1999) Potential causes of arrested succession in Kibale National Park, Uganda: Growth and mortality of seedlings. *African Journal of Ecology*, **37**, 81–92.
- Chuvieco E, Plummer S, Padilla M et al. (2018) Generation and analysis of a new global burned area product based on MODIS 250m reflectance bands and thermal anomalies. *Earth System Science Data*, **10**, 2015–2031.
- Cochrane M a. (2003) Fire science for rainforests. **421**, 913–919.
- Cochrane MA, Alencar A, Schulze MD, Souza CM, Nepstad DC, Lefebvre P, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*, **284**, 1832–1835.
- Crutzen PJ (2002) Geology of mankind. *Nature*, **415**, 23.
- Defries RS, Rudel T, Uriarte M, Hansen M (2010) Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, **3**, 178–181.
- Dirzo R, Raven PH (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, **28**, 137–167.
- FAO (2020) *The State of the World's Forests 2020*. Rome, 188 pp.
- de Andrade RB, Balch JK, Parsons AL, Armenteras D, Roman-Cuesta RM, Bulkan J (2017) Scenarios in tropical forest degradation: carbon stock trajectories for REDD+. *Carbon Balance and Management*, **12**, 6.
- De Faria BL, Brando PM, Macedo MN, Panday PK, Soares-Filho BS, Coe MT (2017) Current and future patterns of fire-induced forest degradation in amazonia. *Environmental Research Letters*, **12**.
- Fauset S, Johnson MO, Gloor M et al. (2015) Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, **6**, 6857.
- Fearnside PM, De Alencastro Graça PML, Leal Filho N, Rodrigues FJA, Robinson JM (1999) Tropical forest burning in Brazilian Amazonia: Measurement of biomass loading, burning efficiency and charcoal formation at Altamira, Para. *Forest Ecology and Management*,

123, 65–79.

- Feldpausch TR, Lloyd J, Lewis SL et al. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381–3403.
- Feng X, Porporato A, Rodriguez-Iturbe I (2013) Changes in rainfall seasonality in the tropics. *Nature Climate Change*, **3**, 811–815.
- Flores BM, Fagoaga R, Nelson BW, Holmgren M (2016a) Repeated fires trap Amazonian blackwater floodplains in an open vegetation state (ed Barlow J). *Journal of Applied Ecology*, **53**, 1597–1603.
- Flores BM, Fagoaga R, Nelson BW, Holmgren M (2016b) Repeated fires trap Amazonian blackwater floodplains in an open vegetation state. *Journal of Applied Ecology*, **53**, 1597–1603.
- Foley JA, DeFries R, Asner GP et al. (2005) Global consequences of land use. *Science*, **309**, 570–574.
- França FM, Ferreira J, Vaz-de-Mello FZ et al. (2020) El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes. *Biotropica*, **52**, 252–262.
- Ganivet E (2020) Growth in human population and consumption both need to be addressed to reach an ecologically sustainable future. *Environment, Development and Sustainability*, **22**, 4979–4998.
- Gibson L, Lee TM, Koh LP et al. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.
- Giglio L, Boschetti L, Roy DP, Humber ML, Justice CO (2018) The Collection 6 MODIS burned area mapping algorithm and product. *Remote Sensing of Environment*, **217**, 72–85.
- Haddad NM, Brudvig LA, Clobert J et al. (2015) Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances*, **1**, e1500052.
- Hansen MC, Potapov P V., Moore R et al. (2013) High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, **342**, 850–853.
- Hansen MC, Wang L, Song XP, Tyukavina A, Turubanova S, Potapov P V., Stehman S V. (2020) The fate of tropical forest fragments. *Science Advances*, **6**, 8574–8585.
- Hardesty J, Myers R, Fulks W (2005) Fire, ecosystems and people: a preliminary assessment of fire as a global conservation issue. *Fire Management*, **22**, 78–87.
- Hosonuma N, Herold M, De Sy V et al. (2012) An assessment of deforestation and forest degradation drivers in developing countries. *Environmental Research Letters*, **7**, 12.
- Houghton R. (2012) Carbon emissions and the drivers of deforestation and forest degradation in the tropics. *Current Opinion in Environmental Sustainability*, **4**, 597–603.
- Hubau W, Lewis SL, Phillips OL et al. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, **579**, 80–87.
- IBGE (2000) ZEE Amazônia Legal | IBGE. *Censo Demográfico*.
- Jimenez JC, Barichivich J, Mattar C, Takahashi K, Santamaría-Artigas A, Sobrino JA, Malhi Y (2018) Spatio-temporal patterns of thermal anomalies and drought over tropical forests driven by recent extreme climatic anomalies. *Philosophical Transactions of the Royal*

*Society B: Biological Sciences*, **373**, 20170300.

- Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, **6**, 1–11.
- Kalamandeen M, Gloor E, Mitchard E et al. (2018) Pervasive Rise of Small-scale Deforestation in Amazonia. *Nature Scientific Reports*, **8**, 1–10.
- Keller M, Palace M, Asner GP, Pereira R, Silva JNM (2004) Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology*, **10**, 784–795.
- Kim DH, Sexton JO, Townshend JR (2015) Accelerated deforestation in the humid tropics from the 1990s to the 2000s. *Geophysical Research Letters*, **42**, 3495–3501.
- Krawchuk MA, Moritz MA, Parisien M-A, Van Dorn J, Hayhoe K (2009) Global Pyrogeography: the Current and Future Distribution of Wildfire (ed Chave J). *PLoS ONE*, **4**, e5102.
- Lewis SL, Brando PM, Phillips OL, van der Heijden GMF, Nepstad D (2011) The 2010 Amazon drought. *Science (New York, N.Y.)*, **331**, 554.
- Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF (2009) Changing Ecology of Tropical Forests: Evidence and Drivers. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 529–549.
- Laurance WF, Camargo JLC, Luizão RCC et al. (2011) The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, **144**, 56–67.
- Laurance WF, Carolina Useche D, Rendeiro J et al. (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature*, **489**, 290–293.
- Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution*, **15**, 332–337.
- Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P (2014) Tropical Forests in the Anthropocene. *Annual Review of Environment and Resources*, **39**, 125–59.
- Marengo JA, Espinoza JC (2016) Extreme seasonal droughts and floods in Amazonia: Causes, trends and impacts. *International Journal of Climatology*, **36**, 1033–1050.
- Matricardi EAT, Skole DL, Costa OB, Pedlowski MA, Samek JH, Miguel EP (2020) Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*, **369**, 1378–1382.
- Mayor P, Pérez-Peña P, Bowler M, Puertas PE, Kirkland M, Bodmer R (2015) Effects of selective logging on large mammal populations in a remote indigenous territory in the northern peruvian amazon. *Ecology and Society*, **20**, 36.
- McMichael CH, Piperno DR, Bush MB, Silman MR, Zimmerman AR, Raczka MF, Lobato LC (2012) Sparse pre-Columbian human habitation in Western Amazonia. *Science*, **336**, 1429–1431.
- Muelbert AE, Brienen RJW, Baker TR et al. (2019) Compositional response of Amazon forests to climate change. *Global Change Biology*, 39–56.
- Nepstad DC, Verssimo A, Alencar A et al. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.

- Nepstad D, Carvalho G, Cristina A et al. (2001) Road paving, fire regime feedbacks, and the future of Amazon forests. *Forest Ecology and Management*, **154**, 395–407.
- Nepstad D, Lefebvre P, Da Silva UL et al. (2004) Amazon drought and its implications for forest flammability and tree growth: A basin-wide analysis. *Global Change Biology*, **10**, 704–717.
- Numata I, Cochrane MA, Souza CM, Sales MH (2011) Carbon emissions from deforestation and forest fragmentation in the Brazilian Amazon. *Environmental Research Letters*, **6**, 044003.
- Oliveras I, Román-Cuesta RM, Urquiaga-Flores E et al. (2017) Fire effects and ecological recovery pathways of Tropical Montane Cloud Forests along a time chronosequence. *Global Change Biology*, 1–15.
- Osone Y, Toma T, Warsudi, Sutodjo, Sato T (2016) High stocks of coarse woody debris in a tropical rainforest, East Kalimantan: Coupled impact of forest fires and selective logging. *Forest Ecology and Management*, **374**, 93–101.
- Pan Y, Birdsey RA, Fang J et al. (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.
- Page SE, Siegert F, Rieley JO, Boehm HD V., Jaya A, Limin S (2002) The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, **420**, 61–65.
- Le Page Y, Morton D, Hartin C et al. (2017) Synergy between land use and climate change increases future fire risk in Amazon forests. *Earth Syst. Dynam.*, **8**, 1237–1246.
- Parrotta JA, Wildburger C, Mansourian S (2012) *Understanding Relationships between Biodiversity, Carbon, Forests and People: The Key to Achieving REDD+ Objectives*, Vol. 31. Vienna, 161 pp. p.
- Pausas JG (2015) Bark thickness and fire regime. *Functional Ecology*, **29**, 315–327.
- Pearson TRH, Brown S, Murray L, Sidman G (2017) Greenhouse gas emissions from tropical forest degradation: An underestimated source. *Carbon Balance and Management*, **12**, 1–11.
- Phillips OL, Heijden G van der, Lewis SL et al. (2010) Drought–mortality relationships for tropical forests. *New Phytologist*, **187**, 631–646.
- Pinard MA, Huffman J (1997) Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology*, **13**, 727–740.
- Pivello VR (2011) The use of fire in the cerrado and Amazonian rainforests of Brazil: Past and present. *Fire Ecology*, **7**, 24–39.
- Poorter L, Bongers F, Aide TM et al. (2016) Biomass resilience of Neotropical secondary forests. *Nature*, **530**.
- PPCDAM (2004) Plano de Acao para a Prevencao e Controle do Desmatamento na Amazonia Legal. 156.
- PRODES (2020) Instituto Nacional de Pesquisas espaciais. Projeto PRODES - Monitoramento da Floresta Amazônica por satélite.
- Ray D, Nepstad D, Brando P (2010) Predicting moisture dynamics of fine understory fuels in a moist tropical rainforest system: results of a pilot study undertaken to identify proxy variables useful for rating fire danger. *New Phytologist*, **187**, 720–732.
- Rifai SW, Girardin CAJ, Berenguer E et al. (2018) ENSO Drives interannual variation of forest

- woody growth across the tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**, 20170410.
- Rowland L, Da Costa ACL, Galbraith DR et al. (2015) Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, **528**, 119–122.
- Sanford RL, Saldarriaga J, Clark KE, Uhl C, Herrera R (1985) Amazon rain-forest fires. *Science*, **227**, 53–55.
- Senior RA, Hill JK, González del Pliego P, Goode LK, Edwards DP (2017) A pantropical analysis of the impacts of forest degradation and conversion on local temperature. *Ecology and Evolution*, **7**, 7897–7908.
- Siegert F, Ruecker G, Hinrichs A, Hoffmann AA (2001) Increased damage from fires in logged forests during droughts caused by El Niño. *Nature*, **414**, 437–440.
- Silva Junior. CHL, Aragão LEOC, Fonseca MG, Almeida CT, Vedovato LB, Anderson LO (2018) Deforestation-induced fragmentation increases forest fire occurrence in central Brazilian Amazonia. *Forests*, **9**.
- Silva Junior CHL, Anderson LO, Silva AL et al. (2019) Fire Responses to the 2010 and 2015/2016 Amazonian Droughts. *Frontiers in Earth Science*, **7**, 1–16.
- Silva Junior CHL, Pessôa ACM, Carvalho NS, Reis JBC, Anderson LO, Aragão LEOC (2021) The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology and Evolution*, **5**, 144–145.
- Silvério D V, Brando PM, Bustamante MMC et al. (2019) Fire, fragmentation, and windstorms: A recipe for tropical forest degradation. *Journal of Ecology*, **107**, 656–667.
- Spracklen D V., Arnold SR, Taylor CM (2012) Observations of increased tropical rainfall preceded by air passage over forests. *Nature*, **489**, 282–285.
- Stark SC, Breshears DD, Aragón S et al. (2020) Reframing tropical savannization: linking changes in canopy structure to energy balance alterations that impact climate. *Ecosphere*, **11**.
- Staver AC, Archibald S, Levin S (2011) Alternative Biome States The Global Extent and Determinants of Savanna and Forest as. *Science*, **334**, 230–232.
- Staver AC, Brando PM, Barlow J et al. (2020) Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire (ed Penuelas J). *Ecology Letters*, **23**, 99–106.
- Steffen W, Crutzen PJ, McNeill JR (2007) The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature? *Ambio*, **36**, 614–621.
- Suarez DR, Rozendaal DMA, De Sy V et al. (2019) Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data. *Global Change Biology*, **25**, 3609–3624.
- Tyukavina A, Hansen MC, Potapov P V., Krylov AM, Goetz SJ (2016) Pan-tropical hinterland forests: Mapping minimally disturbed forests. *Global Ecology and Biogeography*, **25**, 151–163.
- Uhl C, Kauffman JB (1990) Deforestation, Fire Susceptibility, and Potential Tree Responses to Fire in the Eastern Amazon. *Ecology*, **71**, 437–449.
- UNFCCC (2020) REDD+ Web Platform.
- Van Der Werf GR, Randerson JT, Giglio L et al. (2017) Global fire emissions estimates during

- 1997-2016. *Earth System Science Data*, **9**, 697–720.
- Van Nieuwstadt MGL, Sheil D (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology*, **93**, 191–201.
- Withey K, Berenguer E, Palmeira A et al. (2018) Quantifying the immediate carbon emissions from ENSO-mediated wildfires in human-modified tropical forests. *Philosophical transactions of Royal Society B*, **373**, 11.
- Yang Y, Saatchi SS, Xu L et al. (2018) Post-drought decline of the Amazon carbon sink. *Nature Communications*, **9**.
- Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB (2011) Changes in the potential distribution of humid tropical forests on a warmer planet. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 137–160.

### 2 DROUGHT-INDUCED AMAZONIAN WILDFIRES INSTIGATE A DECADAL-SCALE DISRUPTION OF FOREST CARBON DYNAMICS

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# Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics

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## 2.1 ABSTRACT

Drought-induced wildfires have increased in frequency and extent over the tropics. Yet, the long-term (greater than 10 years) responses of Amazonian low-land forests to fire disturbance are poorly known. To understand post-fire forest biomass dynamics, and to assess the time required for fire-affected forests to recover to pre-disturbance levels, we combined 16 single with 182 multiple forest census into a unique large-scale and long-term dataset across the Brazilian Amazonia. We quantified biomass, mortality and wood productivity of burned plots along a chronosequence of up to 31 years post-fire and compared to surrounding unburned plots measured simultaneously. Stem mortality and growth were assessed among functional groups. At the plot level, we found that fire-affected forests have biomass levels 24.8±6.9% below the biomass value of unburned control plots after 31 years. This lower biomass state results from the elevated levels of biomass loss through mortality, which is not sufficiently compensated for by wood productivity (incremental growth þ recruitment). At the stem level, we

found major changes in mortality and growth rates up to 11 years post-fire. The post-fire stem mortality rates exceeded unburned control plots by 680% (i.e. greater than 40 cm diameter at breast height (DBH); 5–8 years since last fire) and 315% (i.e. greater than 0.7 g cm<sup>3</sup> wood density; 0.75–4 years since last fire). Our findings indicate that wildfires in humid tropical forests can significantly reduce forest biomass for decades by enhancing mortality rates of all trees, including large and high wood density trees, which store the largest amount of biomass in old-growth forests. This assessment of stem dynamics, therefore, demonstrates that wildfires slow down or stall the post-fire recovery of Amazonian forests.

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**Keywords:** post-fire dynamics, stem mortality, wood productivity, long-term recovery, fire disturbance, drought

## 2.2 INTRODUCTION

The successful reduction of the deforestation rate in the Brazilian Amazon between 2004-2017 has not been sufficient to reduce disturbance in the remaining forests (Aguiar *et al.*, 2016). Recent studies demonstrate that human-induced disturbances (e.g. wildfires and selective logging) can halve the conservation value and significantly decrease the carbon stocks of remaining Amazonian forests (Berenguer *et al.*, 2014; Barlow *et al.*, 2016; Longo *et al.*, 2016). Moreover, Amazonian forests affected by wildfires are estimated to contribute on average with  $31 \pm 21\%$  of the gross emission values from deforestation, with contributions beyond 50% during drought years (Aragão *et al.*, 2018b). Yet, there is a critical knowledge gap regarding the long-term recovery of carbon stocks in forests affected by anthropogenic disturbances such as fire (Aragão *et al.*, 2014; Berenguer *et al.*, 2014; Barlow *et al.*, 2016).

Humid tropical forests are not a fire-adapted ecosystem (Cochrane, 2003b; Power *et al.*, 2008). Previous studies suggested that wildfires in the Amazon basin have been rare since the start of the Holocene, with fire-return intervals exceeding centuries or millennia (Power *et al.*, 2008; McMichael *et al.*, 2012b). However, over the past three to four decades wildfires have become increasingly prevalent across humid tropical forests, including Amazonia (Jolly *et al.*, 2015b). These tropical fires generally require an anthropogenic source to ignite, which generally comes from agricultural practices (Uhl & Kauffman, 1990). The likelihood of wildfires occurrence is

also increased by forest disturbance, such as selective logging (Uhl & Buschbacher, 1985), and by deforestation that exposes remaining forests to edge effects (Alencar *et al.*, 2015) and reduces rainfall (Aragão, 2012; Spracklen *et al.*, 2012b). In addition, wildfires can be greatly exacerbated by extreme drought events (Uhl & Buschbacher, 1985; Alencar *et al.*, 2006; Aragão *et al.*, 2008; Gatti *et al.*, 2014; Anderson *et al.*, 2015b; Aragão *et al.*, 2018b). For example, during the 2015 El Niño-induced extreme drought 799,293 km<sup>2</sup> of the Brazilian Amazon experienced positive active fire anomalies (Aragão *et al.*, 2018b). Given that extreme droughts are predicted to occur at greater frequency in the Amazon Basin (Malhi & Wright, 2004), wildfires are likely to become even more pervasive (Silvestrini *et al.*, 2011).

These wildfires have a major impact on forest carbon stocks, accounting for the mortality of up to 36% of tree stems and 67% of the biomass loss in central Amazonian forests three years after fires (Barlow *et al.*, 2002; Barlow & Peres, 2006). Fire-affected forests consequently become a global important carbon source: based on the 2010 fire season, it was estimated that 27,555 km<sup>2</sup> of old-growth forests burned in the whole Brazilian Legal Amazon, contributing to 14.8Tg of C emissions to the atmosphere from direct combustion of organic material (Anderson *et al.*, 2015b). Immediately combustible carbon stocks – such as leaf litter and fine woody debris – make up only a very small proportion of forests aboveground carbon stock (Berenguer *et al.*, 2014) and most emissions are committed (0.001 to 0.165 Pg of C), as they are likely to occur years after wildfires as a result of vegetation mortality and its subsequent decomposition (Alencar *et al.*, 2006).

Despite the growing prevalence and importance of wildfires in humid tropical forests, our knowledge of their ecological consequences is constrained by the lack of data in three key areas. First, the longer-term effects of wildfires on forest biomass is not known as most studies to date have focussed on relatively short-term responses of vegetation to fire (Barlow *et al.*, 2012; Sato *et al.*, 2016; Numata *et al.*, 2017; Rappaport *et al.*, 2018). For example, a pan-

tropical assessment suggests there is no recovery of forest carbon stocks within at least five years (de Andrade *et al.*, 2017), while a study on flooded Amazonian forests highlight the potential for fires to impede forest succession in the first 15 years after fire (Flores *et al.*, 2016a). Second, most assessments are one off inventories, meaning ecological processes and stem dynamics in fire-affected forests are very poorly understood. Extensive field assessments in undisturbed Amazonian forests show the importance of repeat surveys, which have enabled researchers to link the spatial variation of forest biomass to stem dynamics such as mortality and recruitment (Baker *et al.*, 2004; Johnson *et al.*, 2016). Finally, there is no data linking post-fire long-term forest dynamics with functional traits. Plant traits such as bark thickness and wood density provide important insights into post-fire changes and the susceptibility of forest ecosystems (Pinard & Huffman, 1997; Barlow *et al.*, 2003c; Midgley *et al.*, 2011; Brando *et al.*, 2012b; Pausas, 2015), especially as they are directly related to carbon storage function (Chave *et al.*, 2014). Recently, an assessment of the impacts of fire and other forest disturbances has shown that wood density remains below baseline conditions for at least 25 years following disturbance, indicating a slow recovery or impeded succession (Berenguer *et al.*, 2018a). Longer term assessments of forest dynamics could provide additional insights into the successional trajectories of burned forests, and their ability to recompose carbon stocks.

We address these knowledge gaps by using a unique large-scale and long-term assessment of forest dynamics, which is based on a set of chronosequences and re-census data from burned and unburned forests in five distinct regions of the Brazilian Amazon. We ask two main research questions:

i) What are the longer-term effects of wildfires on forest biomass (i.e. up to 31 years after the fires)? We address this question by comparing, at the plot-level, the total aboveground biomass, and forest dynamics represented by mortality and wood productivity, between burned and unburned forests. The balance between tree mortality and productivity defines the ability of

these fire-affected forests to recover to pre-disturbance carbon levels and offset carbon emissions.

ii) How do wildfires affect forest growth, recruitment and mortality at stem-level, and what insights do key structural traits such as wood density and stem size (Diameter at Breast Height) provide into the mechanisms underpinning the changes in biomass? We focus on wood density and size because both are important predictors of short-term fire-induced mortality (Barlow *et al.*, 2003c; Brando *et al.*, 2012b) and both are linked to stem growth rates and carbon storage in undisturbed forests (Baker *et al.*, 2003; Fauset *et al.*, 2015). We divided stems into three classes of wood density and size to examine the changes in the probability density functions of growth, recruitment and mortality over time since fire degradation.

Finally, we combine results from both questions to discuss to what extent Amazon forests are recovering from fires.

## 2.3 MATERIALS AND METHODS

### 2.3.1 *Experimental design for field data collection*

We used tree inventory data collected as part of the Fire-Associated Transient Emissions in Amazonia (FATE) network. Since 2009, the FATE network has been monitoring permanent forest plots established in burned forests with different times since wildfire occurrence. Here, we collected and analysed field data from 64 permanent plots across Amazonia, from which we revisited and re-measured 55. All plots are located on old growth non-flooded forests (*Terra Firme*) with 269.3 m median distance from the edge. We examined the terrain elevation and slope within 100 m buffer of each plot using a high resolution (12.5m) digital elevation model (ALOS PALSAR RTC). There is very small slope across the plots (range: 2.8° – 9.4°). Plots ranged from 0.25 to 1 ha. From a total of 64 plots, 29 are in unburned and 35 plots are in burned forests (supplementary material table S1).

We selected burned forest sites based on the inspection of Landsat images (1984-2016) followed by on-the-ground field confirmation. When we did not find evidence of fire in the satellite image for a specific site, but there was charcoal in the ground, we assumed the fire event occurred at the time of the earliest image (i.e. 1984). Because of the high intensity of the 1982-83 El Niño event, when 3.6 million ha were burned in East Kalimantan (Kinnaird & O'Brien, 1998), it is likely that several forested areas elsewhere were affected by wildfires during this period. To enable pairwise comparisons between burned and unburned control sites, both were selected to avoid other anthropogenic disturbances such as selective logging. The unburned control plots, moreover, were carefully chosen to encompass a similar range and heterogeneity of both soils and topography as the burned sites. Independent proxies of fire intensity, such as char height, are not available for plots assessed a long time after fires when many of the affected trees will have died and decomposed. Without this additional information, we assume that all plots were subjected to low intensity understorey wildfires that are the norm in previously undisturbed forests.

Our 31 years chronosequence dataset captures the effect of wildfires driven by El Niño events and North tropical Atlantic warming since the 1980s. The distribution of the FATE plots reflects the spatial occurrence of these major wildfire events (e.g. figure 2.1a) and accessibility. In order to link drought intensity over the last 40 years with wildfire extent, we used re-analysis derived data to calculate Maximum Climatological Water Deficit (MCWD) and satellite derived products of burned area (please see detailed methods in supplementary material method S.1). The data extracted from each plot location, along the burned area and MCWD time series, shows the association between MCWD and burned area at all plots region (figure 2.1b). Figure 1b also demonstrates when each site was sampled relative to the last fire event.

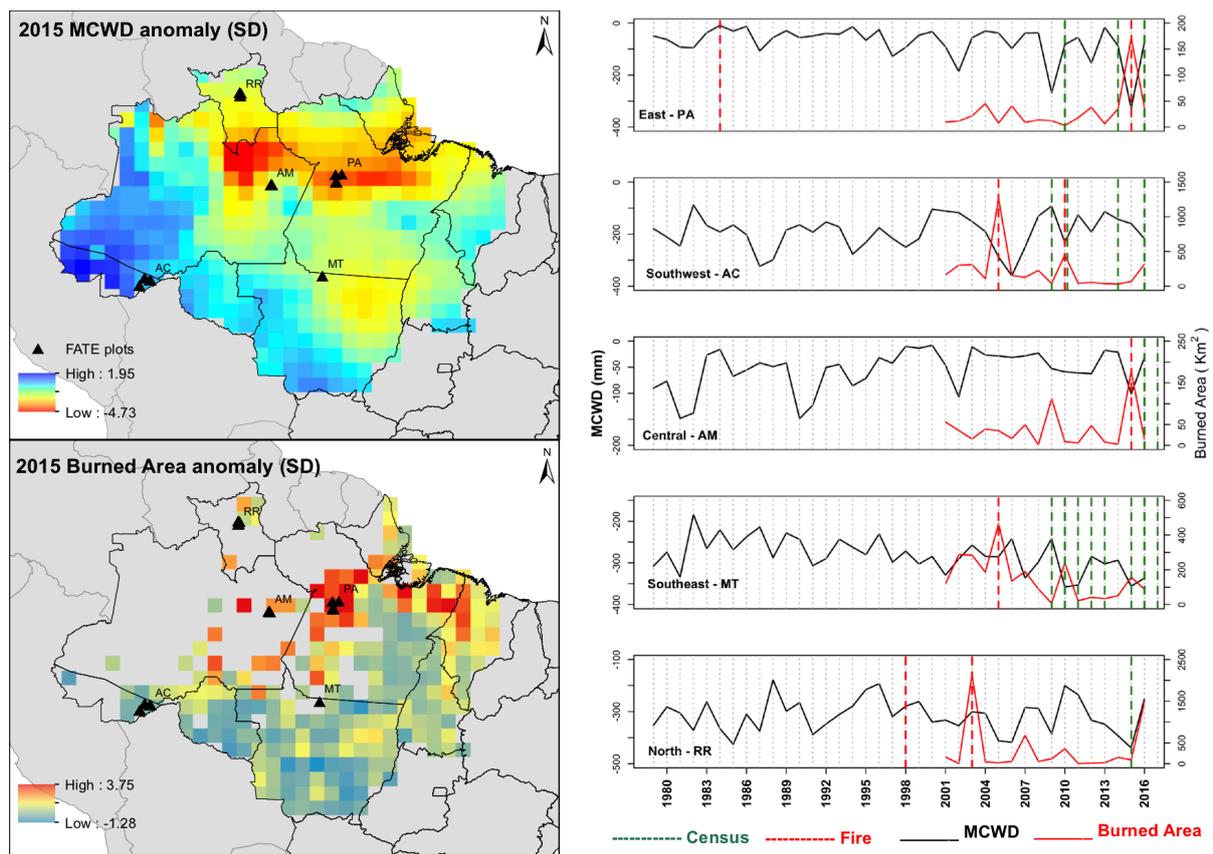


Figure 2.11 Tree inventory plots and overlap of Maximum Cumulative Water Deficit (MCWD) and Burned area (BA) anomalies (sd) over Brazilian Amazon region. MCWD was derived from ERA-Interim and BA derived from MODIS (detailed methods in supplementary material S.1). Left panel: MCWD red values representing extreme drought, or negative anomalies (sd) in relation to 1979-2016 period; BA red values representing extreme large affected areas, or positive anomalies (sd) in relation to 2001-2016 period. Right panel: MCWD and BA variation over time extracted from each plots region, year of the tree inventory and year of fire.

### 2.3.2 Field inventory and total aboveground biomass

The inventory was conducted following the RAINFOR network protocol for the establishment of permanent sample plots (Phillips *et al.*, 2009a). We estimated aboveground biomass (AGB) of 9,836 live trees, palms and lianas with diameter at breast height (DBH)  $\geq 10$  cm. For both burned and unburned forests, total aboveground biomass (TAGB) represent the sum of all trees, palms and lianas AGB, and was estimated using a specific allometric equation for each group,

following (Chave *et al.*, 2014) for trees, (Goodman *et al.*, 2013) for palms, and (Gerwing & Farias, 2000) for lianas. The AGB estimates for palms and lianas were based solely on their diameter, whilst for trees DBH and specific wood density values were used as input variables. We used the global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009) to match specific wood density to each species. For individuals not identified to the species level (~5%), we used the mean value for the species belonging to that genus. Similarly, we used the mean specific wood density of the family for trees not identified at the genus level (Baker *et al.*, 2004). When an accurate identification was not achieved, the plot mean specific wood density was used.

### 2.3.3 *Plot-level assessment of long-term effects of wildfires on forest biomass*

#### 2.3.3.1 QUANTIFICATION OF PLOT-LEVEL FOREST DYNAMICS

To understand the response of old growth forests to wildfires, we evaluated the long-term shifts in forest dynamics at the plot-level. We quantified for all burned and unburned plots the net biomass change (Net TAGB), which is a function of wood productivity (Wp) and mortality (M) of all stems in the plot (Equation 2.1).

$$\text{Net TAGB} = \Sigma Wp - \Sigma M \quad (2.1)$$

The term  $\Sigma M$  corresponds to plot mortality ( $\text{Mg ha}^{-1} \text{y}^{-1}$ ), which was calculated as the amount of the biomass of all stems recorded as dead within a given census interval. The term  $\Sigma Wp$  corresponds to the sum of the values of Wp for all measured stems in the plot and can be decomposed as (Equation 2.2).

$$\Sigma Wp = \Sigma \text{Recruits} + \Sigma \text{Growth} \quad (2.2)$$

$W_p$  ( $\text{Mg ha}^{-1} \text{y}^{-1}$ ) was calculated as the sum of the biomass of stems that recruited during each census interval ( $\Sigma\text{Recruits}$ ) and the sum of the growth in biomass of each stem present in the plot ( $\Sigma\text{Growth}$ ) during this same census interval.

Because census interval varied among plots, rates were weighted by the census interval length. In order to account for trees that both recruited and died during the census interval and also to correct for tree growth prior their death,  $M$  and  $W_p$  values were corrected at a tree-by-tree basis, following methods of (Talbot *et al.*, 2014).

### 2.3.3.2 QUANTIFICATION OF DIFFERENCES BETWEEN BURNED AND UNBURNED FORESTS

To assess if TAGB and dynamics from burned forests recovered to pre-disturbance levels, we quantified the percent of difference between burned and unburned forests. For TAGB and each dynamic parameter, the proportional difference between each burned plot and the mean of unburned plots, was calculated as described below (Equation 2.3):

$$\% \Delta X = \frac{(X_{\text{BU}(i)} - X_{\text{UB}(\text{mean})})}{X_{\text{UB}(\text{mean})}} 100 \quad (2.3)$$

where  $X$  represents the variable of interest (TAGB,  $M$ ,  $W_p$ , and Net TAGB),  $\text{BU}_{(i)}$  is each of the burned plots, and  $\text{UB}_{(\text{mean})}$  is the local mean of all unburned plots sampled in the same region at the same time as the burned plots. The error is presented as standard error of the mean (SE).

### 2.3.3.3 LONG-TERM TRAJECTORIES OF BURNED FORESTS TAGB AND DYNAMICS

We used Generalized additive mixed models (GAMM) to assess the trajectories of TAGB, mortality,  $W_p$  and Net TAGB over the time since last fire chronosequence. We used each individual plot measured repeatedly as a random effect. To assess the direction of the difference (%) in each variable in relation to the control-unburned forests, we used the local polynomial

regression fit (LOESS), choosing the span values based on the minimum residual standard error obtained. All statistical analyses were performed in R 3.3.3 using *gamm4* and *lme4* R packages.

