

Invited review

Tropical peatlands in the anthropocene: Lessons from the past



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ABSTRACT

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The status of tropical peatlands, one of Earth's most efficient natural carbon stores, is of increasing international concern as they experience rising threat from deforestation and drainage. Peatlands form over thousands of years, where waterlogged conditions result in accumulation of organic matter. Vast areas of Southeast Asian peatlands have been impacted by land use change and fires, whilst lowland tropical peatlands of Central Africa and South America remain largely hydrologically intact. To predict accurately how these peatlands may respond to potential future disturbances, an understanding of their long-term history is necessary. This paper reviews the palaeoecological literature on tropical peatlands of Southeast Asia, Central Africa and South America. It addresses the following questions: (i) what were the past ecological dynamics of peatlands before human activity?; (ii) how did they respond to anthropogenic and natural disturbances through the palaeoanthropocene, the period from whence evidence for human presence first appeared?; and, (iii) given their past ecological resilience and current exposure to accelerating human impacts, how might the peatlands respond to drivers of change prevalent in the anthropocene? Through synthesis of palaeoecological records, this review demonstrates how tropical peatland ecosystems have responded dynamically, persisting through fire (both natural and anthropogenic), climatic and human-induced disturbances in the palaeoanthropocene. Ecosystem resilience does, however, appear to be compromised in the past c. 200 years in Southeast Asian peatlands, faced with transformative anthropogenic impacts. In combination, this review's findings present a pantropical perspective on peatland ecosystem dynamics, providing useful insights for informing conservation and more responsible management.

1. Introduction

Tropical peatlands play a major role in the global carbon cycle (Sjögersten et al., 2014). Containing approximately 152 – 288 billion tonnes of carbon (Ribeiro et al., 2021), they represent one of Earth's most efficient terrestrial carbon stores, illustrated by their capacity to contain up to c. 20 times more carbon per hectare than tropical forest (Murdijarso et al., 2019; Saatchi et al., 2011). When hydrologically intact, waterlogged conditions create an anaerobic environment which, along with high acidity and low nutrient content, slow the rate of

organic matter decomposition, leading to the accumulation of peat, a carbon-rich soil (Page and Baird, 2016). Within the last decade, investment in mapping and modelling the carbon dynamics and distribution (Lawson et al., 2015) has increased across the c. 58.7 Mha of peatlands between c. 23.5°N and 23.5°S (modelled by Leifeld and Menichetti, 2018). Research has focused on the three largest tropical areas: Southeast Asia (Koh et al., 2011; Miettinen et al., 2016; Wijedasa et al., 2018); Africa's Central Congo Basin (Dargie et al., 2017); and western Amazonia in South America (Draper et al., 2014) (Fig. 1).

Lowland tropical peatlands are generally covered in dense swamp

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forest, providing habitats for a diversity of plants and animals, many of which are adapted to the low-nutrient, waterlogged conditions (Draper et al., 2018; Posa et al., 2011). They also provide a range of tangible and intangible services to people: fishing grounds (Thornton et al., 2018), water for agriculture and human consumption throughout drier seasons, a range of timber and non-timber forest products (NTFPs) (Posa et al., 2011), and as spaces of cultural significance for local communities (e.g., Schulz et al., 2019a; Thornton et al., 2020).

Over the last half century, the services people have sought from these ecosystems have changed, most notably in Indonesia and Malaysia. In these vast areas of tropical peat swamps, deforestation, drainage, and conversion into commercial plantations have occurred, commonly oil palm and wood pulp for paper production (Koh et al., 2011; Miettinen et al., 2016). This conversion has turned the peatland carbon sink into a huge carbon source (Leifeld and Menichetti, 2018). The transformation of landscapes, from being shaped predominantly by natural processes to anthropogenic drivers, is one of the key indicators used to define the existence and onset of the “Anthropocene” (Corlett, 2015; Ellis et al., 2010; Lewis and Maslin, 2015; Smith and Zeder, 2013), with associated debates on how to manage the emerging novel ecosystems (Clement and Standish, 2018; Folke et al., 2021; Hobbs et al., 2014). To contextualise contemporary changes, understanding how human interactions with these ecosystems have unravelled in the past is important.

For the purpose of this review, the “anthropocene” refers to the last c. 200 years, encompassing the period since the first evidence of transformative human impacts on tropical peatlands. This evidence is from Southeast Asian peatlands (e.g., Cole et al., 2015), where observations at c. 200 years ago noted reductions in typical intact peatland vegetation indicating the compromise of ecosystem resilience by human activity. Analysing human-peatland interaction before and after this point allows exploration of the real and potential impact of people. Patterns of anthropogenic transformative change across tropical peatlands has, however, as in tropical forests (Roberts et al., 2018), occurred at different times in different places. Central African and Amazonian peatlands have not experienced impacts in the same forms or scales as those in Southeast Asia over the last 200 years (Lilleskov et al., 2019). Analysis of these largely intact tropical peatlands provides insights into the non-transformative human interactions with peatlands that are possible (Roberts et al., 2018). In this paper, we contextualise the large-scale, transformative human-peatland interactions of the last 200 years by reviewing and synthesizing the palaeoecological evidence for long-term peatland dynamics and resilience in the face of past human and non-human perturbations. A corresponding paper in progress by Girkin et al. outlines the present and likely future human interactions with peatlands.

2. Palaeoecological insights into the palaeoanthropocene

Palaeoecology is important for understanding contemporary ecological dynamics, exploring ecosystem resilience (e.g., Cole et al., 2014; Davies et al., 2018; Willis et al., 2010) and predicting environmental changes (e.g., Froyd and Willis, 2008; Githumbi et al., 2020; Seddon et al., 2014). It uses a variety of evidence preserved in sediments, for example fossil pollen, to understand past interactions between plants, animals, people and climate (Bennett and Willis, 2001; Birks, 2008). In the wet tropics, where vegetation does not easily burn unaided, fossil charcoal, an important proxy for fire (Whitlock and Larsen, 2002), is used to indicate human activity. Cole et al. (2019) measured various palaeoecological proxies to explore human interaction with tropical peatlands in the Late Holocene, from c. 5,000 Cal. yr BP (Fig. 2). Their record is interpreted to encompass the palaeoanthropocene (open vegetation, a proxy for human-induced deforestation, extends into the deeper past, c. 2500 Cal. yr BP; e.g., Foley et al., 2013) and the more recent anthropocene *sensu lato* (open vegetation, microcharcoal and macrocharcoal concentrations increase, coincident with a decline in peat swamp forest vegetation, from c. 200 Cal. yr BP).

Palaeoecology can be deployed to investigate the local environmental changes that typify the ‘palaeoanthropocene’ (Foley et al., 2013). The palaeoanthropocene defines the interval of Earth’s history when human activities left a mark on the environment, demonstrated in archaeological and palaeoecological records (Streeter et al., 2015), but likely did not contribute to large-scale reorganisations of Earth’s systems, as in the anthropocene. As a “transitional period”, the palaeoanthropocene exhibits asynchronous local manifestations not anchored to the geological timescale in any universal way (Foley et al., 2013). The Holocene series/epoch, in contrast, has an accepted formal definition and date for the base/start – the period from 11,700 years ago up to and including the present day (Walker et al., 2009). The central idea of the palaeoanthropocene is that humans have influenced the dynamics of Earth’s system to some extent throughout prehistory; they are a part of nature and not apart from it.

