ELSEVIER

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco





Leaf-litter production in human-modified Amazonian forests following the El Niño-mediated drought and fires of 2015–2016[★]

Tainá Madalena Oliveira de Morais ^{a,1}, Erika Berenguer ^{b,c,*,1}, Jos Barlow ^{c,d}, Filipe França ^c, Gareth D. Lennox ^c, Yadvinder Malhi ^b, Liana Chesini Rossi ^e, Marina Maria Moraes de Seixas ^f, Joice Ferreira ^{a,f}

- ^a Programa de Pós-Graduação em Ecologia (PPGECO), Universidade Federal do Pará, Belém, PA 66075-10, Brazil
- ^b Environmental Change Institute, School of Geography and the Environment, University of Oxford, OX1 3QY Oxford, UK
- ^c Lancaster Environment Centre, Lancaster University, LA1 4YQ Lancaster, UK
- d Setor de Ecologia e Conservação, Universidade Federal de Lavras, Lavras, MG, Brazil
- ^e Departamento de Ecologia, Universidade Estadual Paulista, 13506-900 Rio Claro, SP, Brazil
- f Embrana Amazônia Oriental, Tray. Dr. Enéas Pinheiro, s/n. CP 48, 66095-100 Belém, PA, Brazil

ARTICLE INFO

Keywords: Wildfire El Niño Drought Litter Amazon Carbon cycling

ABSTRACT

Leaf-litter production is an essential part of the carbon cycle of tropical forests. In the Amazon, it is influenced by climate, presenting high levels during the driest months of the year. However, it is less established how extreme climatic events may impact leaf-litter production in the long term. Even more unclear is how litter production is affected by human-driven disturbances. Here we examine the effects of the 2015-16 El Niño drought and subsequent fires in the leaf-litter production of human-modified Amazonian forests, thus investigating the interactions of a climatic extreme with anthropogenic disturbances on this key process of the Amazonian carbon cycle. We sampled leaf litter from April 2015 until March 2019 across 20 plots located in the eastern Brazilian Amazon, in a total of 11,548 samples. Plots were distributed along a pre-El Niño gradient of human disturbance, including undisturbed, logged, logged-and-burned, and secondary forests. All plots were impacted by the extreme drought caused by the 2015-16 El Niño, and eight were also impacted by understory fires. We found a significant and non-linear relationship between precipitation and monthly leaf-litter production - above 300 mm of monthly precipitation, the production of leaf-litter becomes independent of rainfall. Surprisingly, this relationship was not influenced by pre-El Niño forest disturbance class. During the El Niño, leaf-litter production was higher, decreasing sharply in the following year, especially in El Niño-fire-affected forests. Between 2017 and 2019, all forests experienced a gradual increase in the production of leaf litter. However, the mechanisms behind this increase remain unclear and are likely different between forests affected only by the El Niño drought and those affected by both the drought and fires. Our results suggest that while leaf-litter production may be insensitive to past human disturbances, it is affected, in the short term, by extreme climatic events, especially in forests impacted by El Niño fires.

1. Introduction

Extreme climatic events are becoming increasingly common as the 21st century progresses (IPCC, 2007). The El Niño event of 2015–2016 was one of these events and considered one of the strongest on record (Jimenez et al., 2018), affecting some of the world's most important

ecosystems (França et al., 2020). For example, within the Amazon, temperatures reached 1.5–2 °C above the maximum temperature observed during previous El Niños (Jiménez-Muñoz et al., 2016). This increase in temperature was accompanied by a severe reduction in precipitation, which resulted in widespread drought and a subsequent increase in the occurrence of understory forest fires (Van Schaik et al.,

E-mail address: e.deberenguercesar@lancaster.ac.uk (E. Berenguer).

[★] For a Portuguese version of the abstract, please see the Supplementary Material.

^{*} Corresponding author.

¹ Shared first co-authorship.

2018). In one eastern Amazonian region alone, which represents just 2% of the Amazon's extent, understory fires burned c. one million hectares of forest (Withey et al., 2018).

The importance of these extreme climatic events has resulted in a growing number of studies evaluating how intense drought and resulting understory fires affect carbon cycling rates in Amazonian forests. For instance, some have evaluated changes in post-drought tree recruitment and mortality (Phillips et al., 2009); while others have quantified postfire tree growth (Berenguer et al., 2018), tree mortality (Silva et al., 2018), and consequent impacts on carbon stocks (Berenguer et al., 2014). Yet, while our understanding of stem dynamics is improving, we have a more limited knowledge of other aspects of the forest carbon cycle. Litter - the aggregate input of leaves, twigs, fruits, flowers, and seeds onto the soil surface – for example, is much less studied despite its crucial role in the functioning of tropical rainforests, including nutrients cycling (Osborne et al., 2020), reducing seed predation (Cintra, 1997), influencing seedling establishment (Molofsky and Augspurger, 1992), and providing habitat for a broad range of vertebrates and invertebrates (Gascon, 1996; Vitt and Caldwell, 1994; Silveira et al., 2013).

Litter fall accounts for 3.1–7.3 Mg C ha⁻¹ being cycled every year in Amazonian forests (Araujo-Murakami et al., 2014; Malhi et al., 2009b; Rocha et al., 2014), with leaves being its predominant component (Barlow et al., 2007; Girardin et al., 2014; Selva et al., 2007), corresponding to 67-68% of its total (Chave et al., 2008; Rowland et al., 2018). Leaves of Amazonian trees may fall because they have reached the end of their life span (Chavana-Bryant et al., 2019; Reich et al., 1991), to protect other leaves from herbivory (Williams and Whitham, 1986), to avoid water stress (Smith et al., 2019), or after a tree dies. It is well established that seasonality affects leaf-litter production across the Amazon, with the driest periods seeing the highest levels of leaf fall (Cornforth, 1970; Barlow et al., 2007; Lanuza et al., 2018). As a consequence, during extreme droughts, higher leaf litter indicate stems are water stressed, and that trees are either resorting to leaf abscission as a coping mechanism or are dying. This increased leaf fall leads to more fine fuel being accumulated on the forest floor, thus increasing forest susceptibility to understory fires (Brando et al., 2016).