#### 2.3.4 *Stem-level assessment of growth, recruitment and mortality*

To explore the structural and successional mechanisms driving the long-term changes on TAGB of burned forests, we assessed the empirical probability density function of stem mortality rate and stem growth in three DBH (cm) classes: 10.0 to 19.9, 20 to 39.9 and >40.0; and three specific wood density ( $\text{g cm}^{-3}$ ) classes: 0.1 to 0.49, 0.5 to 0.69 and > 0.7 for both burned and unburned plots. Including all plots from all regions, we divided the dataset into four categories considering the years since last fire (YSLF): 0.75-4; 5-8; 9-11; 12-31 years. For each plot we calculated stem mortality as the exponential mortality coefficient ( $\%y^{-1}$ ) (Sheil & May, 1996), mean stem growth as the annual mean growth ( $\text{cm y}^{-1}$ ) of all living individuals, and stem recruitment as the percentage rate of stems recruited relative to live stems in each census ( $\%y^{-1}$ ). Stem mortality and stem growth from each plot were stratified by classes of diameter, wood density and YSLF. Stem recruitment by plot was stratified by YSLF class, but we only used a grouping based on wood density class, as all recruitment falls into the smallest DBH class. The probability density functions of the unburned and burned plots were compared using the Wilcoxon test for two samples.

## 2.4 RESULTS

### 2.4.1 *The long-term effects of wildfires on forest biomass at plot-level*

During the monitoring period, the biomass of unburned forest plots remained generally unchanged, with exception of forest plots from southeast and east Amazonia that have experienced high mortality in the drought years of 2015 ( $15.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ;  $n=4$ ) and 2016 ( $9.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ;  $n=20$ ) respectively (supplementary material, table S2). In contrast, the biomass of burned forest plots changed greatly with time since fire (table 2.1). Immediate fire effects on TAGB were smaller, with reduction of  $-2.1 \pm 3.9\%$  up to four years post-fire. From 5-8 years since fire, we found a much greater difference in TAGB, with reduction of  $-22.1 \pm 2.9\%$  in burned plots compared to unburned controls. The significantly lower biomass persisted up to 31 years post-fire, when burned plots remained  $24.8 \pm 6.9 \%$  below the baseline value of the control plots (figures 2.2a, 2.2e).

Table 2.1 Mean difference in % ( $\pm$ SE) between each burned plot and unburned mean values of TAGB, mortality, wood productivity (increment and recruitment values in table S3, supplementary material) and Net TAGB.

YSLF categories	Census year	TAGB Stock		TAGB Dynamics			
		TAGB $\Delta\%$	N	Mortality $\Delta\%$	Wood productivity $\Delta\%$	Net TAGB $\Delta\%$	N
(0.75 to 4)	2009; 2011; 2014; 2015; 2016	-2.1(3.9)	42	199.2 (43.5)	4.0(6.9)	-1308.4 (263.1)	17
(5 to 8)	2010; 2011; 2012; 2013; 2016	-22.1(2.9)	26	247.4 (135.6)	30.0(7.8)	-26.8 (212.1)	26
(9 to 11)	2014; 2015; 2016	-17.1(2.9)	12	-8.6 (10.8)	16.7(11.2)	-45.5 (57.2)	12
(12 to 31)	2010; 2014; 2016; 2017	-24.8(6.9)	20	20.7 (33.7)	8.9(8.7)	105.0 (183.3)	10

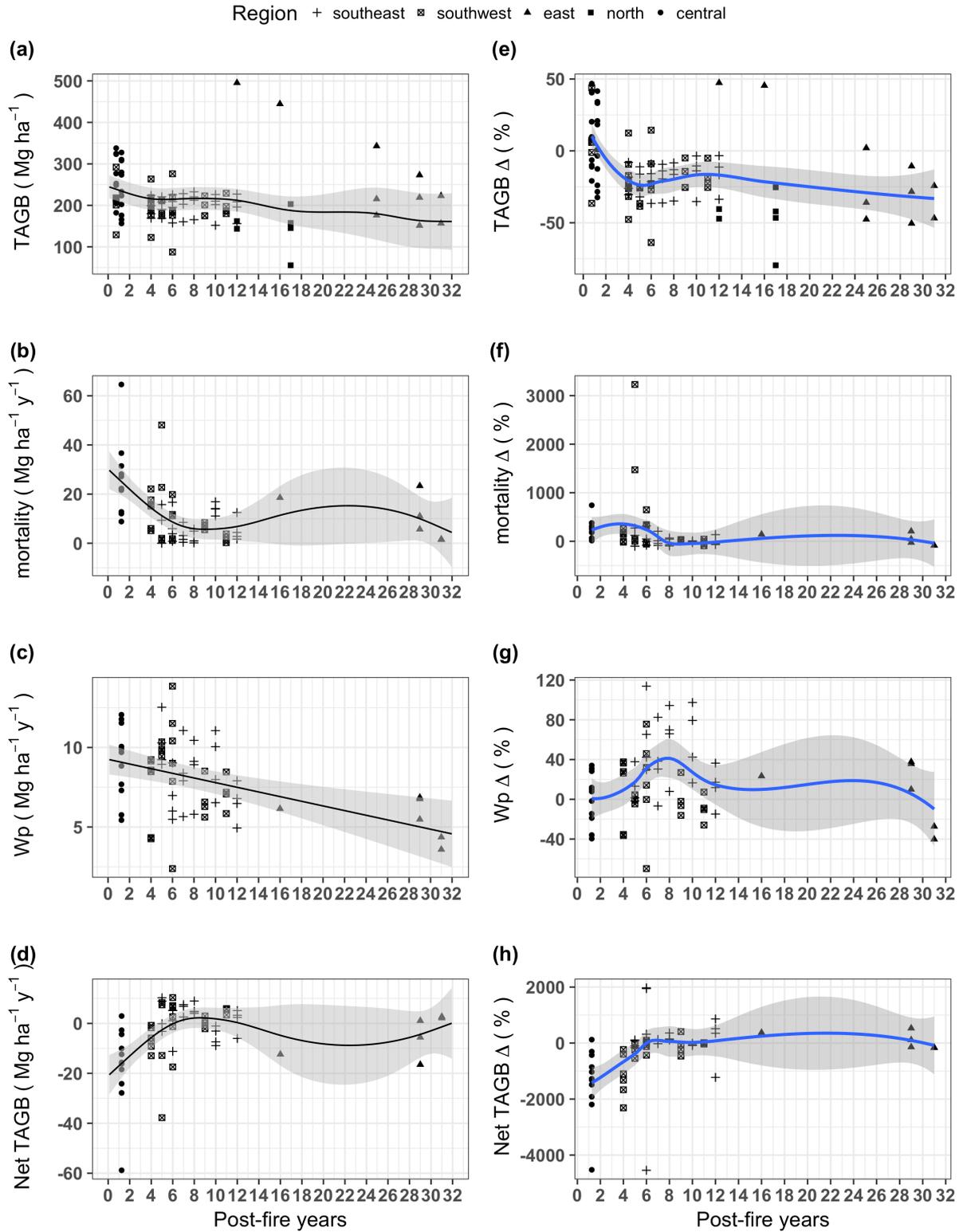


Figure 2.2 GAMM fitted models of burned forests pathways by dependent variables: (a) Total Aboveground Biomass (TAGB), (b) Mortality, (c) Wood productivity (Wp) and (d) Net TAGB; and LOESS fit for percent difference of each variable in relation to unburned forest (e-h).

### 2.4.2 *Uncertainties*

Across pools, the largest uncertainties (table 1) are associated with mortality, due to the large influence exerted by the death of a single large tree. Temporally, and for all variables, there were large uncertainties from 16 to 27 years after fire, where data was lacking (Figures 2.2a-2.2h). It is reassuring that the trajectories predicted along the chronosequence using the GAMM model and LOESS fit agree. All GAMM fitted models intercept and smooth component (YSLF) are statistically significant (table 2.2). While all models are significant (supplementary material, figure S1), residual variability may be associated to the “random” deviations from the predicted values that are not due to plots’ specificities and/or YSLF, suggesting possible association with fire intensity and environment conditions. Accordingly, the large TAGB and mortality variability observed across the plots explains the higher Std. Error found in the intercept and slope of TAGB and mortality models. The fitted model’s effective degrees of freedom values consistently show that burned forests TAGB, mortality and Net TAGB response to time is non-linear, while Wp is linear. For Wp the effective degrees of freedom is equal to 1 meaning linearity for Wp in relation to time.

Table 2.2 GAMM models output by fixed term for intercept and the smooth term YSLF.

		<b>TAGB</b>	<b>Mortality</b>	<b>Wp</b>	<b>Net TAGB</b>
<b>Intercept</b>	Estimate	216.2	11.4	8.1	-3.3
	Std. Error	12.5	1.2	0.3	1.3
	Std. dev.	72.8	0	1.3	0
	Pr(> t )	<2e-16	2.71E-13	<2e-16	0.01
<b>Smooth term (YSLF)</b>	Estimate	-34.2	-21.4	-1.0	19.7
	Std. Error	17.9	9.6	0.3	9.7
	Std. dev.	102.7	22.5	0	22.6
	edf*	5.2	3.5	1	3.5
	p-value	0.000463	0.0002	0.00064	0.000119
<b>Residuals</b>	Std. dev.	12.3	9.9	1.8	10.2

\* effective degrees of freedom

### 2.4.3 *Mortality, recruitment and growth rates at stem-level*

Wildfires had persistent effects on burned forest dynamics at stem-level: from a total of 48 comparisons between burned and unburned forests of stem mortality and growth, 16 were significant ( $p < 0.05$ ), and another five were marginally significant at  $p < 0.10$  (figure 2.3 and 2.4). These significant results were distributed across all classes of time since last fire disturbance, and all classes of tree size and wood density.

Stem mortality was skewed towards zero, but still higher in burned forests when compared to unburned forests. The significantly higher stem mortality was observed across all tree size and wood density classes – but not in all YSLF categories (figure 2.3a, 2.4a). The largest stem mortality differences between burned and unburned forests were observed at 0.75-4 YSF. On average  $22.8 \pm 2.4\%$  of trees from small classes of size (i.e. 10-19.9 cm DBH) and  $23.8 \pm 5.0\%$  of trees with the lightest wood density (i.e. 0.1-0.49 g cm<sup>-3</sup>) died during 0.75-4 YSLF – these mortality rates were 341% and 239% higher than the equivalent size and wood density classes in unburned controls. However, the larger size stems (i.e. >40cm DBH; 5-8 YSLF) and higher wood density classes (i.e. >0.7 g cm<sup>-3</sup>; 0.75-4 YSLF) were also significantly affected in burned forest, being 680% and 315% higher than unburned controls, respectively. Between 9-11 years since the wildfires, small size stems (i.e. 10-19.9 cm DBH) and stems from small (i.e. 0.1-0.49 g cm<sup>-3</sup>) and medium (i.e. 0.5-0.69 g cm<sup>-3</sup>) classes of wood density experienced significant higher mortality in burned forests – these mortality rates were 74%, 173% and 69% higher than unburned controls, respectively.

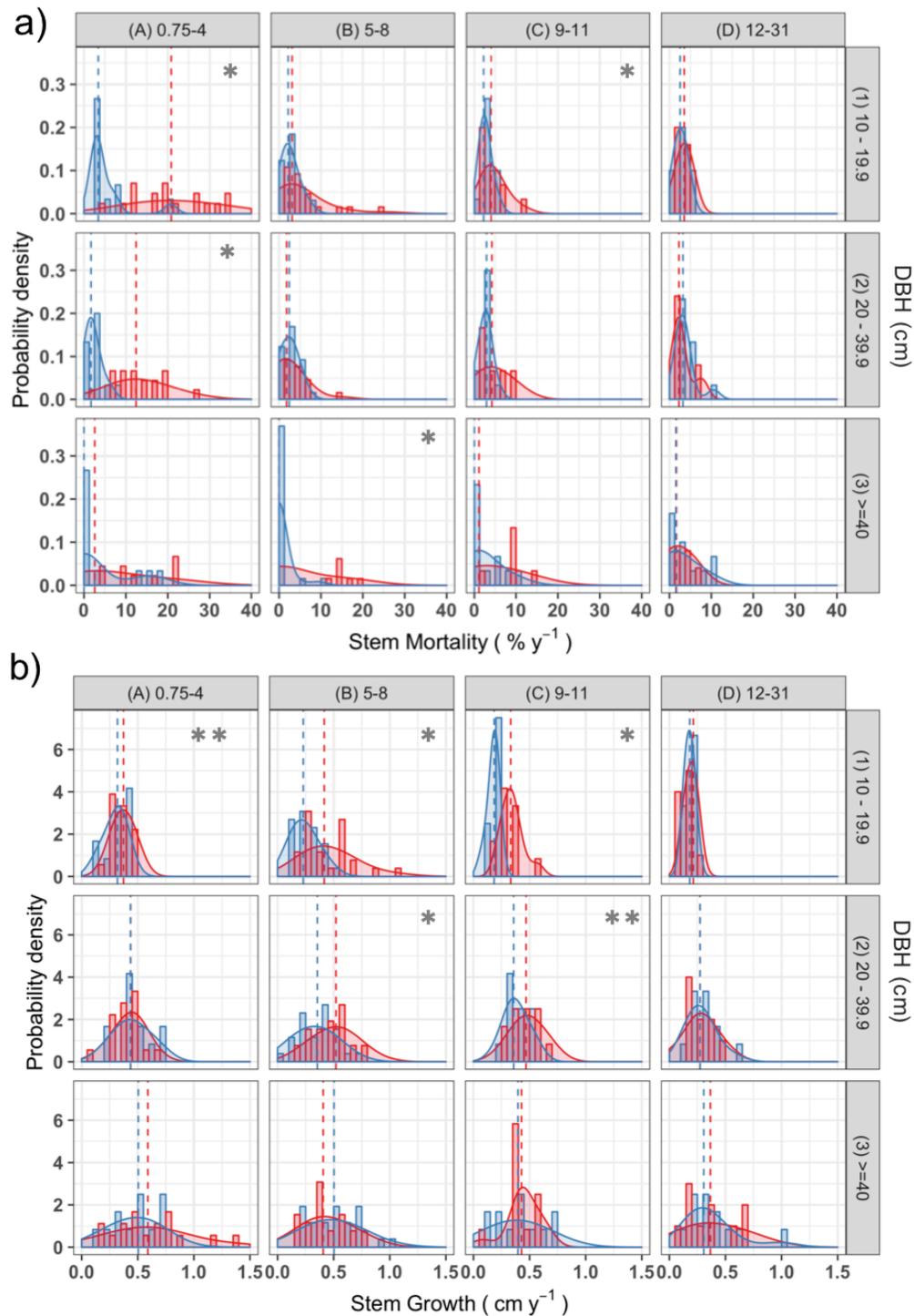


Figure 2.3 Probability density function of: a) Stem Mortality (%y-1) and, b) Stem Growth (cm y-1) by Size classes (DBH: 10.0-19.9; 29.9-39.9; >40.0 cm) in lines and years since last fire (YSLF) classes (0.75-4; 5-8; 9-11; 12-31 years) in columns. Dashed lines represent median, red colour for burned and blue for unburned forests. Significance of Wilcoxon test is represented by: \*  $p < 0.05$  and \*\*  $p < 0.10$ .

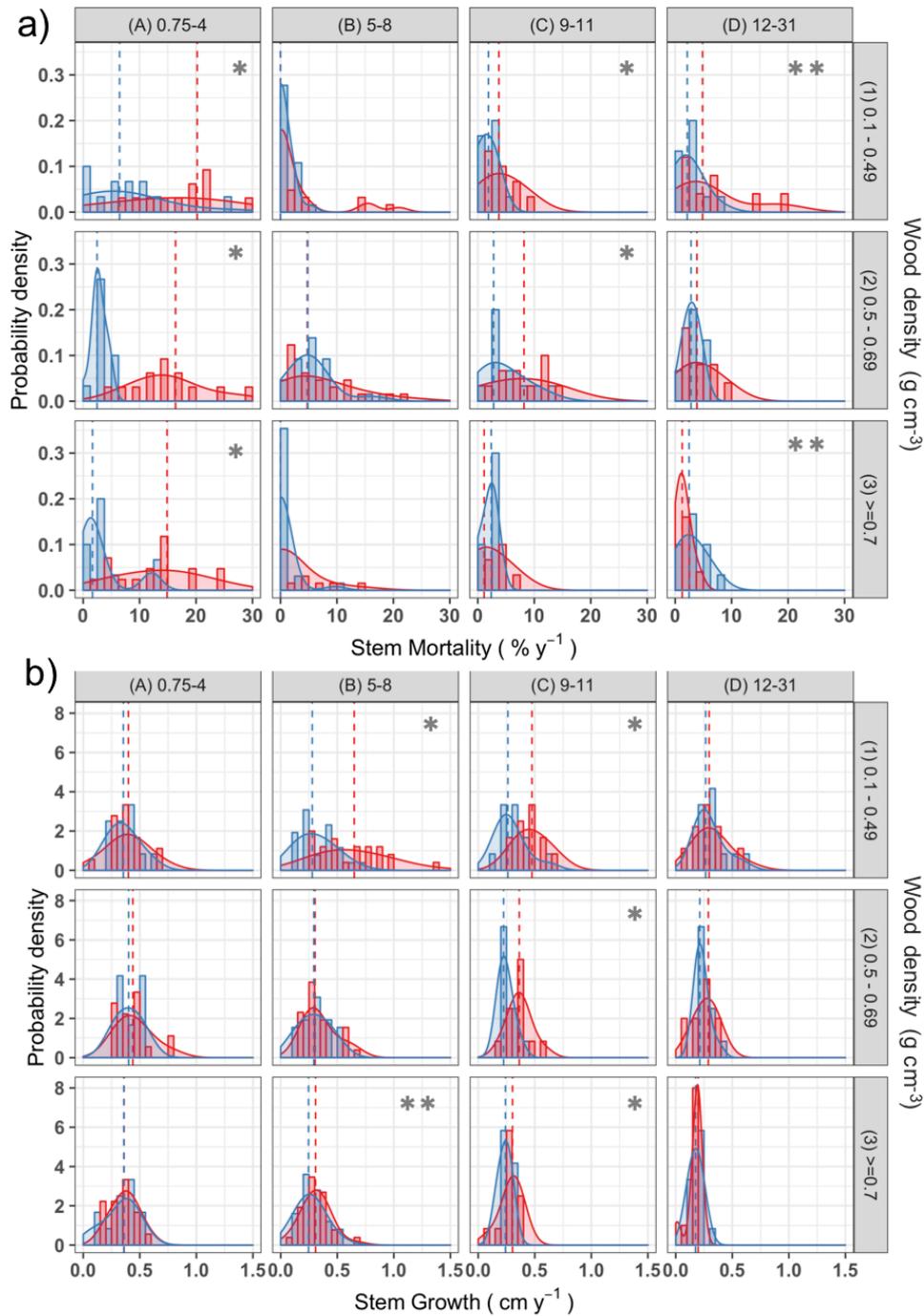


Figure 2.4 Probability density function classes of a) Stem Mortality in (%y-1) and, b) Stem Growth (cm y-1) by Wood Density (WD: 0.1- 0.49; 0.5-0.69; > 0.7 g cm-3) in lines and years since last fire (YSLF) classes (0.75-4; 5-8; 9-11; 12-31 years) in columns. Dashed lines represent median, red colour for burned and blue for unburned forests. Significance of Wilcoxon text is represented by: \* p<0.05 and \*\* p<0.10.

Stem growth followed a normal distribution, and the mean values of burned forests were generally higher than those in unburned forests (figure 2.3b, 2.4b). The greatest difference in stem growth was observed in the small and medium size classes: when compared to unburned controls, mean stem growth was 94.1 and 96.6% higher in burned forests for small size class in the 5-8 and 9-11 YSLF categories, respectively, and 54.2% and 27.0% higher in burned forests for the medium size classes at 5-8 and 9-11 YSLF categories, respectively. Similarly, for the class of low wood density, mean stem growth was 121.1% and 62.1% higher in burned forests than in unburned forests in the 5-8 and 9-11 YSLF categories, respectively. For medium wood density stems, mean stem growth was 50.0% higher in burned forests than in unburned forests at the 9-11 YSLF category. Finally, for high wood density stems, growth was 24.0% and 26.0% higher in burned forests than in unburned forests at 5-8 and 9-11 YSF, respectively.

Stem recruitment was skewed towards zero (supplementary material, figure S2). Overall, mean stem recruitment values were generally higher in burned than unburned forests up to 12 years since last fire (supplementary material, figure S3). There were no significant differences between recruitment in burned and unburned forests when separated by wood density classes.

## 2.5 DISCUSSION

We provide one of the longest post-fire chronosequence assessments of fire-affected Amazonian forests, analysing the most extensive dataset to date. Our findings reveal that burned Amazonian forests persist in a reduced biomass state for at least 31 years since last fire, at which point they store approximately 25% less above-ground biomass than equivalent unburned forests. This decrease in biomass is driven by increases in mortality that are not fully compensated for by the relatively small changes in recruitment and growth rates (table 2.1). The high mortality in burned forests was not exclusively limited to small diameter and light wood trees, but also includes the large-stemmed and hardwood trees which contribute most to

the carbon stock (Baker *et al.*, 2004; Slik *et al.*, 2013; Sist *et al.*, 2014). In contrast, the positive post-fire growth response was predominantly associated with small-medium sized trees and lighter or intermediate classes of wood density - groups that contribute relatively little to overall above-ground carbon stocks. We examine in more detail these findings to understand how the post-fire changes in dynamics rates influence forest biomass in the long-term, and how this is underpinned by mortality, recruitment and growth among functional groups. Finally, we discuss the prospects of long-term slow recovery of Amazonian fire-affected forests and the future of tropical humid forests under the risk of wildfires.

### 2.5.1 *Post-fire changes in forest dynamics and consequences for the long-term recovery of biomass stocks*

Our data show that long-term reduction on TAGB after fire is persistent, but the uncertainties inherent in space-for-time comparisons and delayed mortality of large trees mean it only became fully evident after five years of the fire events. After the initial fire-induced mortality, wood productivity rates in burned forests were higher than unburned controls probably because of the increase in light and nutrients availability to the remaining survivors' trees. However, this initial short-term increase in wood productivity (plot level biomass gain) does not exceed mortality (plot level biomass loss), and is insufficient to counteract the total biomass losses through mortality along the whole chronosequence. Previous studies have raised the question of whether enhanced forest growth, promoted by low-intensity fires, offsets carbon emissions due to post-fire tree mortality (Brando *et al.*, 2016b). Our assessment refutes that: although burned forests were no longer a net carbon source six years after fires, the lack of biomass accumulation from 6-31 years shows they will not recover to pre-fire conditions on decadal time-scales. Our findings also emphasize the importance of longer-term and larger-scale studies to monitor carbon dynamics in burned forests, which are particularly important for

incorporating the variation of mortality and growth rates in C emission models for the growing extent of fire-affected tropical forests.

### 2.5.2 *Post-fire mortality among functional groups with high contribution to biomass stocks*

Wildfires affected the stem mortality rates of small-medium sized trees and all wood density classes in the first YSLF category (0.75-4) of the chronosequence. An initial increase in the mortality of high wood density trees (315%) compared to unburned forests, combined with a late increase in the mortality of large-sized trees (680%), has important impacts upon overall aboveground biomass loss. A burned forest that lost its large-size (figure 2.3a) and high-wood density stems (figure 2.4a) will inevitably store less biomass that it did prior to disturbance (figures 2.2a, 2.2e). As well as corroborating previous studies on the late increase in mortality of large trees (Barlow *et al.*, 2002), we also show for the first time that this process can continue for up to eight years after fire – suggesting that almost all previous studies will have underestimated total biomass loss from fires.

Although previous findings show tree mortality decreased as a function of increasing wood density (Brando *et al.*, 2012b), we show that all wood density classes are at risk of fire-induced mortality, especially in the first 4 years after the burn. It is important to note, our results do not show higher susceptibility of high wood density trees compared to lower wood density trees to post-fire mortality, instead we show higher stem mortality of high wood density trees in burned forests compared to unburned controls. One explanation for this high post-fire mortality across wood density classes reflects the fact that the full range of wood densities can be found in the small (i.e. 10.0-19.9cm DBH) and medium (i.e. 20.0 – 39.9 cm DBH) size classes, which are the fire-susceptible groups. Smaller trees are shown to have thinner bark, which in turn are at more risk of heat stress and fire-induced mortality (Uhl & Kauffman, 1990; Barlow *et al.*, 2003c).

### 2.5.3 *Post-fire stem growth and recruitment*

The significant loss of large size and emergent trees is likely to have triggered the increase in the growth of light-dependent and fast-growing species. As expected, this increase in wood productivity is associated with the stem growth responses of small and medium size trees from all wood density classes, and to a lesser extent to stem recruitment. Although light availability is expected to also benefit new recruits (Walker & Moral, 2003), stem recruitment is less evident and not significantly higher than undisturbed forest in each individual wood density class. However, an ongoing successional process may be occurring within burned forests, as components of wood productivity (recruitment + growth) was higher compared to unburned forests (supplementary material, table S3, figure S3). Our results suggest that pioneer species are colonizing and growing after fire, maintaining a natural forest succession process after disturbance. For instance, the late stem mortality of small trees (i.e. 10-19.9 cm DBH; 9-11 YSLF) and stem growth at mid-long term (i.e. 5-8 and 9-11 YSLF) observed, supports the expected post-disturbance forest succession. However, it is expected that recruitment of old growth species is limited after fire disturbance which negatively affects the forest's ability to recover to its pre-disturbance functional state (Flores *et al.*, 2016a; Berenguer *et al.*, 2018b). Consequently, fire disturbances are likely to shift forest composition and dynamics for much longer than 30 years.

### 2.5.4 *Prospects for forest recovery beyond the time-scale of our data*

Although our data extend to 31 years post-fire, there are reasons to expect slow recovery for many decades beyond this timeframe. First, the Net TAGB in burned forests was close to unburned forests equilibrium in the long-term of the chronosequence, and did not provide any signs of continued recovery. For the recovery to occur gains would need to surpass loss during this stage. Second, the fires killed many large-size and high-wood density trees, which will take the longest to recover; perhaps unsurprisingly we also found that their re-establishment

will take longer than 31 years, and many could take centuries to recover, given the large trees age (200 to 1,400 yr) in undisturbed Amazonian forests (Chambers *et al.*, 1998). However, other unassessed factors could be important and are worthy of further investigation. For example, the destruction of the seedbank by fire and a low seedling survival may act to limit stem recruitment, as previously found in Amazonian flooded forest affected by fire in long-term (Flores *et al.*, 2016a). In addition, remaining seeds from shade-tolerant species have lower chances to germinate in larger canopy gaps (Denslow, 1987). Finally, the reduced biomass stock may result from the dominance of early successional species inhibiting emergent and shade-tolerant species on decadal time scales (Walker & Moral, 2003).

#### 2.5.5 *Post-fire forest recovery limitations and the future of tropical humid forests under the risk of wildfires*

Forest disturbance from fires may interact with a changing climate. For example, burned forests have a more open canopy which allows the entrance of solar radiation. The increasing temperature in the interior of burned forests results in the increase of vapour pressure deficit and evapotranspiration, further exacerbating soil drying (Cochrane, 2003b; Balch *et al.*, 2008). At the same time, the Amazon has seen an increase in drought conditions, limiting water availability (Malhi *et al.*, 2009) and potentially limiting the recruitment of trees (Phillips *et al.*, 2009b). Although Amazonian forests seem to be resilient to dry conditions, it is likely that water limitation can limit their recovery from fire-disturbances (Malhi *et al.*, 2009; Bush, 2017). Whether post-fire succession is permanently arrested or is just occurring at a very slow rate is difficult to ascertain based on the temporal scale of our dataset. As we only assessed individuals  $\geq 10$ cm DBH within 31 years of since the last fires, we are unlikely to detect longer term recovery or the reestablishment of slow growing (high wood density) species. Although, assessments of saplings and seed bank on disturbed Amazonian forests indicates a slowdown or stalled forest recovery (Flores *et al.*, 2016a; Berenguer *et al.*, 2018a). Nonetheless, it is

notable that the stabilisation of recovery after wildfires is in marked contrast to the consistent increases in forest biomass observed in the first decades after disturbance in selectively logged or secondary forests (Bonner *et al.*, 2013; Rutishauser *et al.*, 2015; Poorter *et al.*, 2016b).

## 2.6 CONCLUSIONS

Considering the increase in frequency and intensity of extreme events, such as the 2015/2016 El Niño, associated with increasing fire incidence (Aragão *et al.*, 2018b), our findings highlight the urgent need to avoid fires in humid tropical forests. Our study provides the largest ground-based assessment on patterns of post-fire forest recovery, which is particularly important considering the role of the Amazon in the global carbon cycle. Moreover, in our effort to cover the heterogeneity of once-burned forests subjected to similar fire intensities, our estimates describe a general response of Amazonian old growth *Terra Firme* forests to fire disturbance. However, it is important to state that in our study we investigated the effect of a single fire event on forest dynamics and biomass stocks through time. Recurrent fires are still somewhat rare in the Amazon – in 2010, they only accounted for 16% of all wildfires (Morton *et al.*, 2013). However, recurrent fires are likely to be increasingly prevalent across the Amazon, given the synergies between a drier and hotter climate, the pervasive use of fire in agriculture (Carmenta *et al.*, 2013), and the human-induced disturbances such as selective logging that turn forests more vulnerable to fires due to changes in the microclimate (Uhl & Kauffman, 1990; Berenguer *et al.*, 2014). The combination of these factors will also affect the ability of forests to recovery from fire disturbance.

## 2.7 ACKNOWLEDGMENTS

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## 2.8 SUPPLEMENTARY MATERIAL

**Method S1:** Description of methods applied for MCWD and Burned Area anomaly calculations in figure 2.1.

We used re-analysis data and satellite derived products of burned area to characterize the association between burned areas and drought affected regions over the Amazonia. To perform this analysis we calculated the Maximum Climatological Water Deficit (MCWD) anomalies for 2015 based on precipitation and evapotranspiration data from ERA-Interim reanalysis at 1° spatial resolution from 1979 to 2016 (Dee *et al.*, 2011). For calculation of burned area anomalies for 2015 we used data from MODIS (MCD64A1 product) at 500 m spatial resolution from 2001 to 2016 (Giglio *et al.*, 2006). We calculated MCWD as indicated by (Aragão *et al.*, 2007). Then we aggregated burned area at the MCWD 1° spatial resolution, so we assessed the total burned area for each grid-cell of MCWD. Both MCWD and burned area anomalies were then calculated for 2015 on a pixel-by-pixel basis, as the deviation from the long-term mean calculated from 1979 to 2016 (t) and 2001 to 2016 (t) respectively, normalized by the standard deviation ( $\sigma$ ) as following:

$$\mathbf{X \textit{ Anomaly}} (\mathbf{i, j}) = \frac{\mathbf{X(i,j)} - \mathbf{X(tx)}}{\sigma(\mathbf{tx})(\mathbf{i,j})}$$

Along the time series we plotted the data extracted from plots location and observed coincident peak of BA on the falls of MCWD at all plots region (figure 2.1).

Table S1 Description of permanent sample plots by region with respective Brazilian federal state, number of plots in burned (BU) and un-burned (UB) area, period of measurements, number of repeated census, Years since last fire disturbance (YSLF), total number of census in each region, plot size in hectare.

<b>Region</b>	<b>BU (N)</b>	<b>UB (N)</b>	<b>Census period</b>	<b>Census (N)</b>	<b>YSLF</b>	<b>Census Total</b>	<b>Plot size (ha)</b>
East (PA)	4	6	2010-2016	3	16-31	30	0.25
Central (AM)	11	6	2015-2016	2	0.75 – 1.25	34	0.25
North (RR)	6	3	2015	1	12-17	9	0.25
Southeast (MT)	4	4	2009-2017	7	4-12	56	0.25
Southwest (AC)	10	10	2009-2016	3	0.75-11	60	0.25; 1
<b>Total</b>	<b>35</b>	<b>29</b>	<b>2009-2017</b>	<b>16</b>	<b>0.75-31</b>	<b>189</b>	<b>–</b>

Table S2 Summary of mean values of TAGB stock and dynamics parameters, mortality (M), wood productivity (Wp) and Net TAGB, with s.d. values between parentheses for burned and unburned plots.