This review adopts the palaeoanthropocene, i.e., prior to c. 200 years ago, as a conceptual and temporal framing to explore the spatially asynchronous and idiosyncratic human-peatland interactions in lowland tropical latitudes. Insights from palaeoecological records inform understanding of how these ecosystems could respond to larger-scale, more intensive environmental and climatic perturbations of the anthropocene. This review focuses on the three largest areas of tropical peatlands: Southeast Asia, the Central Congo Basin and Amazonia, with the most published research on palaeoecology and early human-peatland interactions (albeit still limited for the latter two regions). Although studies of peat-forming environments exist elsewhere in tropical

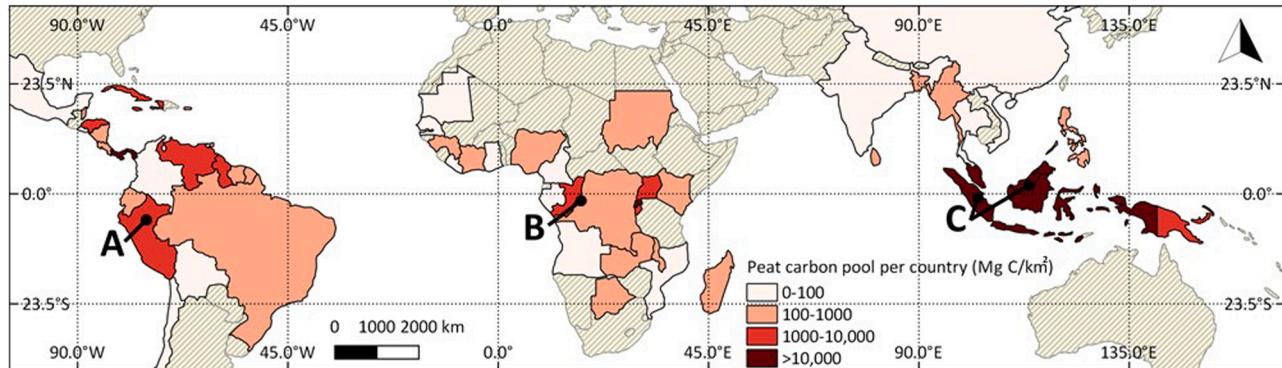


Fig. 1. Estimated peat carbon density (in $\text{Mg C}/\text{km}^2$) for countries in the tropical latitudes for which data exist (grey dashed represents a lack of data). The three main regions of tropical peatlands discussed herein are labelled: A – Amazonia (Peru); B – Central Congo Basin (Democratic Republic of Congo, Republic of Congo); C – Southeast Asia (pointer indicating Sumatra, Indonesia, and Sarawak, Malaysian Borneo).

Data was sourced from Dargie et al. (2017) and Page et al. (2011).

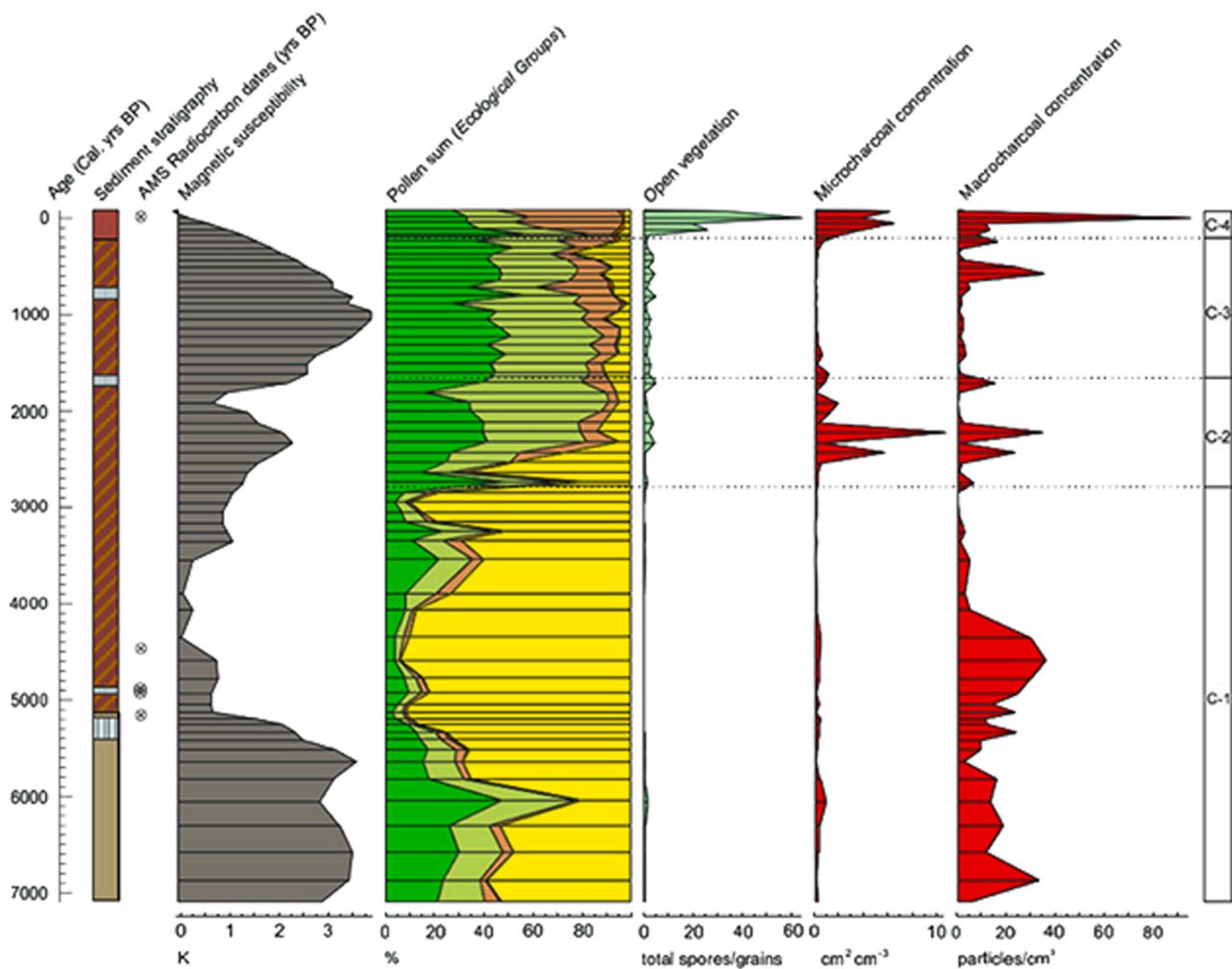


Fig. 2. Results from a palaeoecological study on a peat core from Sarawak, Malaysian Borneo, showing sediment stratigraphy, magnetic susceptibility (grey), pollen sum for five ecological groups (peat swamp forest taxa - green; peat swamp forest pioneer taxa - pale green; degraded peatland taxa – brown; non-peatland/other forest taxa – orange; and, coastal vegetation – yellow; open vegetation – aquamarine, and microcharcoal and macrocharcoal – red. Significant pollen zones are shown for each (labelled C-). Cal. yr(s) BP refers to calendar years before present (i.e., 1950 (Hajdas, 2008)). (For further details, see Cole et al., 2019).

latitudes (including coastal Venezuela and Panama (Phillips et al., 1997), montane Peru (Cooper et al., 2019; Fonkén, 2014) and East Africa (e.g., Mumbi et al., 2014), and across central Africa (e.g., Langan et al., 2019)) few have explored patterns of prehistoric human interaction with these ecosystems (Page and Baird, 2016). This review addresses three questions: (i) what were the past ecological dynamics of the peatlands of lowland Southeast Asia, the Central Congo Basin and Amazonia prior to human activity; (ii) how have they responded to disturbances, both anthropogenic and natural, over time; and, (iii) given their ecological resilience, how might they respond to the drivers of change prevalent in the last c. 200 years? The three broad categories of disturbance emphasized are fire (both natural and anthropogenic), climatic change and other human impacts for which evidence exists in palaeoecological and palaeoenvironmental records. We synthesize the similarities and differences in exposure and responses to disturbance between the three regions. We conclude by identifying future research needs for understanding and enhancing the persistence of these ecosystems.

2.1. Tracing the palaeoanthropocene in tropical peatlands

Despite the paucity of studies exploring past human-peatland interactions in the Central Congo Basin and Amazonia compared to Southeast Asia, this review covers all three regions to develop a pan-

tropical synthesis of peatland ecosystem dynamics and resilience. Table 1 summarises the principle physical, ecological and anthropogenic characteristics of each region.

2.2. Southeast Asia

Indonesia, Malaysia and Papua New Guinea harbour the largest peatland area of Southeast Asia, at 20.6, 2.6 and 1 Mha, respectively (Page et al., 2011). Peatlands in Brunei, Singapore, the Philippines, Vietnam and Thailand together host the remaining 1% (Page et al., 2011). The average peat thickness ranges from 0.5 m (Susanto et al., 2018) to 7 m (Page et al., 2011), but in Indonesia and Malaysia, thicknesses of up to 20 m have been reported (Page et al., 2011; Ruwaimana et al., 2020). Carbon storage in peatlands across Southeast Asia is estimated at 68.5 Pg C (Page et al., 2011b), although estimates vary according to the methods used (Warren et al., 2017). They typically developed in regions where the wet season lasts for nine to ten months and the mean annual precipitation is ≥ 2500 mm (Riley and Page, 2016). Most peat-forming ecosystems in the region are forested, ranging from freshwater swamp forests (Fig. 3A), dominated by *Shorea* spp. and other Dipterocarps, to the communities of stunted trees typical of environments with lower nutrient status and thicker peat, found at the centre of peat domes (Anderson, 1964).

Table 1

Summary characteristics of each tropical peatland region: Southeast Asia, Central Congo Basin and Peruvian Amazon, specifically the Pastaza-Marañón foreland basin (PMFB), for which data is available.

