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ABSTRACT

Background: Fire is known to affect forest biodiversity, carbon storage, and public health today; however, comparable fire histories from across forest regions in Amazonia are lacking. Consequently, the degree to which past fires could have preconditioned modern forest resilience to fire remains unknown.

Aim: We characterised the long-term (multi-millennial) fire history of forests in Amazonia to determine spatial and temporal differences in fire regimes.

Methods: We collated and standardised all available charcoal data extracted from continuously deposited lake sediments (n = 31) to reconstruct a ca. 10,000-year fire history for: (i) north and north-western, (ii) south-western, and (iii) eastern parts of Amazonia.

Results: Charcoal was found across Amazonia, but it was less abundant in the north and north-western regions. Regionally distinct periods of elevated charcoal deposition were identified at between ca. 4000 and 1500 (eastern), 3000–1000 (south-western) and 2500–2000 (north and north-western) years ago.

Conclusions: Forests in eastern and south-western Amazonia have been exposed to fire activity over recent millennia, while the forests in north and north-western Amazonia have grown under conditions largely free of fire activity. Consequently, we hypothesise that the forests in eastern and south-western Amazonia are preconditioned to be relatively more resilient to the threat of increased modern fire activity.

Introduction

Over the last decades fire has become increasingly widespread across many ecosystems in the Amazon basin (Barlow et al. 2020; Berenguer et al. 2021), threatening Earth's most diverse forests (Gentry 1988b; Bass et al. 2010) and the homes and health of ca. 17.5 million people (Smith et al. 2014; Machado-Silva et al. 2020; IBGE (Brazilian Institute of Geography and Statistics) 2019). Forests of the Amazon basin are particularly sensitive to fire impacts, and many plant species are not evolutionarily adapted to withstand recurrent fires (Uhl and Kauffman 1990; Cochrane and Schulze 1999; Barlow and Peres 2008). These forests are also one of Earth's largest carbon sinks (Pan et al. 2011), and Amazonian fires during recent decades have liberated large amounts of carbon into the atmosphere, elevating global atmospheric CO_2 concentrations (Neto et al. 2009; Aragão et al. 2018). The marked uptick in fires in Brazilian Amazonia (= Amazônia Legal, an administrative term in Portuguese, that includes some areas that fall outside of the Amazon basin) in 2019 and 2020 affected air quality as far as São Paulo (over 1000 km away) and were a direct consequence of relaxing the implementation of regulations on deforestation (Escobar 2019; Ferrante and Fearnside 2019). These data have heightened concern about the threat of fire to Amazonian ecosystems and public health (Borunda 2019); however, in the absence of a long-term record of fire history to reference these fires against it remains unclear if, and how far, the modern fires deviate from what forests have may have experienced in the past in the Amazon basin. Specifically, to anticipate the likely ecological impacts of these modern fires, it is important to view them in the context of spatial and temporal variation of fire activity in relation to tree generation time, i.e., centuries to millennia.

Almost all fires within the Amazon basin today are started by people and occur in the dry season, (e.g. Cochrane 2003; Malhi et al. 2014) and this was most often likely also the case in the past (Bush et al. 2008). Humans have been present and using fire in Amazonia for ca. 13,000 years (Roosevelt et al. 1996; Roosevelt 2013), and have been cultivating squashes and manioc since ca. 10,000 years ago and maize since ca. 6500 years ago (Bush et al. 1989; Brugger et al. 2016; Lombardo et al. 2020). Most cultivation in Amazonian forests before European contact (ca. AD 1541) was slash-and-burn (Arroyo-Kalin 2012). Primarily between 2500 and 500 years ago, the peoples of Amazonia formed anthropic soils with elevated soil fertility known as Amazonian Dark Earths (ADE) (Glaser and Woods 2004). As charcoal is a primary component of ADE, burning was required for their formation, although it should be noted that this burning could take place within the forest but was, not necessarily, of the forest

trees, i.e., likely included burning of organic waste or crops. Following European arrival, the human population within the Amazon basin is thought to have collapsed, from an estimated peak of between 5 and 10 million people (Denevan 2014; Koch et al. 2019), and modern (post-AD 1950) land-use practices with fire and machinery for forest clearance were introduced (Hecht 2013). Over recent decades, the expansion of road infrastructure has allowed the spread of deforestation for cultivation and ranching into remote regions (Cochrane and Laurance 2008; Ferrante and Fearnside 2019). The modern human expansion, coupled with recent droughts, has resulted in an increased incidence of fire within the Amazon basin (Silvestrini et al. 2011).