Type	Plots	Region	Census period	Census (N)	YSLF	TAGB (Mg ha <sup>-1</sup> )	M ((Mg ha <sup>-1</sup> y <sup>-1</sup> ))	Wp (Mg ha <sup>-1</sup> y <sup>-1</sup> )	Net TAGB (Mg ha <sup>-1</sup> y <sup>-1</sup> )
<b>Burned plots</b>	AFL_2a	southeast	2009-2017	7	4-12	226.3 (3.7)	8.4(5.4)	10.3(1.6)	1.8(4.0)
	AFL_2b	southeast	2009-2017	7	4-12	198.0 (11.3)	4.1(5.9)	8.3(1.8)	4.1(6.4)
	AFL_2c	southeast	2009-2017	7	4-12	209.0 (7.5)	5.1(6.2)	7.6(1.5)	2.5(6.2)
	AFL_2d	southeast	2009-2017	7	4-12	161.2 (6.7)	8(6.3)	6.5(1.4)	-1.4(6.4)
	BOL_4	southwest	2011-2016	3	0.75-6	277.2(14.4)	9.4(11.7)	8.1(0.4)	-1.2(11.2)
	BOL_5	southwest	2011-2016	3	0.75-6	113.0(22.4)	12.9(9.8)	3.3(1.3)	-9.5(11.1)
	BOL_6	southwest	2011-2016	3	0.75-6	186.5(12.9)	8.7(9.8)	8.7(0.3)	-0.005(10.1)
	HUM_2a	southwest	2009-2016	4	4-11	217.4(10.8)	3.5(2.0)	8.4(1.3)	4.9(3.0)
	HUM_2b	southwest	2009-2016	4	4-11	203.1(5.7)	3.5(4.3)	7.1(2.0)	3.6(5.1)
	HUM_2c	southwest	2009-2016	4	4-11'	179.4(6.4)	9.7(11.4)	7.5(2.2)	-2.2(9.6)
	HUM_2d	southwest	2009-2016	4	4-11	190.1(19.7)	19.3(25.0)	8.4(1.9)	-10.8(23.5)
	MUC_10	north	2015	1	17	157.5			
	MUC_11	north	2015	1	17	203.1			
	MUC_13	north	2015	1	12	162			
	MUC_14	north	2015	1	12	143.6			
MUC_6	north	2015	1	17	145.3				

Type	Plots	Region	Census period	Census (N)	YSLF	TAGB (Mg ha <sup>-1</sup> )	M ((Mg ha <sup>-1</sup> y <sup>-1</sup> )	Wp (Mg ha <sup>-1</sup> y <sup>-1</sup> )	Net TAGB (Mg ha <sup>-1</sup> y <sup>-1</sup> )
	MUC_7	north	2015	1	17	55.4			
	NOC_4	central	2015-2016	2	0.75-1.25	242.9(13.7)	28.1	9.6	-18.4
	NOC_5	central	2015-2016	2	0.75-1.25	332.6(7.4)	22	12	-10
	NOC_6	central	2015-2016	2	0.75-1.25	235.8(17.9)	31.4	7.2	-24.1
	NOC_7	central	2015-2016	2	0.75-1.25	316.8(9.2)	22.2	9.8	-12.3
	NOC_8	central	2015-2016	2	0.75-1.25	316.4(11.8)	21.6	5.4	-16.1
	NOC_9	central	2015-2016	2	0.75-1.25	275.2(2.3)	12.7	10	-2.7
	RCM_4	southwest	2011-2016	3	0.75-6	198.5(14.7)	13.3(2.4)	9.8(0.8)	-3.5(3.2)
	RCM_5	southwest	2011-2016	3	0.75-6	215.9(3.7)	3.1(2.8)	7.9(5.1)	4.7(7.9)
	RCM_6	southwest	2011-2016	3	0.75-6	190(24.3)	16.6(7.7)	11.5(3.3)	-5.1(11.1)
	TIC_4	central	2015-2016	2	0.75-1.25	278.1(1.9)	8.8	11.7	2.9
	TIC_5	central	2015-2016	2	0.75-1.25	173.8(11.7)	27.1	11.5	-15.6
	TIC_6	central	2015-2016	2	0.75-1.25	185.9(41.9)	64.6	5.7	-58.8
	TIC_7	central	2015-2016	2	0.75-1.25	204.6(3.3)	12	7.6	-4.3
	TIC_8	central	2015-2016	2	0.75-1.25	190.2(20.3)	36.6	8.8	-27.8
	TPJ_10	east	2010-2014	2	12-16	469.9(36)	18.5	6.1	-12.3

Type	Plots	Region	Census period	Census (N)	YSLF	TAGB (Mg ha <sup>-1</sup> )	M ((Mg ha <sup>-1</sup> y <sup>-1</sup> ))	Wp (Mg ha <sup>-1</sup> y <sup>-1</sup> )	Net TAGB (Mg ha <sup>-1</sup> y <sup>-1</sup> )
	TPJ_7	east	2010-2014	2	25-29	307.9(49.5)	23.3	6.8	-16.4
	TPJ_8	east	2010-2016	3	25-31	219(3.8)	3.5(3.0)	5.1(2.2)	1.6(0.7)
	TPJ_9	east	2010-2016	3	25-31	161.3(13.1)	6.3(6.6)	4.9(0.8)	-1.4(5.9)
<b>Unburned plots</b>	AFL_1a	southeast	2009-2017	7		264.3(9)	3.9(1.5)	7(2.1)	3.1(1.8)
	AFL_1b	southeast	2009-2017	7		209.4(15.6)	6.3(8.3)	5.6(1.8)	-0.7(8.7)
	AFL_1c	southeast	2009-2017	7		292.5(4.7)	6.1(4)	5.9(1.7)	-0.2(4.6)
	AFL_1d	southeast	2009-2017	7		213.6(17.3)	6.8(8.2)	5.4(1.6)	-1.5(8.6)
	BOL_1	southwest	2011-2016	3		141.9(11.6)	1(0.1)	6(0.7)	4.9(0.5)
	BOL_2	southwest	2011-2016	3		236.1(12.8)	4.7(3.8)	9.4(0.9)	4.7(2.9)
	BOL_3	southwest	2011-2016	3		249.5(14.4)	1.5(1.2)	6.7(1.2)	5.2(2.5)
	HUM_1a	southwest	2009-2016	4		297.2(7.6)	4.2(5.5)	7.7(1.2)	3.5(6.8)
	HUM_1b	southwest	2009-2016	4		269.9(25.8)	1.4(1.7)	10.4(1.6)	9(2.4)
	HUM_1c	southwest	2009-2016	4		263.4(69.1)	15.2(17.8)	8(4.5)	-7.3(20.9)
	HUM_1d	southwest	2009-2016	4		258.5(14.5)	1.9(1)	6.9(2)	5(1)
	MUC_1	north	2015	1		332.8			
	MUC_2	north	2015	1		195.3			
	MUC_3	north	2015	1		287.9			

Type	Plots	Region	Census period	Census (N)	YSLF	TAGB (Mg ha <sup>-1</sup> )	M ((Mg ha <sup>-1</sup> y <sup>-1</sup> )	Wp (Mg ha <sup>-1</sup> y <sup>-1</sup> )	Net TAGB (Mg ha <sup>-1</sup> y <sup>-1</sup> )
	NOC_1	central	2015-2016	2		311.1(0.6)	8.7	10	1.2
	NOC_2	central	2015-2016	2		314.2(5.7)	1.5	9.8	8.3
	NOC_3	central	2015-2016	2		216.6(2.3)	6	9.4	3.4
	RCM_1	southwest	2011-2016	3		339.3(13.6)	2(2.7)	10.8(1.7)	8.7(4.4)
	RCM_2	southwest	2011-2016	3		104.7(7.7)	1.8(0.7)	4.7(0.1)	2.8(0.5)
	RCM_3	southwest	2011-2016	3		215.5(4.8)	1.1(0.8)	5(0.4)	3.8(1.3)
	TIC_1	central	2015-2016	2		213.4(3.6)	2.2	7.5	5.2
	TIC_2	central	2015-2016	2		165.1(3.3)	14.7	10.4	-4.3
	TIC_3	central	2015-2016	2		163.8(4.4)	12.6	6.5	-6.1
	TPJ_1	east	2010-2016	3		371.6(30.5)	15.9(9.5)	3.8(0.8)	-12.2(10.3)
	TPJ_2	east	2010	1		231.8			
	TPJ_3	east	2010-2016	3		204(10.2)	4.5(2)	8.2(2.8)	3.7(0.7)
	TPJ_4	east	2010-2016	3		313.1(10.6)	4.6(5)	5(1.2)	0.3(6.3)
	TPJ_5	east	2010-2016	3		333.7(15.1)	9.8(0.04)	4.9(0.4)	-5(0.3)
	TPJ_6	east	2010	1		518.4			

Table S3 Summary of LOESS model's parameters

<b>LOESS model for TAGB ~ Years since last fire</b>	
Number of Observations: 100	
Equivalent Number of Parameters: 4.73	
Residual Standard Error: 21.16	
Trace of smoother matrix: 5.17 (exact)	
Control settings:	
span : 0.75	
degree : 2	
family : gaussian	
surface : interpolate	cell = 0.2
normalize: TRUE	
parametric: FALSE	
drop.square: FALSE	

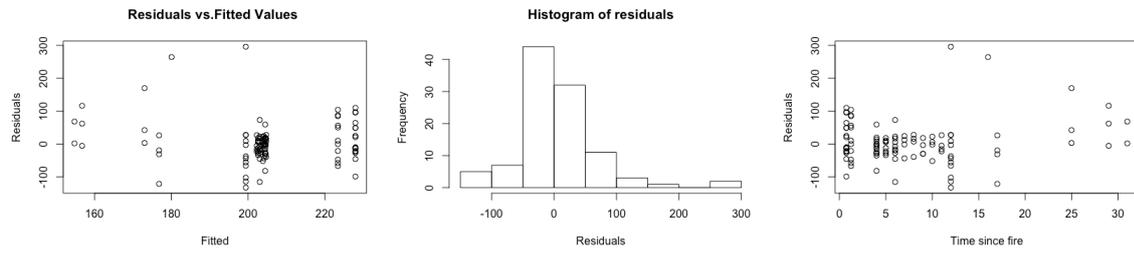
<b>LOESS model for Mortality ~ Years since last fire</b>	
Number of Observations: 65	
Equivalent Number of Parameters: 5.34	
Residual Standard Error: 452.6	
Trace of smoother matrix: 5.86 (exact)	
Control settings:	
span : 0.75	
degree : 2	
family : gaussian	
surface : interpolate	cell = 0.2
normalize: TRUE	
parametric: FALSE	
drop.square: FALSE	

<b>LOESS model for Wood Productivity ~ Years since last fire</b>	
Number of Observations: 65	

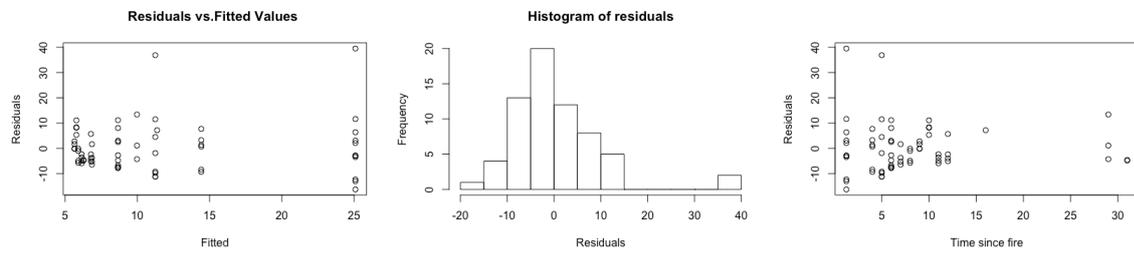
Equivalent Number of Parameters: 5.34	
Residual Standard Error: 34.34	
Trace of smoother matrix: 5.86 (exact)	
Control settings:	
span : 0.75	
degree : 2	
family : gaussian	
surface : interpolate	cell = 0.2
normalize: TRUE	
parametric: FALSE	
drop.square: FALSE	

<b>LOESS model for Net TAGB ~ Years since last fire</b>	
Number of Observations: 65	
Equivalent Number of Parameters: 5.34	
Residual Standard Error: 953.2	
Trace of smoother matrix: 5.86 (exact)	
Control settings:	
span : 0.75	
degree : 2	
family : gaussian	
surface : interpolate	cell = 0.2
normalize: TRUE	
parametric: FALSE	
drop.square: FALSE	

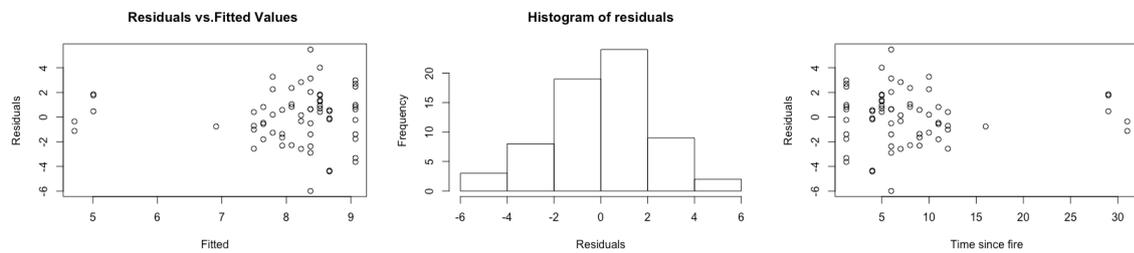
# TAGB



# Mortality



# Wp



# Net TAGB

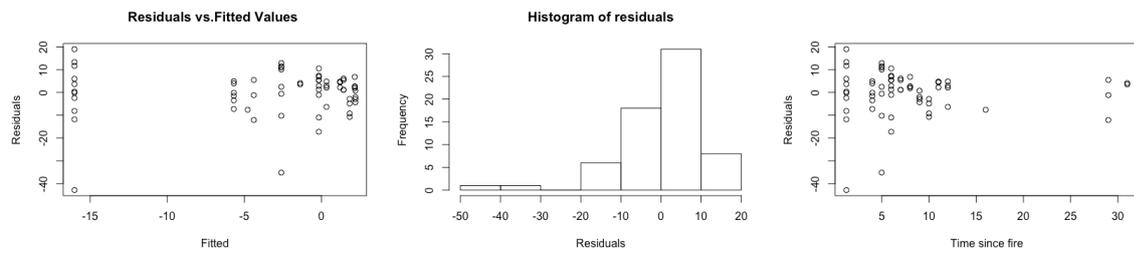


Figure S1 The General Additive Mixed Model validation graphs for TAGB, mortality, Wp and Net TAGB: Residuals homogeneity, normality and independency.

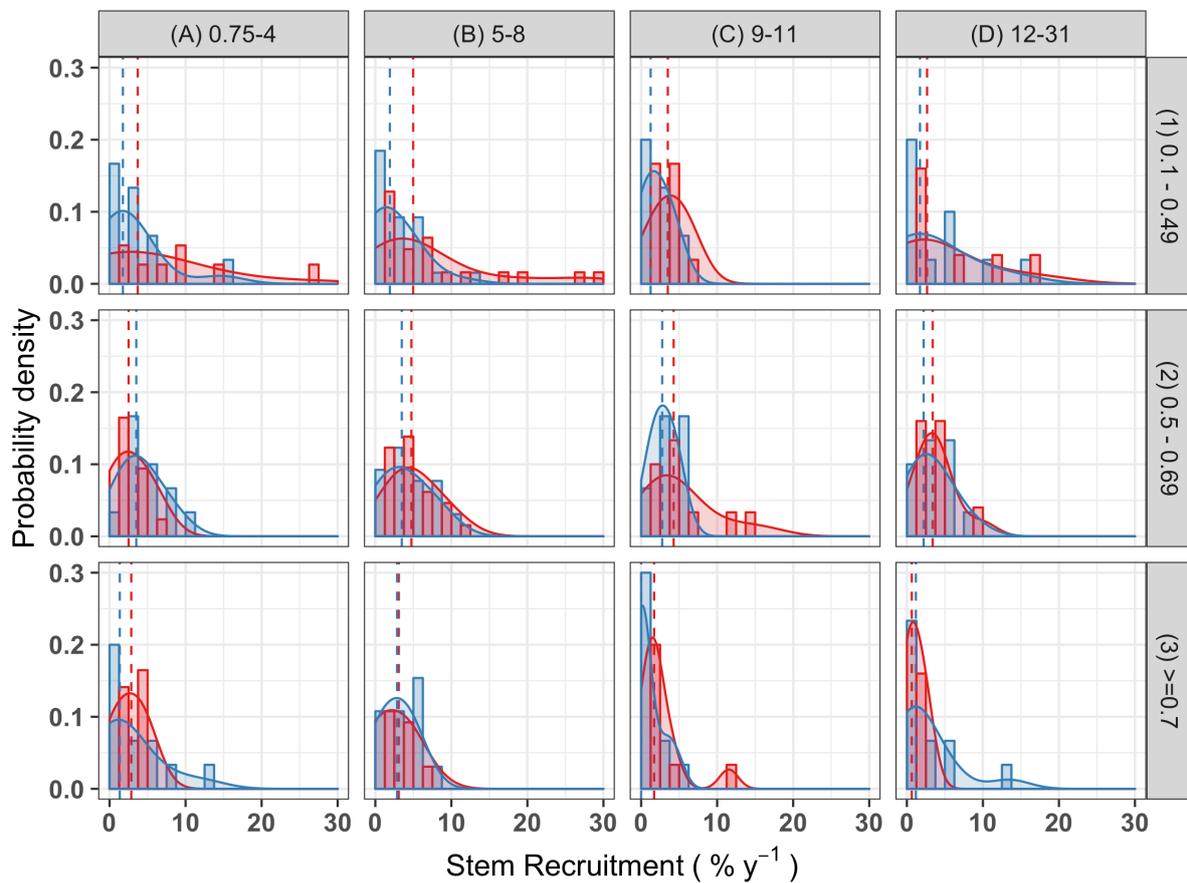


Figure S2 Probability density function of Stem Recruitment (% y<sup>-1</sup>) by Wood Density classes (WD: 0.1 - 0.49; 0.5 - 0.69; > 0.7 g cm<sup>-3</sup>) in lines and years since last fire (YSLF) classes (0.75 - 4; 5 - 8; 9 - 11; 12 - 31 years) in columns. Dashed lines represent median, red colour for burned and blue for unburned forests. Significance of Wilcoxon text represented by: \* p<0.05 and \*\* p<0.10.

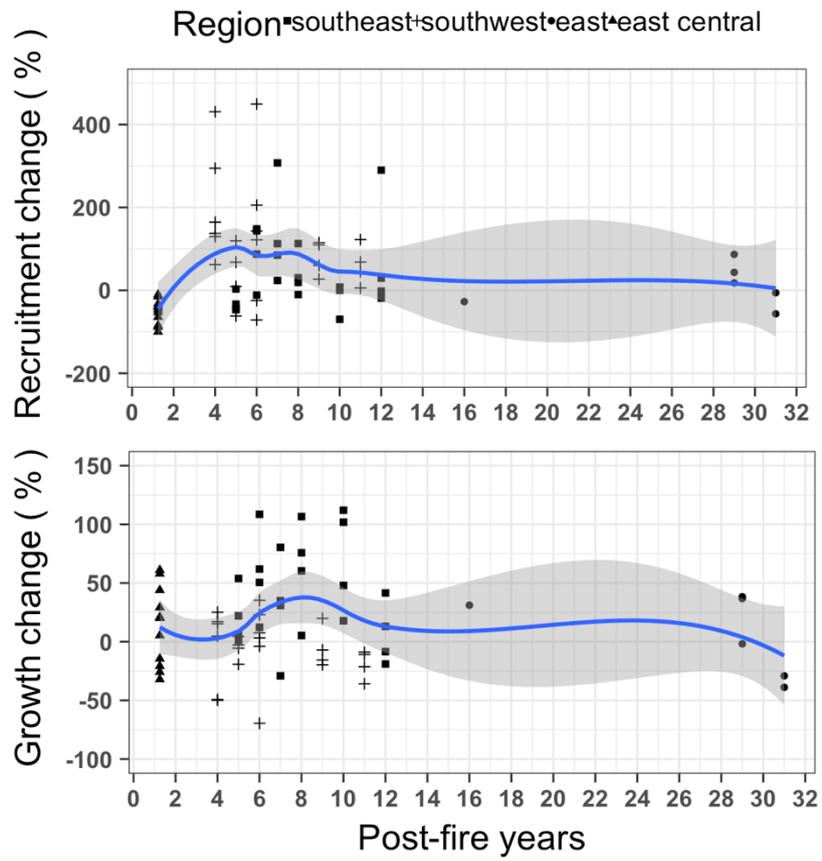


Figure S3 LOESS fit for percent difference of Recruitment and Growth in relation to unburned forest.

## 2.9 REFERENCES

- Aguiar APD, Vieira ICG, Assis TO et al. (2016) Land use change emission scenarios: anticipating a forest transition process in the Brazilian Amazon. *Global Change Biology*, **22**, 1821–1840.
- Alencar A, Nepstad D, Diaz MCV, Alencar A, Nepstad D, Diaz MCV (2006) Forest Understory Fire in the Brazilian Amazon in ENSO and Non-ENSO Years: Area Burned and Committed Carbon Emissions. *Earth Interactions*, **10**, 1–17.
- Alencar AA, Brando PM, Asner GP, Putz FE (2015) Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological Applications*, **25**, 1493–1505.
- Anderson LO, Aragão LEOC, Gloor M et al. (2015) Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought. *Global Biogeochemical Cycles*, **29**, 1739–1753.
- de Andrade RB, Balch JK, Parsons AL, Armenteras D, Roman-Cuesta RM, Bulkan J (2017) Scenarios in tropical forest degradation: carbon stock trajectories for REDD+. *Carbon Balance and Management*, **12**, 6.
- Aragão LEOC (2012) The rainforest's water pump. *Nature*, **489**, 217–218.
- Aragão LEOC, Malhi Y, Barbier N, Lima A, Shimabukuro Y, Anderson L, Saatchi S (2008) Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1779–85.
- Aragão LEOC, Poulter B, Barlow JB et al. (2014) Environmental change and the carbon balance of Amazonian forests. *Biological Reviews*, **89**, 913–931.
- Aragão LEOC, Anderson LO, Fonseca MG et al. (2018) 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, **9**, 536.
- Baker TR, Swaine MD, Burslem DFRP (2003) Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 21–36.
- Baker TR, Phillips OL, Malhi Y et al. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.
- Balch JK, Nepstad DC, Brando PM, Curran LM, Portela O, de Carvalho O, Lefebvre P (2008) Negative fire feedback in a transitional forest of southeastern Amazonia. *Global Change Biology*, **14**, 2276–2287.
- Barlow J, Peres CA (2006) Effects of Single and Recurrent Wildfires on Fruit Production and Large Vertebrate Abundance in a Central Amazonian Forest. *Biodiversity and Conservation*, **15**, 985–1012.
- Barlow J, Peres CA, Lagan BO, Haugaasen T (2002) Large tree mortality and the decline of

- forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.
- Barlow J, Lagan BO, Peres CA (2003) Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, **19**, 291–299.
- Barlow J, Silveira JM, Mestre LAM et al. (2012) Wildfires in Bamboo-Dominated Amazonian Forest: Impacts on Above-Ground Biomass and Biodiversity (ed Bond-Lamberty B). *PLoS ONE*, **7**, e33373.
- Barlow J, Lennox GD, Ferreira J et al. (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, **535**, 144–147.
- Berenguer E, Ferreira J, Gardner TA et al. (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, **20**, 3713–3726.
- Berenguer E, Gardner TA, Ferreira J et al. (2018a) Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests (ed Nardoto GB). *Journal of Ecology*.
- Berenguer E, Gardner TA, Ferreira J et al. (2018b) Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology*, 1–14.
- Bonner MTL, Schmidt S, Shoo LP (2013) A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations. *Forest Ecology and Management*, **291**, 73–86.
- Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Brando PM, Oliveria-Santos C, Rocha W, Cury R, Coe MT (2016) Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. *Global Change Biology*, **22**, 2516–2525.
- Bush MB (2017) The resilience of Amazonian forests. *Nature*, **541**, 167–168.
- Carmenta R, Vermeulen S, Parry L, Barlow J (2013) Shifting Cultivation and Fire Policy: Insights from the Brazilian Amazon. *Human Ecology*, **41**, 603–614.
- Chambers JQ, Higuchi N, Schimel JP (1998) Ancient trees in Amazonia. *Nature*, **391**, 135–136.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Chave J, Réjou-Méchain M, Búrquez A et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, **20**, 3177–3190.
- Cochrane MA (2003) Fire science for rainforests. *Nature*, **421**, 913–919.
- Denslow JS (1987) Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.
- Fauset S, Johnson MO, Gloor M et al. (2015) Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, **6**, 6857.
- Flores BM, Fagoaga R, Nelson BW, Holmgren M (2016) Repeated fires trap Amazonian blackwater floodplains in an open vegetation state (ed Barlow J). *Journal of Applied Ecology*, **53**, 1597–1603.

- Gatti L V., Gloor M, Miller JB et al. (2014) Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*, **506**, 76–80.
- Gerwing JJ, Farias DL (2000) Integrating Liana Abundance and Forest Stature into an Estimate of Total Aboveground Biomass for an Eastern Amazonian Forest. *Journal of Tropical Ecology*, **16**, 327–335.
- Goodman RC, Phillips OL, del Castillo Torres D, Freitas L, Cortese ST, Monteagudo A, Baker TR (2013) Amazon palm biomass and allometry. *Forest Ecology and Management*, **310**, 994–1004.
- Johnson MO, Galbraith D, Gloor M et al. (2016) Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models. *Global Change Biology*, **22**, 3996–4013.
- Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, **6**, 7537.
- Kinnaird MF, O'Brien TG (1998) Ecological Effects of Wildfire on Lowland Rainforest in Sumatra. *Conservation Biology*, **12**, 954–956.
- Longo M, Keller M, dos-Santos MN et al. (2016) Aboveground biomass variability across intact and degraded forests in the Brazilian Amazon. *Global Biogeochemical Cycles*, **30**, 1639–1660.
- Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 311–29.
- Malhi Y, Aragão LEOC, Galbraith D et al. (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 20610–5.
- McMichael CH, Piperno DR, Bush MB, Silman MR, Zimmerman AR, Raczka MF, Lobato LC (2012) Sparse Pre-Columbian Human Habitation in Western Amazonia. *Science*, **336**, 1429–1431.
- Midgley JJ, Kruger LM, Skelton R (2011) How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae “fire-resisters.” *South African Journal of Botany*, **77**, 381–386.
- Morton DC, Le Page Y, DeFries R, Collatz GJ, Hurtt GC (2013) Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **368**, 20120163.
- Numata I, Silva SS, Cochrane MA, d'Oliveira MVN (2017) Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *Forest Ecology and Management*, **401**, 135–146.
- Pausas JG (2015) Bark thickness and fire regime. *Functional Ecology*, **29**, 315–327.
- Phillips O, Baker T, Feldpausch T, Brien R (2009a) Field manual for establishment and remeasurement (RAINFOR). 22.
- Phillips OL, Aragão LEOC, Lewis SL et al. (2009b) Drought sensitivity of the Amazon rainforest. *Science (New York, N.Y.)*, **323**, 1344–7.
- Pinard MA, Huffman J (1997) Fire resistance and bark properties of trees in a seasonally dry

- forest in eastern Bolivia. *Journal of Tropical Ecology*, **13**, 727–740.
- Poorter L, Bongers F, Aide TM et al. (2016) Biomass resilience of Neotropical secondary forests. *Nature*, **530**, 211–214.
- Power MJ, Marlon J, Ortiz N et al. (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, **30**, 887–907.
- Rappaport DI, Morton DC, Longo M, Keller M, Dubayah R, dos-Santos MN (2018) Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation. *Environmental Research Letters*, **13**, 065013.
- Rutishauser E, Hérault B, Baraloto C et al. (2015) Rapid tree carbon stock recovery in managed Amazonian forests. *Current Biology*, **25**, R787–R788.
- Sato L, Gomes V, Shimabukuro Y et al. (2016) Post-Fire Changes in Forest Biomass Retrieved by Airborne LiDAR in Amazonia. *Remote Sensing*, **8**, 839.
- Sheil D, May RM (1996) Mortality and Recruitment Rate Evaluations in Heterogeneous Tropical Forests. *The Journal of Ecology*, **84**, 91.
- Silvestrini RA, Soares-Filho BS, Nepstad D, Coe M, Rodrigues H, Assunção R (2011) Simulating fire regimes in the Amazon in response to climate change and deforestation. *Ecological Applications*, **21**, 1573–1590.
- Sist P, Mazzei L, Blanc L, Rutishauser E (2014) Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. *Forest Ecology and Management*, **318**, 103–109.
- Slik JWF, Paoli G, McGuire K et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, **22**, 1261–1271.
- Spracklen D V., Arnold SR, Taylor CM (2012) Observations of increased tropical rainfall preceded by air passage over forests. *Nature*, **489**, 282–285.
- Talbot J, Lewis SL, Lopez-Gonzalez G et al. (2014) Methods to estimate aboveground wood productivity from long-term forest inventory plots. *Forest Ecology and Management*, **320**, 30–38.
- Uhl C, Buschbacher R (1985) A Disturbing Synergism Between Cattle Ranch Burning Practices and Selective Tree Harvesting in the Eastern Amazon. *Biotropica*, **17**, 265.
- Uhl C, Kauffman JB (1990) Deforestation, Fire Susceptibility, and Potential Tree Responses to Fire in the Eastern Amazon. *Ecology*, **71**, 437–449.
- Walker LR, Moral R del (2003) *Primary succession and ecosystem rehabilitation*. Cambridge University Press, 442 pp.
- Zanne AE, Lopez-Gonzalez G, Coomes DA et al. (2009) Global wood density database. *Dryad*.

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## CHAPTER 3

### 3 ESTIMATING THE MULTI-DECADAL CARBON DEFICIT OF BURNED AMAZONIAN FORESTS

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Photo taken by Erika Berenguer

# Estimating the multi-decadal carbon deficit of burned Amazonian forests

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## 3.1 ABSTRACT

Wildfires in humid tropical forests have become more common in recent years, increasing the rates of tree mortality in forests that have not co-evolved with fire. Estimating carbon emissions from these wildfires is complex. Current approaches rely on estimates of committed emissions based on static emission factors through time and space, yet these emissions cannot be assigned to specific years, and thus are not comparable with other temporally-explicit emission sources. Moreover, committed emissions are gross estimates, whereas the long-term consequences of wildfires require an understanding of net emissions that accounts for post-fire uptake of CO<sub>2</sub>. Here, using a 30-year wildfire chronosequence from across the Brazilian Amazon, we calculate net CO<sub>2</sub> emissions from Amazon wildfires by developing statistical models comparing post-fire changes in stem mortality, necromass decomposition and vegetation growth with unburned forest plots sampled at the same time. Over the 30-year time period, gross emissions from combustion during the fire and subsequent tree mortality and decomposition were equivalent to 126.1 Mg CO<sub>2</sub> ha<sup>-1</sup> of which 73% (92.4 Mg CO<sub>2</sub> ha<sup>-1</sup>) resulted from mortality and decomposition. These emissions were only partially offset by forest growth, with an estimated CO<sub>2</sub> uptake of 45.0 Mg ha<sup>-1</sup> over the same time period. Our analysis allowed us to assign emissions and growth across years, revealing that net annual emissions peak four years after forest fires. At present, Brazil's National Determined Contribution (NDC) for emissions fails to consider forest fires as a significant source, even though these are likely to make a substantial and long-term impact on the net carbon balance of Amazonia. Considering long-term post-

fire necromass decomposition and vegetation regrowth is crucial for improving global carbon budget estimates and national GHG inventories for tropical forest countries.

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**Keywords:** wildfires, tropical forests, stem mortality, committed emissions, decomposition, combustion, CO<sub>2</sub> uptake, net emissions

## 3.2 INTRODUCTION

Wildfires, defined here as uncontrolled understory fires affecting forested areas (Barlow *et al* 2020), were once absent or incredibly rare in humid tropical forests (Cochrane 2003, McMichael *et al* 2012). However, since the 1980s they have been growing in prevalence due to increases in deforestation, forest fragmentation, and widespread use of fire in land management (Goldammer and Seibert 1990, Cochrane *et al* 1999, Mouillot and Field 2005). These factors combined with changes in climate, including increased temperatures and drought frequency, heighten fire probability (Fernandes *et al* 2017, Silva Junior *et al* 2019). It is predicted that by 2050, the Brazilian Amazon will have 16% of its extent affected by wildfires (Brando 2020). Wildfires can lead to large changes in species composition and forest structure (Van Nieuwstadt and Sheil 2005, Balch *et al* 2011, Oliveras *et al* 2018, Barlow and Peres 2008), as well as increasing rates of tree mortality rates by 50% (Barlow *et al* 2003). This is particularly worrying, as in years of extreme drought, emissions resulting from wildfires can be greater than those from deforestation (Alencar *et al* 2006, Anderson *et al* 2015, Aragão *et al* 2018). Given the recent magnitude of tropical wildfires, refined temporal estimates of their associated emissions are crucial for improving national and global carbon budgets.