Region	Area of peatlands (km ²)	Below-ground carbon content (Pg C)	Earliest reported initiation dates (Cal. yr BP)	Dominant peatland form	Major peat-forming vegetation types	Anthropogenic activities	
						palaeoanthropocene (pre-200 Cal. yr BP)	anthropocene (post-200 Cal. yr BP to present)
Southeast Asia	240,000 ^a	68.5 ^b	47,800 ^c	coastal peat domes	Dipterocarp hardwood swamps	some small-scale clearing of peat swamp forest with use of fire, harvesting of NTFPs ^d	fishing, hunting, foraging for NTFPs ^e ; subsistence & industrial logging, drainage, fire, land use change for agriculture & settlement
Central Congo Basin	145,500 ^f	30.6 ^f	c. 10,500 ^f	various ombrotrophic forms and shallow peat domes associated with interfluvial basins ^{g,h}	hardwood & palm swamps	largely unknown (limited evidence)	no large-scale impacts at present, but future threats from mining, logging, deforestation, oil exploration and palm oil plantations ^h
Peruvian Amazon (PMFB)	35,600 ⁱ	3.14 ^j	c. 8870 ^j	various ombrotrophic & minerotrophic forms associated with basins & old river channels	palm swamps, peatland pole forests, open peatlands	no evidence of past impacts on peatland vegetation suggesting minimal interaction	no large-scale impacts at present, but future threats from oil exploration and spills, oil palm plantations, harvestings of NTFPs ^k

^a (Page et al., 2011),

^b (Page et al., 2010),

^c (Ruwaima et al., 2020),

^d (Hapsari et al., 2018),

^e NTFPs - non-timber forest products

^f (Dargie et al., 2017),

^g (Davenport et al., 2020),

^h (Dargie et al., 2019),

ⁱ (Draper et al., 2014),

^j (Lähteenoja et al., 2012),

^k (Roucoux et al., 2017)

2.2.1. Palaeoecological perspective

Peatlands have existed in the interior of Borneo since the late Pleistocene, including some examples that date to 60,000 Cal. yr BP (Anshari et al., 2001; Page et al., 2004; Wüst et al., 2007). The majority of coastal peatlands, however, initiated during the Holocene (Biagioli et al., 2015; Dommain et al., 2011; Hope et al., 2005). Peat accumulation in the coastal plains of Sumatra, Peninsular Malaysia and Borneo was driven by slowing post-glacial sea level rise, which led to the widespread development of mangrove vegetation and consequently the provision of an acidic and flat substrate (Anderson, 1964; Dommain et al., 2011; Horton et al., 2005), and by enhanced precipitation in the middle Holocene (c. 8000–4000 Cal. yr BP) (e.g., Cole et al., 2015; Neuzil, 1997; Sabiham, 1990; Woodroffe, 2000; Wüst and Bustin, 2004). After the sea level highstand (c. 5000 Cal. yr BP), marine regression allowed rapid seaward expansion of peatlands by exposing further suitable land surfaces, i.e., mud flats and sandy coastal plains, which peat swamp forest could colonise (Dommain et al., 2011; Neuzil, 1997).

The development of peatland ecosystems in Southeast Asia was initially assumed to follow the successional pathway of the ‘Anderson model’. That is, a coupled evolution of substrate and vegetation from mangrove swamp to mixed swamp forest then mature peat swamp forest, a model confirmed by palaeoecological studies at multiple sites (Cole et al., 2015; Dommain et al., 2015; Sabiham, 1990). Palaeoecological studies at other sites, however, have shown that alternative development pathways exist, for example, where mangrove soil and vegetation are not essential precursors (e.g., Hapsari et al., 2017; Hope et al., 2005; Taylor et al., 2001). Some peatlands started to form in depressions near rivers, under riparian or lowland forests, which then developed into freshwater swamp forests and subsequently peat swamp forests. This type of peatland is mostly located in the interior beyond the influence of marine conditions, or in coastal locations above the Holocene sea level highstand (+5 m a.s.l.) (Hapsari et al., 2017; Neuzil, 1997; Taylor et al., 2001).

2.2.2. Responses to past disturbances

2.2.2.1. Fire. Fires in Southeast Asian peatlands result from natural (e.g., lightning strikes, Dommain et al., 2015) or anthropogenic causes, or a combination of both (e.g., Anshari et al., 2001; Cole et al., 2019; Hope et al., 2005). Unlike the large-scale fires that now occur annually in some locations (Girkin et al., in progress; Langner and Siegert, 2009; Stolle and Lambin, 2003), however, fire was relatively rare in the past, with a return interval of centuries to millennia (Page and Hooijer, 2016), and probably predominantly ignited by natural sources.

Multiple palaeoecological records suggest that fires did not usually result in the loss of peat (Anshari et al., 2001; Biagioli et al., 2015; Hapsari et al., 2017; Yulianto et al., 2004) or any significant vegetation change. Fires therefore caused limited perturbation to ecosystem function, including carbon accumulation (Anshari et al., 2004, 2001; Biagioli et al., 2015; Cole et al., 2019; Hapsari et al., 2017; Yulianto and Hirakawa, 2006). One exceptional record, from Kutai peatland in Eastern Kalimantan, Indonesia, does provide a rare example of fire-related loss of peat (Hope et al., 2005), akin to the impacts of fire typical of recent decades (Astiani et al., 2018; Page and Hooijer, 2016). Estimations have shown that late Holocene fires (at c. 4400, 3900, 1900, and 1400 Cal. yr BP) may have consumed at least the upper 1 m of peat and prevented recolonization by trees at the burnt site, leading to the formation of lakes (van Eijk et al., 2009; Wösten et al., 2006) and the release of ~25 Tg C (between 0.1 and 3.6 Tg C per fire event; Dommain et al., 2014). These severe fires are the only known examples to date in the palaeoanthropocene.

2.2.2.2. Climatic changes. Climate has served as an important driver of the dynamics of peatlands in Southeast Asia throughout their history (e.g., Anshari et al., 2001, 2004; Hapsari et al., 2017; Page et al., 2009). Multiple studies have shown how moist climates prevalent during the



A



B



C

Fig. 3. . Photographs illustrating one prominent type of peatland ecosystem from each described region: A) *Shorea albida* dominated peat swamp forest, in Sumatra, Indonesia; B) hardwood dominated swamp forest in the Republic of Congo; and, C) *Mauritia flexuosa* dominated palm swamp, locally known as an *aguajá*, in the Peruvian Amazon. (Photo credits: KAH, DH and LESC, respectively.).

late Pleistocene and Holocene contributed to the initiation and continued accumulation of peat in inland Borneo, Sumatra and Peninsula Malaysia (Anshari et al., 2001; Page et al., 2004; Russell et al., 2014). At some sites, however, increased precipitation in the mid Holocene, coupled with sea level rise, caused high water discharge and frequent flooding, inhibiting peat accumulation or eroding existing peat (Anshari et al., 2001; Hapsari et al., 2017). Palaeoecological and palaeoclimate records illustrate the dynamic relationship between precipitation and peat accumulation and show how other factors, such as relative sea level, can influence this relationship.

Dry conditions are considered unfavorable for Southeast Asian peatland persistence. A lower water table and consequent increased decomposition rate reduces peat accumulation (Anshari et al., 2004; Dommain et al., 2014; Mezbahuddin et al., 2014; Page et al., 2004), and droughts increase the risk of peat fires (Dommain et al., 2014; Page et al., 2002). Palaeoecological studies repeatedly report drought-related fire occurrence, though their impact on peatland vegetation is limited (e.g., Anshari et al., 2001; Biagioli et al., 2015; Cole et al., 2015; Hapsari et al., 2017; Yulianto and Hirakawa, 2006; Yulianto et al., 2004). Evidence exists, however, that climatic changes, such as increases in precipitation, caused shifts in the composition of peatland vegetation communities (e.g., Anshari et al., 2001, 2004; Taylor et al., 2001; Wüst and Bustin, 2004).

2.2.2.3. Human impact. In Southeast Asian peatlands, prehistoric human activities are often evident in the palaeoecological archives from the presence of elevated charcoal abundance (e.g., Anshari et al., 2001; Hope et al., 2005; Taylor et al., 2001) and changes in peat swamp forest vegetation. Further support is commonly available from contemporaneous archaeological or historical records (e.g., Cole et al., 2019; Hapsari et al., 2017, 2018; Wüst and Bustin, 2004). Although evidence suggests that humans have been present in the Indo-Malayan archipelago since the late Pleistocene, c. 35,000 Cal. yr BP (Barker et al., 2017; Bellwood, 1997; Hunt and Premathilake, 2012), their activities were mainly shifting cultivation, hunting and gathering, and apparently limited to forest edges and riversides (rivers being key travel routes) until the last few hundred years.