Despite the links between leaf litter and seasonality, few studies have assessed inter-annual changes (c.f. Paudel et al., 2015), which are key to understanding the long-term effects of extreme climatic events on the carbon cycle of tropical rainforests - for example, we currently do not know how quickly leaf litterfall returns to baseline levels after a severe drought. Moreover, the majority of studies in the Amazon have been conducted in undisturbed primary forests (Nebel et al., 2001; Selva et al., 2007), with only one study focusing on litterfall production in secondary forests (da Silva et al., 2018), thus providing limited insights into leaf litter production in human-modified forests. These are increasingly predominant in the region - in the Brazilian Amazon alone, 146,068 km² of primary forests were affected by either selective logging or understory fires between 2007 and 2016 (INPE, 2019); while c. 120,000 km² of secondary forests (i.e. those regenerating after deforestation) regrew between 1985 and 2017 (Nunes et al., 2020). It is therefore crucial to investigate the interaction between climatic and local stressors in the different components of the Amazonian carbon cycle to better understand how the largest rainforest in the world will function in the Anthropocene.

Here, we address these knowledge gaps by undertaking a detailed assessment of leaf-litter production in Amazonian forests. We assessed leaf litter in 20 plots distributed along a gradient of pre-El Niño human disturbance classes (hereafter referred to as pre-EN forest disturbance classes), including undisturbed, logged, logged-and-burned, and secondary forests. The four-year study period (2015–2019) encompassed the El Niño of 2015–2016, allowing us to evaluate the impact of both drought and understory fires on leaf litter, as well as its post-El Niño recovery. During the El Niño, 12 plots were only affected by drought (hereafter called EN-drought-affected), while eight were also affected by wildfires. Although these plots were also affected by drought, we use the

term "EN-fire-affected" to refer to them. We addressed five questions split into two broad groups. First, we explore the phenology of leaf litter production. Here, we ask (1) what is the relationship between monthly rates of leaf litterfall and precipitation, and (2) does this relationship differ (a) between pre-EN forest disturbance classes, (b) between EN-drought-affected and EN-fire-affected forests, and (c) between years? Second, we examine changes in mean leaf-litter production. For this, we use all data following the onset of the El Niño to examine (4) how pre-EN forest disturbance classes and the El Niño impact (i.e. drought alone or drought combined with fire) affect annual leaf-litter production? Finally, we use data of two months that we consistently have sampled across all years, including before the El Niño onset, to examine (5) whether, after three years since the end of the El Niño, average leaf-litter production has returned to pre-El Niño levels?

2. Materials and methods

2.1. Study area

Our study was carried out in the municipalities of Santarém, Belterra and Mojuí dos Campos (hereafter referred to as Santarém region), located in the eastern Brazilian Amazon. The regional climate is hot and humid (Fig. S1) – between January 2000 and December 2019, the average annual temperature was 26.2 °C (Instituto Nacional de Metereologia, 2019). Annual rainfall is around 2200 mm, with a marked dry season generally occurring between August and November, when rainfall <100 mm (Funk et al., 2015; Malhi et al., 2009a). During the 2015–16 El Niño, the dry season was extended to a period of eight months, from June 2015 until January 2016 (Fig. S1B).

The study region occupies an area of c. 6.5 million hectares and still presents large swathes of forests, including two protected areas – the Tapajós National Forest and the Tapajós-Arapiuns Extractive Reserve. However, most of the primary forest outside the protected areas have been previously disturbed by selective logging and understory fires (Gardner et al., 2013). Even parts of these two protected areas have also been affected by human-driven disturbances, including understory fires, which, in 2015–16, burned approximately 12% of the 527,000 ha of the Tapajós National Forest and 28% of the 678,000 ha of the Tapajós-Arapiuns Extractive Reserve (Withey et al., 2018). Secondary forests are also common in the region, representing c. 9% of the forested area in 2015 (Withey et al., 2018).

2.2. Sampling design

We established 20 plots (10×250 m, 0.25 ha each) in *terra firme* forests (Table S1) distributed along a pre-El Niño gradient of forest disturbance, including: undisturbed primary forests (n=5), logged primary forests (n=5), logged-and-burned primary forests (n=5), and secondary forests (n=5). Pre-EN disturbance classes were determined based on a visual analysis of satellite images from 1988 until 2010 (i.e. the year the plots were first established for other studies), combined with an assessment of on-the-ground evidence of past disturbances, such as logging debris and charcoal (See Gardner et al., 2013 for more information). While all 20 study plots were affected by drought during the 2015–16 El Niño, eight of them were also affected by understory fires between November 2015 and January 2016 (Table S2). In EN-fire-affected plots, median flame height varied between 10–20 cm, while the area directly affected by the fires varied between 72–98% (Withey et al., 2018).

In all plots, six litter-fall traps (50×50 cm; 0.25 m 2) were installed in April 2015, resulting in only two sampling months before the onset of the El Niño. Traps were located 1 m above the forest floor and 50 m apart. Litter was sampled bi-weekly until March 2019. At each sampling time, leaves were separated from the rest of the litter and oven dried at 60 °C for 3 days. Finally, leaves were weighed using scales with an accuracy of 0.01 g. To obtain monthly leaf-litter production of each trap

we first divided the leaf mass of each sampling by the number of days since the previous sampling event. We then attributed the daily average to every calendar day between sampling events. Finally, we added the values of all days in each month to obtain the monthly leaf-litter production.

2.3. Data analysis

2.3.1. Leaf-litter phenology

We obtained plot-level monthly precipitation data from CHIRPS (Funk et al., 2015). To calculate monthly precipitation across the whole sampling region, we averaged the rainfall values of each given month across all study plots. We examined the relationship between plot total monthly leaf litter (hereafter, "monthly leaf litter") and precipitation using mixed-effect models. We considered both linear and non-linear relationships by fitting polynomial models of degrees one to five (i.e. from linear to quintic fits) and chose the most parsimonious model as that with the lowest Bayesian Information Criterion score (Burnham and Anderson, 2002). All models included spatial and temporal random effects. Specifically, we included study plot as a random effect to account for the repeated plot sampling. This random effect was crossed with survey month to account for the seasonal nature of leaf litter. We used the results of this analysis to define the 'leaf-litter year' - i.e. the month with the highest precipitation, and therefore the lowest amount of leaf litter, to represent the beginning of the year. By this definition, our leaflitter year began in April and ended in March of the following calendar year. In all subsequent analyses in which year was an explanatory variable, it corresponds to the leaf-litter year.

Next, we considered how the relationship between monthly leaf litter and precipitation varied across pre-EN forest disturbance classes (i.e. undisturbed, logged, logged-and-burned, and secondary forests), El Niño impact (i.e. plots only affected by drought vs those affected by both drought and fire), and years (i.e. 2015/16, 2016/17, 2017/18, and 2018/19). To do so, we added one of the categorical variables (i.e. pre-EN forest disturbance class, El Niño impact, or year) to the most parsimonious monthly leaf-litter-to-precipitation model and constructed 95% confidence intervals for each level of the categorical variables, accounting for both residual and random effect variance. We took the relationship between monthly leaf litter and precipitation to be significantly dependent on the categorical variable if, for at least two levels of the variable, the 95% confidence intervals were non-overlapping. Otherwise, we assumed no statistical difference.