Biodiversity patterns within the Amazon basin are related to climatic gradients (precipitation, temperature), soils, and geology (Gentry 1988a; Ter Steege et al. 2006; Hoorn et al. 2010). The precipitation gradient and dry season length are particularly
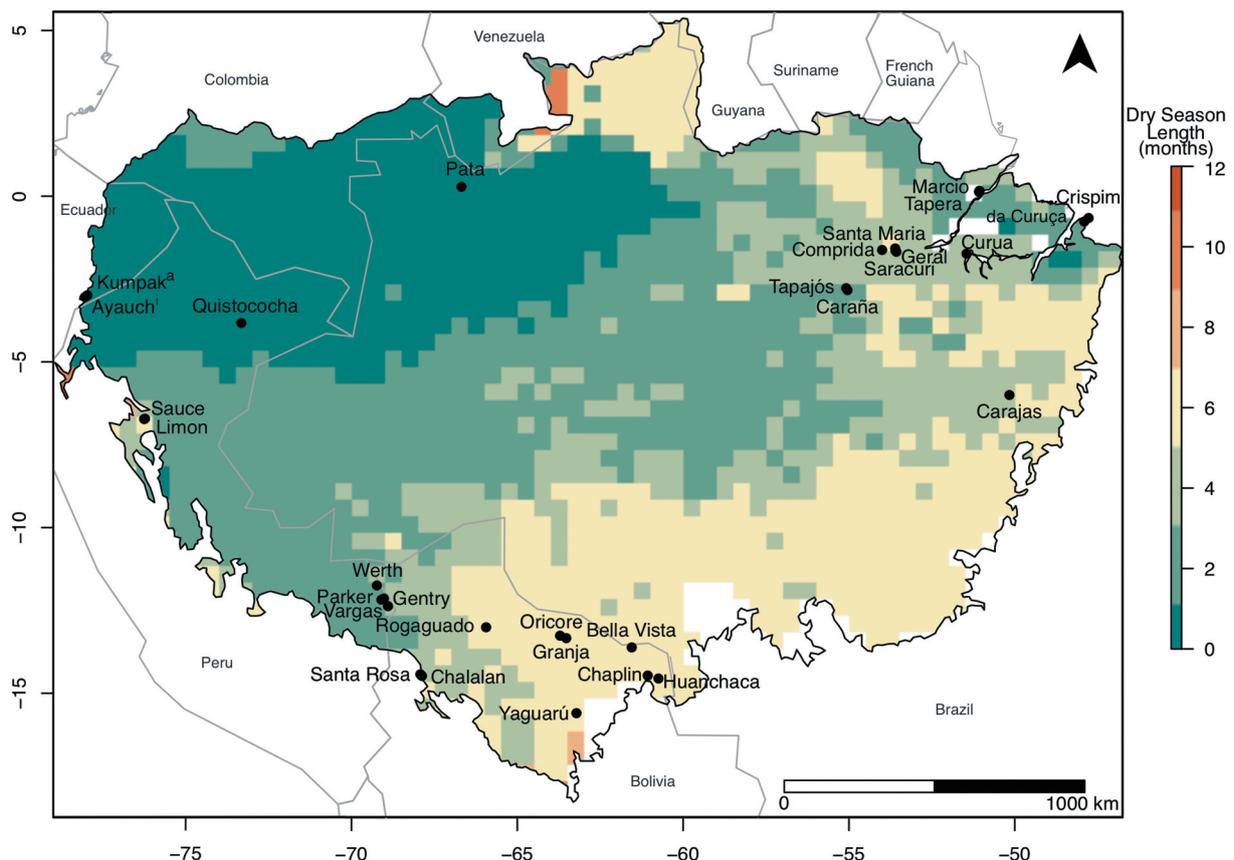
Figure 1. Locations of lake sediment records containing charcoal data within the Amazon basin *sensu stricto*, following (Eva et al. 2005). The sites containing charcoal data are shown in relation to dry season length; number of months receiving less than 100 mm precipitation (Berenguer et al. 2021). Study sites originally published by: Bush et al. (1989), Behling (2001), Behling and Lima Da Costa (2000) Bush et al. (2000) Bush et al. (2007), Bush et al. (2016), Irion et al. (2006), Maezumi et al. (2018b), Mayle et al. (2000), McMichael et al. (2012), Parsons et al. (2018), Urrego et al. (2013) Carson et al. (2014), Brugger et al. (2016), Taylor et al. (2010), Nascimento et al. (2019), De Toledo and Bush (2007), Maezumi et al. (2015), Cordeiro et al. (2008), Behling and Da Costa (2001), Kelly et al. (2018), Maezumi et al. (2018a).

important for determining forest vegetation type and its flammability (Clinebell et al. 1995; Ter Steege et al. 2006; Berenguer et al. 2021) (Figure 1). During the last 10,000 years precipitation across the Amazon basin has varied, notably between 7000 and 4000 cal yr BP the climate it is thought to have been generally drier than today (Wang et al. 2017; Mayle and Power 2008; van Breukelen et al. 2008; Bush et al. 2011). The Holocene changes in climate, and the modern climatic gradient across the Amazon basin, suggest that the probability of fire occurrence and spread has varied regionally through time. Here we collated and standardised charcoal evidence of pre-modern (before AD 1950) fire in Amazonian forests over the last 10,000 years to create regional fire histories for the Amazon basin. We asked how fire occurrence differed across regions and over time in the Amazon basin. We expected that the wetter forests of north and north-western Amazonia have experienced less fire over the past 10,000 years compared with forests in eastern and south-western Amazonia that contain a more pronounced dry season, despite regional variance in past human activity and climate. Moreover, we expected that dry periods (e.g., during the Holocene dry event; 7000–4000 years ago) had more fire than wetter periods. We assess these hypotheses of regional and temporal differences in fire regimes using 10,000 years of charcoal data.