Indicators of human activity in peatlands across Borneo increase synchronously after 1600 Cal. yr BP (Anshari et al., 2001; Hope et al., 2005; Yulianto et al., 2005), supporting archaeological findings (Krigbaum, 2003; Kusmartono et al., 2017; Kusmartono and Oktrivia, 2019). In Tasek Bera peatland, Peninsular Malaysia, two notable changes in vegetation, at c. 2000 Cal. yr BP and over the last 600 years, were attributed to humans, possibly the activities of the Semelai people (Wüst and Bustin, 2004). Meanwhile in Sumatra, very few records of human activities are available for the peatlands during the Holocene (Hapsari et al., 2018, 2017), reflecting the scarcity of people living in and around these densely forested, waterlogged environments before c. 200 years ago (Hope et al., 2005).

In Sungai Buluh, Sumatra, a period of peatland forest openness and slower peat accumulation coincided with the occupation period of the Malaya Empire in the vicinity (1000–600 Cal. yr BP; Hapsari et al., 2017, 2018; Witrianto, 2014). Palaeoecological data and detailed archaeological and historical records of the dynamics of the Malaya Empire have revealed that its people affected the peatland ecosystem through harvesting timber, forest products and fodder, but not draining the peat, converting the forest or using fire excessively to clear it (Hapsari et al., 2018). The Sungai Buluh peatland started to recover after the people of Malaya Empire abandoned the site, c. 600 Cal. yr BP. Its carbon accumulation rate and peat swamp vegetation composition recovered to pre-disturbance states after 60 and 170 years, respectively (Hapsari et al., 2018).

Several records do, however, suggest that people impacted peatlands in this region in irreversibly transformative ways in the late Holocene. A palaeoecological study in Sarawak showed a lack of peat swamp forest

recovery within the last c. 200 years (Cole et al., 2019), contemporaneous with indicators of anthropogenic activity, including elevated levels of burning, and with historical evidence of human activity in the region (Colombijn, 2005; Kaur, 1995). The decline in peat swamp forest taxa at these sites suggests a loss of peatland ecosystem resilience resulting from the intensity of anthropogenic disturbance that occurred several hundred years ago and/or a lack of opportunity for the vegetation to recover due to ongoing human activity (Cole et al., 2015). The latter explanation was supported at sites where records indicate continuous elevated burning (e.g., Cole et al., 2019).

2.2.3. Present status & future threats to peatlands

Following population and economic growth, Southeast Asian peatlands have undergone rapid land use conversion, primarily into agricultural land (Miettinen et al., 2016, 2012). Since 1990, 3.1 Mha of peat swamp forest has been converted into oil palm plantations annually (Miettinen et al., 2016). In 2015, less than 30% (4.6 Mha) of peatlands throughout Sumatra, Peninsular Malaysia and Borneo remained forested, with only 1 Mha considered to be in a pristine condition (Miettinen et al., 2016). Deforestation has led to irreversible peatland degradation, turning the peat into a dry substrate prone to fire and oxidation, and in turn creating a significant source of atmospheric carbon (e.g., Miettinen et al., 2017; Page and Hooijer, 2016; Vetrata and Cochrane, 2020). This process contrasts with the impact of human activities evidenced in palaeoecological records before 200 years ago, where humans used peatlands in a “resilience-friendly” way, i.e., without clearing the forest with fire or draining the ecosystem (Hapsari et al., 2018).

Under current rates of peatland deforestation/conversion and burning (3.1 and 0.5 Mha yr⁻¹, respectively), driven by factors such as the Indonesian Government's biofuel and timber production targets (Bassi et al., 2020; Schoneveld et al., 2019; Surahman et al., 2019), all intact peatland ecosystems across Southeast Asia will have disappeared by 2030, if not earlier (Miettinen et al., 2012; Vetrata and Cochrane, 2020). Fortunately, numerous conservation and restoration efforts are underway (e.g., Global Environment Centre, 2021; “Katingan”, 2021; “Rekoforest”, 2021), with long-term leases (60 + years) to peatland sites. The palaeoecological record from Sungai Buluh in Indonesia, suggests that this length of time may be sufficient for degraded peat swamp forests to re-establish their peat formation and carbon sequestration functions, but not to recover previous levels of biodiversity. For this, a longer period of ecosystem recovery, greater than 170 years, may be necessary (Hapsari et al., 2018).

2.3. Central Congo Basin

The largest known peatland complex in tropical latitudes, covering c. 145,500 km², is in the central Congo basin (Dargie et al., 2017), referred to as the Cuvette Centrale peatland complex. It has only recently been mapped and dated in a single field-based study (Dargie et al., 2017) and there has been little work on peatlands in the wider Congo Basin. Therefore this section is, in parts, necessarily speculative. The peatland complex extends into the east of the Republic of Congo (ROC) (54,700 km²), and the west of the Democratic Republic of Congo (DRC) (90,800 km²). At its centre, the peatland occupies a low-lying hydrological drainage basin of the Congo River and its tributaries. The mean peat thickness is 2.2 m ± 1.61 (St. dev.), with a maximum of 5.9 m. The estimated carbon stored below-ground across the entire Congo peatland complex is 30.6 Pg C (95% CI: 6.3 – 46.8), ~29% of the global tropical peatland carbon stock (Dargie et al., 2017).

Annual rainfall in the Central Congo Basin is 1500–2500 mm yr⁻¹, notably lower than in Amazonia and Southeast Asia (Primack and Corlett, 2005). A range of forest types occur within the peatland complex, though two common peat-forming vegetation communities are the palm-dominated swamp forest (commonly consisting of *Raphia laurentii*) and hardwood swamp forest (dominated by *Uapaca paludosa*, *Carapa*

procera and *Xylopia rubescens*) (Fig. 3B). The trees show adaptations to wet conditions, such as stilts, buttresses and aerial roots (Dargie, 2015).

2.3.1. Palaeoecological perspective

Nine basal radiocarbon dates suggest that the peatland began to form between 10,554–7137 Cal. yr BP, during the African Humid Period (11,700 – 4000 Cal. yr BP), with an increase in rainfall across western and northern Africa (Aleman and Fayolle, 2020; Dargie et al., 2017; Shanahan et al., 2015). Currently no palaeoecological records exist from within the Cuvette Centrale peatlands studied by Dargie et al. (2017). Outside the peatland complex, the closest comparable record is from Ngamakala swamp, in the Bateke Plateaux region (~220 km to the south). Here, Elenga et al. (1994) presented radiocarbon dates from a single core with a peat initiation date of c. 24,000 yr BP (uncalibrated). Thus, dates for peat initiation vary significantly across the Congo Basin as a whole, probably dependant on local environmental conditions, e.g., topographic, hydrological, climatic, and on potentially varying mechanisms of formation.

The lack of palaeoecological records from the Cuvette Centrale peatlands means that the environment within which peat began to accumulate has not yet been explored. However, a single record exists from the Congo fan, at the mouth of the Congo River, representing broad vegetation change across West Equatorial Africa (Jahns, 1996) and may provide insights into the environment within which peat initiated. During the Last Glacial Maximum (c. 21,000–18,000 Cal. yr BP), the climate was cooler and drier, and the Congo fan record is dominated by taxa such as Cyperaceae, Poaceae and *Podocarpus* (Jahns, 1996). With the onset of the African Humid period there was an increase in lowland rain forest taxa, such as *Alchornea*, *Khaya*, *Pterocarpus*, *Celtis* and *Uapaca*, in response to the warmer and wetter climate. The Ngamakala swamp record indicates that peat initiated in a “hydromorphous forest” environment, characterised by a dominance of taxa tolerant of wet conditions, including Sapotaceae and *Syzygium*, and an absence of herbaceous taxa (Elenga et al., 1994). An expansion of “hydromorphous forest” was recorded again after 13,000 yr BP (uncalibrated), corresponding to the onset of the African Humid Period.

The mechanism responsible for the initiation of peat within the Cuvette Centrale remains to be established. Peatland formation likely resulted from terrestrialisation, paludification or a combination of the two. A multicore study at one site, Ekolongouma in the northern Republic of Congo, gives insight into how peat in this region of the Cuvette Centrale expanded laterally following initiation. The oldest (10,555 Cal. yr BP at 3 m depth, 9 km into the peatland) and deepest peat (5.9 m, 17.4 km into the peatland) was recorded towards the centre of the site, with three additional cores taken along a transect showing that the base of the peat becomes progressively younger and shallower towards the peatland margin (Dargie, 2015). Vertical long-term apparent peat accumulation rates also varied (0.36–0.21 mm yr⁻¹), becoming slower towards the peatland margin. Five additional cores taken at different sites across the Cuvette Centrale peatlands revealed peat initiation dates in the early Holocene (c. 9500 – 7200 Cal. yr BP) and accumulation rates ranging from 0.16 to 0.29 mm yr⁻¹ (Dargie et al., 2017).