2.3.2. Average leaf litter fall

To investigate whether monthly leaf litter varied during and after the El Niño, we used a linear mixed-effect model with leaf-litter year as the fixed effect. Given that the El Niño began in June 2015, and consistently with our definition of the leaf-litter year, we took the year in which the El Niño occurred to be from June 2015 to March 2016. To ensure a balanced design, we removed April and May data from all subsequent, post-El Niño years. The random effect structure of this model was as described above: study plot crossed with survey month, and we tested mean differences in monthly leaf litter across years using Tukey's posthoc test with Bonferroni adjustments. Next, we examined whether there were differences in monthly leaf litter across pre-EN forest disturbance classes and El Niño impact during and after the El Niño event. We did this by adding interaction fixed effects between year and pre-EN forest disturbance classes and between year and El Niño impact to the model described above. We tested for differences across years and pre-EN forest disturbance classes and across years and El Niño impact by computing estimated marginal means for the interactions. In this analysis, we removed one outlier from our data. This outlying leaf-litter value was three times larger than any other recorded value across the whole timeseries and 22 times larger than any value recorded in the same month. The removal of this outlier had no bearing on any of our findings.

Finally, for a limited temporal subset of the data, we evaluated

whether monthly leaf litter was different before and after the El Niño. We did this by comparing monthly leaf litter in April and May 2015 (i.e. the available pre-El Niño data) to monthly leaf litter in April and May in all subsequent years (i.e. 2016–2018), using a linear mixed-effect model with study plot as the random effect. We tested mean differences in the April-May monthly leaf litter across years using Tukey's post-hoc test with Bonferroni adjustments. All analyses were run in R version 3.6.0.

3. Results

3.1. Relationship between leaf litter and precipitation

Monthly leaf litter was significantly and non-linearly related to precipitation – in months which precipitation levels were greater than c. 300 mm, leaf litter was largely independent of it (Fig. 1). For lower precipitation levels, leaf litter increased markedly. This relationship was held across all pre-EN forest disturbance classes and types of El Niño impact (Fig. 2). Over time, all forests continued to present a similar relationship between leaf litter and precipitation, with higher rates of leaf litterfall during drier months. This pattern was not significantly different across all sampled years (Fig. S2).

3.2. Leaf-litter production during and after the El Niño

During the El Niño year (i.e. 2015/16), monthly leaf litter was significantly higher than in the following three years (Fig. 3). Specifically, monthly leaf litter declined significantly in the first year after the El Niño (2016/17) and increased thereafter. This pattern seemed to be driven by the type of El Niño impact – in 2016/17, EN-fire-affected forests presented significantly lower levels of leaf litter than EN-drought-affected forests (Fig. 4). Pre-EN forest disturbance class did not influence leaf litter neither during nor after the 2015–2016 El Niño (Fig. S3).

3.3. Comparison between pre- and post-El Niño leaf litter

There were no significant differences in pre- and post-El Niño

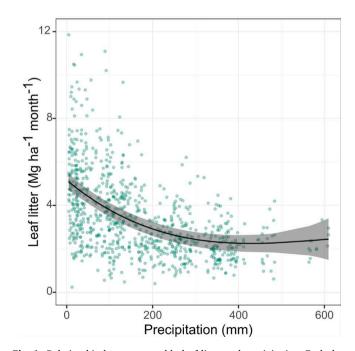


Fig. 1. Relationship between monthly leaf litter and precipitation. Each data point represents the monthly leaf litter of each of the 20 study plots across the four years of sampling. The fitted line represents the model fit and the shaded area the 95% confidence interval.

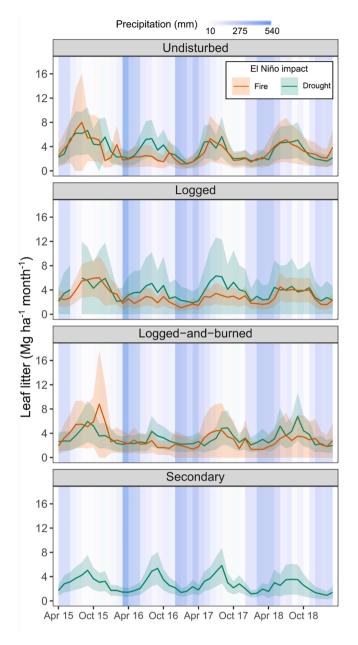


Fig. 2. Relationship between monthly leaf litter and precipitation through time between pre-EN forest disturbance classes and El Niño impacts. Monthly leaf litter from April 2015 until March 2019 across undisturbed (n = 5), logged (n = 5), logged-and-burned (n = 5) and secondary (n = 5) forests. Green lines represent the mean monthly leaf litter of EN-drought-affected plots, while orange lines represent EN-fire-affected plots. Shaded areas show confidence intervals (95% CI). The blue background shading exhibits monthly precipitation, with lighter tones showing drier periods and darker tones the wetter ones across the whole sampled region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

monthly leaf litter in April and May (Fig. S4). However, mean monthly leaf-litter production was lowest in April-May 2016 (i.e. in the year following the El Niño) before increasing to values more consistent with those seen prior to the El Niño.

4. Discussion

Leaf-litter production is one of the best studied ecosystem processes in tropical forests, and litter traps are integrated into many forest monitoring protocols. However, to date most research investigating

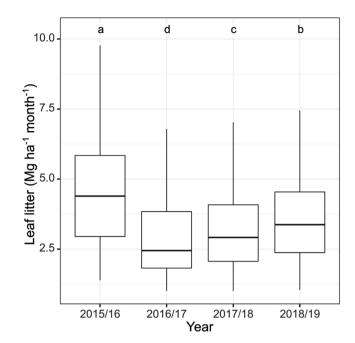


Fig. 3. Monthly leaf litter across the four different leaf-litter years. Each leaf-litter year period corresponds from June to March (see methods), thus 2015–16 encompasses the whole El Niño period. Different letters across different leaf-litter year indicate a significant difference in monthly leaf litter across each leaf-litter year, following Tukey's post-hoc test with Bonferroni adjustments.

patterns of leaf-litter production in the Amazon has been conducted in undisturbed forests (Girardin et al., 2014; Selva et al., 2007), and no studies have evaluated the long-term effects of an extreme climatic event – although some have explored the effect of a long-term experimental drought on litterfall dynamics (Brando et al., 2008; Rowland et al., 2018). Additionally, we are not aware of any study that has explored the possibility of an interaction between previous disturbance events, and droughts and fires related to climatic extremes. Our study, while lacking long-term data from before the El Niño event, provides three important insights into how leaf-litter production responds to climatic and local stressors. We explore these in turn, before examining some of the remaining uncertainties.