Although it is recognized that tropical wildfires can significantly contribute to global climate change (Page *et al* 2002, Nepstad *et al* 2008, Brando *et al* 2020), their carbon emissions remain absent from most national and global-level accounting systems. For example, the official Brazilian System for Registering National Greenhouse Gases (GHG) Emissions (SIRENE, in Portuguese) and the Brazilian System for Estimating Emissions of GHG (SEEG, in Portuguese)

do not account for wildfire-related emissions (MCTIC 2017, Azevedo *et al* 2018). There are two key knowledge gaps. The first is spatial; despite recent advances in remote sensing techniques (e.g. Anderson *et al* 2015, Hawbaker *et al* 2017, Chuvieco *et al* 2018, Reiche *et al* 2018) fire-emission datasets such as the Global Fire Emission Database (GFED) (van der Werf *et al* 2010), still rely on burned area products that can underestimate low-intensity understory wildfires in closed-canopy forests by up to 11 times (e.g. see Withey *et al* 2018). The second is temporal; most estimates of emissions focus on immediate emissions from combustion (e.g. Withey *et al* 2018) or estimates of committed emissions from mortality (Barlow *et al* 2003, Alencar *et al* 2006, Anderson *et al* 2015), but no studies have yet attempted to quantify the dynamics of post-fire forest carbon fluxes in humid tropical forests. This study addresses this second knowledge gap.

In Amazonia, during wildfire events, the immediate emissions from combustion of leaf litter and woody debris are likely to be dwarfed by the committed emissions resulting from tree mortality and subsequent decomposition. Tree mortality remains above-baseline levels for at least seven years after the fires (Silva *et al* 2018a). The subsequent decomposition of these dead trees will lead to CO<sub>2</sub> being emitted over decades later (Chambers *et al* 2000). These longer-term emissions could be partially or completely offset throughout a largely unquantified phase of post-fire regeneration, which is initially dominated by pioneers (Berenguer *et al* 2018, Barlow and Peres 2008), but later by slow growth higher wood density tree species (Silva *et al* 2018a). Without quantifying these processes, it is not possible to assign CO<sub>2</sub> emissions from wildfires to specific years, limiting our ability to compare emissions resulting from wildfires to those resulting from other sources, such as deforestation. This lack of temporal detail also hinders effective tracking of country-level emissions targets under the Paris Agreement commitments (UNFCCC, 2016). Furthermore, a better understanding of the temporal

progression of wildfire-related emissions would allow us to estimate their influence on the fraction of CO<sub>2</sub> in the atmosphere, elucidating previously unknown sources and sinks.

Here, we provide the first evidence-based assessment of the temporal basis of gross and net CO<sub>2</sub> emissions resulting from Amazonian wildfires. We use a unique field-based dataset of trees, palms and lianas in four different regions in the Brazilian Amazon, where stem mortality, growth and recruitment have been assessed since 2009. We focused on CO<sub>2</sub> fluxes resulting from growth and decomposition of woody components, which store the largest Carbon content with the longest residence time in the forest. We develop a novel statistical approach to estimate year-to-year net CO<sub>2</sub> emissions from burned forests. For all four regions, nearby undisturbed forests were considered as our baseline for forest dynamics, allowing us to separate the marginal influence of fires from confounding drought effects, and other variation across sites. We address the following questions: (i) What is the temporal pattern of gross CO<sub>2</sub> emissions resulting from fire-induced stem mortality and decomposition? (ii) What is the contribution of post-fire stem recruitment and growth to long-term CO<sub>2</sub> uptake? (iii) What is the multi-decadal net CO<sub>2</sub> flux of burned forests given the relative contribution of combustion and decomposition-related CO<sub>2</sub> emissions and post-fire CO<sub>2</sub> uptake? To answer question (i), we used empirical models (Silva *et al* 2018a) to describe post-fire stem mortality rates, incorporating a decomposition constant rate previously estimated for the central Amazon (Chambers *et al* 2000). For question (ii), we used the Chapman-Richard function to model post-fire tree growth and estimate how much CO<sub>2</sub> is taken up by vegetation over time. For question (iii), we used data from questions (i) and (ii) to model the net CO<sub>2</sub> flux following Amazonian wildfires over a 30-year period and evaluate the model by conducting an uncertainty analysis. Finally, we compare our estimates of decomposition-derived emissions with previous estimates of combustion-related emissions

### 3.3 METHODOLOGY

#### 3.3.1 *Study region and field measurements*

Our dataset was collected in four different regions across the Brazilian Amazonia (figure 3.1), with permanent plots (0.25 ha) located in both burned (BF, n = 27) and unburned (UF, n = 24) *terra firme* primary forests (Table S.M. 1). Burned forests were only affected by fire once, between 1-30 years prior to sampling. Fire occurrence was checked in Landsat images dating from 1970's and during field work by checking evidence in the ground (e.g. charcoal, charred stems) and confirming sites history with local community. Plots in unburned forests were located near burned ones (1.3–34.6 km) and sampled at the same time. In all plots, we measured all live stems (trees, palms and lianas; 7,527)  $\geq 10$  cm of diameter at 1.3m height. Aboveground biomass (AGB) were estimated according to Silva *et al* (2018), using specific allometric equations for trees (Chave *et al* 2014), palms (Goodman *et al* 2013) and lianas (Gerwing and Farias 2000). The AGB was estimated for all live stems in the plots, with the use of specific wood density and diameter for trees and only diameter for palms and lianas. We quantified plot-level AGB growth by adding the AGB of stems recruited with the AGB gain of live stems within censuses. The plot-level AGB losses due to stem mortality were quantified by adding the AGB of all dead stems (downed and standing) within censuses. The number of times each plot was revisited varied (2–6 times), as well as the time interval between censuses (1–4 years). Corrections at the plot level were applied in order to account for stem recruitment and mortality not measured between censuses, as well as for stem-level growth prior to mortality, following Talbot *et al* (2014).

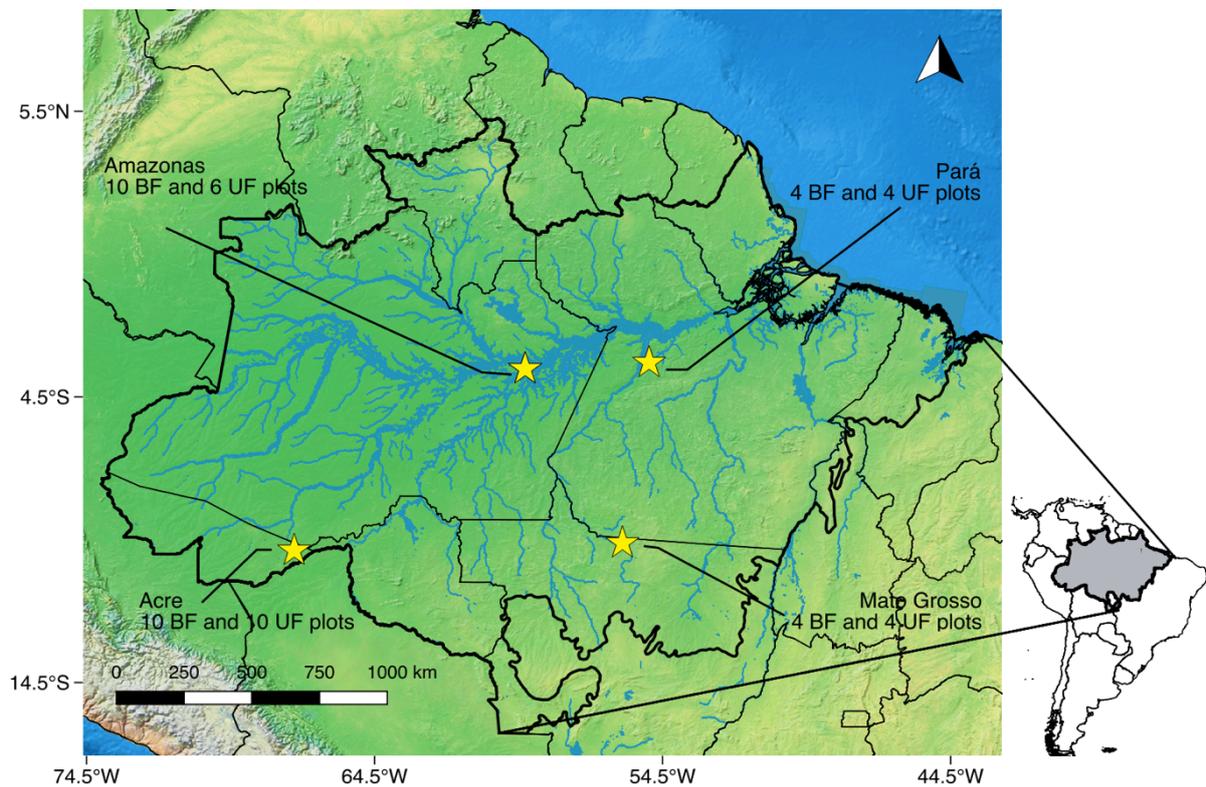


Figure 3.1 Location of our four regions in: Amazonas state where wildfires occurred during the 2015/2016 El Niño and forest censuses started by the same time (2015), Pará state where the latest wildfires occurred in 1998 and the earliest in 1985, and forest censuses started in 2010, Mato Grosso state where wildfires occurred during the 2005 drought and forests censuses started in 2009, and Acre state where wildfires occurred during the 2005 drought and censuses started in 2009.

### 3.3.2 *Estimating gross CO<sub>2</sub> emissions*

#### 3.3.2.1 FIRE-INDUCED ABOVEGROUND NECROMASS PRODUCTION.

Aboveground necromass production (AGN<sub>p</sub>, Mg ha<sup>-1</sup> y<sup>-1</sup>) is defined as being the same as the annual AGB loss due to stem mortality, from all causes, including downed and standing dead stems. The fire-induced AGN<sub>p</sub> (fAGN<sub>p</sub>) is determined by subtracting the AGN<sub>p</sub> of the control, unburned plots from AGN<sub>p</sub> of each burned plot after the fires,

$$fAGNp_{(i)} = AGNp_{BF(i)} - \overline{AGNp_{UF}} \quad (\text{Eq. 3.1})$$

where  $AGNp_{BF(i)}$  refers to annual AGNp of the *i*th plot of burned forest and  $\overline{AGNp_{UF}}$  refers to the average annual AGNp of all unburned forest plots measured in the same region at the same time of BF plots. This allows us to exclude the influence from spatial (e.g. soil fertility) and temporal (e.g. droughts) drivers on fAGNp.

We used a non-linear least squares regression and a standard exponential decay function to model fAGNp,

$$fAGNp_{(t)} = fAGNp_{(t=0)} \cdot e^{(-kt)} \quad (\text{Eq. 3.2})$$

where *t* is years since fire, and *k* is the rate at which fAGNp reduces over time. The regression analysis was done using the *nls* function from the *stats* R package (R Core Team 2019), S.M.2.

### 3.3.2.2 ABOVEGROUND NECROMASS DECOMPOSITION.

#### **Removing combusted necromass from subsequent decomposition emissions in burned forests**

Combustion during understory wildfires removes c. 73% of forest necromass stocks (Withey *et al.* 2018). The vast majority of this necromass would have been emitted at a later date during decomposition. To avoid accounting for this loss twice (as both combustion and decomposition), we estimated the decomposition that would have occurred each year over the 30 years (see supplementary material figure S.M.1). This estimate was based on published estimates of the combustion completeness of coarse woody debris (CWD), fine woody debris (FWD) and leaf litter stocks in central Amazonia (Withey *et al.* 2018). The decomposition of the AGN stocks that were combusted was done by the following equation:

$$cAGNd_{(t)} = b \cdot cAGN \cdot e^{(-b \cdot t)} \quad (\text{Eq. 3.3})$$

where  $b$  is a constant decomposition rate estimated for unburned forests in central Amazonia (Chambers *et al* 2000),  $cAGN$  is combusted necromass stock that would have been emitted by decomposition, and  $t$  is years since fire. The removal of  $cAGNd$  from total decomposition emissions is demonstrated in next section Eq. 3.4

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### Decomposition of annual necromass inputs

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Over a decadal-time scale, changes in stem mortality mean there is a decreasing amount of above-ground necromass being produced in burned forests ( $fAGNp$ ). After the first year, the fraction of  $AGN$  that decomposed at each year is added to the fractions decomposed in the previous years. Therefore, relative to unburned forests, the total losses by decomposition  $fAGNd$  ( $\text{Mg CO}_2 \text{ ha}^{-1} \text{ y}^{-1}$ ), occurring in burned forests at a given time  $t$  is the sum of all decomposed fractions (present and previous) minus the  $cAGNd$  at a given time  $t$  (see Eq. 3.3),

$$fAGNd_{(t)} = \left( \sum_{t=1}^t (b \cdot fAGNp_{(t)} \cdot e^{(-b \cdot t)}) \right) - cAGNd_{(t)} \quad (\text{Eq. 3.4})$$

with all symbols defined as above.  $fAGNd$  was then converted into gross  $\text{CO}_2$  emissions, using 0.5 as the biomass to carbon conversion factor (Penman *et al* 2003) and then by multiplying the value obtained by 3.67 (the ratio between C and  $\text{CO}_2$  molecular weights) as the  $\text{CO}_2$  conversion factor.

### 3.3.3 Estimating $\text{CO}_2$ uptake by stem growth and recruitment

Aboveground biomass growth ( $AGBg$ ) is defined as the annual increment in  $AGB$  due to stem growth plus the  $AGB$  of recruited stems. Here, to estimate the fire-induced changes to growth rates ( $fAGBg$ ) we used a similar relationship as Eq. 3.1,

$$fAGBg_{(i)} = AGBg_{BF(i)} - \overline{AGBg_{UF}} \quad (\text{Eq. 3.5})$$

where  $AGBg_{BF(i)}$  is the annual AGBg of every *ith* plot of burned forest and  $\overline{AGBg_{UF}}$  is the average annual AGBg of all unburned forest plots measured in the same region at the same time of BF plots. To model the process of post-fire forest growth according to the pattern observed in  $fAGBg$  over the years since fire, we fitted a Chapman-Richard growth function (Richards 1959), which is widely used in forestry to model tree population growth (Pommerening and Muszta 2016). We used a non-linear least squares regression to estimate the function parameters (S.M.2) as per  $fAGNp$ . We used the first derivative of this function to model the annual AGB growth rates of forests after the fire,

$$fAGBg_{(t)} = gmax \cdot (1 - e^{(-gt)})^{(c-1)} \cdot (c \cdot g \cdot e^{(-gt)}) \quad (\text{Eq. 3.6})$$

where  $gmax$  is the maximum growth the forest could reach corresponding to the inflection point of the cumulative function,  $g$  is the mean growth rate,  $c$  is a nondimensional parameter controlling the curve shape and the location of the inflection point, and other symbols defined as above.  $fAGBg$  is converted to  $CO_2$  uptake as per  $fAGNd$ . We use  $CO_2$  uptake instead of sequestration as the longevity of this sink remains uncertain.

### 3.3.4 *Net CO<sub>2</sub> emissions and the relative contribution of combustion*

Net  $CO_2$  emissions were calculated by subtracting the modelled  $CO_2$  uptake from the modelled  $CO_2$  gross emissions. We compared the relative contributions of our estimates of the net and gross  $CO_2$  emissions (derived just from necromass decomposition) with published estimates of immediate  $CO_2$  emissions deriving from the combustion of CWD, FWD and leaf litter in central Amazonia (Withey *et al* 2018). We used the cumulative values of each emission component to estimate their relative contribution over the 30 years.

For all analysis, we quantified and propagated uncertainties throughout the model outputs (see supplementary material S.M.4).

## 3.4 RESULTS

### 3.4.1 *Temporal pattern of gross CO<sub>2</sub> emissions from fire-induced stem mortality and decomposition*

Immediately after fires, necromass production rates increased by  $22.4 \pm 4.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$  above the levels of unburned forests (>4-fold the UF plots' necromass), and then declined over time at a constant rate of  $0.32 \pm 0.08 \text{ yr}^{-1}$  (Figure 3.2a and supplementary material tables S.M.2 and 3). Overall, the nonlinear regressions fit the fAGNp field data well (RSE =  $6.63 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ; df=61). The initial necromass stock was the most important parameter for short-term changes in fAGNp, while the contribution from reduction rates ("k" in Eq. 3.2) increased over time and was the most important parameter for the long-term changes (supplementary material Figure S.M.8).

One year after fires, the CO<sub>2</sub> emissions from necromass decomposition occurred at the rate of  $0.27 \pm 1.95 \text{ Mg ha}^{-1} \text{ y}^{-1}$ , as a result of low necromass stocks. New necromass stocks are produced in subsequent years as a result of delayed stem mortality, triggering new decomposition processes that will emit CO<sub>2</sub> (see supplementary material Figure S.M.2). Gross CO<sub>2</sub> emissions reached their peak five years after fire ( $8.13 \pm 1.1 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ y}^{-1}$ ), and then decreased over time, approaching the baseline levels 30 years after the fire event (Figure 3.2b).

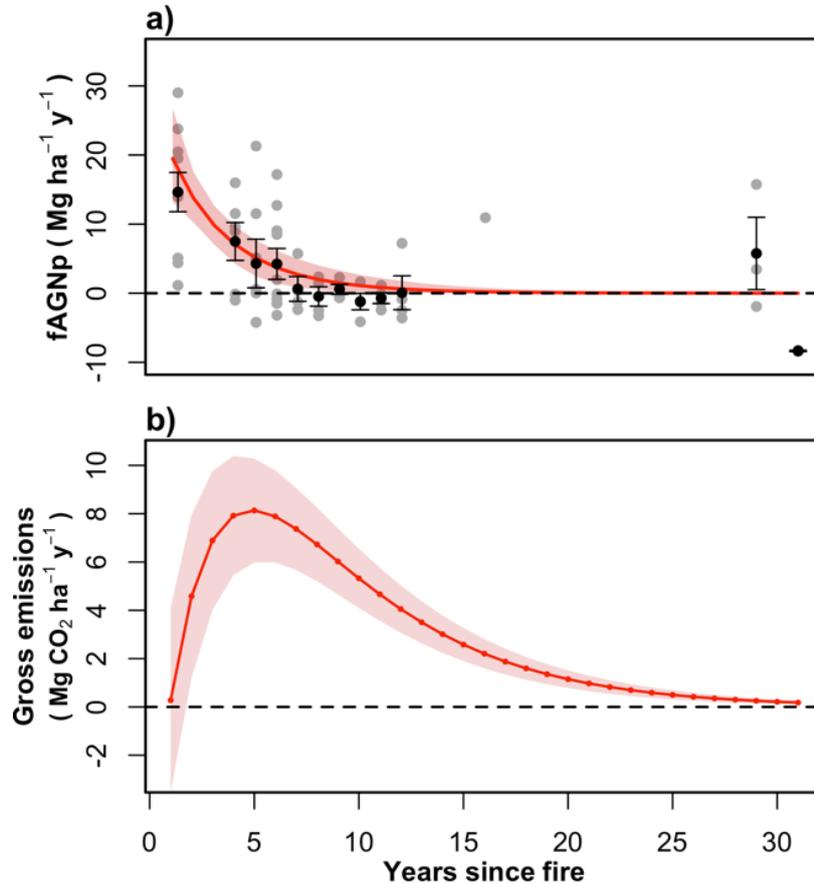


Figure 3.2 a) Fitted model for predicting fire-induced necromass production (fAGNp). The grey dots are estimated fAGNp from field observations ( $n = 61$ ) derived from the comparison between burned forest plots and locally measured unburned forest plots (Eq.1), black dots with bars are the mean  $\pm$  standard error, and the red shaded area represents the 95% CI of the model. The dashed black line represents the necromass baseline in undisturbed primary forests. b) Total CO<sub>2</sub> gross emissions (solid line) resulting from the sum of previous and present emissions per year and the subtraction of cAGN.

### 3.4.2 *Temporal pattern of gross CO<sub>2</sub> uptake due to post-fire recruitment and growth*

AGB growth in burned forests increased above baseline levels accumulating the maximum of  $22.5 \pm 7.41 \text{ Mg ha}^{-1}$  in 30 years. AGBg slowly declined and reached baseline levels between 20-25 years after the fire (Figure 3.3). When burned forests AGBg peaked, CO<sub>2</sub> was taken up at the maximum rate of  $5.59 \pm 1.33 \text{ Mg ha}^{-1} \text{ y}^{-1}$  (Figure 4A).

The nonlinear model fit the fAGBg data well ( $RSE = 2.21 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ;  $df=50$ ). However, the nondimensional parameter related to the time and size of the growth peak (“c” in Eq. 3.6) had the greatest variation ( $17.9 \pm 18.4$ ; supplementary material tables S.M.6 and 7). All the three parameters in the Chapman-Richard function ( $g_{max}$ ,  $k$ ,  $c$  in Eq. 3.6) controlling the forest growth had similar contributions (supplementary material S.M.9) at the maximum growth (inflection point).

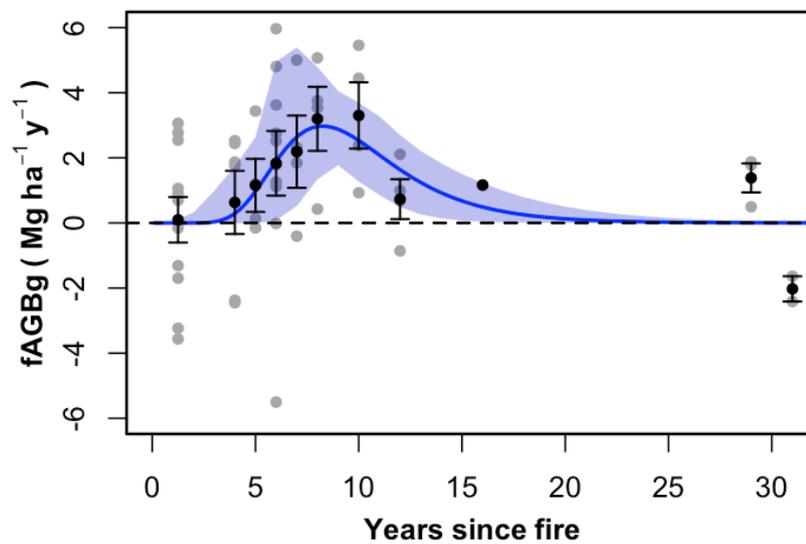


Figure 3.3 Fitted model (Chapman-Richard) for predicting fire-induced biomass growth (fAGBg). The grey dots are estimated fAGBg from field observations ( $n = 50$ ), derived from the comparison between burned forest plots and locally measured unburned forest plots (Eq.5), black dots and bars are the mean  $\pm$  standard error, and red shaded area represent the 95% CI of the model. The dashed black line represents the baseline growth in undisturbed primary forests.

### 3.4.3 *Multi-decadal net CO<sub>2</sub> flux from burned forests: comparing the contribution of combustion and decomposition-related CO<sub>2</sub> emissions with post-fire CO<sub>2</sub> uptake*

The balance between gross emissions and uptake results in net CO<sub>2</sub> emissions that peaked four years after the fire, with the release of  $7.51 \pm 1.39 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ y}^{-1}$  to the atmosphere (Figure

3.4a). After that, the net CO<sub>2</sub> emissions decline sharply due to increases in CO<sub>2</sub> removals. Net CO<sub>2</sub> emissions converged with baseline levels towards the end of the 30-year period. However, when we combined our estimates of CO<sub>2</sub> emissions resulting from dead-wood decomposition with those from the combustion of woody debris and leaf litter (33.64 Mg CO<sub>2</sub> ha<sup>-1</sup>, see Withey *et al* 2018), both cumulative gross and net CO<sub>2</sub> emissions remained above baseline levels (Figure 3.4b). We therefore estimate a cumulative gross emission of *c.* 126.1 Mg CO<sub>2</sub> ha<sup>-1</sup> for 30 years after a fire event. Cumulative CO<sub>2</sub> uptake only offsets 35% of these emissions (45.0 Mg CO<sub>2</sub> ha<sup>-1</sup>) within the same timeframe. Decomposition-related emissions account for approximately 58% (47.4 Mg CO<sub>2</sub> ha<sup>-1</sup>) of total net emissions. The inclusion of net decomposition-related emissions doubles the emission estimates from combustion seven years after the fire took place.

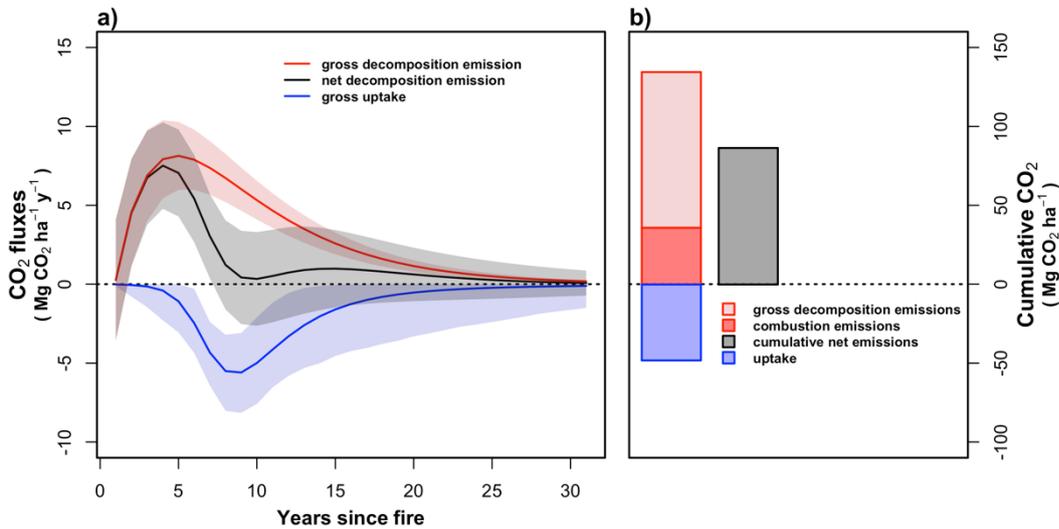


Figure 3.4 a) CO<sub>2</sub> fluxes (Mg ha<sup>-1</sup> y<sup>-1</sup>) from wildfires. Gross emissions (red line) are the total emissions derived from necromass decomposition each year after the burn, CO<sub>2</sub> uptake (blue line) is the CO<sub>2</sub> taken up through above-ground biomass growth, and net CO<sub>2</sub> (black line) is the balance between gross CO<sub>2</sub> emissions and uptake. b) Cumulative CO<sub>2</sub> (Mg ha<sup>-1</sup>) emissions and uptake over 30 years. Emissions from combustion (dark red) represent a single emission during the burn while gross decomposition emissions (light red) are the cumulative decomposition from all necromass stocks produced in 30 years, accounting for 73% of total gross emissions. Uptake (blue) offsets part (35%) of total emissions resulting in above baseline values (81 Mg CO<sub>2</sub> ha<sup>-1</sup>) of net emissions (dashed black).

## 3.5 DISCUSSION

### 3.5.1 *Improving emission estimates from Amazonian wildfires*

Our approach provides a calibrated method for integrating Amazonian wildfires into national and global emission databases. At present, in humid tropical forests, GFED focuses on emissions from deforestation fires and assumes that wildfires are carbon neutral in the long term, with regrowth offsetting respiration of woody debris and leaf litter (Landry and Matthews 2016). Also, the currently omitted CO<sub>2</sub> emissions and removals, from post-fire stem mortality, growth and recruitment, in SIRENE and SEEG could be resolved by employing the approach

proposed here. The omission of wildfire-related emissions is important: for example, while the emissions from the 2.6 million hectares of Amazonian forests affected by the 1998 wildfires (Alencar *et al* 2006) would have been ignored by GFED, SEEG and SIRENE, our analysis suggests that this single event will have emitted 0.17-0.25 Pg of CO<sub>2</sub> to the atmosphere by 2030, even without considering subsequent recurrent wildfires or deforestation. These are equivalent to 18-27% of Brazil's intended contribution in 2030 (i.e., 0.9 Pg of CO<sub>2</sub>, see UNFCCC 2016) under the Paris agreement. Following these estimates, the CO<sub>2</sub> emissions resulting from 2010 and 2015-2016 wildfires, if properly accounted for, would have direct implications for Brazil's ability to meet its Nationally Determined Contributions (NDC). Furthermore, as these emissions databases can be used for fire representation in dynamic global vegetation models, the omissions shown here may significantly impact the carbon budget of tropical countries, if complemented by accurate wildfire mapping.

### ***3.5.2 The importance of avoiding further degradation in burned forests***

Across the 30-year period, burned forests acted as net CO<sub>2</sub> source, and cumulative net emissions were far higher than uptake. The average net annual emissions of burned forests over a 30-year period were 1.52 Mg CO<sub>2</sub> ha<sup>-1</sup> y<sup>-1</sup>, which is approximately 36% of the estimated annual sink of old-growth secondary forests across tropical American rainforests (Suarez *et al* 2019). These long-term positive emissions are also due to the non-recovery of biomass stocks to pre-disturbance levels shown in Silva *et al* (2018). However, despite these emissions, regenerating burned forests also remain an important part of any strategy to mitigate carbon losses from degradation. Allowing burned forests to regrow offsets 35% of all decomposition- and combustion-related emissions over the 30-year period, and, unlike secondary forest, does not require expensive tree planting or incur opportunity costs from the abandonment of agricultural land. The protection of burned forests from further disturbances and/or clearance

may also offer other important ecosystem services, such as maintenance of hydrological cycling (Brando *et al* 2019), as well as providing habitat for biodiversity – albeit at a lower level than in undisturbed primary forests (Berenguer *et al* 2014, Barlow *et al* 2016, Ferreira & Lennox *et al* 2018, França *et al* 2020). Yet, protecting these forests from clearance has recently become more challenging — since 2012, deforestation rates have risen 16% on average (PRODES 2020) and burned forests are often located at the agricultural frontier where they may be more susceptible to clearance. Likewise, protecting burned forests from further disturbances is far from straightforward, since burned forests are more vulnerable to windstorms (Silvério *et al* 2019) and are increasingly susceptible to repeated fires (Alencar *et al* 2011, Morton *et al* 2013, Silva *et al* 2018b, Cochrane *et al* 1999), which is likely to be exacerbated by climate change (Fonseca *et al* 2019). If burned forests burn again, the consequences for CO<sub>2</sub> emissions are likely to be far worse. These recurrent fires are often much more intense, leading to much higher levels of tree mortality (Barlow and Peres 2004, Cochrane *et al* 1999), a high turnover of species composition towards pioneer species (Barlow and Peres 2008), and slower rates of post-fire carbon uptake through regrowth (Balch *et al* 2013).

### 3.5.3 *Quantifiable uncertainties*

While we present the first temporal estimate of emissions from Amazonian wildfires, we also recognise that many uncertainties remain. These include particularly the uncertainties associated with the growth parameters, especially relating to the phase when burned forests reach their peak of CO<sub>2</sub> uptake relative to unburned forests, where the confidence intervals were especially high (“c” in Eq. 3.6; supplementary material table S.M.3). There are many reasons for such high uncertainty: post-disturbance growth is a complex process, and post-disturbance growth rates are known to vary significantly by species (Berenguer *et al* 2018), across regions (e.g. Poorter *et al* 2016), and can be affected by environmental factors including

fire intensity and canopy openness (Brando *et al* 2019, Balch *et al* 2013), or even climate change or climate anomalies (Phillips *et al* 2009, Elias *et al* 2020). Although we tracked mortality over time in our burned plots, additional variability could have stemmed from the lack of samples in forests before they burned (e.g. França *et al* 2016). However, these pre-fire samples are only achievable by chance or through experimental fires, and the data-spread (figure 3.2 and 3.3) suggests our field observations are representative of some of the main environmental gradients within Amazonian forests (Johnson *et al* 2016). Finally, temporal limitations in the dataset represent a further source of uncertainty and our estimates of emission and regrowth are highly uncertain beyond 15 years since fire. Narrowing this uncertainty remains challenging, as many of the sites impacted by 1980's and 1998 El Nino events have either been deforested, selectively logged or burned again (e.g. see Bullock *et al* 2020).

Decomposition rates are also a source of uncertainty. We propagated the decomposition rate uncertainty measured in undisturbed forests, as decomposition rates in burned forests are unknown. Yet, the decomposition rates in burned forests may differ due to (1) drier microclimate brought on by changes in forest structure and canopy openness (Uhl and Kauffman 1990, Barlow and Peres 2008); (2) changes in decomposer community structure, including invertebrates (Ashton *et al* 2019) and microbes, relating to changes in pH and microclimate (Carvalho *et al* 2016); (3) changes in the litter quality, especially as wood density negatively affects decomposition rates in undisturbed forests (Chao *et al* 2009, Chambers *et al* 2000), and at least part of the mortality is related to short-lived lower wood density species that colonise rapidly after fires (Silva *et al* 2018a); and (4) stem mode of death, which impacts wood decomposition rates because dead stems standing and suspended from the ground have much slower decomposition rates than downed stems (Gora *et al* 2019). None of these potential drivers of change in decomposition rates has been previously investigated or quantified in burned humid tropical forests.