Materials and methods

We obtained fire histories from charcoal particles extracted from lake sediments that had accumulated over the last ca. 10,000 years, and were recovered between 1989 and 2014 (Online Supplementary Data Sheet). The spatial distribution of lakes that provide Amazonian fire histories is limited (Figure 1) because of the rarity of suitable lakes for study, i.e., those containing stratigraphically intact sediments that span the last several thousand years. Despite the rarity of available lake sediment records, 31 records of pre-modern fire activity, based on charcoal material preserved within lake sediments, were available within the Amazon basin *sensu stricto* (Figure 1); defined as lowland tropical rainforests located at elevations less than 500 m above sea level and with drainage eventually flowing into the Amazon River (Eva et al. 2005). These 31 sites span the major moisture gradient and are geographically clustered into north and north-western Amazonia, south-western Amazonia, and eastern Amazonia (Figure 1).

Charcoal identified within lake sediments provides the most temporally continuous and intact archives of fire history (Whitlock and Larsen 2001). The charcoal data available from Amazonian forests were compiled from the Global Charcoal Database (www.palaeofire.org) and other published records (for references see Online Supplementary Data Sheet; Figure 1). Bringing together these charcoal records, which have been collected by researchers over the last ca. 30 years, poses two key challenges: (i) temporal integration (related to sampling effort and chronological control), and (ii) metric integration (related to the different approaches used to quantify the charcoal recovered).

Charcoal data recovered from the study sites were originally analysed at varying temporal resolutions due to differences in: (i) the sedimentation rates at the sites, (ii) the level of investigator effort available, and (iii) the objectives of the original study. The differences in sub-sampling mean that some records can have >100 samples while others only one sample within the same time window. To show these variations, we displayed the charcoal data with varying bar sizes to represent the time window represented by each sample (Figure 2).

The variety of methods used by different researchers to parameterise the abundance of charcoal within the sediments precludes direct quantitative comparison based on the raw datasets (see Online Supplementary Data Sheet for details). Broadly speaking the charcoal data recovered from the 31 lake sediment cores can be classified into two broad groups: (i) macro-charcoal (particles >160 μm), and (ii) micro-charcoal (particles <160 μm) (Whitlock and Larsen 2001). These differences between datasets require that all be standardised to the same scale (Marlon et al. 2016). We used proportional relative scaling to document the relative shifts within each charcoal dataset, and compare these relative shifts across sites (McMichael et al. 2021a). Proportional relative scaling standardises the charcoal measurements from each lake sediment to a scale of 0 to 100; however, importantly this approach retains the 0 value to represent the absence of fire, and scales the maximum value relative to the number of samples containing charcoal within the sequence, and so avoids rare charcoal finds events in largely charcoal free sediments being upweighted. Consequently, this approach allows differences between datasets caused by factors such as laboratory procedure, catchment size, and sediment properties to be better compared (McMichael et al. 2021a). After scaling each charcoal

record, we constructed a composite fire record over the last 10,000 years for the lake sediment records in north and north-western Amazonia (n = 6), south-western Amazonia (n = 13), and eastern Amazonia (n = 12). The composite was created using 500-yr time intervals to account for various levels of temporal uncertainty (related to sampling resolution and/or age control) within the lake sediment records, which results from different numbers of ^{14}C dates used to build the chronology or differences in sampling frequency between sites. We tested the statistical difference between the charcoal data of the three regions within each time interval using a one-way ANOVA with a minimum of three sites per group. We used an unbalanced Tukey test if the ANOVA indicated significant differences (Sokal 1995).