4.1. El Niño effects on leaf litter are strongest when a forest burns

In EN-fire-affected forests, trees faced the combined impact of severe water stress, as a consequence of the El Niño drought, and high mortality rates as a consequence of the fires, resulting in high levels of leaf-litter production in the El Niño year. In the following year, we recorded a strong reduction in leaf-litter production in EN-fire-affected forests (Fig. 3), being even lower than that in EN-drought-affected forests (Fig. 4). This is likely a consequence of the low number of surviving stems in EN-fire-affected forests (Barlow et al., 2003). Two and three years after the El Niño, leaf-litter production increased in EN-fireaffected forests and became statistically similar to that found in ENdrought-affected forests. This recovery could be a consequence of the recruitment of a large number of pioneer species following the fires (Barlow and Peres, 2008), which tend to have very big leaves with short life spans (Reich et al., 1991), such as those from the genus Cecropia or Aparisthmium. As such, the similarity in post-El Niño leaf-litter production between forests affected by drought and those affected by both drought and fire needs to be interpreted with caution, as it is likely underpinned by very different mechanisms.

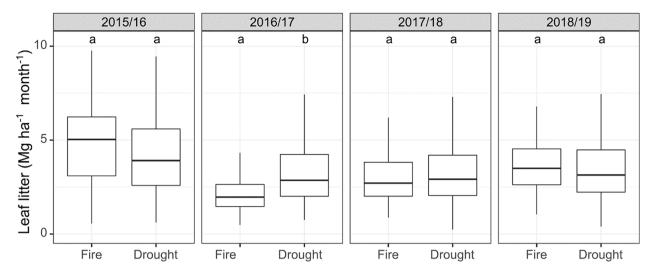


Fig. 4. Differences between monthly leaf litter and El Niño impact within each leaf-litter year. Each leaf-litter year period corresponds from June to May (see methods), thus 2015–16 encompasses the whole El Niño period. El Niño impacts include forests affected by both drought and fire, and those just affected by drought. Letters represent Tukey's post-hoc test with Bonferroni adjustments. The same letter across El Niño impacts within each leaf-litter year indicate no significant difference in monthly leaf litter, while the different letters in 2016/17 represent a significant difference in monthly leaf litter between El Niño impacts in that particular year.

4.2. Leaf-litter production is generally insensitive to past human disturbance

Human-modified forests, when compared to undisturbed ones, present a different plant community composition (Barlow and Peres, 2008; Laurance et al., 2006), dominated by pioneers with acquisitive functional traits (Carreño-Rocabado et al., 2012) – i.e. species that grow fast (Berenguer et al., 2018) and have high leaf turnover rates (Galia Selaya et al., 2008). Additionally, pioneers tend to have narrower hydraulic safety margins, being more likely to die during a drought (Santiago et al., 2018). As a consequence, we expected that both disturbed primary and secondary forests would present higher levels of leaf-litter production throughout the year, due to the greater presence of species with short leaf life spans, and particularly during extreme droughts, given their greater likelihood to suffer embolism.

Despite the reasons outlined above, our results show that the production of leaf litter is relatively insensitive to past human disturbance: leaf fall in undisturbed, logged, logged-and-burned, and secondary forests held similar phenological responses to precipitation during the four years of our study (Fig. S2), and presented similar variations in average leaf-litter production before, during and after the El Niño event (Figs. 2, 3 and S3). However, there is great variability in monthly leaf production when precipitation is <300 mm (Fig. 1). One possible explanation for the relationship between leaf litterfall and precipitation being held constant is that higher leaf turnover rates in disturbed primary and secondary forests are offset by the higher amount of leaves found in undisturbed forests (Sirri et al., 2019). However, it is also possible that leaf-litter production remains one of the most resilient ecosystem processes, rapidly recovering after either human or climatic disturbances. This would align with results from drought experiments in Amazonian forests, in which a significant decline in leaf-litter production was only observed after three to four years of rainfall exclusion (Brando et al., 2008; Rowland et al., 2018), and it promptly returned to baseline levels as soon as rainfall was re-established. It is also consistent with results from experimental burns in forests in the southern Amazon, where litter production remained similar to that in unburned forests during the first two years after the fires (Balch et al., 2008). At the beginning of our study, in 2015, our secondary forests aged between 18 to over 25; and the last disturbance in primary forests occurred between 13 to over 30 years ago: likely being enough time for leaf-litter production to reach the same levels as those observed in undisturbed forests.

4.3. The leaf-fall phenology of EN-drought- and EN-fire-affected forests is insensitive to change

Across the Amazon, leaf-litter production increases as precipitation decreases (Barlow et al., 2007; Lanuza et al., 2018). Trees likely use leaf abscission as a protection mechanism from drought when they are water stressed – i.e. the fewer leaves, the less amount of water is lost through transpiration (Smith et al., 2019; Wagner et al., 2017). We show that all pre-EN forest disturbance classes showed a similar response to rainfall (Fig. S2), with leaf-litter production increasing sharply around 200 mm of rainfall (Fig. 1). The similarity of responses across pre-EN disturbance classes is surprising (Fig. 2) – pioneers tend to have narrower hydraulic safety margins, and are more likely to suffer embolism and die during a drought (Santiago et al., 2018), suggesting that forests dominated by pioneers would show a different threshold of leaf-litter production to low rainfall. The fact they did not suggests that, at the stand-level, both undisturbed forests and disturbed primary and secondary forests may share similar responses to water stress. However, it could also mean that the forests in our region are all below the threshold at which present-day climatic variables have a big impact on key ecosystem processes (Sullivan et al., 2020).

4.4. Uncertainties

Despite our four years study, it remains unclear whether leaf-litter production returned to pre-El Niño levels. There are two key reasons for this. First, the recovery of litter fall is likely to be confounded by ongoing tree mortality – this is particularly evident in EN-fire-affected plots (e.g. Silva et al. 2018), but even EN-drought-affected plots may experience delayed mortality (Phillips et al., 2010). Second, our experimental design – set up to assess forest disturbance classes without prior knowledge of the effects of the El Niño in our region – means we have only limited data on pre-El Niño conditions. While the data from April and May are comparable across years (Fig. S4), they are also from one of the wettest periods of the annual cycle, when forests are least likely to show effects in relation to rainfall (Fig. 2). There is also the question of whether the relationship between leaf litterfall with temperature and radiation would present the same patterns as that of precipitation – an issue that requires further investigation.