Although vegetation is the most disturbance-sensitive carbon pool in the forest (Berenguer *et al* 2014), uncertainties could also be reduced by evaluating other components of forest carbon cycle. For example, FWD and leaf litter, which corresponds to 34% of total NPP in undisturbed forests (Malhi *et al* 2009), is assumed to decompose at the rate of CWD. This makes the decay time of FWD and litter in our model longer (5 years) than that expected (6 months – 2 years; Malhi *et al* 2011), causing a delay in the emissions. Moreover, not all carbon from woody debris and leaf litter is released as CO<sub>2</sub> to the atmosphere; part of it is biologically transformed and locked up in the soil or leached to groundwater. The net dissolved organic carbon (DOC) export from forest soil is, however, a very small component of the forest carbon cycle (0.003 – 1.9% of total NPP; Malhi *et al* 2009). While burned forests' soil carbon pool does not differ from unburned forests (Berenguer *et al* 2014), increases in DOC may be expected for burned forests. Further carbon release can be also expected through CH<sub>4</sub> emissions from termite activity and anaerobic decay of wood and litter. However, anaerobic activity increase is unlikely in free-draining *terra-firme* forests where oxygen is not limiting, and the production of CH<sub>4</sub> in *terra-firme* forests represents a small component of the carbon cycle (0.005 – 0.06%; Malhi *et al* 2009), and the sources have not been identified (do Carmo *et al* 2006). While changes in CH<sub>4</sub> emission due to termites is a possibility, this has not been investigated in burned humid tropical forests.

Another important set of uncertainties go beyond our approach and relate to the spatiotemporal scaling of our results. For example, wildfires are mostly missed by active fire counts and estimates of burned area derived from satellite measures (Anderson *et al* 2015), meaning that we lack a reliable large-scale and historical mapping of fire scar coverage across Amazonia. Furthermore, even if fires are mapped with the use of improved techniques (Morton *et al* 2011, Anderson *et al* 2015, Withey *et al* 2018), pre-fire forest conditions will play an important role in determining fire intensity and mortality (Barlow *et al* 2012, Brando *et al* 2016). Forests that

have experienced disturbances from logging or fires prior to the satellite era may harbour large fuel loads, resulting in more intense fires, albeit with lower initial carbon stocks. However, this source of uncertainty may remain unresolved due to the lack of both on-the-ground and remote sensing data. Mortality is also likely to be higher near forest edges, where necromass accumulation is higher (Brando *et al* 2019).

### 3.6 CONCLUSION

Most estimates of wildfire-related CO<sub>2</sub> emissions account for committed emissions without considering the temporal evolution of stem mortality, the time taken for the subsequent decomposition of dead biomass, and the amount taken up by regrowth. By incorporating long-term field-data on biomass gains and losses, we developed an approach that addresses these knowledge gaps, showing that decomposition-related emissions make a significant contribution to the total CO<sub>2</sub> emitted and are only partially offset (~35%) by post-fire forest regrowth in 30 years. Our approach allows the scaling-up of the net CO<sub>2</sub> emissions resulting from wildfires across the Amazon basin, providing a way of incorporating them into both national and global carbon budgets and databases. This, however, depends on the enhancement of forest fire detection and mapping.

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### 3.8 SUPPLEMENTARY MATERIAL

Table SM1 Summary of permanent plots located in burned (BF) and undisturbed (UF) primary forests from across four regions in the Brazilian Amazonia. The measurements varied over time

Region	Censuses year	Fire year	BF plots (N)	UF plots (N)	Mean distance between BU and UN plots (Km)
southeast (MT)	2010, 2011, 2012, 2013, 2015, 2017	2005	4	4	1.3
east (PA)	2010, 2014, 2016	1985, 1998	4	4	34.6
southwest (AC)	2010, 2014, 2016	2005, 2010	10	10	2.1
central (AM)	2015, 2016	2015	10	6	3.0

#### Method SM2 – Description of methods for fitting the nonlinear models

For fitting the AGNp (necromass) and AGBg (live biomass) nonlinear models, the *nls* function in R required we set the starting values for the regression. For the AGNp model, the starting values were  $fAGNp_{(t=0)} = 40$ , and  $k = 0.5$ , and for the AGBg model they were  $gmax = 30$ ,  $g = 0.3$  and  $c = 10$ .

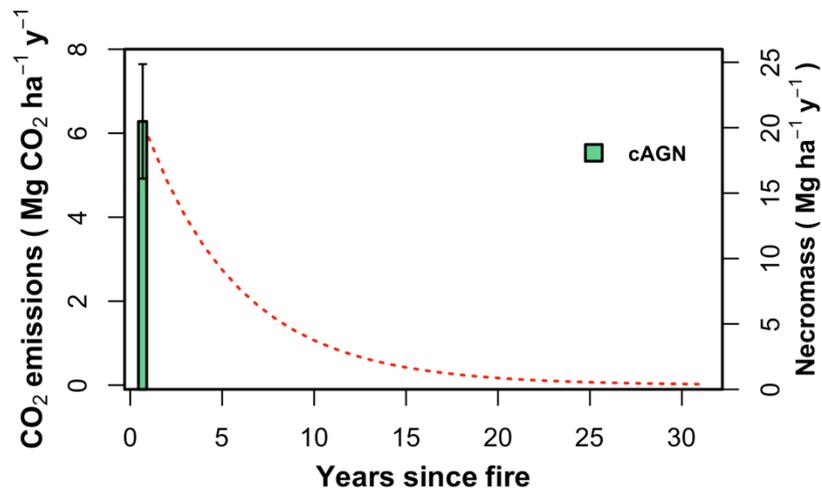


Figure SM1 Combusted necromass (cAGN) that would have decomposed (green bar) in the right y-axis, and the associated CO<sub>2</sub> emissions derived from the decomposition (red dashed line) in left y-axis.

#### Method S.M. 4 Description of methods for estimating uncertainties

We assumed the main proportion of errors to come from the estimated parameters rather than the independent variable “years since fire”. To quantify and propagate the uncertainties from estimated parameters to the model’s output we: (i) used a non-parametric bootstrap approach (nlsBoot function from the nlstools R package (Baty et al 2015)) for obtaining bootstrapped parameters estimates by fitting the non-linear models on each resampled dataset; and (ii) propagated the errors from the parameters and obtained summary statistics (mean, standard deviation (sd) and 95% confidence interval [CI]) by doing a Monte Carlo simulation (n = 100,000) using the function propagate from the R package propagate (Spiess 2018). Each of the processes estimated (i.e. necromass production, annual gross emissions, biomass growth, annual sequestration, and annual net emissions) have their mean values and 95% CI reported accounting for errors propagated from the parameters. To compute uncertainty for gross emissions, we ran simulations for each of the emissions curves starting at a different time step,

propagating the error from necromass production and the error ( $0.026 \text{ year}^{-1}$ ) associated with the decomposition rate reported by Chambers *et al* 2000. Since total gross emissions result from summed means of annual emissions at each time step, we computed the total error by adding errors in quadrature at each time step, assuming they are uncorrelated and normally distributed. Following the error propagation rule, we square-rooted the sum of the squared errors and then estimated the 95% CIs. We estimated errors and 95% CIs for net emissions in the same manner. Finally, we considered the contribution matrix, rescaled to sum up to 1, for assessing each parameter's contribution to the respective model output.

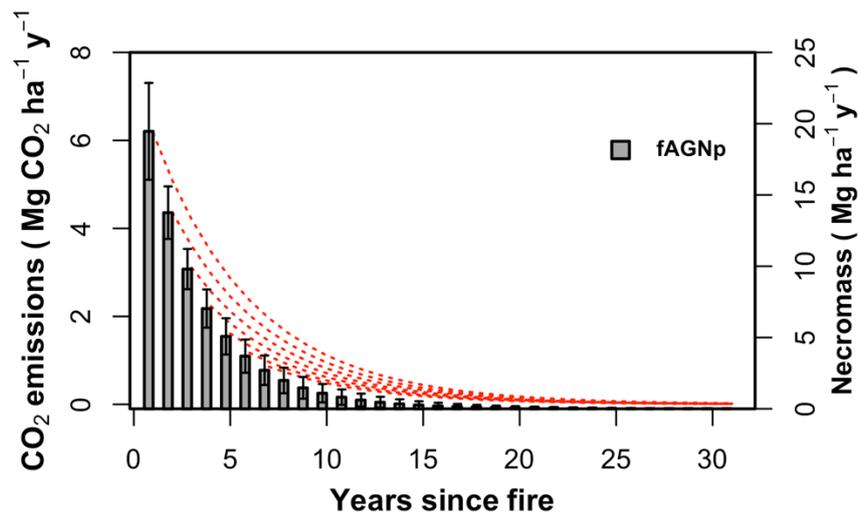


Figure SM2 Fire-induced necromass production (fAGNp) over the years since fire represented by grey bars in the right y-axis; and the associated concurrent CO<sub>2</sub> emissions derived from decomposition represented as red dashed lines in left y-axis.

Table SM2 Output summary of estimated parameters in non-linear least square regression models

	<b>Parameters</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>fAGNp model</b>	<b>a*</b>	22.39	4.56	4.91	7.17e-06 ***
	<b>b</b>	0.33	0.08	3.98	0.000189 ***
<b>fAGBg model</b>	<b>gmax</b>	22.47	7.42	3.03	0.00388 **
	<b>g</b>	0.35	0.14	2.44	0.01837 *
	<b>c</b>	17.92	18.43	0.97	0.33563

\*a is fAGNp at t=0 in Eq.2

Table SM 3 Bootstrap statistics for models estimate parameters

Median of bootstrap estimates and percentile confidence intervals				
		Median	2.5%	97.5%
	<b>a*</b>	22.87	14.95	33.77
<b>fAGNp model</b>	<b>b</b>	0.33	0.20	0.56
	<b>gmax</b>	22.99	11.25	57.01
<b>fAGBg model</b>	<b>g</b>	0.37	0.09	0.85
	<b>c</b>	21.60	2.67	489.21

\*a is fAGNp at t=0 in Eq.2

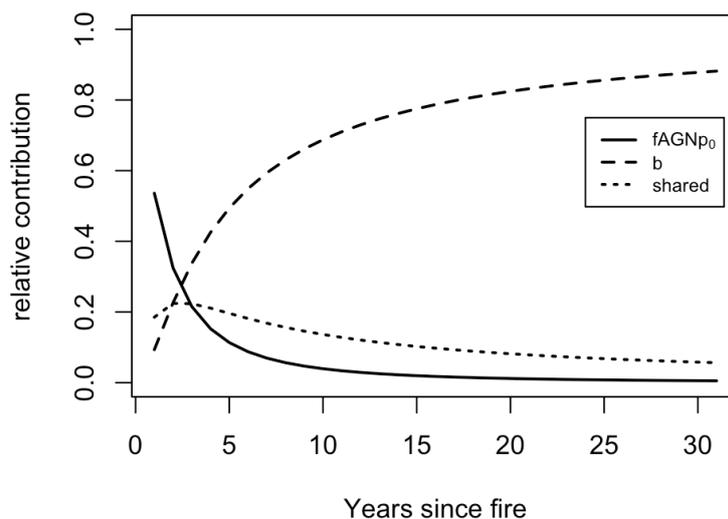


Figure SM3 Relative contribution of estimated parameters to necromass model output



Figure SM4 Relative contribution of estimated parameters to growth model output

### 3.9 REFERENCES

- Alencar A, Asner G P, Knapp D and Zarin D 2011 Temporal variability of forest fires in eastern Amazonia *Ecol. Appl.* **21** 2397–412
- Alencar A, Nepstad D and Diaz M C V 2006 Forest Understorey Fire in the Brazilian Amazon in ENSO and Non-ENSO Years: Area Burned and Committed Carbon Emissions *Earth Interact.* **10** 1–17
- Anderson L O *et al.* 2015 Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought *Global Biogeochem. Cycles* **29** 1739–53
- Aragão L E O C *et al.* 2018 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions *Nat. Commun.* 1–12
- Ashton L A, Griffiths H G M, Parr C L, Evans T A, Didham R K, Hasan F, Teh Y A, Tin H S, Vairappan C S and Eggleton P 2019 Termites mitigate the effects of drought in tropical rainforest *Science (80-. )*. **177** 174–7
- Azevedo T R *et al.* 2018 SEEG initiative estimates of Brazilian greenhouse gas emissions from 1970 to 2015 *Sci. Data* **5** 1–43
- Balch J K, Massad T J, Brando P M, Nepstad D C and Curran L M 2013 Effects of high-frequency understorey fires on woody plant regeneration in southeastern Amazonian forests *Philos. Trans. R. Soc. B Biol. Sci.* **368**
- Balch J K, Nepstad D C, Curran L M, Brando P M, Portela O, Guilherme P, Reuning-Scherer J D and de Carvalho O 2011 Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon *For. Ecol. Manage.* **261** 68–77

- Barlow J, Berenguer E, Carmenta R and França F 2020 Clarifying Amazonia's burning crisis *Glob. Chang. Biol.* **26** 319–21
- Barlow J *et al.* 2016 Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation *Nature* **535** 144–7
- Barlow J, Peres C a., Lagan B O and Haugaasen T 2003 Large tree mortality and the decline of forest biomass following Amazonian wildfires *Ecol. Lett.* **6** 6–8
- Barlow J and Peres C A 2004 Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests ed Y Malhi and O L Phillips *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* **359** 367–80
- Barlow J and Peres C A 2008 Fire-mediated dieback and compositional cascade in an Amazonian forest *Philos. Trans. R. Soc. B Biol. Sci.* **363** 1787–94
- Barlow J, Silveira J M, Mestre L A M, Andrade R B, Camacho D'Andrea G, Louzada J, Vaz-de-Mello F Z, Numata I, Lacau S and Cochrane M A 2012 Wildfires in bamboo-dominated Amazonian forest: Impacts on above-ground biomass and biodiversity *PLoS One* **7** e33373
- Berenguer E, Ferreira J, Gardner T A, Aragão L E O C, De Camargo P B, Cerri C E, Durigan M, Oliveira R C De, Vieira I C G and Barlow J 2014 A large-scale field assessment of carbon stocks in human-modified tropical forests *Glob. Chang. Biol.* **2005** 1–14
- Berenguer E, Malhi Y, Brando P, Cordeiro A, Ferreira J, França F, Chesini Rossi L, Seixas M, Barlow J, 2018 Tree growth and stem carbon accumulation in human-modified Amazonian Forests *Philos. Trans. R. Soc. B Biol. Sci.* **373** 20170308
- Brando P M, Oliveria-Santos C, Rocha W, Cury R and Coe M T 2016 Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest *Glob. Chang. Biol.* **22** 2516–25
- Brando P M *et al.* 2019 Prolonged tropical forest degradation due to compounding disturbances: Implications for CO<sub>2</sub> and H<sub>2</sub>O fluxes *Glob. Chang. Biol.* **25** 2855–68
- Brando P M, Soares-Filho B, Rodrigues L, Assunção A, Morton D, Tuchsneider D, Fernandes E C M, Macedo M N, Oliveira U and Coe M T 2020 The gathering firestorm in southern Amazonia *Sci. Adv.* **6** eaay1632
- Bullock E L, Woodcock C E, Souza C and Olofsson P 2020 Satellite-based estimates reveal widespread forest degradation in the Amazon *Glob. Chang. Biol.* **26** 2956–69
- do Carmo J B, Keller M, Dias J D, de Camargo P B and Crill P 2006 A source of methane from upland forests in the Brazilian Amazon *Geophys. Res. Lett.* **33** 2–5
- Carvalho T S, Jesus E da C, Barlow J, Gardner T A, Soares I C, Tiedje J M and Moreira F M de S 2016 Land use intensification in the humid tropics increased both alpha and beta diversity of soil bacteria *Ecology* **97** 2760–71
- Chambers J Q, Higuchi N, Schimel J P, Ferreira L V. and Melack J M 2000 Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon *Oecologia* **122** 380–8
- Chao K-J, Phillips O L, Baker T R, Peacock J, Lopez-Gonzalez G, Vásquez Martínez R, Monteagudo A and Torres-Lezama A 2009 After trees die: quantities and determinants of necromass across Amazonia *Biogeosciences* **6** 1615–26
- Chave J *et al.* 2014 Improved allometric models to estimate the aboveground biomass of

- tropical trees *Glob. Chang. Biol.* **20** 3177–90
- Chuvieco E, Lizundia-Loiola J, Pettinari M L, Ramo R, Padilla M, Tansey K, Mouillot F, Laurent P, Storm T, Heil A and Plummer S 2018 Generation and analysis of a new global burned area product based on MODIS 250m reflectance bands and thermal anomalies *Earth Syst. Sci. Data* **10** 2015–31
- Cochrane M A 2003 Fire science for rainforests *Nature* **421** 913–9
- Cochrane M A, Alencar A, Schulze M D, Souza C M, Nepstad D C, Lefebvre P and Davidson E A 1999 Positive feedbacks in the fire dynamic of closed canopy tropical forests *Science* (80-. ). **284** 1832–5
- Elias F *et al.* 2020 Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes *Ecology* **101**
- Fernandes K, Verchot L, Baethgen W, Gutierrez-Velez V, Pinedo-Vasquez M and Martius C 2017 Heightened fire probability in Indonesia in non-drought conditions: the effect of increasing temperatures *Environ. Res. Lett.* **12** 054002
- Ferreira J *et al.* 2018 Carbon-focused conservation may fail to protect the most biodiverse tropical forests *Nat. Clim. Chang.* **8** 744–9
- Fonseca M G, Alves L M, Aguiar A P D, Arai E, Anderson L O, Rosan T M, Shimabukuro Y E and Aragão L E O e C 2019 Effects of climate and land-use change scenarios on fire probability during the 21st century in the Brazilian Amazon *Glob. Chang. Biol.* **25** 2931–46
- França F, Louzada J, Korasaki V, Griffiths H, Silveira J M and Barlow J 2016 Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles ed R Mac Nally *J. Appl. Ecol.* **53** 1098–105
- França F M *et al.* 2020 El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes *Biotropica* [btp.12756](https://doi.org/10.1111/btp.12756)
- Gerwing J J and Farias D L 2000 Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest *J. Trop. Ecol.* **16** 327–35
- Goldammer J G and Seibert B 1990 The Impact of Droughts and Forest Fires on Tropical Lowland Rain Forest of East Kalimantan *Fire in the Tropical Biota. Ecological Studies (Analysis and Synthesis)* (Springer-Verlag Berlin Heidelberg) pp 11–31
- Goodman R C, Phillips O L, Del Castillo Torres D, Freitas L, Cortese S T, Monteagudo A and Baker T R 2013 Amazon palm biomass and allometry *For. Ecol. Manage.* **310** 994–1004
- Gora E M, Kneale R C, Larjavaara M and Muller-Landau H C 2019 Dead Wood Necromass in a Moist Tropical Forest: Stocks, Fluxes, and Spatiotemporal Variability *Ecosystems* **22** 1189–205
- Hawbaker T J *et al.* 2017 Mapping burned areas using dense time-series of Landsat data *Remote Sens. Environ.* **198** 504–22
- Johnson M O *et al.* 2016 Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models *Glob. Chang. Biol.* **22** 3996–4013
- Landry J-S and Matthews H D 2016 Non-deforestation fire vs. fossil fuel combustion: the source of CO<sub>2</sub> emissions affects the global carbon cycle and climate responses *Biogeosciences* **13** 2137–49

- Malhi Y *et al.* 2009 Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests *Glob. Chang. Biol.* **15** 1255–74
- Malhi Y, Doughty C and Galbraith D 2011 The allocation of ecosystem net primary productivity in tropical forests *Philos. Trans. R. Soc. B Biol. Sci.* **366** 3225–45
- McMichael C H, Piperno D R, Bush M B, Silman M R, Zimmerman A R, Raczka M F and Lobato L C 2012 Sparse pre-Columbian human habitation in Western Amazonia *Science (80-. )*. **336** 1429–31
- MCTIC 2017 *Estimativas Anuais de Emissões de Gases de Efeito Estufa no Brasil* (Brazilian National Report, Brasilia, DF)
- Morton D C, DeFries R S, Nagol J, Souza C M, Kasischke E S, Hurtt G C and Dubayah R 2011 Mapping canopy damage from understory fires in Amazon forests using annual time series of Landsat and MODIS data *Remote Sens. Environ.* **115** 1706–20
- Morton D C, Le Page Y, DeFries R, Collatz G J and Hurtt G C 2013 Understorey fire frequency and the fate of burned forests in southern Amazonia *Philos. Trans. R. Soc. B Biol. Sci.* **368**
- Mouillot F and Field C B 2005 Fire history and the global carbon budget: a 10x 10 fire history reconstruction for the 20th century *Glob. Chang. Biol.* **11** 398–420
- Nepstad D C, Stickler C M, Soares-Filho B and Merry F 2008 Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point *Philos. Trans. R. Soc. B Biol. Sci.* **363** 1737–46
- Oliveras I *et al.* 2018 Fire effects and ecological recovery pathways of tropical montane cloud forests along a time chronosequence *Glob. Chang. Biol.* **24** 758–72
- Page S E, Siegert F, Rieley J O, Boehm H D V., Jaya A and Limin S 2002 The amount of carbon released from peat and forest fires in Indonesia during 1997 *Nature* **420** 61–5
- Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, Buendia L, Miwa K, Ngara T, Tanabe K and Wagner F 2003 *Good practice guidance for land use, land-use change and forestry*. ed F Penman *et al* (Institute for Global Environmental Strategies)
- Phillips O L *et al.* 2009 Drought Sensitivity of the Amazon Rainforest *Science (80-. )*. **323** 1344–7
- Pommerening A and Muszta A 2016 Relative plant growth revisited: Towards a mathematical standardisation of separate approaches *Ecol. Modell.* **320** 383–92
- Poorter L *et al.* 2016 Biomass resilience of Neotropical secondary forests *Nature* **530** 211–4
- PRODES 2020 Instituto Nacional de Pesquisas espaciais. Projeto PRODES - Monitoramento da Floresta Amazônica por satélite
- R Core Team 2019 R: The R Project for Statistical Computing
- Reiche J, Verhoeven R, Verbesselt J, Hamunyela E, Wielaard N and Herold M 2018 Characterizing Tropical Forest Cover Loss Using Dense Sentinel-1 Data and Active Fire Alerts *Remote Sens.* **10** 777
- Richards F J 1959 Growth function for empirical use *J. Exp. Bot.* **10** 290–300
- Silva C V J *et al.* 2018a Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics *Philos. Trans. R. Soc. B Biol. Sci.* **373** 20180043
- Silva Junior C H L, Anderson L O, Silva A L, Almeida C T, Dalagnol R, Pletsch M A J S,

- Penha T V., Paloschi R A and Aragão L E O C 2019 Fire Responses to the 2010 and 2015/2016 Amazonian Droughts *Front. Earth Sci.* **7** 97
- Silva S S da, Fearnside P M, Graça P M L de A, Brown I F, Alencar A and Melo A W F de 2018b Dynamics of forest fires in the southwestern Amazon *For. Ecol. Manage.* **424** 312–22
- Silvério D V., Brando P M, Bustamante M M C, Putz F E, Marra D M, Levick S R and Trumbore S E 2019 Fire, fragmentation, and windstorms: A recipe for tropical forest degradation ed D Edwards *J. Ecol.* **107** 656–67
- Suarez D R *et al.* 2019 Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data *Glob. Chang. Biol.* **25** 3609–24
- Talbot J *et al.* 2014 Methods to estimate aboveground wood productivity from long-term forest inventory plots *For. Ecol. Manage.* **320** 30–8
- Uhl C and Kauffman J B 1990 Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon *Ecology* **71** 437–49
- UNFCCC 2016 *Brazil Intended Nationally Determined Contribution*
- van der Werf G R, Randerson J T, Giglio L, Collatz G J, Mu M, Kasibhatla P S, Morton D C, DeFries R S, Jin Y and van Leeuwen T T 2010 Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009) *Atmos. Chem. Phys.* **10** 11707–35
- Van Nieuwstadt M G L and Sheil D 2005 Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia *J. Ecol.* **93** 191–201
- Withey K *et al.* 2018 Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests *Philos. Trans. R. Soc. B Biol. Sci.* **373** 20170312

## 4 A NOVEL SPATIAL-TEMPORAL APPROACH TO ESTIMATE CO<sub>2</sub> EMISSIONS FROM AMAZONIAN FOREST FIRES

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# A novel spatio-temporal approach to estimate CO<sub>2</sub> emissions from Amazonian forest fires

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## 4.1 ABSTRACT

Although emissions from Land Use, Land-Use Change and Forestry (LULUCF) are the major source of CO<sub>2</sub> emissions in Brazil, Amazonian wildfires are still not accounted for in global and national systems. A key reason for this is the lack of integration between combustion emissions and long-term carbon fluxes (i.e. post-fire decomposition emissions and uptake from regrowth). Here, we combined information on Amazonian wildfires with a large-scale dataset of carbon stocks from human-modified forests. We developed a spatio-temporal approach to quantify CO<sub>2</sub> emissions from forest fires based on the carbon stocks of the Amazonian forests within a selected landscape in the eastern of Amazonia region. We first developed a combustion model based on the empirical relationship between aboveground biomass (AGB) and necromass. We then integrated this into a model previously developed for quantifying post-fire emissions. We tested our approach using a high-resolution burned area map and quantified the CO<sub>2</sub> net emissions from 1987 to 2007 within the selected landscape. By evaluating the model's output, we show: (i) the largest combustion emissions are from burned forests with the largest AGB stocks; and (ii) the largest decomposition emissions are from burned forests in the lower and upper range of AGB. Forests with high levels of AGB accounted for only 34% of all burned area by 2007, but their relative contribution to combustion and decomposition emissions was 57% and 34.5%, respectively. Our results show that by using our spatio-temporal approach, total emissions from forests fires could be incorporated into the Brazilian Carbon budget.

**Keywords:** burned area, combustion emissions, decomposition emissions, upscaling, tropical forest, biomass.

## 4.2 1. INTRODUCTION

Across the tropics, LULUCF is a major source of greenhouse gases (GHG) emissions. Brazil, for example, is the world's 6<sup>th</sup> largest emitter of GHG, and c. 40% of those emissions are derived from LULUCF (SEEG, 2020). Most of those emissions are from deforestation and degradation of humid tropical forests in the Amazon basin, which store ~100 Pg of carbon in biomass and necromass (Feldpausch *et al.*, 2012). The assessments of CO<sub>2</sub> emissions from these tropical forests are mainly based on annual satellite assessments of deforestation, which have been ongoing since the 1980's (PRODES, 2020). Currently, annual CO<sub>2</sub> emissions and removals from LULUCF in Brazil are estimated following IPCC guidelines by the environment ministry system (SIRENE, 2017) and a parallel independent system developed by several national and international non-governmental institutions (SEEG, 2020, Azevedo *et al.*, 2018).

Although both platforms cover national and subnational emissions, neither includes emissions from Amazonian wildfires. This is a potentially important omission; the fire crisis in the Brazilian Amazon has received increasing attention in recent years (Barlow *et al.*, 2019), and forest fires could contribute to more than half of deforestation gross emissions (Aragão *et al.*, 2018) or even to 57% of global LULUCF in 2010 (Friedlingstein *et al.*, 2010; Aragão *et al.*, 2018). Moreover, while the prevalence of fires is declining in some parts of the world (Andela *et al.*, 2017) it is increasing in humid tropical forests (Jolly *et al.*, 2015; Le Page *et al.*, 2017). As rainforest vegetation is not fire-adapted, even low-intensity fires result in very high rates of tree mortality (Barlow *et al.*, 2003; Brando *et al.*, 2012).

Although Earth System models and carbon budgets include fire emissions from global databases (GFED, GFAS), both carbon accounting systems underestimate emissions from forest fires. Part of the reason for this stems from the challenges of mapping fire extent (Chapter

2), but these global fire databases are also unable to estimate the long-term carbon deficit of burned forests (Silva *et al.*, 2018). Estimating long-term carbon dynamics in burned forests requires integrating emissions from the combustion of necromass with the longer-term carbon balance resulting from tree mortality, decomposition, and carbon uptake through regrowth (Silva *et al.*, 2020). While recent assessments of burned forest plots in Amazonia have provided key estimates of these processes (Withey *et al.*, 2018; Silva *et al.*, 2020), we still lack a mode of scaling them up spatially to estimate basin-wide emissions over time. Achieving this requires estimating emissions components across the full range of undisturbed and human-modified Amazonian forests, which vary greatly in aboveground biomass (AGB) (Baker *et al.*, 2007; Quesada *et al.*, 2012; Berenguer *et al.*, 2014).

Scaling post-fire dynamics as function of forests structure is crucial, since the AGB of forests will determine the amounts of CO<sub>2</sub> emitted through the relationship of AGB with fuel stocks and levels of tree mortality (Chao *et al.*, 2009, Palace *et al.* 2012, Barlow *et al.*, 2012, Brando *et al.*, 2016). This is because combustion emissions will be influenced by pre-fire necromass stocks (Cochrane *et al.*, 1999), while post-fire necromass available for decomposition will be dependent on pre-fire biomass stocks (Palace *et al.*, 2012; Osone *et al.*, 2016). Once burned, high mortality would be expected in low AGB forests because fire intensity is high in opened and dry forests, and in extremely high AGB forests, because the species composition of these are particularly sensitive to fire (Cochrane, 2001; Brando *et al.*, 2012). Finally, the post-fire susceptibility to mortality of trees would define the amounts of AGB loss across a gradient of forests AGB. Larger trees take longer to die after fires than smaller stemmed trees (Barlow *et al.* 2003, Silva *et al.* 2018), so forests with less AGB are likely to have a lower portion of their biomass susceptible to delayed mortality and thus lose less AGB in the long-term.

In this study, we develop a novel spatial-temporal approach to scale-up immediate and long-term CO<sub>2</sub> emissions from wildfires based on our prior knowledge of the effects of fire on forests

structure. Our first objective was to model combustion and decomposition emissions as a function of pre-fire AGB. We achieved this in multiple steps by: (i) compiling all the field-based information known from previous assessments of biomass and necromass in Amazonian burned forests to estimate necromass stocks and combustion emissions from the fraction of necromass burned; (ii) using a dataset from prior studies detailing biomass loss after forest fires to quantify the relationship between initial biomass and emissions one year after fire (iii); combining the initial biomass loss (step ii) with post-fire temporal changes in biomass (Silva *et al.* 2020) using the relationships between large tree abundance and plot biomass to determine the extent to which a forest is susceptible to delayed mortality; and (iv) offsetting regrowth as modelled by Silva *et al.* (2020). Our second objective was to demonstrate that these combustion and decomposition emissions can be applied spatially, we then applied the models to a 21-year time-series of burned area in an eastern Amazonian landscape.

### 4.3 METHODS

We developed and tested a spatio-temporal approach which the overview is shown in figure 4.0. Each step of the development and application of our approach is described in more detail in the sections 4.3.1 and 4.3.2. In general, we used field-based datasets from different sources (topic *b* in section 4.3.1), which allowed us to calibrate a linear regression for modelling the combustion emissions from pre-fire AGB (topic *c*), and non-linear regressions to model initial AGB loss and the susceptibility to delayed mortality from pre-fire AGB (topics *d* and *f*). The models developed in topics *d* and *f* were used in the adjustment of the necromass equation to a wider range of forests (topic *e*). The adjusted necromass equation was then used in topic *g* for estimating gross CO<sub>2</sub> emissions. The CO<sub>2</sub> uptake was estimated independently (topic *h*) of the other steps. In section 4.3.2 we show how we applied our approach to a test landscape by using three spatial datasets, (burned area, forest cover and AGB), which sources and specifications are described in topic *b* from section 4.3.2. The spatial data processing (topic *c* in section 4.3.2)

involved selecting burned areas in lands covered with forests and applying the models from section 4.3.1 using the AGB spatial data as the main variable for estimating the gross CO<sub>2</sub> emissions and uptake over our wildfire time-series of 21 years.