Results

The north and north-western Amazonian sites yielded lower overall relative abundances of charcoal during the last c. 10,000 years in comparison with the south-western and eastern sites (Figures 2–3);
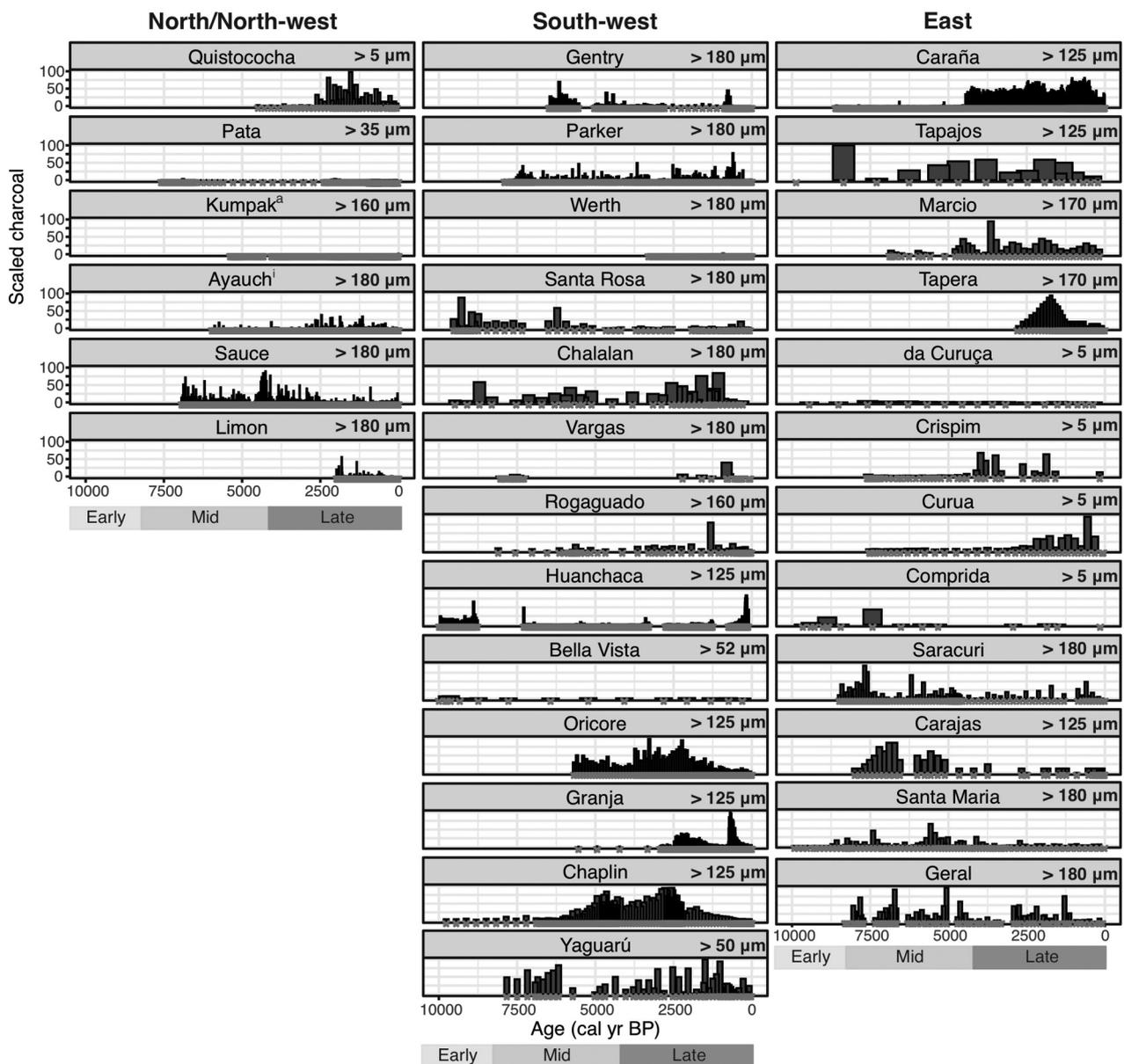
Figure 2. Charcoal data obtained from lake sediments from across the Amazon basin grouped by geographic region (Figure 1) and ordered top to bottom by dry season length (short to long). Width of bars indicates the temporal sampling resolution of each record. Grey X's indicate samples analysed, i.e., grey X but no bar indicates no charcoal was found in the sample, no grey X indicates no sample examined/available. Size of charcoal fraction examined in each record indicated in microns (μm). Further, information on the type of charcoal data and the age vs. depth control can be found in the Online Supplementary Data Sheet. Early, Mid and Late notations below the time axis indicate the divisions of the Holocene following Walker et al. (2019).

notwithstanding the differences in the number of sites among the regions. In the everwet forests of north and north-western Amazonia (dry season length 0 months, except Sauce and Limon which is 5 months; Figure 1), two sites showed a near absence of charcoal in the past (Kumpak[a] and Pata) (Figure 2). The remaining sites had similar trends in their fire histories. Lake Ayauch[i] contained an increase in charcoal abundance between c. 3000 and c. 500 cal yr BP, and Quistococha ('-cocha' = lake) charcoal abundance peaked in between c. 2000 and c. 550 cal yr BP. Lake Sauce was the exception, containing relatively higher abundances of charcoal between c. 7000–2500 cal yr BP (Figure 2). The regional composite of fire history for the northern and north-western region showed the highest fire occurrence between c. 2500–2000 cal yr BP (Figure 3).