Our research also does not explore the mechanisms underpinning post-El Niño leaf-litter production. The recovery of the litter cycling

processes in burned forests could be an important and under-studied aspect of forest regeneration, helping replenish soil nutrients and part of the physical structure of the organic layer; albeit the litter chemical composition of burned and unburned forests may differ. However, the fast recovery of leaf-litter production in EN-fire-affected forests, when their canopy is still dominated by gaps created by high and long-lasting tree mortality (Barlow and Peres, 2008; Silva et al., 2018) can increase the vulnerability of these forests to further fire events. In a gappier forest, the microclimate is hotter and drier (Uhl and Kauffman, 1990), causing a more rapid desiccation of the leaf litter during the dry season. Previous studies have shown that a dry litter layer (i.e. <23% moisture) is the best predictor of forest susceptibility to fire (Ray et al., 2005). Another source of uncertainty regarding litter production and forest flammability is the predicted longer and more intense dry seasons across most of the Amazon Basin (Duffy et al., 2015). Our results suggest that all forests, regardless of disturbance, will experience a higher leaf-litter production in drier periods, resulting in greater availability of fine fuel. The combination of a drier climate and an abundance of fuel may increase the risk of fire in Amazonian forests.

5. Conclusion

Tropical forests face the twin threats of local human disturbance events and climate change, including extreme climatic events (Barlow et al., 2018; França et al., 2020). Previous research has shown that some aspects of these ecosystems are very sensitive to changes, presenting a marked decline in aboveground carbon stocks and severe alterations in forest structure (Berenguer et al., 2014). We provide evidence suggesting that leaf-litter production remains relatively insensitive to past anthropogenic changes, and there is no evidence that forest disturbance modifies responses to climatic stresses associated with El Niño events. The apparent resilience of litter production to drought is important as exceptional dry periods are becoming more frequent across the Amazon Basin (Duffy et al., 2015). Conversely, understory fires had a much greater effect on leaf-litter production, adding to a growing set of evidence that suggests these fires are one of the greatest threats to the functioning of Amazonian forests.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful for the following for financial support: Instituto Nacional de Ciência e Tecnologia - Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0); Empresa Brasileira de Pesquisa Agropecuária - Embrapa (SEG: 02.08.06.005.00); the Fundação de Amparo à Pesquisa do Estado de São Paulo - FAPESP (2012/51509-8 and 2012/51872-5); the UK government Darwin Initiative (17-023), The Nature Conservancy; the UK Natural Environment Research Council (NERC; NE/F01614X/1, NE/G000816/1, NE/K016431/1, and NE/ P004512/1); the BNP Paribas Foundation's Climate and Biodiversity Initiative (Project Bioclimate); and the Brazilian Research Council (CNPq-CAPES; Prevfogo-IBAMA 441949/2018-5 [Sem-Flama], MCIC 420254/2018-8 [Resflora] and 441659/2016-0 [PELD-RAS]). TMOM was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES). -EB and JB were funded by H2020-MSCA-RISE (691053-ODYSSEA). FF was funded by CAPES CNPq-PELD (scholarships: 88887.186650/2018 00 and 88887.358233/2019 00). YM was supported by ERC Advanced Investigator Grant GEM-TRAIT (321131) and by the Jackson Foundation. We would like to thank the Large-Scale Biosphere-Atmosphere Program (LBA) for logistical and infrastructure support during field measurements. We are deeply

grateful to all our field and laboratory assistants. We also thank all collaborating land owners for their support and access to their land. This is paper #88 of the Rede Amazônia Sustentável publication series. The datasets used in this paper are available at: https://figshare.com/article s/dataset/Leaf-litter_production_in_human-modified_Amazonian_forest s_following_the_El_Ni_o-mediated_drought_and_fires_of_2015_2016/ 14770992.

Appendix A. Supplementary material

Supplementary data to this article can be found online at $\frac{\text{https:}}{\text{doi.}}$ org/10.1016/j.foreco.2021.119441.

References

- Araujo-Murakami, A., Doughty, C.E., Metcalfe, D.B., Silva-Espejo, J.E., Arroyo, L., Heredia, J.P., Flores, M., Sibler, R., Mendizabal, L.M., Pardo-Toledo, E., Vega, M., Moreno, L., Rojas-Landivar, V.D., Halladay, K., Girardin, C.A.J., Killeen, T.J., Malhi, Y., 2014. The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. Plant Ecol. Divers. 7, 55–69. https://doi. org/10.1080/17550874.2013.798364.
- Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., de Carvalho, O., Lefebvre, P., 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. Glob. Chang. Biol. 14, 2276–2287. https://doi.org/10.1111/j.1365-2486-2408.01655.x
- Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L., Economo, E.P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A.C., Parr, C.L., Wilson, S.K., Young, P.J., Graham, N.A.J., 2018. The future of hyperdiverse tropical ecosystems. Nature 559, 517–526. https://doi.org/10.1038/s41586-018-0301-1.
- Barlow, J., Gardner, T.A., Ferreira, L.V., Peres, C.A., 2007. Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. For. Ecol. Manage. 247, 91–97. https://doi.org/10.1016/j.foreco.2007.04.017.
- Barlow, J., Peres, C., Lagan, B., Haugaasen, T., 2003. Large tree mortality and the decline of forest biomass following Amazonian wildfires. Ecol. Lett. 6, 6–8.
- Barlow, J., Peres, C.A., 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. Philos. Trans. R. Soc. Lond. B Biol. Sci. 363, 1787–1794. https://doi.org/10.1098/rstb.2007.0013.
- Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E., Durigan, M., De Oliveira, R.C., Vieira, I.C.G., Barlow, J., 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. Glob. Chang. Biol. 20, 3713–3726. https://doi.org/10.1111/gcb.12627.
- Berenguer, E., Malhi, Y., Brando, P., Cardoso Nunes Cordeiro, A., Ferreira, J., França, F., Chesini Rossi, L., Maria Moraes de Seixas, M., Barlow, J., Cordeiro, A.C.N., Ferreira, J., França, F., Rossi, L., Seixas, M.M.M., Barlow, J., 2018. Tree growth and stem carbon accumulation in human-modified Amazonian Forests. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170308 https://doi.org/10.1098/rstb.2017.0308.
- Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., Camargo, P., 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philos. Trans. R. Soc. B Biol. Sci. 363, 1839–1848. https://doi.org/10.1098/rstb.2007.0031.
- Brando, P.M., Oliveria-Santos, C., Rocha, W., Cury, R., Coe, M.T., 2016. Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. Glob. Chang. Biol. 1–9 https://doi.org/10.1111/gcb.13172.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A
 Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York,
 NY USA
- Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J.C., Poorter, L., 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. J. Ecol. 100, 1453–1463. https://doi.org/10.1111/j.1365-2745.2012.02015.
- Chavana-Bryant, C., Malhi, Y., Anastasiou, A., Enquist, B.J., Cosio, E.G., Keenan, T.F., Gerard, F.F., 2019. Leaf age effects on the spectral predictability of leaf traits in Amazonian canopy trees. Sci. Total Environ. 666, 1301–1315. https://doi.org/ 10.1016/i.scitotenv.2019.01.379.
- Chave, J., Olivier, J., Bongers, F., Châtelet, P., Forget, P.M., Van Der Meer, P., Norden, N., Riéra, B., Charles-Dominique, P., 2008. Above-ground biomass and productivity in a rain forest of eastern South America. J. Trop. Ecol. 24, 355–366. https://doi.org/10.1017/S0266467408005075.
- Cintra, R., 1997. Leaf litter effects on seed and seedling predation of the palm Astrocaryum murumuru and the legume tree Dipteryx micrantha in Amazonian forest. J. Trop. Ecol. 13, 709–725. https://doi.org/10.1017/S0266467400010889.
- Cornforth, I.S., 1970. Leaf-fall in a tropical rain forest. J. Appl. Ecol. 7, 603. https://doi. org/10.2307/2401982.
- da Silva, W.B., Périco, E., Dalzochio, M.S., Santos, M., Cajaiba, R.L., 2018. Are litterfall and litter decomposition processes indicators of forest regeneration in the neotropics? Insights from a case study in the Brazilian Amazon. For. Ecol. Manage. 429, 189–197. https://doi.org/10.1016/j.foreco.2018.07.020.
- Duffy, P.B., Brando, P., Asner, G.P., Field, C.B., 2015. Projections of future meteorological drought and wet periods in the Amazon. Proc. Natl. Acad. Sci. 112, 13172–13177. https://doi.org/10.1073/pnas.1421010112.