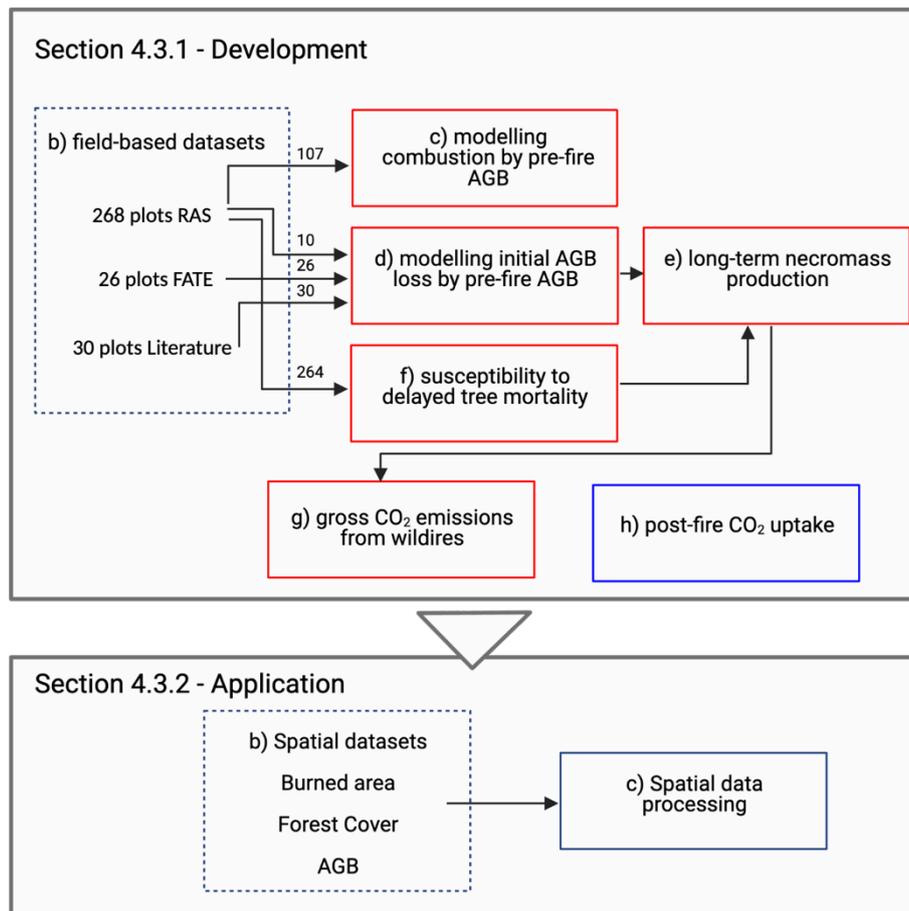


Figure 4.0 Main steps of the development and the application of our spatio-temporal approach for estimating CO<sub>2</sub> emissions from Amazonian wildfires. Red boxes represent steps associated with CO<sub>2</sub> emissions estimates and the blue box is an independent step for estimating CO<sub>2</sub> uptake. AGB: Aboveground biomass, RAS: Rede Amazônia Sustentável network, FATE: Fire-Associated Transient Emissions in Amazonia network

#### 4.3.1 *The spatio-temporal approach for quantifying the CO<sub>2</sub> fluxes of burned forests*

##### a) The basis for quantifying net CO<sub>2</sub> emissions

We integrated two approaches to quantify the emissions from (i) combustion and, (ii) decomposition of forest necromass. These two types of emissions occur separately in time and depend on different factors (figure 4.1). For example, combustion emissions depend on the relative proportions of coarse and fine woody material that constitute necromass stocks, and the combustion efficiency of these components during the fires. We quantify combustion emissions in section (c) using data from Withey et al 2018. For quantifying the decomposition emissions, we used an approach adapted from (Silva *et al.* 2020), that quantifies post-fire woody necromass production by tree mortality, and growth using non-linear models. We adapted these models to estimate the CO<sub>2</sub> fluxes of burned forests relative to unburned forests. The integration of the combustion emissions with the post-fire emissions are described with more details in the next section. The carbon emissions and uptakes are reported in CO<sub>2</sub> equivalent unit.

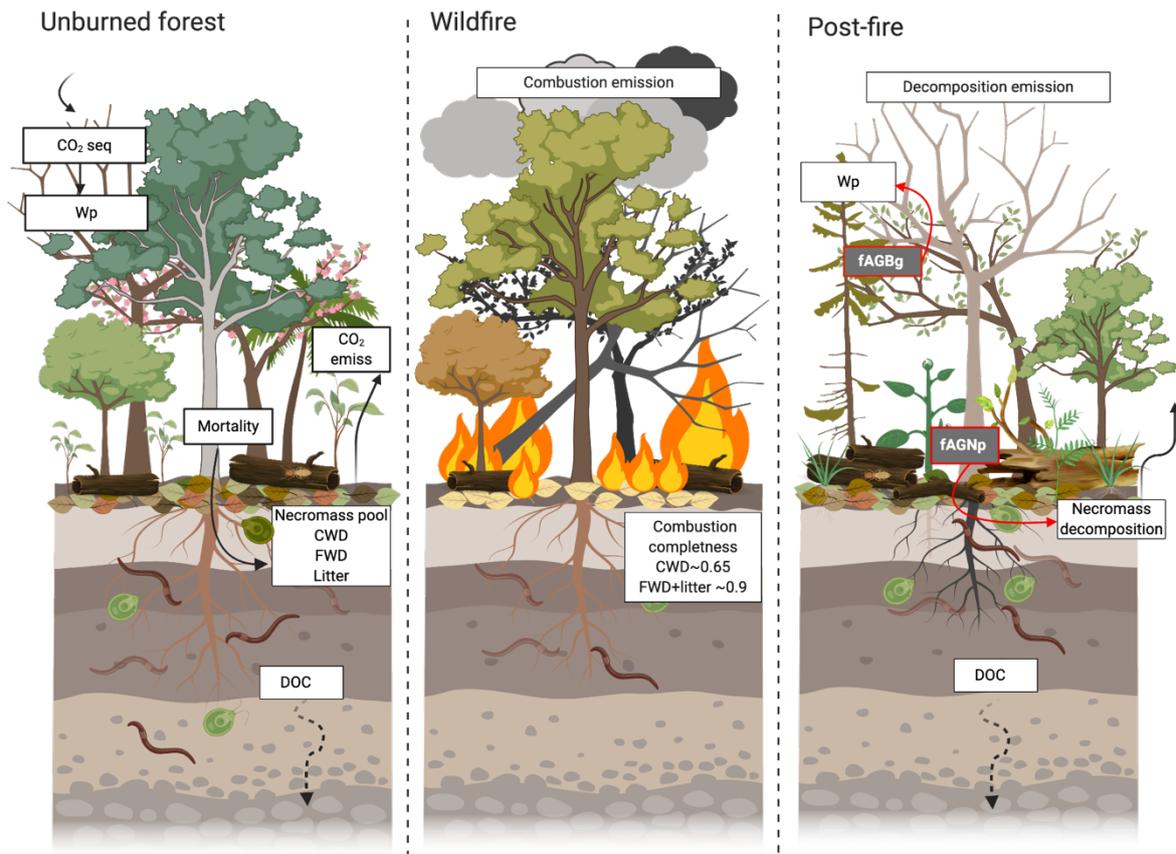


Figure 4.1 The changes in forest carbon fluxes (left panel) after wildfires. During wildfires (centre panel), large amounts of carbon are released to the atmosphere by the combustion of necromass components (coarse wood debris (CWD) and fine wood debris (FWD)). The combustion completeness of each component determines the amounts of emissions and is based on an experiment in pre- and post-uncontrolled fires in central Amazonia (Withey et al. 2018). After the fires (right panel), the burned forests carbon fluxes are changed relative to the balanced undisturbed forests fluxes (left panel). Fire-induced AGB growth (fAGBg) increases wood productivity (Wp) levels, resulting in increased CO<sub>2</sub> uptake. Similarly, fire-induced aboveground necromass production (fAGNp) increases necromass pools, in turn increasing decomposition emissions. Part of the carbon from the necromass decomposition stays in the soils as dissolved organic carbon (DOC).

## b) Field-based datasets

We compiled three sets of forest plots data. The first dataset is a collection of 30 plots from unburned and burned sites (one year since fire) from previous studies (Brando et al., 2014, Berenguer et al., 2014, Alencar et al. 2011). The second and third datasets are from the existing forest plots networks Fire-Associated Transient Emissions in Amazonia (FATE; 26 plots) and Rede Amazonia Sustentável (RAS; 268 plots). In total, 324 plots were assessed, among them 26 plots were sampled before and after fires, 20 plots were sampled in burned forests to be compared with unburned control plots ( $n = 20$ ), and another 258 plots were measured in degraded and undisturbed forest. The plots comprised six forest types: undisturbed, secondary, once-burned, repeatedly burned, logged and burned, secondary burned. The plot-level AGB was quantified by aggregating stem-level AGB following allometric equation for trees Chave *et al.*, 2014, palms (Goodman *et al.*, 2013), and for lianas (Gerwing and Farias, 2000). The plot-level AGB of the first dataset (30 plots from literature), varied in AGB allometric equations as we did not have access to stems-level data.

c) Modelling combustion emissions by pre-fire AGB

For the analysis described in this section we used a selection of 107 plots from the RAS network dataset where both AGB and necromass stocks were measured. To quantify carbon losses from the combustion of necromass on the forest floor we first estimated the relationship between both plot-level coarse wood debris (CWD;  $\geq 10$  cm diameter at one extremity) and fine wood debris (FWD;  $\geq 2$  and  $< 10$  cm diameter at both extremities) with AGB (figure 4.2). The positive linear relationship between AGB and both woody debris components, CWD and FWD, was determined by a null intercept linear regression ( $R^2=0.5$ ,  $p<0.01$ ;  $R^2=0.65$ ,  $p<0.01$ , respectively). The estimated coefficient of each regression was then used for quantifying FWD and CWD stocks as a proportion of AGB.

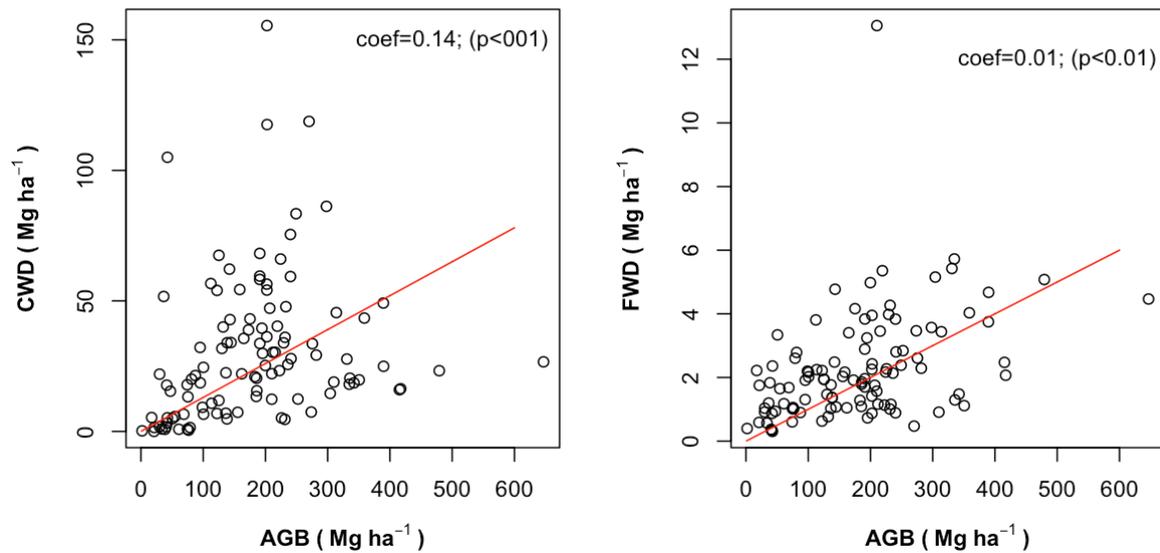


Figure 4.2 The relationship between above ground biomass (AGB) and necromass components: coarse woody debris (CWD; on the left) and fine woody debris (FWD; on the right) from 107 plots (Rede Amazônia Sustentável network), allocated in human-modified and old-growth forests. A linear model (red line) with null-intercept was fitted to estimate each necromass component from AGB stocks. The linear models estimate that CWD is on average 14% of AGB and FWD is 1% of AGB.

We used combustion completeness factors from (Withey *et al.* 2018) to quantify the proportion of each component, CWD and FWD consumed by the fires. Finally, we estimated the total CO<sub>2</sub> emissions from combusted necromass (CN) by adding the emissions from FWD and CWD, according to:

$$CN = (FWD \cdot CCf) + (CWD \cdot CCc) \quad (\text{Eq. 4.1})$$

where, CCf the combustion completeness of FWD, and CCc is the combustion completeness of CWD.

d) Modelling initial AGB loss as function of pre-fire AGB

For the analysis described in this section we used the collection of 30 plots from literature, 26 from FATE and 10 from RAS network. We modelled the initial (within one year) post-fire AGB loss resulting from tree mortality as a function of the forest's pre-fire AGB, therefore capturing variation in the responses of different types of forests (including human-modified and undisturbed) to fire. We collated data from all plots where forest AGB was measured within one year since the fires, and fitted a linear and a non-linear model, constrained to go through the intercept at zero. We fitted the models using the *nls* and *lm* functions from the *stats* R package (R CoreTeam, 2019). The two models were statistically similar in terms of fit (linear RSE 48.6; non-linear RSE 47.8) and plausibility (linear AIC = 490.98; non-linear AIC 490.33). We chose to focus on the non-linear model as it had a better fit to the data and matched our a priori expectations that mortality would be higher at the extremes of the data (low and very high biomass forests) (figure 4.3).

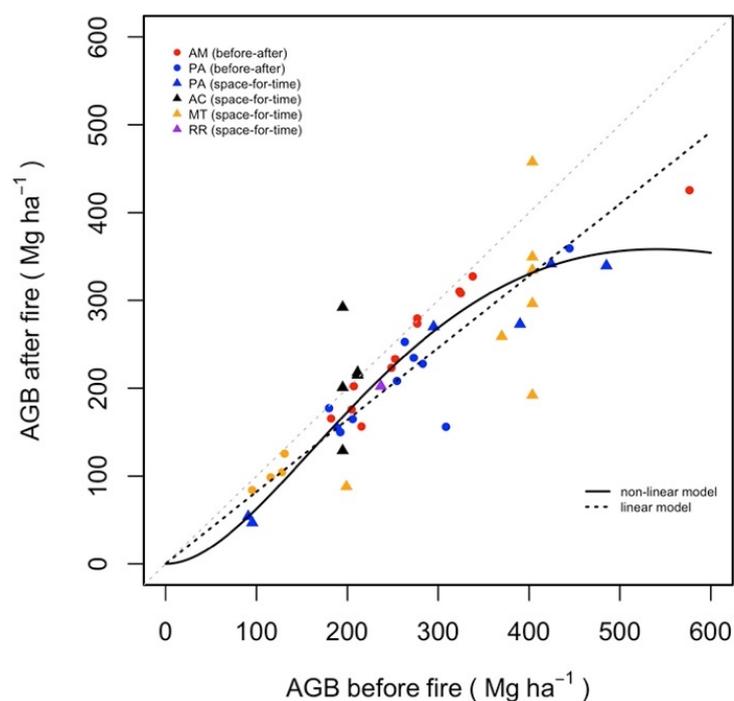


Figure 4.3 A non-linear and a linear model for quantifying initial above ground biomass (AGB) losses from 5 sites in Brazilian Amazonia (Amazonas (AM), Pará (PA), Acre (AC), Mato-

Grosso (MT) and Roraima (RR). Both models were fitted to data from 66 plots, of which 26 were measured before and after fires, and 40 were burned-control pairs from space-for-time studies. The dataset is a compilation of all studies that assessed the initial effects of Amazonian fires on AGB stocks to our knowledge (Brando et al., 2014, Berenguer et al., 2014, Alencar et al. 2011) and plots from FATE and RAS network. The non-linear model showed a slightly better fit to the data.

e) Determining longer-term necromass production

This analysis is applied to spatial data and field-based data was not used. The initial AGB loss in section (d) was used to determine the longer-term necromass production (AGNp) for beyond one year since fire. We used the standard negative exponential decay function from Silva *et al.* 2020 (Chapter 3), that describes the reduction of mortality rates up to 30 years after fires:

$$AGNp = a * t^{-k} \quad (\text{Eq. 4.2})$$

where,  $AGNp$  is the necromass production by tree mortality,  $a$  is the y-intercept,  $t$  is the time since last fire, and  $k$  is the decay constant estimated previously as 0.32 by Silva *et al.* 2020. To estimate the y-intercept  $a$  of Eq. 4.2, we replaced our modelled initial AGB loss (section d) with the AGNp at  $t=1$ . In doing so, the y-intercept  $a$  of the AGNp function, and thus the long-term AGNp, are dependent on pre-fire AGB.

f) Susceptibility to delayed tree mortality

In this analysis we used 264 plots from RAS network dataset. We determined the extent to which a burned forest that lost part of its AGB during the first year after a fire is susceptible to delayed mortality. To do this we first examined the proportion of plot-level AGB that is composed of large trees AGB (> 40cm DBH). We chose >40cm as our cut off as in Chapter 2 we suggest that stems larger than this show delayed mortality. We used 150 Mg ha<sup>-1</sup> as the

AGB threshold above which forests would be more susceptible to delayed mortality because 150 Mg ha<sup>-1</sup> was the minimum AGB of the forest plots used for parametrizing the AGNp function in Silva et al., 2020. We obtained 52% as the mean proportion of AGB held within large trees in > 150 Mg ha<sup>-1</sup> plots. We then fitted an asymptotic model, by using the *nls* function from *stats* R package, to estimate the mean proportion of AGB held within large trees in < 150 Mg ha<sup>-1</sup> plots (figure 4.4). We estimated the susceptibility to delayed mortality of <150 Mg ha<sup>-1</sup> forests AGB according to:

$$SM(\%) = 1/(0.52/(a - (a)^{-c*AGB})) \quad (\text{Eq. 4.3})$$

where *SM (%)* is the proportion of forest AGB susceptible to delayed mortality, *a* is an estimated coefficient from the fitted asymptotic model describing the maximum proportion (1.04±0.11, p<0.01), and *c* is an estimated coefficient describing the increase rate of SM (0.003±0.0004, p<0.01). The AGNp in a given forest at a given time after fire was limited by the SM.

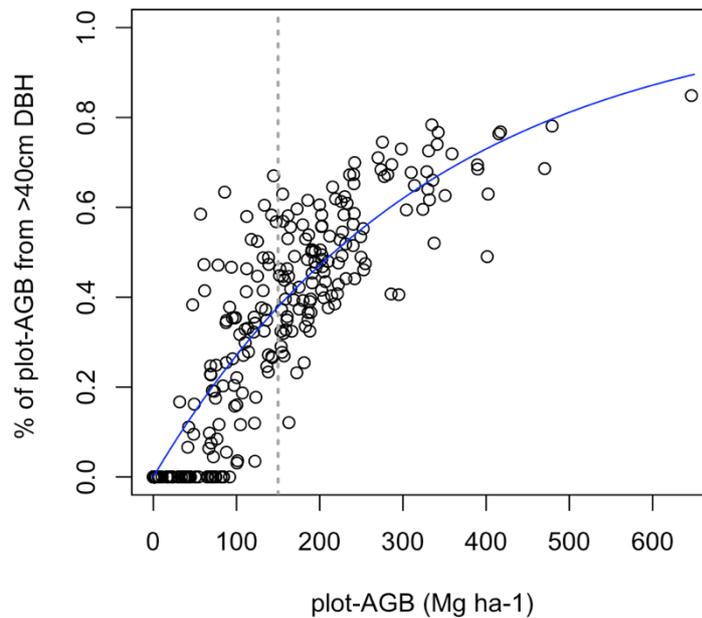


Figure 4.4 The asymptotic model (blue line) used for estimating forests susceptibility to fire-induced delayed mortality of forests with  $<150 \text{ Mg ha}^{-1}$  (dashed grey line) in Eq 4.3. The model was fitted to 264 plots from Rede Amazônia Sustentável network, and estimates the proportion of aboveground biomass (AGB) held in large trees ( $>40\text{cm}$  diameter at breast height (DBH)) based on AGB at the plot-level. The model shows that as plot-level AGB increases, a larger proportion of AGB concentrated in large trees is expected, and that the relationship is asymptotic.

#### g) Gross CO<sub>2</sub> emissions from wildfires

The gross CO<sub>2</sub> emissions were estimated by combining the emissions estimated from combustion (section c) and from decomposition. We used the model for estimating gross decomposition emissions from Silva *et al.* 2020 (Chapter 3). We summed all decomposed necromass fractions (cumulatively) and, to avoid double-counting, we removed the decomposition fractions that would have occurred if necromass was not combusted. We estimated gross CO<sub>2</sub> emissions resulting from combustion emissions from a current fire with the additional necromass decomposition from previous fires.

#### h) Post-fire CO<sub>2</sub> uptake

The post-fire CO<sub>2</sub> uptake was estimated according to Silva *et al.* 2020 (Chapter 3), and only varied over time. As there was insufficient data to modify the parameters (maximum growth ( $g_{max}$ ), mean growth rate ( $g$ ), and curve inflection point ( $c$ )), the post-fire uptake was fixed for the whole range of AGB. The values of growth rates are relative to the growth measured in the undisturbed forests plots used for parametrizing the uptake equation in chapter 3.

### 4.3.2 *Quantifying the total net emissions in an Amazonian landscape*

#### a) Test landscape

Our test landscape was a single Landsat scene from Pará state in the eastern part of the Brazilian Amazon, surrounding the cities of Tailândia and Tome-Açu (figure 4.5). This region was affected by wildfires in 1993, and several studies have focussed on it (Cochrane *et al.* 1993, Cochrane *et al.* 2001, Alencar *et al.*, 2011). The typical forests in the region are evergreen lowland (terra-firme), and the climate is tropical with an annual precipitation of 1500-2000 mm and a distinct dry season from July to December . The landscape suffered both large-scale and fish-bone patterns of deforestation, resulting in widespread agricultural lands and highly fragmented human-modified forests.

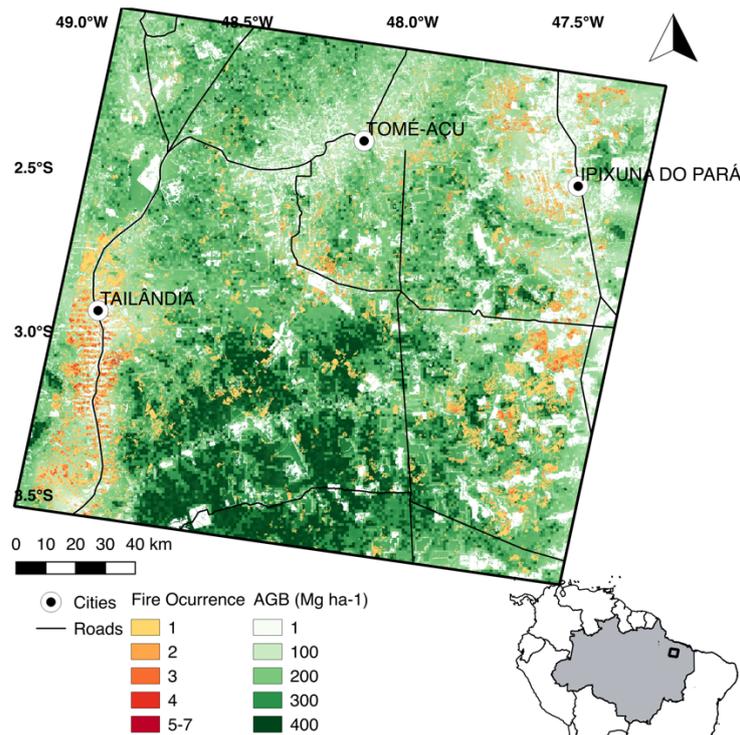


Figure 4.5 Study area in the surroundings of Tailândia, PA, eastern of Amazonia region. The fire occurrence from 1987 to 2007 is shown on a scale of 1-7, according to fire frequency by yellow to red shading. The range of initial (1987) biomass (Mg ha<sup>-1</sup>) is show by green shading.

#### b) Spatial datasets

For scaling up the wildfres emissions we used three sets of spatial data: (i) burned area maps, developed by Alencar *et al.* 2011 using a routine (CLAS-BURN) that classified wildfires in a 30-m resolution Landsat scene (path row 223\_62) from 1987 to 2007. This fire mapping methodology is currently being applied to generate a dataset covering the whole Amazon biome (Ane Alencar, personal communication). However, at the time we tested our approach, data for the entire basin were still unavailable. (ii) Forest cover maps (FC) derived from the Brazilian Annual Land-Use and Land-Cover Mapping project (MapBiomass, 2019), produced from a classification of pixel-per-pixel of Landsat satellite images using machine learning algorithms. This dataset is available through Google Earth Engine, and covers Brazil's area extent and is available from 1985. (iii) The 1-km resolution AGB map for the early 2000s

developed by Avitabile *et al.*, 2016 covering the pan-tropical region. The pre-processing of the spatial data is given in detail in the next section.

c) Spatial data processing

The processing of spatial data started with the reclassification of the input datasets to obtain binary maps. The land cover and burned area maps were reclassified to extract only fires in forested areas each year. The AGB map was previously processed (Smith *et al.*, 2020) to infill the areas deforested before 2000's with the mean AGB of the 10 km<sup>2</sup> surrounding area. The processing was run 21 times, equivalent to the number of years in our time-series. At each step (year), input data was pre-processed, and used for producing auxiliary and final outputs (figure 4.6). After pre-processing inputs, we applied our field-based models to calibrate auxiliary outputs: (i) the time since fire (TSF); (ii) the combustion emissions depending on AGB; (iii) the necromass produced (AGN) depending on pre-fire updated AGB layer; (iv) the forest AGB growth (AGBg) depending on TSF; (v) the updated AGB after removing losses and adding gains. The auxiliary inputs were then processed to generate final outputs: (i) the combustion layer was added to decomposition (derived from AGN); (ii) the uptake layer was derived from AGBg; and (iii) net emissions were produced by combining gross and uptake layers. Hence, at each step, forest cover and burned areas were new external inputs, whereas the AGB layer was being updated and used as a recycled input. By the end of processing, we had the time-series layers for combustion emissions, gross emissions, uptake and net emissions.

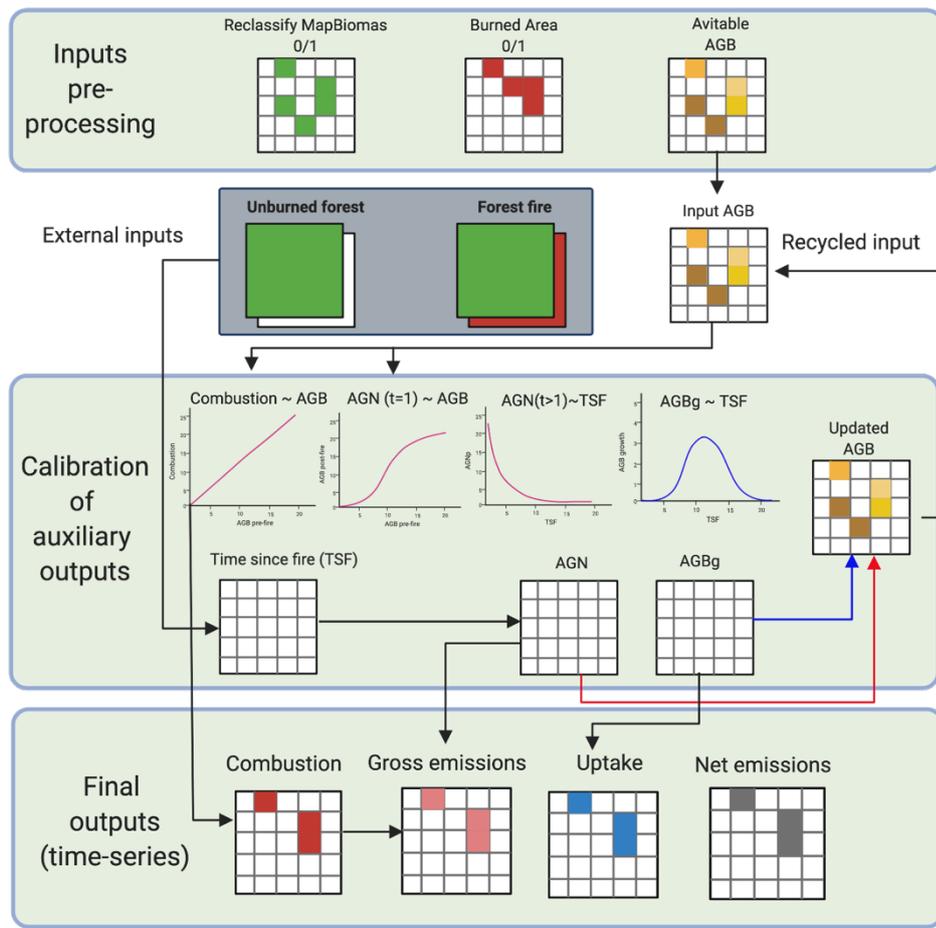


Figure 4.6 The processing flow of the spatial data. A time-series of 21 years was processed in a loop where at each step (year), new input data for forest cover and burned area was used to compute emissions across the extent of forest fires and over time since fire (TSF) . At each step, the aboveground biomass (AGB) dataset was updated by deducting mortality (red arrow) and adding growth (blue arrow), and used for estimating emissions from combustion and decomposition. The functions for estimating aboveground necromass (AGN) and aboveground biomass growth (AGBg) are described in sections (e) and (h) from topic 4.3.1.

## 4.4 RESULTS

### 4.4.1 *Evaluating modelled emissions patterns over time and along a gradient of AGB stocks*

Combustion emissions only occur in the year of the fire, and increased linearly by 0.2 Mg CO<sub>2</sub> ha<sup>-1</sup> with each Mg increase in AGB stocks of burned forests (figure 4.7a,b). This linear function

is a simple outcome of the relationship between necromass (FWD and CWD) and AGB in human-modified and undisturbed Amazonian forests (Figure 4.3). The post-fire lag in mortality and decomposition means that gross and net decomposition emissions vary over time and with AGB. Their non-linear relationship with AGB reflects the non-linear pattern of mortality from plots across Amazonia (Figure 4.3), and results in decomposition emissions that: i) increase with AGB up to c. 90 Mg ha<sup>-1</sup>; ii) decrease with AGB from >90 to c. 250 Mg ha<sup>-1</sup>; and iii) increase with AGB above 250 Mg ha<sup>-1</sup> to the maximum. These three different trajectories are explained by the levels of initial post-fire mortality, which are (i) relatively high in forests with the lowest AGB stocks; (ii) lowest in forests with AGB ranging from 200-300 Mg ha<sup>-1</sup> (iii) and highest in forests with AGB >300 Mg ha<sup>-1</sup> (Figure 4.4).

The non-linear relationship means that gross and net decomposition emissions are negative one year after the fires in burned forests with AGB stocks ranging from 179 to 388 Mg ha<sup>-1</sup> (figure 4.7a,b). These negative emissions result from the foregone decomposition resulting from combustion, which removes a portion the necromass that would have decomposed. In subsequent years, gross and net emissions in burned forests are generally positive across the gradient of AGB, with the exception of forests with very low pre-fire AGB stocks (<18 Mg ha<sup>-1</sup>), where CO<sub>2</sub> uptake by growth is larger than emissions by decomposition (figure 4.7b). Over time, cumulative gross and net fluxes (figure 4.7c,d), including combustion emissions, increase following a similar pattern as annual emissions. In 30 years, we estimate that the largest emissions are from the forests with AGB stocks ranging 50-150 and >350 Mg ha<sup>-1</sup>.

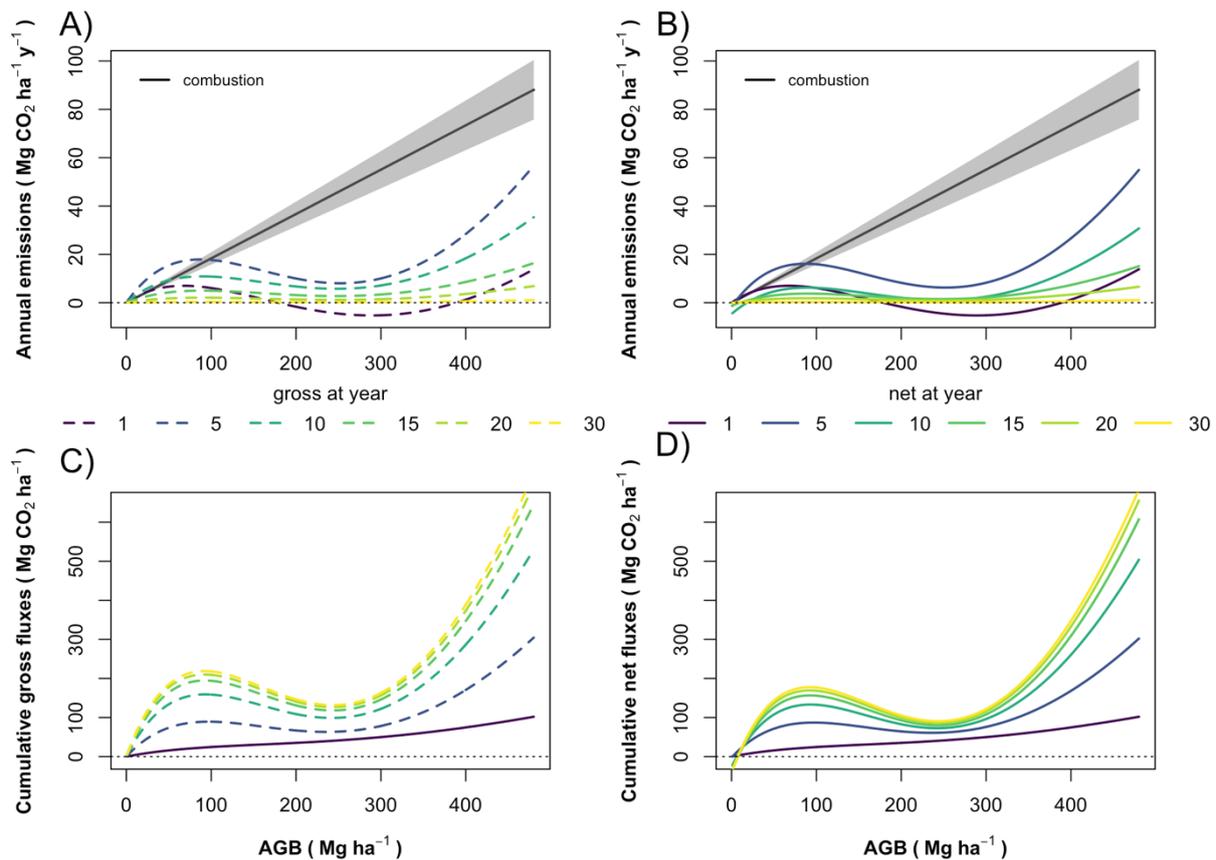


Figure 4.7 Over a period of 30 years since fire (in the colour palette) and across aboveground (AGB) stocks (Mg ha<sup>-1</sup>) the estimated a) Annual gross emissions from decomposition (dashed lines) and combustion (black line, shaded grey area is the CI 95%); b) Net emissions from decomposition; c) Cumulative gross fluxes with addition of combustion emissions, and d) Cumulative net fluxes with addition of combustion emissions.