The south-western region of Amazonia contains sites from across a sharp gradient in seasonal precipitation (dry season length 3–7 months), but with those sites closer to the eastern Andean flank having less seasonal variation in rainfall (Figure 1). Lake Werth had a general lack of charcoal (Figure 2). The timing of relatively higher charcoal abundances within the records in south-western Amazonia fell into four time periods: (i) early Holocene (ca. 10,000–7000 cal yr BP) at Huanchaca, Santa Rosa, and Yaguaru, (ii) mid Holocene (ca. 7000–2000 cal yr BP) at Chaplin and Oricore, (iii) late Holocene
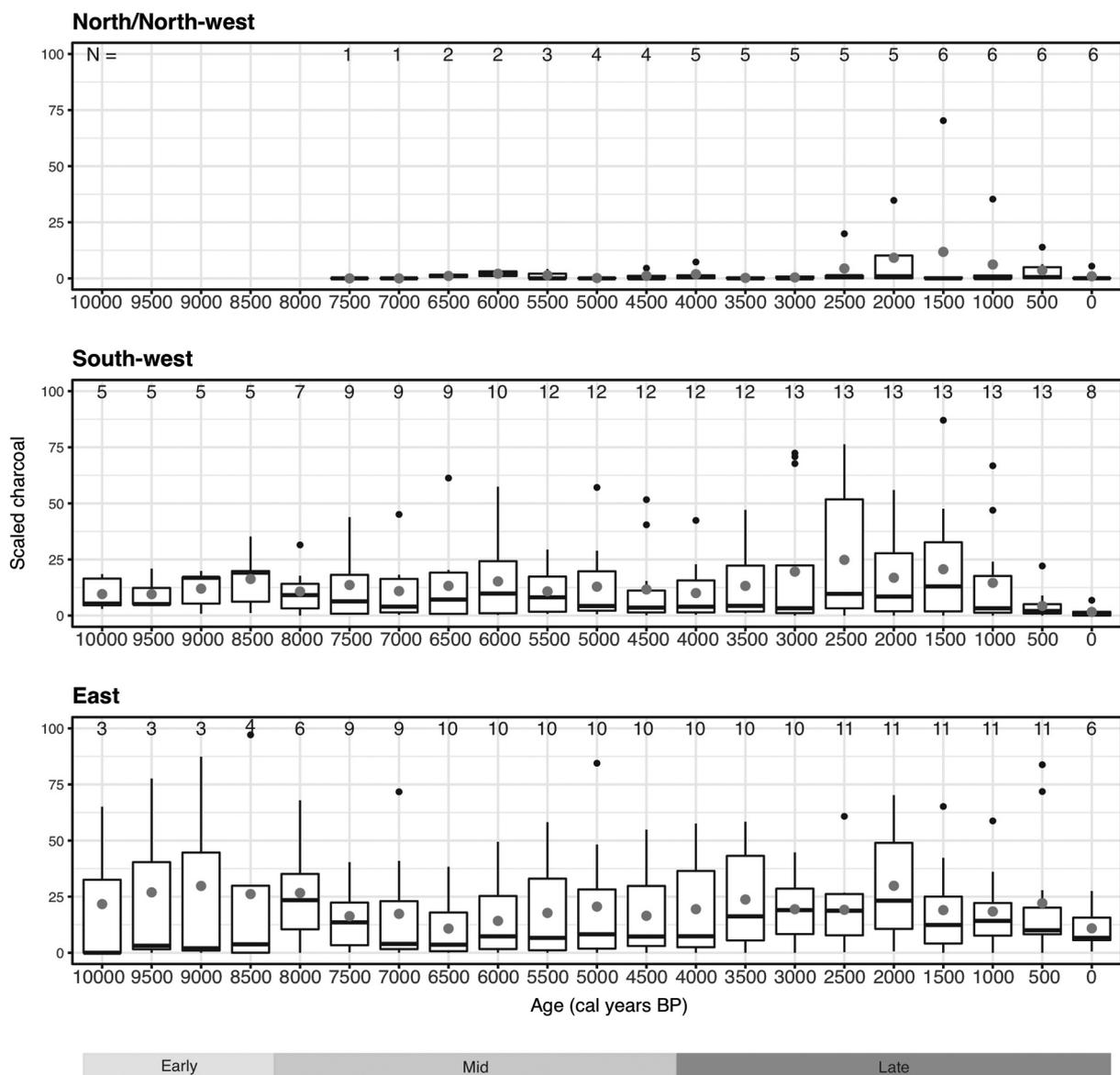
Figure 3. Composite fire histories for the north and north-western, south-western, and eastern Amazon Basin. Boxplots (quartiles; thick horizontal black bar, median; grey dot, mean; black dot, outliers) show the variation of charcoal abundance within 500-year time windows, and the number of records is shown above each time bin. Number of records available for each time bin indicated at the top of each panel (N =). See Figure 2 for the scaled charcoal data from individual sites within each region. Early, Mid and Late notations below the time axis indicate the divisions of the Holocene following Walker et al. (2019).

(2500–1000 cal yr BP) at Chalalan, Granja, Parker and Yaguaru, and (iv) ca. 500 cal yr BP at Huanchaca (Figure 2). The regional composite indicated the highest overall abundance of fires between c. 3500–1000 cal yr BP, with a notable decline after 1000 cal yr BP in the south-west and eastern regions (Figure 3).

The eastern region of Amazonia is seasonally dry today (dry season length 3–5 months; Figure 1) and the lake sediment records contained higher abundances of charcoal compared with other regions (Figures 2–3). Curua was the only lake that had relatively low abundances of charcoal in this region. The highest abundances of charcoal were found in the early Holocene (ca. 10,000–7000 cal yr BP) at Carajas, Comprida, Geral, Saracuri and Tapajos, during the mid and late Holocene (7000–1000 cal yr BP) at Caranã, Crispim, Tapera, and Marcio (Figure 2). The regional composite record for eastern Amazonia indicated that fires in the past were most common in this region between ca. 3500–1000 cal yr BP, and also in the early Holocene prior to 8000 years ago (Figure 3), though note that the number of records for this period was low.

Statistical analyses of the differences in the charcoal data between the time windows within each region (unbalanced Tukey test; Online Supplementary Data Sheet) resulted only the most recent time window (499–0 years ago) to be significantly different.

Discussion

We compiled regional fire histories for the Holocene across 31 sites in the Amazon basin using charcoal datasets covering the last 10,000 years before present to assess variation in fire occurrence across time and regions. The number of datasets currently available (n = 31), and spatial biases in distribution, mean that these data should not be viewed as providing a complete representation of past fire across the Amazon basin; however, the data that are available do span important climatic and environmental gradients and therefore allow us to decern major trends in the fire histories. Specifically, the available data that fell into three broad geographic regions (north/north-western, south-western, and eastern) and spanned the precipitation gradient across the Amazon basin. These datasets reveal both intra- and inter-regional variability in the fire histories of the forests in the Amazon basin.