- França, F.M., Benkwitt, C.E., Peralta, G., Robinson, J.P.W., Graham, N.A.J., Tylianakis, J. M., Berenguer, E., Lees, A.C., Ferreira, J., Louzada, J., Barlow, J., 2020. Climatic and local stressor interactions threaten tropical forests and coral reefs. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190116. https://doi.org/10.1098/rstb.2019.0116.
- Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., Michaelsen, J., 2015. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. Sci. Data 2, 150066. https://doi.org/10.1038/sdata.2015.66.
- Galia Selaya, N., Oomen, R.J., Netten, J.J.C., Werger, M.J.A., Anten, N.P.R., 2008. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. J. Ecol. 96, 1211–1221. https://doi.org/10.1111/j.1365-2745.2008.01441.x.
- Gardner, T.A., Ferreira, J., Barlow, J., Lees, A.C., Parry, L., Vieira, I.C.G., Berenguer, E., Abramovay, R., Aleixo, A., Andretti, C., Aragão, L.E.O.C., Araújo, I., de Ávila, W.S., Bardgett, R.D., Batistella, M., Begotti, R.A., Beldini, T., de Blas, D.E., Braga, R.F., Braga, D. de L., de Brito, J.G., de Camargo, P.B., Campos Dos Santos, F., de Oliveira, V.C., Cordeiro, A.C.N., Cardoso, T.M., de Carvalho, D.R., Castelani, S.A., Chaul, J.C. M., Cerri, C.E., Costa, F. de A., da Costa, C.D.F., Coudel, E., Coutinho, A.C., Cunha, D., D'Antona, A., Dezincourt, J., Dias-Silva, K., Durigan, M., Esquerdo, J.C.D.M., Feres, J., Ferraz, S.F. de B., Ferreira, A.E. de M., Fiorini, A.C., da Silva, L.V.F., Frazão, F.S., Garrett, R., Gomes, A.D.S., Gonçalves, K. da S., Guerrero, J.B., Hamada, N., Hughes, R.M., Igliori, D.C., Jesus, E. da C., Juen, L., Junior, M., Junior, J.M.B. de O., Junior, R.C. de O., Junior, C.S., Kaufmann, P., Korasaki, V., Leal, C.G., Leitão, R., Lima, N., Almeida, M. de F.L., Lourival, R., Louzada, J., Nally, R. Mac, Marchand, S., Maués, M.M., Moreira, F.M.S., Morsello, C., Moura, N., Nessimian, J., Nunes, S., Oliveira, V.H.F., Pardini, R., Pereira, H.C., Pompeu, P.S., Ribas, C.R., Rossetti, F., Schmidt, F.A., da Silva, R., da Silva, R.C.V.M., da Silva, T.F.M.R., Silveira, J., Siqueira, J.V., de Carvalho, T.S., Solar, R.R.C., Tancredi, N.S.H., Thomson, J.R., Torres, P.C., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Viana, C., Weinhold, D., Zanetti, R., Zuanon, J., 2013. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. Philos. Trans. R. Soc. Lond. B Biol. Sci. 368, 20120166.
- Gascon, C., 1996. Amphibian litter fauna and river barriers in flooded and non-flooded Amazonian rain forest. Biotropica 28, 136. https://doi.org/10.2307/2388779.
- Girardin, C.A.J., Espejob, J.E.S., Doughty, C.E., Huasco, W.H., Metcalfe, D.B., Durand-Baca, L., Marthews, T.R., Aragao, L.E.O.C., Farfán-Rios, W., García-Cabrera, K., Halladay, K., Fisher, J.B., Galiano-Cabrera, D.F., Huaraca-Quispe, L.P., Alzamora-Taype, I., Eguiluz-Mora, L., -Revilla, N.S., Silman, M.R., Meir, P., Malhi, Y., 2014. Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. Plant Ecol. Divers. 7, 107–123. doi: 10.1080/17550874.2013.820222.
- INPE, 2019. DEGRAD [WWW Document]. http://www.obt.inpe.br/degrad/. URL http://www.obt.inpe.br/degrad/.
- Instituto Nacional de Metereologia, 2019. INMET Estações Automáticas [WWW Document]. URL http://www.inmet.gov.br/portal/index.php?r=estacoes/estacoes Automaticas.
- IPCC, 2007. Climate Change 2007: The Physical Basis. Summary for Policy Makers. Proc. Alp. Snow Work. Munich, Oct. 5–6, Ger. | HeBIS-Verbundkatalog 8, 142.
- Jiménez-Muñoz, J.C., Mattar, C., Barichivich, J., Santamaría-Artigas, A., Takahashi, K., Malhi, Y., Sobrino, J.A., van der Schrier, G., 2016. Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. Sci. Rep. 6, 33130. https://doi.org/10.1038/srep33130.
- Jimenez, J.C., Barichivich, J., Mattar, C., Takahashi, K., Santamaría-Artigas, A., Sobrino, J.A., Malhi, Y., 2018. Spatio-temporal patterns of thermal anomalies and drought over tropical forests driven by recent extreme climatic anomalies. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170300. https://doi.org/10.1098/rstb.2017.0300.
- Lanuza, O., Casanoves, F., Zahawi, R.A., Celentano, D., Delgado, D., Holl, K.D., 2018. Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of recovery. Biotropica. https://doi.org/10.1111/btp.12533.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., Capretz, R.L., 2006. Rain forest fragmentation and the proliferation of successional trees. Ecology 87, 469–482.
- Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C., Meir, P., 2009a. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proc. Natl. Acad. Sci. U.S.A. 106, 20610–20615. https://doi.org/10.1073/pnas.0804619106.
- Malhi, Y., Aragão, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., da COSTA, A.C.L., Hutyra, L.R., Oliveira, P., Patiño, S., Pyle, E.H., Robertson, A.L., Teixeira, L.M., 2009b. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Glob. Chang. Biol. 15, 1255–1274. doi: 10.1111/j.1365-2486.2008.01780.x.
- Molofsky, J., Augspurger, C.K., 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73, 68–77. https://doi.org/10.2307/ 1938721
- Nebel, G., Dragsted, J., Vega, A.S., 2001. Litter fall, biomass and net primary production in flood plain forests in the Peruvian Amazon. For. Ecol. Manage. 150, 93–102. https://doi.org/10.1016/S0378-1127(00)00683-6.
- Nunes, S., Oliveira, L., Siqueira, J., Morton, D.C., Souza, C.M., 2020. Unmasking secondary vegetation dynamics in the Brazilian Amazon. Environ. Res. Lett. 15, 034057 https://doi.org/10.1088/1748-9326/ab76db.
- Osborne, B.B., Nasto, M.K., Soper, F.M., Asner, G.P., Balzotti, C.S., Cleveland, C.C., Taylor, P.G., Townsend, A.R., Porder, S., 2020. Leaf litter inputs reinforce islands of nitrogen fertility in a lowland tropical forest. Biogeochemistry 147, 293–306. https://doi.org/10.1007/s10533-020-00643-0.
- Paudel, E., Dossa, G.G.O., Xu, J., Harrison, R.D., 2015. Litterfall and nutrient return along a disturbance gradient in a tropical montane forest. For. Ecol. Manage. 353, 97–106. https://doi.org/10.1016/j.foreco.2015.05.028.

- Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. a, van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D. a, Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. Ter, Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C. a, Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science 323(80-.), 1344–1347. doi: 10.1126/science.1164033.
- Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, Á.C.A., Chao, K.J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N., Patiño, S., Peh, K.S.H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R., Vilanova, E., 2010. Drought-mortality relationships for tropical forests. New Phytol. 187, 631–646. doi: 10.1111/j.1469-8137.2010.03359.x.
- Ray, D., Nepstad, D., Moutinho, P., 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. Ecol. Appl. 15, 1664–1678.
- Reich, P.B., Uhl, C., Walters, M.B., Ellsworth, D.S., 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia 86, 16–24. https://doi.org/10.1007/BF00317383.
- Rocha, W., Metcalfe, D.B., Doughty, C.E., Brando, P., Silvério, D., Halladay, K., Nepstad, D.C., Balch, J.K., Malhi, Y., 2014. Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). Plant Ecol. Divers. 7, 25–40. https://doi.org/ 10.1080/17550874.2013.798368.
- Rowland, L., da Costa, A.C.L., Oliveira, A.A.R., Almeida, S.S., Ferreira, L.V., Malhi, Y., Metcalfe, D.B., Mencuccini, M., Grace, J., Meir, P., 2018. Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics. J. Ecol. 106, 1673–1682. https://doi.org/10.1111/1365-2745.12931.Santiago, L.S., De Guzman, M.E., Baraloto, C., Vogenberg, J.E., Brodie, M., Hérault, B.,
- Santiago, L.S., De Guzman, M.E., Baraloto, C., Vogenberg, J.E., Brodie, M., Hérault, B., Fortunel, C., Bonal, D., 2018. Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. New Phytol. 218, 1015–1024. https://doi.org/10.1111/nph.15058.
- Selva, E.C., Couto, E.G., Johnson, M.S., Lehmann, J., 2007. Litterfall production and fluvial export in headwater catchments of the southern Amazon. J. Trop. Ecol. 23, 329–335. https://doi.org/10.1017/S0266467406003956.
- Silva, C.V.J., Aragão, L.E.O.C., Barlow, J., Espirito-Santo, F., Young, P.J., Anderson, L.O., Berenguer, E., Brasil, I., Foster Brown, I., Castro, B., Farias, R., Ferreira, J., França, F., Graça, P.M.L.A., Kirsten, L., Lopes, A.P., Salimon, C., Scaranello, M.A., Seixas, M., Souza, F.C., Xaud, H.A.M., 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. Philos. Trans. R. Soc. B Biol. Sci. 373, 20180043. https://doi.org/10.1098/rstb.2018.0043.
- Silveira, J.M., Barlow, J., Andrade, R.B., Louzada, J., Mestre, L.A., Lacau, S., Zanetti, R., Numata, I., Cochrane, M.A., 2013. The responses of leaf litter ant communities to wildfires in the Brazilian Amazon: a multi-region assessment. Biodivers. Conserv. 22, 513–529. https://doi.org/10.1007/s10531-012-0426-8.
- Sirri, N.F., Libalah, M.B., Momo Takoudjou, S., Ploton, P., Medjibe, V., Kamdem, N.G., Mofack, G., Sonké, B., Barbier, N., 2019. Allometric models to estimate leaf area for tropical African broadleaved forests. Geophys. Res. Lett. 46, 8985–8994. https://doi. org/10.1029/2019GL083514.
- Smith, M.N., Stark, S.C., Taylor, T.C., Ferreira, M.L., Oliveira, E., Restrepo-Coupe, N., Chen, S., Woodcock, T., Santos, D.B., Alves, L.F., Figueira, M., Camargo, P.B., Oliveira, R.C., Aragão, L.E.O.C., Falk, D.A., McMahon, S.M., Huxman, T.E., Saleska, S.R., 2019. Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. New Phytol. 222, 1284–1297. https://doi.org/10.1111/nph.15726.
- Sullivan, M.J.P., Lewis, S.L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A.C., Ewango, C.E.N., Hubau, W., Marimon, B., Monteagudo-Mendoza, A., Qie, L., Sonké, B., Martinez, R.V., Baker, T.R., Brienen, R.J.W., Feldpausch, T.R., Galbraith, D., Gloor, M., Malhi, Y., Aiba, S.-I., Alexiades, M.N., Almeida, E.C., de Oliveira, E.A., Dávila, E.Á., Loayza, P.A., Andrade, A., Vieira, S.A., Aragão, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., Ashton, P., Aymard C., G., Baccaro, F.B., Banin, L.F., Baraloto, C., Camargo, P.B., Barlow, J., Barroso, J., Bastin, J.-F., Batterman, S.A., Beeckman, H., Begne, S.K., Bennett, A.C., Berenguer, E., Berry, N., Blanc, L., Boeckx, P., Bogaert, J., Bonal, D., Bongers, F., Bradford, M., Brearley, F.Q., Brncic, T., Brown, F., Burban, B., Camargo, J.L., Castro, W., Céron, C., Ribeiro, S.C., Moscoso, V.C., Chave, J., Chezeaux, E., Clark, C.J., de Souza, F.C., Collins, M., Comiskey, J.A., Valverde, F.C., Medina, M.C., da Costa, L., Dančák, M., Dargie, G.C., Davies, S., Cardozo, N.D., de Haulleville, T., de Medeiros, M.B., del Aguila Pasquel, J., Derroire, G., Di Fiore, A., Doucet, J.-L., Dourdain, A., Droissart, V., Duque, L.F., Ekoungoulou, R., Elias, F., Erwin, T., Esquivel-Muelbert, A., Fauset, S., Ferreira, J., Llampazo, G.F., Foli, E., Ford, A., Gilpin, M., Hall, J.S., Hamer, K.C., Hamilton, A.C., Harris, D.J., Hart, T.B., Hédl, R., Herault, B., Herrera, R., Higuchi, N., Hladik, A., Coronado, E.H., Huamantupa-Chuquimaco, I., Huasco, W.H., Jeffery, K.J., Jimenez-Rojas, E., Kalamandeen, M., Djuikouo, M.N.K., Kearsley, E., Umetsu, R.K., Kho, L.K., Killeen, T., Kitayama, K., Klitgaard, B., Koch, A., Labrière, N., Laurance, W., Laurance, S., Leal, M.E., Levesley, A., Lima, A.J.N., Lisingo, J., Lopes, A.P., Lopez-Gonzalez, G., Lovejoy, T., Lovett, J.C., Lowe, R., Magnusson, W.E., Malumbres-