#### 4.4.2 Applying the burned forest emissions model to an Amazonian landscape

From 1987 to 2007, 2973.9 km<sup>2</sup> of forests burned in the test landscape (total area = 27148 km<sup>2</sup>; Figure 4.5). From these, 20% burned twice and 6% burned at least three times. We estimated that these fires resulted in total net emissions of 16.9 Tg CO<sub>2</sub>, of which 10.5 Tg CO<sub>2</sub> resulted from combustion. Over the 21-year time series, combustion and decomposition emissions were strongly affected by burned area extent, with decomposition emissions showing a marked lag (figure 4.8a).

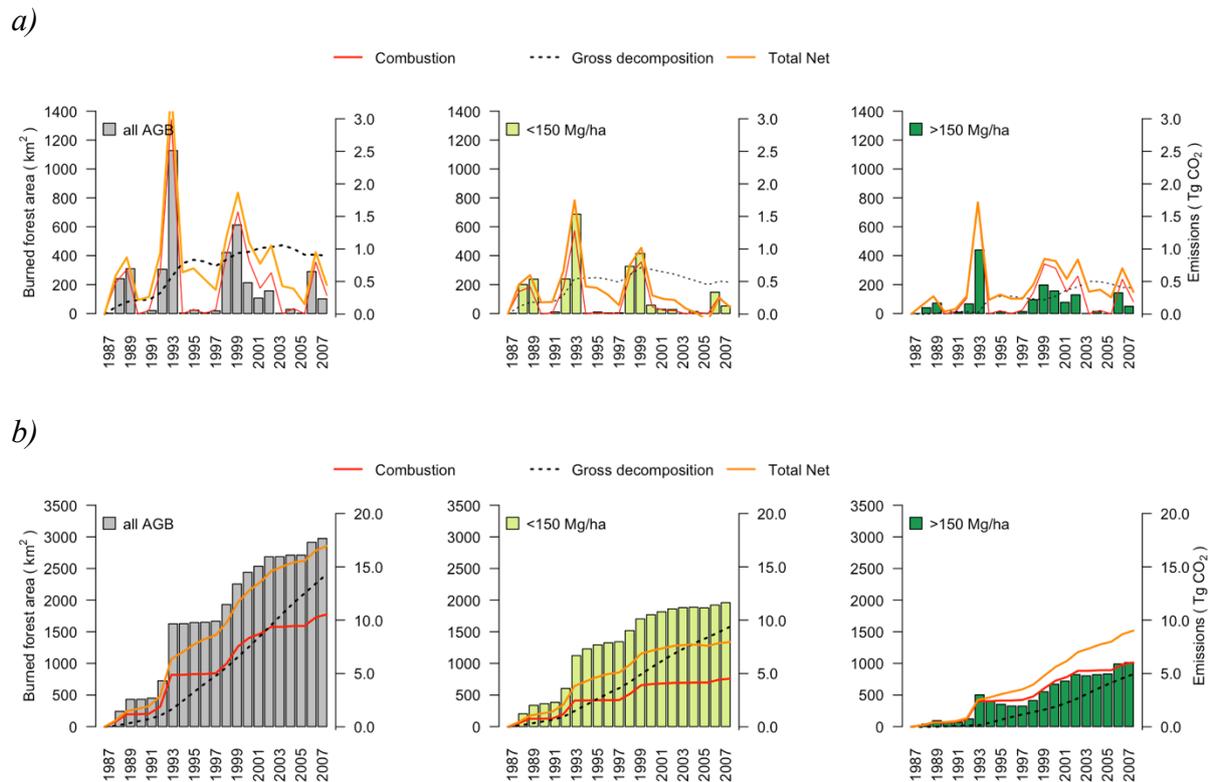


Figure 4.8 a) Annual burned area (bars) from the study area, combustion (red line), gross decomposition (dashed black line) and total net (orange line) emissions from all forests, low AGB (<150Mg/ha) and high AGB (>150Mg/ha) forests; b) Cumulative burned area, and respective cumulative emissions by type of forest – all forests, low and high AGB.

Pre-fire AGB stocks were an important determinant of emissions. Overall, a larger area burned in low AGB forest (<150 Mg ha<sup>-1</sup>) than in high AGB forests (>150 Mg ha<sup>-1</sup>), but high AGB forests emitted the largest CO<sub>2</sub> amounts by combustion due to their greater levels of necromass. For example, by 2007, high AGB forests had emitted 9 Tg CO<sub>2</sub>, the equivalent to 53% of total net emissions within the test landscape (figure 4.9), even though they only contributed 34% to the burned area. The relative importance of high AGB forests was marginally higher for combustion emissions (57%) than decomposition emissions (34.5%) over this time period. Pre-fire AGB of the forests also determined when the peak in decomposition emissions

occurred. Low AGB forests were the major CO<sub>2</sub> source up until 1997, yet total net emissions from high AGB forests increased in their importance after that, from 1999 to 2007. As such, some of the emissions from decomposition remained committed (and hence unaccounted for) at the end of the time series.

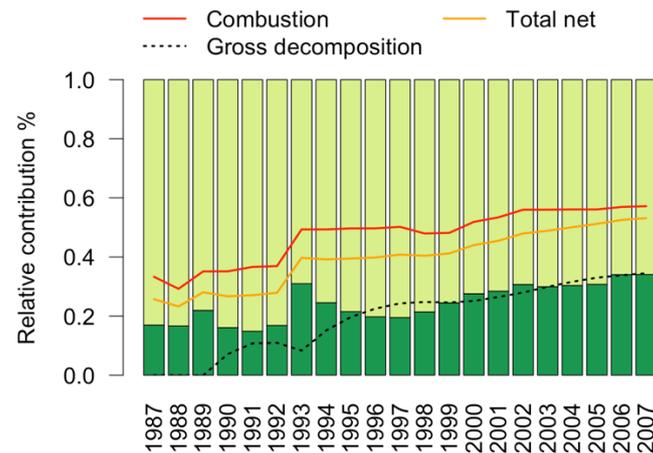


Figure 4.9 Relative contribution of low aboveground biomass (light green) and high aboveground biomass (dark green) forests to cumulative (21 years) burned area (bars), combustion (red line), gross (dotted black line) and total net emissions (orange line).

#### 4.5 DISCUSSION

We propose an approach that integrates a comprehensive synthesis of biomass loss after Amazonian wildfires (Figure 4.3), detailed field data on biomass and necromass in human-modified tropical forests (Berenguer *et al.* 2014) and temporal assessments of changes in biomass over time (Silva *et al.* 2018, 2020) to simulate combustion and decomposition emissions over a spatial-temporal scale. We show how our novel approach can be scaled up using maps of above ground biomass and time series of burned areas. We further discuss the impact of Amazonian forest complexities on estimated fire emissions and examine the prospects for applying our approach to other landscapes given the uncertainties in our model

and the data required to refine it. We finally discuss the implications of our estimates for Brazil's plan on climate change.

#### 4.5.1 *The implications of pre-fire AGB for net emissions*

The total net emissions from fires simulated in our models were strongly determined by the statistical model linking initial mortality model with pre-fire AGB demonstrated in section (d) topic 4.3.1. Thus, according to our models simulations, the highest emissions are expected in forests with the greater initial mortality, i.e. the lowest AGB forests (<200 Mg ha<sup>-1</sup>) and the highest AGB forests (>350 Mg ha<sup>-1</sup>). The high AGB forests have a marked contribution over a 30-year period, with cumulative net emissions exceeding 208 Mg CO<sub>2</sub> ha<sup>-1</sup>. While the impacts of these emissions are high for even a small area, there are two reasons why fire likelihood is lower in high AGB forests. First, high AGB forests are rarer, and represent only c. 12% of all forests in Amazonia (Avitabile *et al.* 2016 data). Second, high AGB forests are likely to be undisturbed, and their intact canopy means they are more likely to maintain humid understories than disturbed (and therefore lower biomass) forests (Uhl & Kauffman, 1990).

Our model outcomes also suggest that the fires will release lower quantities of CO<sub>2</sub> over 30 years in forests where AGB ranges from 200-350 Mg ha<sup>-1</sup>. These forests have a broad spatial coverage and account for 56% of remaining forests in 2000 (Avitabile *et al.*, 2016 data), Although these mid-range AGB forests are likely to retain closed canopies and persist in wetter and less seasonal regions, (Cochrane *et al.*, 2001, Krawchuk *et al.*, 2009, Brando *et al.* 2012), the existence of data for burned forests in this biomass class of our analysis shows they do burn (e.g. figure 3), especially during extreme drought events (Silva *et al.*, 2018, Berenguer *et al.*, 2018).

Fire-induced mortality in the Amazon is determined by fire intensity, duration and tree survival traits (Cochran *et al.*, 1993). The combination of the highest loads of dry necromass (Chao *et*

*al.*, 2009) and a species composition with the least fire-resistance traits (Barlow *et al.*, 2003; Balch *et al.*, 2011; Staver *et al.*, 2020) would reasonably exacerbate combustion and decomposition emissions in the forests with the maximum AGB. By contrast, forests with intermediate levels of AGB (200-350 Mg ha<sup>-1</sup>) hold relatively lower necromass stocks and emit less by combustion and, if subjected to a shorter fire duration and/or less intense fire, they are likely to have increased tree survival rates. A different process may occur in forests with the lowest AGB that, even though they have the lowest necromass, burn with severe fire intensity because necromass is very dry in more open canopy, resulting in higher mortality and decomposition emissions.

#### 4.5.2 *Caveats and knowledge gaps*

Wildfire net emissions are for the first time scaled up to an Amazonian landscape with accurate temporal and spatial data. However, there are a number of caveats that concern the scaling of these emissions to the whole of the Amazon basin. Particularly, combustion emissions are essentially associated to necromass stocks. We estimated necromass stocks from a large sample of plots measured in our studied region. The relationship of necromass with AGB was weak, but the statistical modelling could be refined by adding other important explanatory variables to the model, such as climate and soil descriptive variables and disturbance level and age (Chao *et al.*, 2009, Palace *et al.*, 2012). Applying these combustion emissions to other landscapes require adjusting the necromass-AGB relationship, which is highly variable (Baker *et al.*, 2007; Chao *et al.*, 2009), especially in disturbed forests (Palace *et al.*, 2012,). Although our estimates of necromass have many uncertainties, in our study area we suspect our combustion emissions are conservative, as we do not account for accumulated necromass from previous fires but instead use the necromass-AGB relationship when fires were recurrent (26% of all burned area). Furthermore, in our models we used the only measurements of necromass stocks in pre- and post-uncontrolled Amazonian fires (Whithey *et al.*, 2018).

However, combustion completeness depends on pre-fire fuel moisture (Ray *et al.*, 2010), which is not known across the study region or Amazon. This is a challenging knowledge gap to address, as assessments of combustion completeness in uncontrolled fires are only achievable by chance, and experimental fires are logistically challenging and would need to be conducted across a range of climatic conditions and with differing species compositions.

The form of the relationship between pre-fire AGB and initial mortality is not totally clear, however, the initial mortality is determinant of delayed mortality, and the accuracy of the linear or non-linear models needs to be better understood. While our non-linear model estimates high mortality in extremely high AGB forests, which represent only 12% of all Amazonian forests (Avitabile *et al.*, 2016), the linear model estimates higher mortality in the AGB range (200 to 400 Mg ha<sup>-1</sup>) that occupies more than one half of Amazonia (Avitabile *et al.*, 2016). We suspect both models result in similar overall outputs, but the implications of using one or the other requires further consideration.

Our analysis attempts to assign emissions to a given year, which means some of the emissions resulting from necromass decomposition will remain unaccounted for at the end of a given time series. The extended emissions and uptake beyond a given studied period should be considered, especially when high forests with AGB stocks are burned, as these are the largest contributors to longer-term emissions. To account for the lagged emissions over 30yr time, the estimates in Silva *et al.*, 2020 can be used, which shows a total of 92.4 Mg CO<sub>2</sub> ha<sup>-1</sup> emissions resulting from mortality and decomposition in forests > 150 Mg ha<sup>-1</sup>.

Estimates of net emissions can be further improved by refining estimates of post-fire regrowth. The major CO<sub>2</sub> uptake estimated within our approach is attributed to low AGB forests, as these have limited delayed mortality. However, we simulated all forests growing at the same rate, because the limited information available on post-fire growth of disturbed forests (Barlow &

Peres, 2008; Berenguer *et al.*, 2018a; Silva *et al.*, 2020) is not enough to create a statistical relationship with pre-fire AGB. Our estimated AGB regrowth rates change over time, but it is reassuring that at their maximum ( $2.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ) they are similar to the mean growth rates estimated for selectively logged forests ( $2.6 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ; e.g. Rutishauser *et al.*, 2015) and older secondary rainforests in tropical America ( $2.3 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ; e.g. Suarez *et al.*, 2019). The responses of heavily disturbed forests affected by recurrent fires could be very different, and as our estimates are from once-burned forests (Silva *et al.*, 2020) we may be overestimating the regrowth. Higher intensity fires in disturbed forests kill many more of the original trees (Cohrane *et al.*, 2001; Barlow and Peres, 2004) and could impede succession by depleting the seed bank of forest species (Flores *et al.*, 2016; Berenguer *et al.*, 2018b). Finally, we excluded fire impacts in secondary forests (those regrowing after deforestation) in our simulations; these represented just 7% of all burned forests in our study area, but may make a much larger contribution across the Amazon – especially if they are more likely to burn, as suggested by Ray *et al.*, 2010. While a suite of recent studies have advanced our understanding of the carbon accumulation potential of secondary forests (Nunes *et al.*, 2020; Smith *et al.*, 2020; Wang *et al.*, 2020), their responses to fires remain largely unquantified.

#### 4.5.3 *Accounting for forest fire emissions in Brazil's climate policy*

Amazonian fire CO<sub>2</sub> emissions and uptake are an important part of the carbon cycle and should be included to the Brazil's LULUCF accounting systems. The approach we developed represents a progress over the current estimates because it integrates all major emissions, from immediate and long-term processes, that can be derived from wildfires into high resolution burned area data. The application of our approach in the Amazonian landscapes can provide a first step for the country to include these emissions in their accounting systems and it would allow avoided fires to be integrated into policies promoting payments for ecosystem services, such as REDD+.

Integrating fire emissions could also assist policy makers and stakeholders to develop better strategies for making Brazil's carbon balance economically efficient. For example, Brazil wants to restore and reforest 12 million ha by 2030 to mitigate carbon emissions and achieve its NDC target (MMA, 2017). Pará state alone could contribute over 40% of this target (Pará State Law 941, 2020). If these 5 Million ha regrow at an estimated rate of 2.2 Mg C ha<sup>-1</sup> y<sup>-1</sup> (Lennox *et al.*, 2018) over the first 30 years, then they would take up 40 Million t carbon from the atmosphere. We estimate that the same benefit would be accrued by avoiding forest fires across an area just 2.5 times the size of our test landscape equivalent to our test landscape over 21 years. The benefits of fire avoidance are likely to be even greater considering the higher levels of forest biodiversity in primary forests compared to secondary forest (Barlow *et al.*, 2007; Lennox *et al.*, 2018), and the very high costs of forest restoration, which are on average US\$1,500/ha (Imazon, 2017).

#### 4.6 CONCLUSION

Until now, there has been no spatially explicit method for incorporating forest fire emissions into Brazil's carbon accounting from LULUCF and assigning those emissions to specific years. We develop the first approach with a minimum requirement of spatial data that is already available. While the approach is preliminary and requires refinement, we were able to apply it to a test landscape, revealing for the first time how fire emissions progress over time across disturbed and old-growth forests, and how this is affected by regrowth. Applying our models could have important implications for policies in tropical forest countries, by highlighting the advantages of reducing forest fires over and above other climate change mitigation approaches.

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#### 4.8 REFERENCES

- Alencar A, Asner GP, Knapp D, Zarin D (2011) Temporal variability of forest fires in eastern Amazonia. *Ecological Applications*, **21**, 2397–2412.
- Andela N, Morton DC, Giglio L et al. (2017) A human-driven decline in global burned area. *Science*, **356**, 1356–1362.
- Aragão LEOC, Anderson LO, Fonseca MG et al. (2018) 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, **9**, 536.
- Avitabile V, Herold M, Heuvelink GBM et al. (2016) An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology*, **22**, 1406–1420.
- Azevedo TR, Costa C, Brandão A et al. (2018) SEEG initiative estimates of Brazilian greenhouse gas emissions from 1970 to 2015. *Scientific Data*, **5**, 1–43.
- Baker TR, Honorio Coronado EN, Phillips OL, Martin J, Van Der Heijden GMF, Garcia M, Silva Espejo J (2007) Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia*, **152**, 495–504.
- Balch JK, Nepstad DC, Curran LM et al. (2011) Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management*, **261**, 68–77.
- Barlow J, Peres CA (2004) Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: Management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 367–380.
- Barlow J, Peres C a (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1787–1794.
- Barlow J, Peres CA, Lagan BO, Haugaasen T (2003) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.
- Barlow J, Gardner TA, Araujo IS et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18555–18560.
- Barlow J, Silveira JM, Mestre L a M et al. (2012) Wildfires in bamboo-dominated Amazonian forest: impacts on above-ground biomass and biodiversity. *PloS one*, **7**, 11.
- Barlow J, Berenguer E, Carmenta R, França F (2019) Clarifying Amazonia’s burning crisis. *Global Change Biology*, **00**, 1–3.
- Berenguer E, Ferreira J, Gardner TA et al. (2014) A large-scale field assessment of carbon

- stocks in human-modified tropical forests. *Global Change Biology*, **20**, 3713–3726.
- Berenguer E, Malhi Y, Brando P et al. (2018a) Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**.
- Berenguer E, Gardner TA, Ferreira J et al. (2018b) Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology*, 1–14.
- Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Brando PM, Oliveria-Santos C, Rocha W, Cury R, Coe MT (2016) Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. *Global Change Biology*, **22**, 2516–2525.
- Chao KJ, Phillips OL, Baker TR et al. (2009) After trees die : quantities and determinants of necromass across Amazonia. *Biogeosciences*, **6**, 1615–1626.
- Chave J, Réjou-Méchain M, Búrquez A et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, **20**, 3177–3190.
- Cochrane M a. (2001) Synergistic Interactions between Habitat Fragmentation and Fire in Evergreen Tropical Forests. *Conservation Biology*, **15**, 1515–1521.
- Cochrane MA, Alencar A, Schulze MD, Souza CM, Nepstad DC, Lefebvre P, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*, **284**, 1832–1835.
- Feldpausch TR, Lloyd J, Lewis SL et al. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381–3403.
- Flores BM, Fagoaga R, Nelson BW, Holmgren M (2016) Repeated fires trap Amazonian blackwater floodplains in an open vegetation state. *Journal of Applied Ecology*, **53**, 1597–1603.
- Friedlingstein P, Houghton RA, Marland G et al. (2010) *Update on CO2 emissions*, Vol. 3. 811–812 pp.
- Gerwing JJ, Farias DL (2000) Integrating Liana Abundance and Forest Stature into an Estimate of Total Aboveground Biomass for an Eastern Amazonian Forest. *Journal of Tropical Ecology*, **16**, 327–335.
- Goodman RC, Phillips OL, del Castillo Torres D, Freitas L, Cortese ST, Monteagudo A, Baker TR (2013) Amazon palm biomass and allometry. *Forest Ecology and Management*, **310**, 994–1004.
- Imazon (2017) Avaliação e modelagem econômica da restauração florestal no estado do Pará. <https://imazon.org.br/avaliacao-e-modelagem-economica-da-restauracao-florestal-no-estado-do-para/>.
- Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, **6**, 1–11.
- Krawchuk MA, Moritz MA, Parisien M-A, Van Dorn J, Hayhoe K (2009) Global Pyrogeography: the Current and Future Distribution of Wildfire (ed Chave J). *PLoS ONE*,

4, e5102.

- Lennox GD, Berenguer E, Gardner TA et al. (2018) Second rate or a second chance ? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. 5680–5694.
- MapBiomass (2019) Mapbiomas Brasil. <https://mapbiomas.org/>.
- MMA (2017) *PLANAVEG - Plano Nacional de Recuperação da Vegetação Nativa*. Brasília, DF, Brazilian Government Report, 823 pp.
- Nunes S mia, Oliveira L, Siqueira J o., Morton DC, Souza CM (2020) Unmasking secondary vegetation dynamics in the Brazilian Amazon. *Environmental Research Letters*, **15**, 034057.
- Osono Y, Toma T, Warsudi, Sutedjo, Sato T (2016) High stocks of coarse woody debris in a tropical rainforest, East Kalimantan: Coupled impact of forest fires and selective logging. *Forest Ecology and Management*, **374**, 93–101.
- Le Page Y, Morton D, Hartin C et al. (2017) Synergy between land use and climate change increases future fire risk in Amazon forests. *Earth Syst. Dynam*, **8**, 1237–1246.
- Palace M, Keller M, Hurtt G, Frohling S (2012) A Review of Above Ground Necromass in Tropical Forests. *Tropical Forests*, 215–252.
- Pará State Law 941 S (2020) Plano Estadual Amazônia Agora, Decreto 941, 3 de Agosto 2020.
- PRODES (2020) Instituto Nacional de Pesquisas espaciais. Projeto PRODES - Monitoramento da Floresta Amazônica por satélite. <https://terrabrasilis.dpi.inpe.br/>.
- Quesada C a., Phillips OL, Schwarz M et al. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**, 2203–2246.
- R Core Team 2019 R: The R Project for Statistical Computing
- Ray D, Nepstad D, Brando P (2010) Predicting moisture dynamics of fine understory fuels in a moist tropical rainforest system: results of a pilot study undertaken to identify proxy variables useful for rating fire danger. *New Phytologist*, **187**, 720–732.
- Rutishauser E, Hérault B, Baraloto C et al. (2015) Rapid tree carbon stock recovery in managed Amazonian forests. *Current Biology*, **25**, R787–R788.
- SEEG (2020) *Impacto da Pandemia de COVID-19 nas emissões de gases de efeito estufa no Brasil*. Climate Observatory Report, 1–25 pp.
- Silva CVJ, Aragão LEOC, Barlow J et al. (2018) Drought-induced Amazonian wildfires promote long-term disruption of forest carbon dynamics. *Philosophical transactions of Royal Society B*, **373**, 12.
- Silva CVJ, Aragao LEOC, Young PJ et al. (2020) Estimating the multi-decadal carbon deficit of burned Amazonian forests. *Environmental Research Letters*, **in press**, 1–10.
- SIRENE, MMA (2017) *SIRENE - Sistema de Registro Nacional de Emissões*. Brazilian Government Report, 60 pp.
- Smith CC, Espírito-Santo FDB, Healey JR, Young PJ, Lennox GD, Ferreira J, Barlow J (2020) Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Global Change Biology*, gcb.15352.
- Staver AC, Brando PM, Barlow J et al. (2020) Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire (ed Penuelas J). *Ecology Letters*, **23**, 99–106.

- Suarez DR, Rozendaal DMA, De Sy V et al. (2019) Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data. *Global Change Biology*, **25**, 3609–3624.
- Uhl C, Kauffman JB (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology*, **71**, 437–449.
- Wang Y, Ziv G, Adami M et al. (2020) Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon. *Nature Sustainability*, **3**, 290–295.
- Withey K, Berenguer E, Palmeira A et al. (2018) Quantifying the immediate carbon emissions from ENSO-mediated wildfires in human-modified tropical forests. *Philosophical transactions of Royal Society B*, **373**, 11.

5 GENERAL DISCUSSION



## 5.1 GENERAL DISCUSSION

Wildfires in humid tropical forests are one of the most critical environmental problems of this century that could define the future of the tropical forest biome and the world's climate (Jolly *et al.*, 2015). This thesis provides a detailed and multi-scale understanding of the impact of forest fires on the carbon balance of humid tropical forests by modelling their effects on individual stems, all the way up to their landscape-level effects on the carbon balance of Amazonian humid tropical forests. To achieve this, I started by assessing field data from across five Amazonian states (Chapters 2 and 3) and then combined this with large-scale field studies (Berenguer *et al.*, 2014) and literature assessments of all the studies to date on fires in the Amazonian forests, including data from the largest long-term fire experiment in burned forests. The key findings outlined below can support the development of governmental strategies to halt fires in tropical forests and curb carbon emissions. For simplicity, I discuss the outcomes from each chapter in terms of carbon, although the results of chapter 2 are reported in biomass ( $\text{Mg ha}^{-1}$ ) and chapters 3 and 4, which relate to emissions, are  $\text{Mg CO}_2 \text{ ha}^{-1}$ .

### 5.1.1 Key findings

#### **Chapter 2 - The long-term disruption of carbon dynamics in burned forests**

In Chapter 2, I addressed the following questions:

What are the longer-term effects of wildfires on forest biomass? How do wildfires affect forest growth, recruitment, and mortality at stem level, and what insights do key structural traits such as wood density and stem size (DBH) provide into the mechanisms underpinning the changes in biomass?

This is a published chapter in which my co-authors and I show that drought-induced wildfires reduce above ground carbon stocks by 25% for at least 30 years. These changes in carbon stocks result from the major changes in carbon dynamics, including the increases in the

mortality of high wood density and large stems that occurs for many years after the fire. We also quantified the increase in stem recruitment and woody growth of pioneer species; as these are early successional species, then the carbon held within them is likely to have a short residence time. Losses outweigh carbon gains in the short-term (1-8 years after the fires), but in the long-term, these rates are equivalent to baseline levels, suggesting the forests may have returned to a balanced state. However, this long-term carbon balance occurs before the carbon stocks have recovered to pre-fire levels, suggesting that forests are unlikely to recover in the following decades or longer.

### **Chapter 3 - Revealing the magnitude of temporal net carbon emissions after fires**

In chapter 3, the main question was:

What is the multi-decadal net CO<sub>2</sub> flux of burned forests given the relative contribution of combustion and decomposition-related CO<sub>2</sub> emissions and post-fire CO<sub>2</sub> uptake?

On the basis of findings from chapter 2, in Chapter 3 (in press) my co-authors and I show the magnitude of temporal carbon net emissions in burned forests, as the balance between the decomposition of dead stems (necromass) and post-fire re-growth. We propose non-linear models that show that, following the combustion emissions, there is a large pulse of carbon released to the atmosphere through decomposition of dead woody material, with emissions peaking at c. 5 years after the fires. We show that after 30 years, the carbon emissions from the decomposition of necromass are responsible for up to 73% of all fire-induced carbon emissions (including combustion). Post-fire regrowth represents an offset of 35% of all fire-induced carbon emissions. We conclude that delayed mortality makes a significant contribution to net emissions and that it needs to be incorporated into carbon accounting systems, including carbon inventories and Earth System Models.

## **Chapter 4 - A spatial-temporal approach to scaling-up combustion and decomposition emissions of carbon**

In chapter 4, I was interested in extending the models developed in chapter 3 to an Amazonian landscape context, as preparation for incorporating it into a basin-wide assessment of fire emissions. A landscape unit that included undisturbed and human-modified forests was used to test a spatial-temporal approach that integrates a combustion model with the net decomposition model developed in chapter 3.

In this chapter, I present a unique approach that could be used by the Brazilian accounting systems to incorporate Amazonian forest fires, an unaccounted-for carbon source, in their GHG inventories. The approach showed that the largest combustion emissions were released from forests with the highest aboveground biomass stocks, as necromass (available fuel to burn) increased with biomass. I show that high-biomass forests make a significant contribution to decomposition emissions, as biomass loss from tree mortality was greatest at the highest levels of forest biomass. Decomposition emissions were also very important in low biomass forests, as the model I proposed predicted high rates of initial tree mortality in these forests. At the landscape level, the relative contribution of high biomass forests to burned area was only 34%, but these forests were responsible for 57% of all fire-induced carbon emissions.

### **5.1.2 Implications of research findings to national conservation strategies and climate-change policies**

#### **5.1.2.1 THE MAIN CONSERVATION PRIORITY**

Besides the urgency in avoiding deforestation, this thesis findings highlight that avoiding wildfires in humid tropical forests, especially in those with high biomass, should be one of the main priorities for climate change mitigation – these forests do not recover on decadal time-scales, and therefore represent an important long-term carbon source (Chapter 4). While the

prevention of wildfires in Amazonia represents one of the greatest challenges in the near hotter, drier future (Fonseca *et al.*, 2019), strategic actions directed to tackle illegal deforestation-fires and support for fire-free methods in agriculture can potentially reduce fire risk (Barlow *et al.*, 2019; Spínola *et al.*, 2020). In order to achieve this, it is crucial to understand the role of different ignition sources, so efforts are directed where they are most needed (Barlow *et al.*, 2019).

The use of fire by smallholders in swidden-agriculture can be an important ignition source during extreme drought years, and thus alternatives has been suggested, such as tractor-driven vegetation management (Davidson *et al.*, 2008) and agroforestry systems (Pollini, 2009). However, these are not always viable and there are important social aspects to be considered. For example, fire-dependant agriculture has been carried out for millennia, and it only became threatening more recently because of increasing flammability of humid forest caused by climate-change and increased forest degradation. In order to establish efficient policy implementation (Carmenta *et al.*, 2013), inclusive management and financial support is crucial (Spínola *et al.*, 2020).

Directing efforts to control deforestation-fires may be even more critical. In the last two years, increased fire detections were mainly associated to increases in deforestation (Alencar *et al.*, 2019; Barlow *et al.*, 2019), and as most active fire was detected in public lands and large-scale deforested areas in private lands, illegal deforestation is suggested to be a major cause (Alencar *et al.*, 2019). There is a clear failure in controlling deforestation at the moment (Silva Junior *et al.*, 2021), which is worrying not only because of what the forest loss represents directly, but also because deforestation fires represent a risk of increasing forest wildfires (Aragão *et al.*, 2008, Barlow *et al.*, 2019).

#### 5.1.2.2 A SECONDARY CONSERVATION PRIORITY

In chapter 3, I highlight allowing burned forests to recover is important and should be additional priority as these represent a significant strategy to mitigate carbon from degradation. Yet, avoiding clearance of these forests is challenging, given the current increasing deforestation rates (Barlow *et al.*, 2019) and trends in the beginning of this century associating burned forests and deforestation (Aragão *et al.*, 2008). Recently, it was estimated that 26% of degradation (natural and anthropogenic) and deforestation in the Amazon basin occurred in secondary or regenerating forests between 1995 and 2017 (Bullock *et al.*, 2020). Although burned forests were not distinguished from other types of degradation, this clearly show a significant portion of the carbon sequestered by regenerating forests is not persistent. Bullock *et al.* (2020) also showed that 30% of intact forests subjected to degradation end up being degraded one more time before a second phase of regeneration (figure 5.1).