Interpretation of charcoal recovered from lake sediments

Our compilation of charcoal from lake sediments combines charcoal abundance data that have been compiled using multiple methodologies and over many years. The principal difference in these methodological approaches is the parameterisation of abundance of either macroscopic (>160 μm) or microscopic (<160 μm) charcoal fragments. Macro- and micro-charcoal particles have different dispersal characteristics; larger particles generally travel smaller distances (Palmer and Northcutt 1975; Whitlock and Larsen 2001). Macro-charcoal particles can travel up to ca. 10 km when significant updraughts are generated from large fires (Whitlock and Larsen 2001), but if the fires burn at a low intensity, this charcoal fraction probably reflects within-catchment deposition (Clark and Royall 1996). Regional fire activity can be represented by micro-charcoal particles that can travel tens or hundreds of kilometres (Palmer and Northcutt 1975). Almost all studies on charcoal deposition and dispersal, however, have been derived from temperate forests, mountainous regions, or savanna regions (e.g. (Palmer and Northcutt 1975; Clark 1988; Ohlson and Tryterud 2000; Whitlock and Larsen 2001; Tinner et al. 2006; Duffin et al. 2008; Leys et al. 2015, 2017). These settings are all quite different from tropical evergreen lowland rain forests, which have a thick tree canopy, high tree density, relatively little wind, and occur on flat or undulating terrain (Kricher 2011). Due to these structural and topographic characteristics in the Amazon basin we anticipate that macro-charcoal and micro-charcoal particles travel smaller distances than reported for other regions (i.e., less than 10 km from the lake where they are deposited). However, the dispersal characteristics of charcoal from any given fire are dependent on weather conditions at the time of the event (e.g., wind speed and direction), the geographic configuration of the depositional environment at that time (e.g., inflows to or outflows from the lake), and the type of fire (e.g., forest vs. non-forest fires). Given the range of different methodological approaches, geographic variation, and environmental variation among sites, it is impossible to precisely quantify the source area of the charcoal entering each lake. Though it seems that most of the charcoal, either micro- or macro-, entering a lake within an Amazon rainforest environment is likely predominantly derived from within a 10-km radius because of the strong influence of the local

vegetation structure. Thus, we consider the datasets compiled in this study comparable for the purpose of interpreting the fire history of Amazonia.

Amazonian fire histories

A striking pattern in the charcoal dataset is the high variability at the sub-regional (landscape) scale. For example, in south-western Amazonia, lakes Bella Vista, Chaplin and Huanchaca are all located within ca. 100 km of each other but indicate highly contrasting fire histories. Bella Vista (evergreen forest) contains almost no charcoal, Chaplin (evergreen forest) has charcoal peaks in the mid-Holocene, and the highest abundances of charcoal at Huanchaca (palm forest within Cerrãdao/savannah woodland) occurs in the early Holocene and ca. 500 cal yr BP. The same pattern of contrasting sub-regional fire histories is also evident in the forested regions of south-western Amazonia at Lakes Gentry, Parker, Vargas, and Werth, which all lie within 100 km of each other (Bush et al. 2008, 2011). In this region, combined charcoal and vegetation histories indicate that the areas surrounding Lake Gentry were the likely settlement hub in the pre-Columbian era, though forests around Parker were also burned. There was a near-absence of fire at Vargas and Werth. Similar variability is also found when assessing the fire and vegetation histories of Lakes Geral, Saracuri, and Santa Maria in the eastern Amazon (Bush et al. 2007a). Lake Geral was the most heavily used site; evidence of forest burning was lower and maize cultivation was absent at the other lakes (Bush et al. 2007). Sub-regional variability in fire histories can even be seen in the wettest forests of north-western Amazonia. Lakes Ayauch[i] and Kumpak[a] are located within 30 km of each other and have completely contrasting fire and vegetation histories. Lake Ayauch[i] has a ca. 6500-year history of fire and cultivation (Bush et al. 1989), whereas Kumpak[a] was primarily fire-free with brief periods of pre-Columbian maize cultivation (Akesson 2019). This indicates that differences in fire histories may be more strongly determined by local scale differences in human presence than by regional-scale differences in climate.

If climate were driving the overall trend in fires within our regions (for example by changing the frequency of lightning ignition, or flammability through drying) we would anticipate a consistent trend within each region. We therefore interpret the high variability of charcoal data from within all three as indicating that humans were required, and

responsible, for the ignition in Amazonian forests fires through the Holocene. Charcoal was mostly absent from at least one lake sediment record in each region. These data support previous ideas that fire rarely occurs without human ignition in the aseasonal wetter north and north-western forests, and occurs with much higher frequency in the drier forests and savannas, such as in south-western and eastern Amazonia, when humans are present in the landscape (Ramos-Neto and Pivello 2000; Bush et al. 2008). However, the strong link between people and fire in Amazonian forests coupled with the presence of charcoal, even in relatively low amounts, in most of the 31 lake sediment records during much of the last 10,000 years leads us to infer that that people were present at these sites, supporting previous findings (Bush and Silman 2007; Bush et al. 2008; Mayle and Power 2008; McMichael and Bush 2019). The patterns of charcoal abundances documented within a single lake, and in lakes within the same region, show that biomass burning has increased and decreased over the last 10,000 years irrespective of climate change, and did not increase linearly or exponentially in the late-Holocene with expanding human populations (Goldberg et al. 2016).