2.3.2. Responses to past disturbances

2.3.2.1. Fire.

The absence of palaeoecological records from within the Cuvette Centrale peatlands means that the presence and role of fire within this ecosystem remains to be established. The Congo Basin as a whole is one of the most lightning-prone regions on earth (Albrecht et al., 2016) and has a long history of hominin occupation (Crevecoeur et al., 2014) providing possible sources of fire ignition. Studies from outside the Cuvette Centrale peatlands, but within the wider Congo Basin, suggest that fires in the past have apparently occurred in forested regions (including swamp forests) under two scenarios. Firstly, fires occurred during periods of reduced precipitation or drought (Hubau

et al., 2015). Secondly, they occurred during periods of increased anthropogenic activity (Brncic et al., 2007; 2009). While these studies provide a palaeoecological view of fire in forested regions within the wider Congo Basin, studies from within the Cuvette Centrale are desperately needed in order to quantify and explore the role of fire within the peatlands in the past.

2.3.2.2. Climatic changes. Palaeoclimatic records from the Cuvette Centrale peatlands are non-existent, therefore we point to data from marine cores and studies outside the peatlands, which provide evidence for strong climatic changes in central Africa (e.g., Gasse, 2000; Maley and Brenac, 1998; Schefuß et al., 2005; Shanahan et al., 2015; Weijers et al., 2007). Major dry and cool periods during the Last Glacial Maximum (c. 21,000–18,000 Cal. yr BP) and Younger Dryas (c. 12,900–11,700 Cal. yr BP), have apparently caused tropical rainforests to contract and form a mosaic with savanna ecosystems (Elenga et al., 1994) or become more open environments (Runge, 1996). Humid and cool environments may have allowed forests to persist with more open canopies, abundant shrubs and herbaceous understorey vegetation (Jahns et al., 1998; Mercader et al., 2000). The onset of the African humid period (11,700 Cal. yr BP) in the Congo Basin was marked by the expansion of forest and a shift to denser forest cover (Mercader et al., 2000). Vincens et al. (2005) and Jansen et al. (1995) supported this scenario and inferred a general humidification and increase in rainfall at this time across central Africa that promoted the expansion and diversity of rainforest and forested swamp environments. The basal peat radiocarbon dates from the Cuvette Centrale (between 10,554 and 7137 Cal. yr BP) suggest that peatlands were among the ecosystem types that expanded during the African Humid Period (11,700 – 4000 yr BP) (Aleman and Fayolle, 2020; Shanahan et al., 2015). Present day rainfall within the Cuvette Centrale is lower when compared to other tropical peatlands, suggesting to Dargie et al. (2017) that the peatland establishment/expansion was potentially largely climatically driven. Additional palaeoclimatic and palaeoecological records are needed from within the Cuvette Centrale, the Congo Basin and central Africa as a whole, to provide a clearer picture of climatic and vegetation change.

2.3.2.3. Human impact. The extent to which past societies have used and modified the forests of the Congo Basin is largely undocumented, and no literature exists on the Cuvette Centrale peatlands. However, human populations have been likely active in the region since at least 3000 years ago. Pits containing pottery sherds and oil palm and *Canarium* nuts, have been found to extend into the equatorial forest interior along the Ubangui River (Phillipson, 2005), with most archaeological evidence for settlement confined to river banks and forest fringes in this and other regions of the wider Congo Basin, e.g., Gabon, Cameroon and Southern Central African Republic (Bostoen et al., 2015). Palynological and climatic evidence, combined with numerous studies on the oral traditions and linguistics of the region, highlight the estimated timing and routes through which Bantu-speaking populations first spread across the Congo Basin. From c. 3500 Cal. yr BP, and peaking c. 2500 Cal. yr BP, evidence suggests the opening up of forests and the expansion of savannas, created a fragmented forest structure and possible corridors that facilitated Bantu population expansion (Bostoen et al., 2015; de Luna, 2016; Maley, 2002; Maley and Willis, 2010). Bantu speakers likely largely followed familiar environments (e.g., open forest, wooded savannah and grassland), but more recent evidence also showed adaptation to denser forest environments (de Luna, 2017). Although it is clear that there is a long history of human influence on *terra firme* environments within the wider Congo Basin, the history and even present day impacts on the Cuvette Centrale peatlands remains to be explored.

2.3.3. Present status & future threats to peatlands

Currently, the peatlands of the central Congo Basin experience little disturbance and remain largely intact. Dargie et al. (2019), however,

gave a detailed account of the present threats and conservation priorities for the Congo Basin peatlands. They highlighted changing land use, logging, oil and gas exploration, dam building and infrastructure developments as activities that could transform these ecosystems in the near future. Despite the current low levels of human intervention, ~75 million people reside within the Congo Basin region, 60% of which live in rural areas (Megevand et al., 2013). Peat forests play a role in supporting some of this population, as a source of bushmeat, fuel, fruit and medicines (Dargie et al., 2019). Research is needed to better understand how human populations use and value these peatlands today, and where future threats may arise.

Even if destructive human activities are not currently prevalent in the peatlands, ongoing climatic changes may have significant impact. Annual mean rainfall has declined since 1979, and the length of the boreal summer dry season in the Congo Basin has increased. This trend is related to an amplification of warming over the Sahara, causing what were previously warm and wet conditions in the region to become drier (Cook et al., 2020). Drier conditions could inevitably lead to an increase in peatland fires. While fire frequency is expected to be low in Congolese swamp forest environments, palaeoecological records from the region indicate that past increases in fire activity were associated with periods of increased aridity, the expansion of savanna environments and increased human activity. Therefore, if conditions continue to dry and anthropogenic impacts increase, peatland fires could become a significant threat in the future.

Drier conditions can also lead to a reduction in peat accumulation. In the future, if rainfall reduces and seasonality increases, causing water tables to drop and peatlands to dry, peat accumulation rates could slow, which would reduce the carbon sink capacity of the region. Keeping the peatlands wet and protecting them from intensive and large-scale anthropogenic impact is a conservation priority.

2.4. Amazonia

The majority of Amazonian peatlands are located within the Pastaza-Marañón foreland basin (PMFB) in northern Peru, covering an estimated $35,600 \pm 2133 \text{ km}^2$ (Draper et al., 2014). The low-lying topography of the $100,000 \text{ km}^2$ basin is characterized by high precipitation (2000–3000 mm yr⁻¹) and frequent flooding, which favours peat formation. Peat accumulates in the PMFB in highly dynamic floodplain settings and in a range of vegetation types, including herbaceous open peatlands, seasonally flooded forest, mixed swamp forest, palm swamp forest (Fig. 3C), and pole forest (Kelly et al., 2017, 2018b; Lähteenoja et al., 2012, 2009; Lähteenoja and Page, 2011; Lawson et al., 2014; Roucoux et al., 2013; Swindles et al., 2018b). Peat depths of up to 7.5 m have been reported in the basin (Lähteenoja and Page, 2011). The most recent estimate of carbon contained within the PMFB is 3.14 (0.44 – 8.15) Pg C (Draper et al., 2014). With addition of the below-ground carbon stocks in other Amazonian peatlands, these ecosystems are an important component of the Amazon basin carbon balance.

A smaller area of peatlands occurs in the meandering belt of the Madre de Dios River in southern Peru, covering 294 km^2 (Householder et al., 2012). Individual peatlands in the Madre de Dios region range in size from 10 to 3500 ha, and the mean peat depth is estimated at $2.5 \text{ m} \pm 1.8 \text{ m}$, though peat thicknesses of up to 9 m have been reported (Householder et al., 2012). The deepest peats are documented in areas that today support dense swamp forest dominated by *Mauritia flexuosa*, whereas more shallow peats (<3.5 m) were documented in areas of open mire vegetation (Householder et al., 2012).

In Brazilian Amazonia, peatlands with varying peat thickness (10 – 210 cm) have been recorded in the middle Negro River basin (Lähteenoja et al., 2013). Shallow peats ($\leq 80 \text{ cm}$ depth) have also been reported underlying flooded forests in the upper Negro River basin in northern Amazonia (Dubroeucq and Volkoff, 1998). Farther north still, studies have documented tropical wetlands with abundant peatlands in the lower Orinoco River Delta, Venezuela (Aslan et al., 2003;

Vegas-Vilarrúbia et al., 2010). Peat-forming vegetation ranges from palm forests and herbaceous vegetation growing on thicker peat layers (5–10 m) (Aslan et al., 2003; Vegas-Vilarrúbia et al., 2010), to swamp forest and shrublands on thinner peats (<150 cm) (Vegas-Vilarrúbia et al., 2010). Lähteenoja et al. (2013) have suggested that the lesser extent of reported peatlands in central Amazonia, compared with western Amazonia, could be explained by a number of factors, including rainfall and hydrology, tectonic conditions, topography, minerogenic subsoil type and the frequency of fires.