Olarte, J., Manzatto, Â.G., Marimon, B.H., Marshall, A.R., Marthews, T., de Almeida Reis, S.M., Maycock, C., Melgaço, K., Mendoza, C., Metali, F., Mihindou, V., Milliken, W., Mitchard, E.T.A., Morandi, P.S., Mossman, H.L., Nagy, L., Nascimento, H., Neill, D., Nilus, R., Vargas, P.N., Palacios, W., Camacho, N.P., Peacock, J., Pendry, C., Peñuela Mora, M.C., Pickavance, G.C., Pipoly, J., Pitman, N., Playfair, M., Poorter, L., Poulsen, J.R., Poulsen, A.D., Preziosi, R., Prieto, A., Primack, R.B., Ramírez-Angulo, H., Reitsma, J., Réjou-Méchain, M., Correa, Z.R., de Sousa, T.R., Bayona, L. R., Roopsind, A., Rudas, A., Rutishauser, E., Abu Salim, K., Salomão, R.P., Schietti, J., Sheil, D., Silva, R.C., Espejo, J.S., Valeria, C.S., Silveira, M., Simo-Droissart, M., Simon, M.F., Singh, J., Soto Shareva, Y.C., Stahl, C., Stropp, J., Sukri, R., Sunderland, T., Svátek, M., Swaine, M.D., Swamy, V., Taedoumg, H., Talbot, J., Taplin, J., Taylor, D., ter Steege, H., Terborgh, J., Thomas, R., Thomas, S.C., Torres-Lezama, A., Umunay, P., Gamarra, L.V., van der Heijden, G., van der Hout, P., van der Meer, P., van Nieuwstadt, M., Verbeeck, H., Vernimmen, R., Vicentini, A., Vieira, I.C.G., Torre, E.V., Vleminckx, J., Vos, V., Wang, O., White, L.J.T., Willcock, S., Woods, J.T., Wortel, V., Young, K., Zagt, R., Zemagho, L., Zuidema, P.A., Zwerts, J.A., Phillips, O. L., 2020. Long-term thermal sensitivity of Earth's tropical forests. Science 368(80-.), 869-874. doi: 10.1126/science.aaw7578.

Uhl, C., Kauffman, J., 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. Ecology 71, 437–449.

- Van Schaik, E., Killaars, L., Smith, N.E., Koren, G., Van Beek, L.P.H., Peters, W., Van Der Laan-Luijkx, I.T., 2018. Changes in surface hydrology, soil moisture and gross primary production in the Amazon during the 2015/2016 El Niño. doi: 10.1 098/rsth 2018 0084
- Vitt, L.J., Caldwell, J.P., 1994. Resource utilization and guild structure of small vertebrates in the Amazon forest leaf litter. J. Zool. 234, 463–476. https://doi.org/ 10.1111/j.1469-7998.1994.tb04860.x.
- Wagner, F.H., Hérault, B., Rossi, V., Hilker, T., Maeda, E.E., Sanchez, A., Lyapustin, A.I., Galvão, L.S., Wang, Y., Aragão, L.E.O.C., 2017. Climate drivers of the Amazon forest greening. PLoS ONE 12. https://doi.org/10.1371/journal.pone.0180932.
- Williams, A.G., Whitham, T.G., 1986. Premature leaf abscission: an induced plant defense against gall aphids. Ecology 67, 1619–1627. https://doi.org/10.2307/ 1939093
- Withey, K., Berenguer, E., Palmeira, A.F., Espírito-Santo, F.D.B., Lennox, G.D., Silva, C.V. J., Aragão, L.E.O.C., Ferreira, J., França, F., Malhi, Y., Rossi, L.C., Barlow, J., 2018. Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170312. https://doi.org/10.1098/rstb.2017.0312.