The absence of clear trends among sites of a given region explains the lack of statistically significant differences between time windows within each region, i.e. for all time periods every region has site with/without fire. The lack of an overarching trend also suggests that climatic drying was not the dominant control on fire, although climate changes may have enhanced fire activity around particularly sensitive sites. For example, there is no consistent increase in fire activity related to generally drier conditions in Amazonia between 7000 and 4000 cal yr BP (mid-Holocene dry event).

Though charcoal peaks did not occur synchronously within regions, several patterns of regional fire emerge from the dataset. A main difference is the low levels of past fire in north and north-western Amazon basin compared with the south-western and eastern regions. The available data for north and north-western Amazonia only span the last 7500 years, and so unfortunately the rarity of fire cannot be assessed for the early Holocene, which was a particularly dry period in the region (van Breukelen et al. 2008). Charcoal records from the mid-elevation (1000–3000 m above sea level) Andean forests adjacent to north-western Amazonia show that fire was

nearly absent during the early Holocene at some sites (McMichael et al. 2021b) but present at others during the late glacial period (Montoya et al. 2018).

Several lake sediment records from the south-western and eastern Amazon basin extended into the early Holocene, and show that charcoal was present and abundances were increasing through time. These data agree with previous archaeological findings (Glaser and Woods 2004). The earliest evidence of people in Amazonia is over 10,000 years old and has been found in the south-western (Capriles et al. 2019; Lombardo et al. 2020) and eastern regions (Roosevelt 1991; Roosevelt et al. 1996). Further, the majority of archaeological sites found in the early Holocene tended to be located in the seasonal forests near the savannas (southern and south-western Amazonia) or along the main Amazon river channel in eastern Amazonia (McMichael and Bush 2019; Iriarte et al. 2020).

Across all regions, fire activity increased between ca. 2500 and 2000 cal yr BP, though this time window extends from ca. 3500–1000 cal yr BP in the south-western and eastern regions. The highest prevalence of fire across the Amazon basin appears to be coincident with the rise in the formation of anthropic soil types called Amazonian Dark Earths (ADE) around 2000 cal yr BP (Glaser and Woods 2004). ADE were created by adding charcoal to the soils, along with organic waste and pottery shards (Glaser and Woods 2004; Woods et al. 2009). ADE contain increased nutrient levels compared with typical Amazonian oxisols or latosols, making them more suitable for cultivation (Arroyo-Kalin 2012). ADE are most commonly found in eastern and central Amazonia, suggesting that the use of fire in these forests has been more frequent than in areas that tend to lack ADE, such as north and north-western Amazonia (McMichael et al. 2014). The increases in ADE frequency and increases in charcoal found in our lake sediment records in south-western and eastern Amazonia during the period of 2500–500 cal yr BP also correspond with increases in the frequency of macro- and micro-botanical evidence of cultivation across the basin (Piperno 2011), suggesting that expanding human populations introduced fire into more Amazonian forests at this time.

The fire histories across the 31 sites show a generally lower prevalence during the last ca. 1000 years. Although the low temporal resolution of the time intervals used does not allow details to be discerned, this broadly support the idea that pre-Columbian land use was changing, and perhaps population densities were decreasing, centuries before the arrival of Europeans. Densities of ^{14}C dated material from archaeological sites begin to decrease in frequency around 800 cal yr BP (Arroyo-Kalin 2012; McMichael and Bush 2019; Riris 2020), suggesting that many of the known sites were abandoned ca. 300 years before the European colonisation that began c. AD 1600 (Bush et al. 2021). Recent syntheses of pollen and charcoal data from a subset of the lakes (n = 9) analysed by Bush et al. (2001) revealed that the decrease in charcoal found around AD 950–1350 (600–300 years ago) was coincident with signals of site abandonment and reforestation that were larger in magnitude than those associated with European colonisation. The causes for the abandonment of sites and reforestation remain unknown.

An alternative explanation for the declining fire activity after 2000 yr BP is the shift from initial clearance of old-growth forest to the clearance of agricultural lands and young secondary forests. An observation from fire histories in western Amazonian lakes was that the first inferred wave of forest clearance and modification produced far more charcoal than subsequent management of cultivated lands (Bush et al. 2017). The very early fire in eastern Amazonia at 10,000–9000 cal BP is heavily influenced by charcoal found at Lake Comprida. An increase in fire activity occurs in all regions in either the 2500 or 2000 cal BP time windows which aligns with an increase in the formation of ADE (Neves et al. 2004), and a well-established spread of regional cultivational activity (e.g., Roosevelt 2013). The decline in charcoal occurrence thereafter does not necessarily indicate a declining population, but it does suggest a slowing of initial forest clearance and/or a shift in the type of material being burnt. Even if slowing, the trend towards forest clearance being more widespread than forest recovery continued until c. 1000 cal BP (Bush et al. 2021). We do not consider it likely that this slowing was due to all old-growth forests already being cleared as so many of the lake catchments show modest or intermittent exploitation. Rather, it may be that improved cultivational practices, intensified use of agricultural land, an adoption of agroforestry, and/or a shift to

using the forest as a resource rather than something to be cleared (Balée 1989; de Souza et al. 2019; Iriarte et al. 2020) were factors slowing deforestation.