2.4.1. Palaeoecological perspective

Limited palaeoecological studies of peatlands across Amazonia are available, though the number is increasing. The oldest documented extant peatland is the ombrotrophic peat dome at Aucayacu in the PMFB, which has been dated to c. 8900 Cal. yr BP. It contains peats up to 7.5 m thick (Lähteenoja and Page, 2011; Swindles et al., 2018b) and is characterised by pole forest today. The palaeoecological record shows that the environment developed from open water wetland, to inundated forest swamp c. 6600 Cal. yr BP, to a raised peat dome after c. 3900 Cal. yr BP (Swindles et al., 2018b).

Quistococha, a small lake located 120 km north-east of Aucayacu within the PMFB, occupies an abandoned arm of the Amazon River and is today surrounded by a permanently waterlogged closed-canopy palm swamp dominated by *Mauritia flexuosa* and *Mauritiella armata* palms (Räsänen et al., 1991; Roucoux et al., 2013). The swamp contains peat up to 4.9 m thick (Lähteenoja et al., 2009b). The palaeoecological record shows that peat initiated c. 2200 Cal. yr BP, after which a marginal fen and/or floating mat with the presence of disturbance and floodplain taxa developed (Lawson et al., 2014; Roucoux et al., 2013). After 2100 Cal. yr BP, the site transitioned into forest vegetation tolerant of deep flooding (Roucoux et al., 2013). When deep flooding ceased after 1000 Cal. yr BP, a palm swamp, dominated by *Mauritia flexuosa*, developed. Despite a general long-term trend of infilling and afforestation at the Quistococha swamp, the palaeoecological record shows times of reversals characterised by short-term increased abundances of open taxa at c. 1700 – 1400 Cal. yr BP and 1150 – 1000 Cal. yr BP, possibly caused by either decreased flooding depth or the development of permanent pools with fen and/or floating mat vegetation (Roucoux et al., 2013).

San Jorge, an ombrotrophic peatland located about 20 km southwest of Quistococha in the PMFB, contains peats of up to 2.4 m thick (Kelly et al., 2018b; Swindles et al., 2018a). The peatland has a domed structure and is characterized by pole forest vegetation. This raised peatland is surrounded by *Mauritia flexuosa*-dominated palm swamp (Kelly et al., 2017; Lähteenoja et al., 2009a). The site may have been located within an active channel of the Amazon c. 3000 years ago, which then moved progressively farther away until the site developed into a floodplain swale or lake (Kelly et al., 2017). Peat initiation occurred c. 2290 Cal. yr BP with development of an open-canopy forest and marginal lake-side and/or a floating mat vegetation. After 650 Cal. yr BP, palm-dominated swamp forest was established at San Jorge (Kelly et al., 2017). The pollen and geochemical records show the establishment of pole forest and predominantly rain-fed, ombrotrophic conditions after 200 Cal. yr BP (Kelly et al., 2017).

2.4.2. Responses to past disturbances

2.4.2.1. Fire. Natural fires are almost non-existent in western Amazonia, as wet conditions of lowland rainforest limit the spread of ignition (Bush et al., 2007). Palaeo-fires in western Amazonia have thus repeatedly been connected to anthropogenic land use, and fossil charcoal has served as a strong indicator of human presence in these landscapes (Bush et al., 2016; Kelly et al., 2018a, 2018b; McMichael et al., 2012; Urrego et al., 2013). At Aucayacu, studies have identified charcoal fragments in three intervals during the last 4500 years, inferred to represent anthropogenic activity at these times (Swindles et al., 2018b).

Charcoal fragments were rare in the peat profiles retrieved at San Jorge and Quistococha (Kelly et al., 2017; Roucoux et al., 2013). Kelly et al. (2018b) documented them in the lake record in sediments, however, dated to c. 2450 Cal. yr BP. These dates are contemporaneous with the oldest archaeological evidence at the site (Rivas Panduro, 2006; Rivas Panduro et al., 2006). Higher abundances of charcoal were found between c. 2180 and 90 Cal. yr BP, with lower charcoal concentrations after 90 Cal. yr BP (Kelly et al., 2018a, 2018b). Although the charcoal record suggests that people were consistently present in the Quistococha area until the present day, the lake and peat pollen records preserve no evidence for extensive disturbance of the peatland vegetation or deforestation of the local landscape until modern times (Kelly et al., 2018a, 2018b; Roucoux et al., 2013). Further palaeoecological studies are required to assess the extent to which this is representative of peatlands in the wider region, beyond the pollen catchment of Quistococha.

2.4.2.2. Climatic changes. Climate change can be difficult to detect in Amazonian peatlands due to the dynamic nature of floodplain settings (Räsänen et al., 1991; Roucoux et al., 2013). Studies have reported direct effects of climate, however, from some palaeoecological sites in the PMFB (e.g., Kelly et al., 2017; Swindles et al., 2018a, 2018b). These effects are mainly evident through alterations in peat accumulation and decomposition rates, linked to climate-induced ecohydrological changes.

Three drought periods are known from the record of the ombrotrophic peat dome at Aucayacu in northern Peru (Swindles et al., 2018b). During the first two periods, drier conditions have apparently increased the peat accumulation rate and caused two different ecohydrological shifts. The first drought, c. 6600 – 6100 Cal. yr BP, coincided with a shift from an open water wetland to a forest swamp, whereas the second, c. 4900 – 3900 Cal. yr BP, with a shift from a minerotrophic forest swamp to ombrotrophic raised peat dome. The timing of the first two droughts in the Aucayacu record coincided with droughts reported from Lake Sauce in western Amazonia (Bush et al., 2016; Correa-Metrio et al., 2010) and low lake levels from Lake Titicaca in the High Andes (Baker et al., 2005).

The Aucayacu site was influenced by a third drought period, c. 1800 – 1100 Cal. yr BP, which led to a cessation of peat accumulation within the ombrotrophic dome and increased peat decomposition, suggested by the presence of a hiatus in the sediment core (Swindles et al., 2018b). A decline in peat accumulation rate is also documented from the peat dome at San Jorge, 200 km to the east, c. 1300 – 400 Cal. yr BP (Kelly et al., 2017). The drying climate likely caused the water table to lower, leading to an increased rate of peat and litter decay (Kelly et al., 2017). The transition to ombrotrophic conditions at San Jorge after c. 200 Cal. yr BP, is partly explainable by a shift to less precipitation or fluvial influence (Swindles et al., 2018a). This shift apparently occurred at Aucayacu, when the swamp forest there transitioned to pole forest and the mire became ombrotrophic at a time of climatic drying (Swindles et al., 2018b). At Quistococha, the formation of a palm swamp at c. 1000 Cal. yr BP has been linked to reduced flooding depth, which could result from a drier climate. In this case, however, the more parsimonious explanation is a decline in fluvial influence caused by river channel migration (Roucoux et al., 2013).

2.4.2.3. Human impact. People have inhabited Amazonia for at least 13,000 years (Roosevelt, 2013), with the first evidence of maize cultivation dated to c. 6500 Cal. yr BP in Bolivia (Brugger et al., 2016) and c. 6320 Cal. yr BP in Peru (Bush et al., 2016). Past human activity in Amazonia caused landscape changes through deforestation (Laurance et al., 2004), burning (Bush et al., 2015), creation of anthropogenic soils (*terra pretas*; Glaser and Woods, 2004; Neves et al., 2004), aquaculture, raised fields (Erickson, 2006), earthworks (Pärsinen et al., 2009), mound building (Rostain, 2012), enrichment of useful species (Clement et al., 2015; Levis et al., 2018, 2017; Roosevelt, 2013), and cultivation

(Brugger et al., 2016; Bush et al., 2016; Bush and Colinvaux, 1988). In aseasonal western Amazonia, settlements were often temporally and spatially intermittent compared with more distinct dry season settings. Localized disturbance was strongly influenced by distance from rivers, lakes, seasonal flood-plains, and savannas (Åkesson et al., 2021; Bush et al., 2007; Bush and Colinvaux, 1988; Kelly et al., 2018a, 2018b; McMichael et al., 2012b, 2015, 2012a; Roucoux et al., 2013).