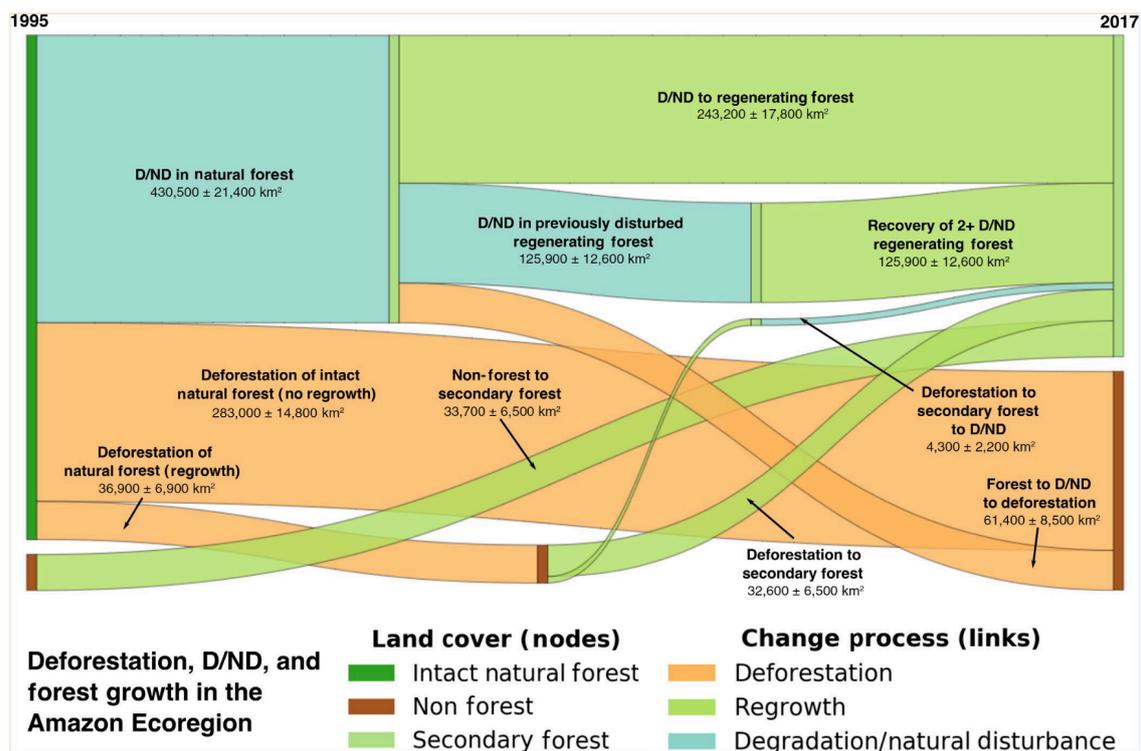


Figure 5.1 The trajectories of intact natural forests subjected to deforestation and degradation or natural disturbance (D/ND) in Amazonia from 1995 to 2017. Adapted from Bullock et al. 2020.

Burned forests are susceptible to further disturbances (Cochrane, 2003; Alencar *et al.*, 2011). Findings from chapter 4 also support this for the landscape analysed, where the majority (65%) of burned forests were low biomass forests, and repeated fires were high (26%). In chapter 4, I also show that burned forests with low biomass contribute significantly to carbon emissions in the short-term through the mortality and decomposition of trees that died immediately after fires. These results reinforce the importance of avoiding further fires in previously disturbed forests.

#### 5.1.2.3 CONSERVATION INITIATIVES AND CLIMATE POLICIES

Recently, a pilot program for payment for ecosystem services has been instated by the Brazilian Government (Floresta +, in Portuguese; MMA, 2018), where c. 96 million USD received from the Green Climate Fund (GCF) will be used to pay public and private lands for preserving and restoring forests. The GCF funds were allocated based on REDD+ results achieved by Brazil in the Amazon biome in 2014 – 2015 (MMA, 2018). The findings from this thesis suggests that the success of such program and other REDD+ investments strongly depend on reducing forest wildfires. By failing to avoid fire-degradation in Amazonia, Brazil will miss a great opportunity to attract more investment in their forests (Aragão & Shimabukuro, 2010). However, curbing Amazonian wildfires will require efforts at multiple levels – e.g. globally, by mitigating climate-change, nationally, by promoting fire-free productive lands as well as curbing illegal deforestation, and locally by effectively managing smallholders fire-use and promoting social justice.

Furthermore, in the proposal Brazil submitted to GCF the set baseline against which to measure LULUCF emissions reductions and the reported results from REDD+ were based on gross emissions from deforestation (MMA, 2018). Nonetheless, incorporating forest degradation

emissions and removals by vegetation regrowth is essential for reducing biases and is likely to become more strongly required in the UNFCCC protocols for REDD+ results-based payment. The approach proposed in this thesis for incorporating post-fire carbon fluxes in accounting systems (chapter 4) could be useful for improving proposals for GCF and reporting results from conservation initiatives under UNFCCC requirements. Reducing uncertainties associated with forest degradation is a recognized area for future improvement by the Brazilian Working Group on REDD+ (WG), and something likely to be required in future from tropical countries seeking results-based payment by GCF. Brazil's WG argue this is complex because of limitations associated with assessing changes in carbon stocks, and due to the short time series of its degradation mapping system (DEGRAD; MMA, 2018). While mapping degradation is beyond the objectives of this thesis, recent advances in remote sensing analysis have made some progress (e.g. Bullock *et al.* 2020, Andela *et al.*, 2020). The results presented here could be combined with these novel fire-mapping efforts to provide detailed fire-associated carbon fluxes. It is important to note that although forest wildfires are a growing type of degradation, the integration of multiple degradation types and the associated emissions is fundamental in future.

### 5.1.3 Future research priorities

In this thesis, I present a general understanding about forest responses to fire (tree mortality and growth) using the largest field-based dataset to date, and many additional data sources in Brazilian Amazonia. The models proposed in chapter 3 and the spatio-temporal approach tested in chapter 4 are also useful for estimating wildfires emissions in other Amazonian countries and perhaps in other tropical countries. To apply the spatio-temporal approach there is a minimum requirement for ground data, which is plot-level biomass and necromass stocks and mortality and growth rates measured in permanent plots. In terms of spatial data, forest cover, burned area and aboveground biomass are the minimum data required. Yet, the models

proposed in this thesis have limitations for applications to tropical forests more widely. To overcome these limitations and be able to apply the models developed in this thesis to the Amazon basin and other tropical forest context, future research should prioritize the following topics.

#### 5.1.3.1 IMPROVING OUR UNDERSTANDING AT THE REGIONAL LEVEL OF LONG-TERM PATTERNS

While the general understanding provided in this thesis reduced uncertainty and targeted several important knowledge gaps, additional research at the regional level, capturing the direct and long-term (decadal) effects of fire on forest structure, would be useful to provide a more detailed knowledge on regional biotic and abiotic stressors of recovery pathways. In order to achieve that, sampling understorey fires at the regional level is crucial, however, is not simple. In this thesis, we relied on chronosequence comparisons at plot-level that were also monitored over time, but the most reliable assessments of change use a before-after approach (França *et al.*, 2016). This, however, can only occur in two ways: by chance, when permanent forest plots are accidentally burned (Berenguer *et al.*, 2018); or by experimental fires which are logistically challenging and may not reproduce wildfire conditions that reflect the rest of the Amazon if they are conducted in non-drought years (Brando *et al.*, 2016) or too late in the season, after the first rains and moisture limit fire spread and intensity (Ray *et al.*, 2010). Chronosequence studies have more uncertainties, but are useful when successional trajectory exceeds investigator lifespan (Walker *et al.*, 2010). Up to now, a great amount of knowledge about humid forests responses to fire has been acquired from short-term studies at the regional level (Uhl & Kauffman, 1990; Kauffman, 1991; Barlow *et al.*, 2003; Cochrane, 2003; Barlow & Peres, 2004; Balch *et al.*, 2011; Brando *et al.*, 2012; Berenguer *et al.*, 2018). However, field-based long-term assessments are key, and thus the expansion of permanent-plots network.

#### 5.1.3.2 THE LONGER-TERM RECOVERY OF FORESTS

Supporting other studies (Barlow & Peres, 2008; Flores *et al.*, 2016; Oliveras *et al.*, 2017; Berenguer *et al.*, 2018) I show post-fire recovery, even after single understorey wildfires, is a slow process that will not occur for decades (chapter 2). Post-degradation forest recovery is of much interest, and our knowledge on mortality is more advanced than on regrowth. Although several studies have quantified post-degradation regrowth, only few have attempted to measure the effects of biotic and abiotic drivers (e.g. Berenguer *et al.* 2018). There is clear evidence that post-fire growth is dominated by low wood-density species (Berenguer *et al.* 2018 and chapter 2). However, a key question still remains: Is the regeneration of slow-growing (high wood density) species impeded, or this is this just a slow process that is not captured in our studied timeframe? While studying long-lived forest trees is inherently challenging, new insights into the recovery of these species, could be gained by evaluating changes in the dynamics of small trees, saplings and the seed bank. I highlight growth as being a particularly complex process to model (chapter 4), and a better understanding of how this process is affected by environmental stressors could greatly improve CO<sub>2</sub> uptake models, reducing the uncertainties in post-fire net emissions.

#### 5.1.3.3 UNBURNED BASELINE, COMBUSTION COMPLETENESS, DECOMPOSITION RATES, AND OTHER UNCERTAINTIES

In Chapter 2, estimates of carbon losses and gains in burned forests are presented relative to the unburned (or undisturbed) forest baseline. Although I assumed the baseline is static over time, based on non-significant changes in most unburned plots, it is important to note that recent research, based on a large-scale dataset of permanent forest plots, indicate undisturbed forests have changed in recent decades (Phillips *et al.*, 2009, Brienen *et al.*, 2015). These changes are highlighted by a decline in the carbon sink of 321 plots in the Amazon forest, and are a consequence of both increased mortality and reduced growth rates (Brienen *et al.*, 2015). While there is no such long-term data to assess these changes in burned forests, given

permanent plots in burned sites date from 2009, it is reasonable to expect burned forests would follow at least the same directional change observed by Brienen *et al.* (2015) in undisturbed forests, or present larger increases in mortality (Brando *et al.*, 2014, Brando *et al.*, 2019). This means the difference in mortality, estimated in Chapter 2, between burned and unburned forests, is unlikely to have reduced over time, as is the case for the difference in woody productivity between burned and unburned forests. Consequently, the carbon flux estimates presented in Chapter 3 are conservative. The decline in carbon sink strength of undisturbed, drought-affected forests since the 1990s (Brienen *et al.*, 2015, Hubau *et al.*, 2020), means the recovery of carbon stocks to pre-fire levels may be affected and take longer than previously thought.

In chapter 3 and 4, I show combustion emissions are a critical component of wildfires emissions. Combustion completeness from slash-burn experiments is commonly used to calibrate the deforestation emissions estimated in burning emissions databases and Earth system models (Guild *et al.*, 1998; Van Leeuwen *et al.*, 2014). Yet, combustion completeness in slash-burn experiment does not reproduce the conditions of understory fires, where fuel is composed of decomposing dry necromass. Only one study has quantified this in Amazonia (Withey *et al.*, 2018), which we used in the estimates produced in chapter 3 and 4, but measuring this component in other regions is a critical knowledge gap for future research.

The decomposition of woody debris is a critical a component of carbon cycle (Chambers *et al.*, 2000; Keller *et al.*, 2004; Chao *et al.*, 2009; Palace *et al.*, 2012), but this has not yet been investigated in burned forests. In chapter 3, I highlight the uncertainties associated with using decomposition rates from undisturbed primary forests. Therefore, future research should focus on quantifying woody debris decomposition in burned forests and evaluate the importance of the multiple factors that affect decomposition rates after fires. In addition to that, it is important to also evaluate the fraction of burned wood that remains in the soil as charcoal and have a

much lower decomposition rate since its major resistance to microbial degradation (Singh *et al.*, 2010).

Finally, future research could focus on other minor components of the burned forests carbon cycle that could influence the fluxes estimates shown in this thesis. For example, small trees (e.g. <10 cm in DBH) contributes to 10% of standing biomass (Phillips *et al.*, 1998) and this proportion is omitted in our carbon dynamics estimates. Similarly, the FWD and leaf litter NPP should be assessed, as well as the alternative carbon pathways such as to soil and groundwater and other sources of carbon such as CH<sub>4</sub> by termites.

#### 5.1.3.4 EXTENDING OUR KNOWLEDGE BEYOND WILDFIRES

The effects of fires in humid tropical forests shown in chapter 2 are possibly much greater than those from other type of forest disturbance. However, in many cases fire interacts with other types of degradation, for example, most forest edges and logged forests are eventually affected by fires (Nepstad *et al.*, 1999; Silva Junior. *et al.*, 2018), and burned forests can be more severely affected by windstorms than intact forests (Silvério *et al.*, 2019). In this thesis, we assessed the impacts of fire excluding other types of degradation (e.g. logging, multiple fires, edge effect, droughts). This brings to attention the importance of investigating degradation under the perspective of human-modified forests which contemplate forests under various levels of disturbance caused by different degradation drivers (e.g. Berenguer *et al.*, 2014). Categorising the different types of degradation is useful. For example, in chapters 2 and 3 we focused only in single fire events rather than assessing repeated fires or multiple disturbances. This can help estimating the magnitude of specific effects such as resulting emissions, and for understanding rates of recovery. However, future field-based research should focus on integrating methodologies the promote the understanding of multiple interactive disturbance events, their associated impacts and forests recovery rates. For example, secondary forests are becoming widespread, and although much is known about their extent (Silva Junior *et al.*,

2020; Smith *et al.*, 2020) and growth rates (Elias *et al.*, 2019), little is known about how much these forests are affected by fire, or how fires affect mortality and growth rates. The application of the models proposed in this thesis require we understand better the recovery of forests under different levels of disturbance and secondary forests that are eventually affected by fire.

#### 5.1.3.5 MAPPING THE EXTENSION OF FIRES AND OTHER FORMS OF DEGRADATION

Mapping understorey fires in Amazonia is the ultimate prerequisite for adequately quantifying associated emissions and thus improving carbon budgets estimates. Achieving that is not trivial as processing a large volume of high spatial resolution data (30 m) is required. Additionally, mapping understorey fire scars by using high spatial resolution data can be challenging. The persistence of changes in the spectral signature of fire-affected forest canopy is variable, and in many cases fire scars are difficult to be detected because of cloud cover and fast regeneration of pioneers between satellite imaging dates (Alencar *et al.*, 2011). The carbon flux estimates presented in chapter 4 are based in a high resolution burned area map, however, it is important to note that the map used may also have omission errors, although this is one of the most accurate fire maps available. In order to understand the effects mapping limitations might have on basin-wide carbon flux estimates, using the approach proposed in chapter 4, it is important to consider omissions and commissions errors from the chosen fire map. To date, only few maps are available, and none provide a time-series dataset covering the entire Amazon biome. For example, GABAM only mapped the 2015 fires (Long *et al.*, 2019); TREES maps do not cover the entire biome and only mapped fires from 2006 to 2016 (Anderson *et al.*, 2015); other maps cover longer periods but focuses on specific regions (Alencar *et al.*, 2011; Silva *et al.*, 2018b). More recently the extent of degradation for the Amazon biome was provided (Bullock *et al.* 2020), although fire is not explicitly differentiated from other forms of degradation. Matricardi *et al.*, (2020) differentiated fires and logging for the Brazilian Amazon, however, estimates of large drought-induced wildfires are not evident and the analysis ended in 2014.

Advancing remote sensing techniques are essential to improve emission estimates from all disturbances.

## 5.2 CONCLUSIONS

This thesis provides a comprehensive evidence-based understanding of the impacts of wildfires on stem dynamics and carbon budgets of tropical humid forests. The long-term disruption of forest carbon stocks and the long-term increased carbon emissions have significant implications for conservation strategies and climate-change mitigation policies. Protecting intact old-growth forests, especially those with high biomass, is the main priority for avoiding the greatest wildfires emissions (Chapter 4). However, it is important to note that carbon-focused conservation strategies may fail to protect many species in low-carbon highly diverse forests (Ferreira et al., 2018). Additionally, the protection of burned forests is of great importance for mitigating carbon emissions from combustion and decomposition processes.

The knowledge on carbon emissions from forest fires developed in this thesis was used to develop a preliminary bookkeeping approach that can be scaled across the Amazon and influence national conservation policies. Although some parts of this approach require further improvements, it provides a way of incorporating Amazonia's wildfires emissions into Brazil's LULUCF budget. Brazil is a leading country in REDD+ schemes and many countries will base their deforestation and degradation carbon accounting on Brazil's methodology. Incorporating forest fires and other forms of degradation emissions, as well as vegetation regrowth removals, to tropical countries accounting systems, is vital for adapting climate-change policies and meeting the 2°C threshold agreed in the Paris Agreement.

## 5.3 REFERENCES

- Alencar A, Asner GP, Knapp D, Zarin D (2011) Temporal variability of forest fires in eastern Amazonia. *Ecological Applications*, **21**, 2397–2412.
- Alencar A, Moutinho P, Arruda V, Balzani C, Ribeiro J (2019) Amazônia em Chamas: Onde está o Fogo. *Nota técnica do Instituto de Pesquisa Ambiental da Amazônia (IPAM)*, 12.
- Andela N, Morton DC, van der Werf GR et al. (2020) Improved daily accuracy from a new VIIRS-based, near-real time GFED emissions product. *EGUGA*, 12237.
- Anderson LO, Aragão LEOC, Gloor M et al. (2015) Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought. *Global Biogeochemical Cycles*, 1739–1753.
- Aragão LEOC, Shimabukuro YE (2010) The incidence of fire in Amazonian forests with implications for REDD. *Science (New York, N.Y.)*, **328**, 1275–8.
- Aragão LEOC, Malhi Y, Barbier N, Lima A, Shimabukuro Y, Anderson L, Saatchi S (2008) Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1779–85.
- Balch JK, Nepstad DC, Curran LM et al. (2011) Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management*, **261**, 68–77.
- Barlow J, Peres CA (2004) Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: Management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 367–380.
- Barlow J, Peres C a (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1787–1794.
- Barlow J, Peres CA, Lagan BO, Haugaasen T (2003) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**, 6–8.
- Barlow J, Berenguer E, Carmenta R, França F (2019) Clarifying Amazonia’s burning crisis. *Global Change Biology*, **00**, 1–3.
- Berenguer E, Ferreira J, Gardner TA et al. (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, **20**, 3713–3726.
- Berenguer E, Malhi Y, Brando PM et al. (2018) Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire. *Proceedings of the Royal Society B: Biological Sciences*.
- Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Brando PM, Oliveria-Santos C, Rocha W, Cury R, Coe MT (2016) Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. *Global Change Biology*, **22**, 2516–2525.
- Brando PM, Paolucci L, Ummenhofer CC et al. (2019) Droughts , Wildfires , and Forest Carbon Cycling: A Pantropical Synthesis. *Annual Review of Earth and Planetary Sciences*, 555–581.
- Brienen RJW, Phillips OL, Feldpausch TR et al. (2015) Long-term decline of the Amazon

carbon sink. *Nature*, **519**.

- Bullock EL, Woodcock CE, Souza C, Olofsson P (2020) Satellite-based estimates reveal widespread forest degradation in the Amazon. *Global Change Biology*, **26**, 2956–2969.
- Carmenta R, Vermeulen S, Parry L, Barlow J (2013) Shifting Cultivation and Fire Policy: Insights from the Brazilian Amazon. *Human Ecology*, **41**, 603–614.
- Chambers JQ, Higuchi N, Schimel JP, Ferreira L V., Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.
- Chao KJ, Phillips OL, Baker TR et al. (2009) After trees die : quantities and determinants of necromass across Amazonia. *Biogeosciences*, **6**, 1615–1626.
- Cochrane M a. (2003) Fire science for rainforests. **421**, 913–919.
- Davidson EA, Sá TD de A, Carvalho CJR, Figueiredo R de O, Kato M do SA, Kato OR, Ishida FY (2008) An integrated greenhouse gas assessment of an alternative to slash-and-burn agriculture in eastern Amazonia. *Global Change Biology*, **14**, 998–1007.
- Elias F, Ferreira J, Lennox GD et al. (2019) Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes. *Ecology*, **0**.
- Ferreira J, Lennox GD, Gardner TA et al. (2018) Carbon-focused conservation may fail to protect the most biodiverse tropical forests. *Nature Climate Change*, **8**, 744–749.
- Flores BM, Fagoaga R, Nelson BW, Holmgren M (2016) Repeated fires trap Amazonian blackwater floodplains in an open vegetation state (ed Barlow J). *Journal of Applied Ecology*, **53**, 1597–1603.
- Fonseca MG, Alves LM, Aguiar APD et al. (2019) Effects of climate and land-use change scenarios on fire probability during the 21st century in the Brazilian Amazon. *Global Change Biology*, **25**, 2931–2946.
- França F, Louzada J, Korasaki V, Griffiths H, Silveira JM, Barlow J (2016) Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Journal of Applied Ecology*, **53**, 1098–1105.
- Guild LS, Kauffman JB, Ellingson LJ, Cummings DL, Castro EA, Babbitt RE, Ward DE (1998) Dynamics associated with total aboveground biomass, C, nutrient pools, and biomass burning of primary forest and pasture in Rondônia, Brazil during SCAR-B. *Journal of Geophysical Research Atmospheres*, **103**, 32091–32100.
- Hubau W, Lewis SL, Phillips OL et al. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, **579**, 80–87.
- Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, **6**, 1–11.
- Kauffman JB (1991) Survival by Sprouting Following Fire in Tropical Forests of the Eastern Amazon. *Biotropica*, **23**, 219.
- Keller M, Palace M, Asner GP, Pereira R, Silva JNM (2004) Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology*, **10**, 784–795.
- Van Leeuwen TT, Van Der Werf GR, Hoffmann AA et al. (2014) Biomass burning fuel consumption rates: A field measurement database. *Biogeosciences*, **11**, 7305–7329.

- Long T, Zhang Z, He G et al. (2019) 30 m Resolution Global Annual Burned Area Mapping Based on Landsat Images and Google Earth Engine. *Remote Sensing*, **11**, 489.
- Matricardi EAT, Skole DL, Costa OB, Pedlowski MA, Samek JH, Miguel EP (2020) Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*, **369**, 1378–1382.
- MMA (2018) *Funding proposal*. Brazilian Government Report, 101 pp.
- Nepstad DC, Verssimo A, Alencar A et al. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Oliveras I, Román-Cuesta RM, Urquiaga-Flores E et al. (2017) Fire effects and ecological recovery pathways of Tropical Montane Cloud Forests along a time chronosequence. *Global Change Biology*, 1–15.
- Palace M, Keller M, Hurtt G, Frolking S (2012) A Review of Above Ground Necromass in Tropical Forests. *Tropical Forests*, 215–252.
- Phillips OL, Aragão LEOC, Lewis SL et al. (2009) Drought sensitivity of the Amazon rainforest. *Science (New York, N.Y.)*, **323**, 1344–7.
- Phillips OL, Malhi Y, Higuchi N et al. (1998) Changes in the Carbon Balance of Tropical Forests: Evidence from Long-Term Plots. *Science*, **282**, 439 LP – 442.
- Pollini J (2009) Agroforestry and the search for alternatives to slash-and-burn cultivation: From technological optimism to a political economy of deforestation. *Agriculture, Ecosystems and Environment*, **133**, 48–60.
- Ray D, Nepstad D, Brando P (2010) Predicting moisture dynamics of fine understory fuels in a moist tropical rainforest system: results of a pilot study undertaken to identify proxy variables useful for rating fire danger. *New Phytologist*, **187**, 720–732.
- Silva CVJ, Aragão LEOC, Barlow J et al. (2018a) Drought-induced Amazonian wildfires promote long-term disruption of forest carbon dynamics. *Philosophical transactions of Royal Society B*, **373**, 12.
- Silva SS da, Fearnside PM, Graça PML de A, Brown IF, Alencar A, Melo AWF de (2018b) Dynamics of forest fires in the southwestern Amazon. *Forest Ecology and Management*, **424**, 312–322.
- Silva CVJ, Aragao LEOC, Young PJ et al. (2020) Estimating the multi-decadal carbon deficit of burned Amazonian forests. *Environmental Research Letters*, **in press**, 1–10.
- Silva Junior. CHL, Aragão LEOC, Fonseca MG, Almeida CT, Vedovato LB, Anderson LO (2018) Deforestation-induced fragmentation increases forest fire occurrence in central Brazilian Amazonia. *Forests*, **9**.
- Silva Junior CHL, Heinrich VHA, Freire ATG et al. (2020) Benchmark maps of 33 years of secondary forest age for Brazil. *Scientific Data*, **7**, 1–9.
- Silva Junior CHL, Pessôa ACM, Carvalho NS, Reis JBC, Anderson LO, Aragão LEOC (2021) The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology and Evolution*, **5**, 144–145.
- Silvério D V, Brando PM, Bustamante MMC et al. (2019) Fire, fragmentation, and windstorms: A recipe for tropical forest degradation. *Journal of Ecology*, **107**, 656–667.
- Singh N, Abiven S, Schmidt MWI (2010) Mechanisms of charcoal degradation during its initial stages of decomposition. **12**, 2010.

- Smith CC, Espírito-Santo FDB, Healey JR, Young PJ, Lennox GD, Ferreira J, Barlow J (2020) Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Global Change Biology*, gcb.15352.
- Spínola J, Soares da Silva MJ, Assis da Silva JR, Barlow J, Ferreira J (2020) A shared perspective on managing Amazonian sustainable-use reserves in an era of megafires (ed Leverkus AB). *Journal of Applied Ecology*, **00**, 1–7.
- Uhl C, Kauffman JB (1990) Deforestation, Fire Susceptibility, and Potential Tree Responses to Fire in the Eastern Amazon. *Ecology*, **71**, 437–449.
- Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725–736.
- Withey K, Berenguer E, Palmeira A et al. (2018) Quantifying the immediate carbon emissions from ENSO-mediated wildfires in human-modified tropical forests. *Philosophical transactions of Royal Society B*, **373**, 11.

#### 5.4 APPENDIX – OTHER OUTCOMES

ARTICLE

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OPEN

# 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions

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Tropical carbon emissions are largely derived from direct forest clearing processes. Yet, emissions from drought-induced forest fires are, usually, not included in national-level carbon emission inventories. Here we examine Brazilian Amazon drought impacts on fire incidence and associated forest fire carbon emissions over the period 2003–2015. We show that despite a 76% decline in deforestation rates over the past 13 years, fire incidence increased by 36% during the 2015 drought compared to the preceding 12 years. The 2015 drought had the largest ever ratio of active fire counts to deforestation, with active fires occurring over an area of 799,293 km<sup>2</sup>. Gross emissions from forest fires ( $989 \pm 504$  Tg CO<sub>2</sub> year<sup>-1</sup>) alone are more than half as great as those from old-growth forest deforestation during drought years. We conclude that carbon emission inventories intended for accounting and developing policies need to take account of substantial forest fire emissions not associated to the deforestation process.

Research



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## Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests

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Wildfires produce substantial CO<sub>2</sub> emissions in the humid tropics during El Niño-mediated extreme droughts, and these emissions are expected to increase in coming decades. Immediate carbon emissions from uncontrolled wildfires in human-modified tropical forests can be considerable owing to high necromass fuel loads. Yet, data on necromass combustion during wildfires are severely lacking. Here, we evaluated necromass carbon stocks before and after the 2015–2016 El Niño in Amazonian forests distributed along a gradient of prior human disturbance. We then used Landsat-derived burn scars to extrapolate regional immediate wildfire CO<sub>2</sub> emissions during the 2015–2016 El Niño. Before the El Niño, necromass stocks varied significantly with respect to prior disturbance and were largest in undisturbed primary forests (30.2 ± 2.1 Mg ha<sup>-1</sup>, mean ± s.e.) and smallest in secondary forests (15.6 ± 3.0 Mg ha<sup>-1</sup>). However, neither prior disturbance nor our proxy of fire intensity (median char height) explained necromass losses due to wildfires. In our 6.5 million hectare (6.5 Mha) study region, almost 1 Mha of primary (disturbed and undisturbed) and 20 000 ha of secondary forest burned during the 2015–2016 El Niño. Covering less than 0.2% of Brazilian Amazonia, these wildfires resulted in expected immediate CO<sub>2</sub> emissions of approximately 30 Tg, three to four times greater than comparable estimates from global fire emissions databases. Uncontrolled understorey wildfires in humid tropical forests during extreme droughts are a large and poorly quantified source of CO<sub>2</sub> emissions.

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## Combining LiDAR and hyperspectral data for aboveground biomass modeling in the Brazilian Amazon using different regression algorithms



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Carbon stock

## ABSTRACT

Accurate estimates of aboveground biomass (AGB) in tropical forests are critical for supporting strategies of ecosystem functioning conservation and climate change mitigation. However, such estimates at regional and local scales are still highly uncertain. Airborne Light Detection And Ranging (LiDAR) and Hyperspectral Imaging (HSI) can characterize the structural and functional diversity of forests with high accuracy at a sub-meter resolution, and potentially improve the AGB estimations. In this study, we compared the ability of different data sources (airborne LiDAR and HSI, and their combination) and regression methods (linear model - LM, linear model with ridge regularization - LMR, Support Vector Regression - SVR, Random Forest - RF, Stochastic Gradient Boosting - SGB, and Cubist - CB) to improve AGB predictions in the Brazilian Amazon. We used georeferenced inventory data from 132 sample plots to obtain a reference field AGB and calculated 333 metrics (45 from LiDAR and 288 from HSI) that could be used as predictors for statistical AGB models. We submitted the metrics to a correlation filtering followed by a feature selection procedure (recursive feature elimination) to optimize the performance of the models and to reduce their complexity. Results showed that both LiDAR and HSI data used alone provided relatively high accurate models if adequate metrics and algorithms are chosen (RMSE = 67.6 Mg.ha<sup>-1</sup>, RMSE% = 36%, R<sup>2</sup> = 0.58, for the best LiDAR model; RMSE = 68.1 Mg.ha<sup>-1</sup>, RMSE% = 36%, R<sup>2</sup> = 0.58, for the best HSI model). However, HSI-only models required more metrics (5–12) than LiDAR-only models (2–5). Models combining metrics from both datasets resulted in more accurate AGB estimates, regardless of the regression method (RMSE = 57.7 Mg.ha<sup>-1</sup>, RMSE% = 31%, R<sup>2</sup> = 0.70, for the best model). The most important LiDAR metrics for estimating AGB were related to the upper canopy cover and tree height percentiles, while the most important HSI metrics were associated with the near infrared and shortwave infrared spectral regions, particularly the leaf/canopy water and lignin-cellulose absorption bands. Finally, an analysis of variance (ANOVA) showed that the remote sensing data source (LiDAR, HSI, or their combination) had a greater effect size than the regression algorithms. Thus, no single algorithm outperformed the others, although the LM method was less suitable when applied to the HSI and hybrid datasets. Results show that the synergistic use of LiDAR and hyperspectral data has great potential for improving the accuracy of the biomass estimates in the Brazilian Amazon.

## TROPICAL FOREST

## Long-term thermal sensitivity of Earth's tropical forests

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The sensitivity of tropical forest carbon to climate is a key uncertainty in predicting global climate change. Although short-term drying and warming are known to affect forests, it is unknown if such effects translate into long-term responses. Here, we analyze 590 permanent plots measured across the tropics to derive the equilibrium climate controls on forest carbon. Maximum temperature is the most important predictor of aboveground biomass (−9.1 megagrams of carbon per hectare per degree Celsius), primarily by reducing woody productivity, and has a greater impact per °C in the hottest forests (>32.2°C). Our results nevertheless reveal greater thermal resilience than observations of short-term variation imply. To realize the long-term climate adaptation potential of tropical forests requires both protecting them and stabilizing Earth's climate.

The response of tropical terrestrial carbon to environmental change is a critical component of global climate models (1). Land-atmosphere feedbacks depend on the balance of positive biomass growth stimulation by CO<sub>2</sub> fertilization (i.e., β) and negative responses to warmer temperatures and any change in precipitation (i.e., γ). Yet the climate response is so poorly constrained that it remains one of the largest uncertainties in Earth system models (2, 3), with the temperature sensitivity of tropical land carbon

stocks alone differing by >100 Pg C °C<sup>−1</sup> among models (2). Such uncertainty impedes our understanding of the global carbon cycle, limiting our ability to simulate the future of the Earth system under different long-term climate mitigation strategies. A critical long-term control on tropical land-atmosphere feedbacks is the sensitivity to climate of tropical forests (a key component of γ), where about 40% of the world's vegetation carbon resides (4).

The sensitivity to environmental change of tropical biomass carbon stocks, rates of production, and the persistence of fixed carbon can all be estimated by relating their short-term and interannual responses to variation in climate (5–7). These sensitivities are then used to con-

strain longer-term projections of climate responses (2). Such approaches typically find that higher minimum temperatures are strongly associated with slower tree growth and reduced forest carbon stocks, likely owing to increased respiration at higher temperatures (7–9). Tropical forest carbon is also sensitive to precipitation (10), with, for example, increased tree mortality occurring during drought events (11).

Yet the sensitivity of ecosystems to interannual fluctuations may be an unreliable guide to their longer-term responses to climate change. Such responses will also be influenced by physiological acclimation (12), changes in demographic rates (13), and shifts in species composition (14). For example, both respiration

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