The relevance of regional Holocene fire histories to modern Amazonian vegetation

The fire histories presented here show a long-term differences in fire frequency in the south-western and eastern regions of Amazonia compared with those in the north and north-west. This long-term difference in fire activity driven by human activity along the precipitation gradient is likely responsible for some of the inter-regional variability seen in modern ecological surveys. For example, Amazonian (and many rainforest) plant species are typically not evolutionarily adapted to fire because of its rarity on geological timescales (Uhl and Kauffman 1990). On timescales relevant to tree life cycles and generations the introduction of fire can cause significant species turnover, and repeated fire can result in a less diverse and more fire tolerant plant community through modification of the seed bank (Barlow and Peres 2008; Barlow et al. 2020). Indeed, within a time record of 7,000 years in the Peruvian Amazon, periods of high fire activity led to increased abundance of fire-avoiding and fire-tolerant species (e.g., that are taller and have larger seeds) (van der Sande et al. 2019). The lower prevalence of fire activity in the northern and north-western region also correlates with the relatively thinner bark (Staver et al. 2009), as species with thin bark are more susceptible to fire damage (Rosell 2016). The relatively higher abundance of thin barked tree species in northern and north-western Amazonia supports the idea that these forests contain fewer, and less abundant, fire tolerant species than other regions. Consequently, we anticipate that the plant species in the north and north-western region are more fire-sensitive and are likely the most vulnerable to change from the introduction of fire by humans relative to other regions of Amazonia (Bush and Lovejoy 2007). Hence, we hypothesise that the lower long-term prevalence of past fire in the northern and north-western regions is positively correlated with the presence of less fire tolerant species, and a relatively higher tree species diversity (Bass et al. 2010; Gentry 1988a; Pan et al. 2011).

In the south-western and eastern regions fire has been introduced, or enhanced, through a long history of human landscape management if inferred from the relatively higher abundance of charcoal. Modern

ecological studies have shown that fire events can act as a selective pressure on plant trait composition in Amazonian forests, e.g. central Amazonia (Barlow et al. 2003) and southern Amazonia (Brando et al. 2012). Therefore, the pre-modern fire history of south-western and eastern Amazonia likely means that the plants that in the previously occupied areas of these regions today already have some adaption to cope with fires, i.e. some selection and turnover has already occurred when the fires were first introduced. However, even in the regions that were relatively more densely occupied in the pre-Columbian era based on the archaeological findings (Denevan 2014) we infer, from the absence of charcoal in parts of the sediment record from some lakes, that not all sites may have been occupied all the time. The absence, infrequent occurrence, and/or low abundance of charcoal in many sites across the Amazon basin, and within the northern and north-western region in particular, leads us to suggest that fires were scarce in the past. The implication of this being that introducing fire, or increasing its frequency and intensity, in modern times will likely to cause strong shifts in species composition and biodiversity in many places. Potentially including a loss of beta diversity due to landscape homogenisation (Solar et al. 2015), and an increase of biogeographic barriers due to landscape fragmentation (Bush et al. 2008).

Most of the charcoal records in the Amazon basin contain relatively low sampling frequency and consequently low temporal resolution over the recent centuries (Bush et al. 2021); charcoal samples per site for the last ca. 100 years (since AD 1850) range from 0 (Chalalan, Huanchaca, Tapajos) up to 44 (Kumpak[a]), with a mode of 1 when all 31 sites are considered. This makes it hard to directly link past fire histories with modern fire regimes or modern forest composition and structure using currently available datasets. The ecological importance of fire in the forests of the Amazon basin is well-documented, and integrating the effect of long-term fire trajectories with observed ecological parameters will require more emphasis on obtaining well-dated sediments and increasing effort in reconstructing decadal-scale fire patterns over the last 2000 years. Generating high-resolution fire records particularly over the last c. 300 years would also allow direct comparisons with historical documents, as has been demonstrated in Mauritius (Gosling et al. 2017) and on the eastern Andean flank (Loughlin et al. 2018).

Conclusions

We assessed 10,000 years of fire history for 31 sites across the Amazon basin and found that although fire was found across the basin, it was more prevalent in the south-western and eastern regions compared with the northern and north-western region. The observed variation likely relates to the relatively wetter climate and shorter/absent dry season in the north and north-western region. Notwithstanding the inter-regional differences, we found the variation among sites within different regions was large. This intra-regional variation was likely driven by differences in human presence and activity. The relative scarcity of exposure to fire of forests in north and north-western Amazonia over the generation time of the trees suggests that these forests are likely the most vulnerable to modern introduction and increase of fire activity by people.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data and Materials Availability

We acknowledge the use of charcoal data obtained from the Global PaleoFire Database (https://paleofire.org). All data are available in the Online Supplementary Data Sheet at: www.doi.org/10.6084/m9.figshare.14890851 (Gosling et al. 2021). The authors declare no competing interests.

Author contributions

WDG, CNHM and SYM conceived the ideas; all authors compiled data; BH, SYM and CNHM generated figures; WDG and CNHM wrote the draft manuscript, and all authors contributed to editing it.

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