For the PMFB region, little evidence suggests prehistoric human impact on peatland vegetation or peat accumulation (Kelly et al., 2018a, 2018b; Roucoux et al., 2013). Fossil charcoal is only sparsely identified at Aucayacu, Quistococha, and San Jorge, and no cultivars (e.g., maize and manioc) were found in the peat core pollen records. Despite the scarcity of anthropogenic signatures in these palaeoecological records, an archaeological site has been excavated adjacent to Quistococha, revealing fragments of pottery, charcoal, cobs of corn, and phytoliths of palms and grasses dated to two distinct intervals: c. 2690 – 2350 Cal. yr BP and c. 1880 – 1740 Cal. yr BP (Rivas Panduro, 2006; Rivas Panduro et al., 2006). *Terra pretas* have also been identified in the area. People occupied the Lower and Upper Ucayali River region in the PMFB from at least c. 3950 Cal. yr BP to early post-Columbian times and practiced manioc cultivation, experimented with maize cultivation and traded with Andean and Amazonian civilizations (Coomes et al., 2020; Lathrap, 1970; Raymond, 1988).

With European arrival after AD 1492, Amazonia suffered substantial losses in human population (90 – 95% decline) due to warfare, disease, and slavery (Clement, 1999; Dobyns, 2017). Industrialization, demands for raw materials (e.g., rubber, mining, and timber), cattle ranching and agriculture created a surge of settlers to Amazonia. This surge caused extensive deforestation and resource depletion after AD 1850 (e.g., Laurance et al., 2005; Nepstad et al., 1997; Weinstein, 1983).

2.4.3. Present status & future threats to peatlands

The documented peatlands in Amazonia remain largely intact (Roucoux et al., 2017). Contemporary evidence suggests that harvesting of the *Mauritia flexuosa* fruit, known locally as *aguaje*, from peat-forming palm swamps, can be unsustainable where it involves felling of the female, fruit-bearing individuals (Bhomia et al., 2018). Although this harvesting technique is now discouraged where possible, it remains prevalent and problematic (Romulo et al., 2022; Virapongse et al., 2017). Many other subsistence activities taking place in the PMFB peatlands today appear to be more sustainable (e.g., Schulz et al., 2019a, 2019b), and have limited, apparently non-transformative, impacts on the peatlands. Further study of the effects of peatland use (e.g., resource harvesting and hunting) are required, however, to accurately assess the extent to which these apparently low impact activities affect peatland ecosystem function.

Although for the most part, the peatlands of the PMFB today are still hydrologically intact, they remain threatened by several types of anthropogenic activity (Roucoux et al., 2017). Industrial-scale agriculture is currently peripheral to most peatlands, but the availability of new technologies and investment opportunities can put pressure on wetlands to become commercially productive. Pervasive within tropical latitudes, oil palm plantations may be a key driver of habitat loss (Glinskis and Gutiérrez-Vélez, 2019). Increased transport infrastructure also poses threat to this currently isolated, inaccessible region. Plans are underway to extend the road network within the PMFB, cutting through some of the most carbon-rich ecosystems in the Peruvian Amazon (Coronado et al., 2021) and enabling access to forest, which has proven devastating for ecosystems elsewhere in Amazonia (Barber et al., 2014; Gallice et al., 2019). Investigations of the threat of climate change in this region is also underway (Marengo et al., 2018), but more work is needed to understand the effect that predicted changes in seasonal patterns of precipitation and flooding could have on the peatlands, especially given the variety of potential responses evident in palaeoecological records (Kelly et al., 2017; Roucoux et al., 2013; Swindles et al., 2018b). Mining and transportation of oil and gas across remote parts of Amazonia will likely

continue to pollute forests and wetlands in at least the near future (e.g., Sierra Praeli, 2020), with as yet unknown consequences for the long-term ecosystem function of peatlands (Baker et al., 2020; Roucoux et al., 2017).

3. Synthesis across three tropical peatland regions

Pathways for the development of peatlands share fundamental features across all three continents. The patterns of ecohydrological development and ecological succession involving the colonisation of freshwater anoxic environments are particularly relevant, by flood-tolerant herbs, palms and trees, commonly progressing to vegetation dominated by palms and trees tolerant of low-nutrient, acidic environments as ombrotrophic conditions develop. However, important differences (Fig. 4) also exist. For example, the peatlands in each region, and each peatland within each region, have a unique initiation date (Fig. 4) and development pathway that differs in detail, determined by the local climatic, geological, hydrological and ecological conditions, and history. The development of coastal peat swamp forests in Southeast Asia was closely linked to global sea level changes. The inland peatlands of Central Africa was more directly attributable to local climate and specifically, precipitation. In Amazonia, continual migration and switching of river channels has alternately created and truncated opportunities for peat to accumulate over time. Synthesising examples from across the tropics also demonstrates several universal patterns in ways that people have interacted with peatlands through the Holocene, and in the responses of peatland ecosystems.

Firstly, people have been living in the vicinity of all of these peatlands for much of the Holocene with the presumed palaeoanthropocene extending through the majority of this epoch. As in temperate regions, most historic and pre-historic human activity associated with the tropical peatlands probably happened on their margins, where the peat is shallower and the land more accessible and amenable to exploitation (Page and Baird, 2016).

Secondly, the difference in the effect of fires on peatlands in the deeper palaeoanthropocene versus the more recent anthropocene is stark. In the past, fires were generally rare in these ecosystems whereas today, they are driving significant change, though currently limited to the peatlands in Southeast Asia (Page and Hooijer, 2016). Throughout much of the Holocene, the forest vegetation apparently recovered after periods of burning. Only one study reported a possible effect of fire on the peat substrate itself (from Indonesia, Hope et al., 2005). Burning before c. 200 years ago has been associated with both natural and anthropogenic causes (Fig. 4) (Brncic et al., 2009; Hapsari et al., 2018; Hubau et al., 2015; Kelly et al., 2017). But towards the present day, in those peatlands that exemplify contemporary ecosystem changes occurring across tropical forested biomes (e.g., Cole et al., 2019; Malhi et al., 2014), fire events have increased in frequency and are linked to a lack of recovery of peatland vegetation, due to their greater intensity and coupling with deforestation and other disturbances.

One driver of change with still largely unknown directions and consequences, is climate. Across the three tropical peatland areas, climate has fluctuated between wetter and drier periods, equating to more or less favourable conditions for peat accumulation, respectively. In Amazonia, drier conditions have resulted in declines and even hiatuses in peat accumulation (Kelly et al., 2017; Swindles et al., 2018b). In the Central Congo Basin, increased aridity and prolonged drought also apparently caused a hiatus, and to a reduced ability of the peatland ecosystem to recover from burning (Hubau et al., 2015). By contrast, and somewhat counter-intuitively, at Aucayacu in northern Peru, periods of regional climatic drying appear to have encouraged peat accumulation in the flooded forest swamp phase. Later, however, after the transition to ombrotrophy and thus establishment of different ecohydrological conditions, a similar regional drought caused a pronounced slowing of peat accumulation (Swindles et al., 2018b). This pattern illustrates the complexity of peatland responses to climatic and other

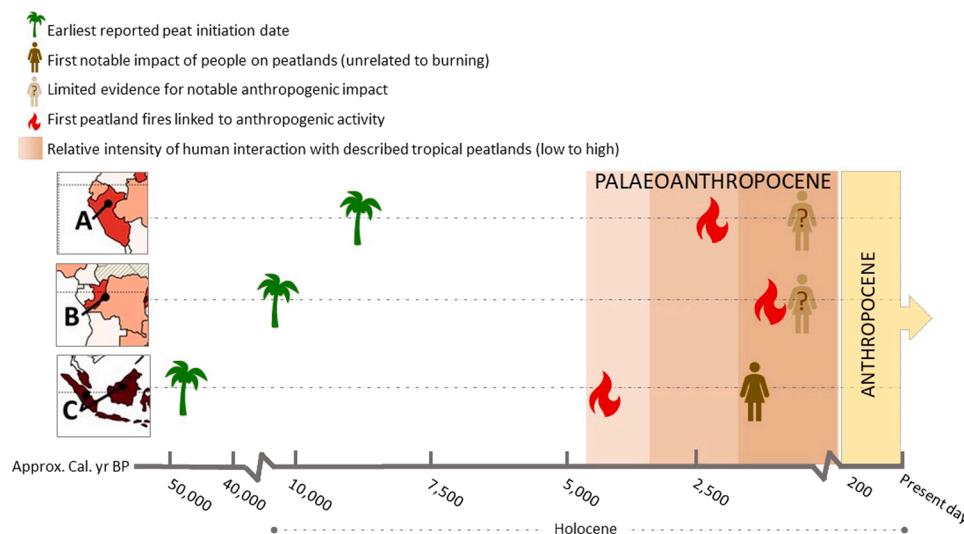


Fig. 4. A timeline of the key events evidenced from the reviewed palaeoecological records from the tropical peatland regions, A – Amazonia (Peru), B – Central Congo Basin (Democratic Republic of Congo, Republic of Congo), and C - Southeast Asia (Indonesia, Malaysia). (For information on the regional images, see Fig. 1.) The timeline demonstrates the approximate temporal placement of the presumed palaeoanthropocene and anthropocene periods, as conceptualised in this review, relative to the Holocene (last c. 11,700 years). (See Girkin et al., in progress, for a corresponding review pertaining to the anthropocene.).

environmental drivers. Many, likely interacting factors have potential to influence the trajectory of peatland ecohydrological change. It also further highlights the importance of understanding local conditions.

3.1. Insights for the anthropocene

The palaeoecological records synthesized in this review demonstrate the temporary nature of the effects of people and of environmental change on tropical peatlands through the palaeoanthropocene. The low intensity of these effects has also enabled the ecosystems to recover. By contrast, notably in Southeast Asia, evidence from human interactions with tropical peatlands in the last c. 200 years illustrates an intensification of impacts and a lack of ecosystem recovery (Fig. 5). Can insights from the earlier palaeoanthropocene help to predict how peatlands might respond to anthropogenic perturbations and climate change in the future?

In terms of anthropogenic perturbations, palaeoecological data indicate that tropical peatland vegetation has persisted through periods

of human presence in the landscape, including episodes of burning associated with both anthropogenic and natural drivers (Fig. 5). The dynamics of tropical peatlands in the last c. 200 years, however, reveal a different story (Girkin et al., in progress). The perturbations observed within this more recent anthropocene period in the tropical peatland region of Southeast Asia, which has undergone the most transformation, apparently differ in two significant ways from those of the palaeoanthropocene. These differences provide important and cautionary insights for understanding how Central African and Amazonian peatlands could respond if exposed to similar perturbations (Lilleskov et al., 2019).

Firstly, the intensity and spatial extent of impacts are larger today. Smaller-scale clearances of peatland vegetation characterised the deforestation practices of the palaeoanthropocene, whereas clear-felling of forest over large areas is common where peatlands are converted to commercial plantations (e.g., Goldstein, 2016). Drainage canals are constructed and maintained, using mechanised vehicles, often in extensive networks (Hooijer et al., 2012; Ritzema et al., 1998). No

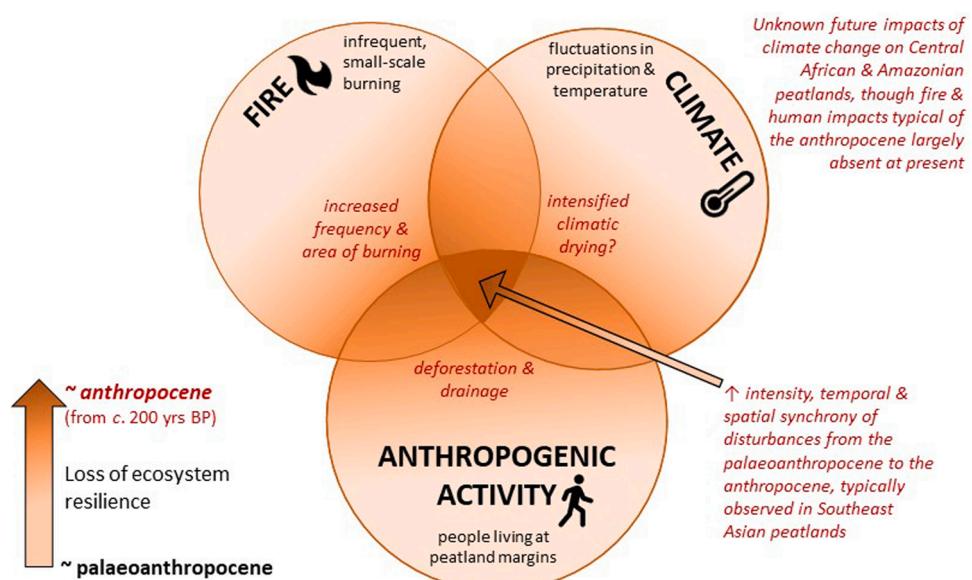


Fig. 5. The three main forms of disturbance to tropical peatlands explored in this review, within the: (i) palaeoanthropocene (black text); and (ii) anthropocene (red text). A loss of resilience of peatland ecosystems in response to the differing intensities and combinations of disturbances in the last c. 200 years compared to those observed prior to this, in the palaeoanthropocene, is illustrated by many peatlands in Southeast Asia.

evidence is available for deliberate peatland drainage before 200 years ago, and certainly not on this scale. Fires have greatly increased in intensity and geographical spread since the 1980s in Southeast Asian peatlands. Their frequency is becoming uncoupled from regional El Niño Southern Oscillation (ENSO) related climatic drying (Gaveau et al., 2014), with extensive burning now taking place annually. The fire regimes of the palaeoanthropocene are characterised by much lower intensity fires with longer return intervals. Consensus is also emerging that the rate of change and predicted elevations in temperature resulting from future anthropogenic global warming are unprecedented for the period in which the tropical peatlands have been extant.

The second major difference is the synchronous and summative nature of contemporary perturbations that rarely occur in isolation (e.g., Loisel et al., 2020; Wijedasa et al., 2017). In many cases, ongoing anthropogenic climate change is the backdrop to large-scale land use change (Fig. 5). Ecosystem conversion disrupts the hydrological and ecological integrity of the peatland unit and its fundamental system of self-regulation (Dommain et al., 2010). Under drier and warmer conditions where sources of ignition are more common in the landscape, peatlands will unlikely recover without significant human intervention (e.g., Graham and Page, 2018; Page et al., 2009).

With respect to the responses of tropical peatlands to climate change, palaeoenvironmental records indicate that future changes in precipitation could cause hiatuses in carbon accumulation. Several records (e.g., Anshari et al., 2001; Hapsari et al., 2017; Swindles et al., 2018b) indicate which climatic and hydrological conditions favour renewed peat accumulation or the development of new peatland sites, i.e., where the water table is at the surface and peat-forming vegetation can grow. These records also demonstrate that the outcome of climatic perturbations on a peatland's carbon balance, i.e., organic matter accumulation relative to decay, depends on the hydrological regime of the peatland. A dry interval, for example, would affect ombrotrophic (rain-fed) and minerotrophic (river-fed) peatlands differently. For coastal peatlands, sea-level rise may counter potential gains in organic matter accumulation triggered by warmer and wetter conditions through flooding low-lying ecosystems, e.g., in Sarawak, Malaysian Borneo (Hooijer et al., 2015).

Fundamentally, the palaeoenvironmental records reviewed in this paper demonstrate that peatlands can recover from major climatic changes. They can also recover from incidences of human impact and from burning, albeit of much lower intensities of disturbance than are typically experienced by Southeast Asian peatlands today. These records contain scenarios for how people and peatlands can coexist over long timescales, with the potential to illustrate alternative futures for human-peatland interactions in the anthropocene.

3.2. Research priorities

Palaeoecology provides multiple 'natural experiments' in which the variables of ecology, hydrology, climate, and human activity come together in different combinations at different times, and at different sites. The resulting effects on ecosystem functions, such as carbon sequestration, are measurable. These measurements can contribute to our understanding of how peatlands will respond to future, primarily anthropogenic, environmental changes by contextualising the effects of natural versus anthropogenic processes on tropical peatlands. High resolution palaeoecological records provide information on how long peatlands took to recover from different kinds of disturbance in the past and on the details of ecological recovery. In addition, high resolution radiocarbon dating reveals past patterns of carbon sequestration and carbon emissions from tropical peatlands. This is important because limited knowledge is available of where, when and how peatlands in the past transitioned from serving as a carbon sink to a carbon source (Hooijer et al., 2010; Wang et al., 2018), making it difficult to judge the relative contribution of natural versus anthropogenic factors to these shifts. Although it is well understood that climatic drying can cause a

peatland's water table to fall below the surface for significant parts of the year, a situation unconducive for peat accumulation, our ability to predict exactly how ongoing anthropogenic climate change will influence carbon sequestration across tropical peatlands in the near future remains limited (Loisel et al., 2020). The results of both natural and computer-simulated experiments exploring the carbon cycle, where palaeoecological data are useful to parameterize models, are of increasing importance as every nation is encouraged to account for and minimise their greenhouse gas emissions. Peatlands are a significant, if as yet poorly quantified contributor to or mitigator of these emissions (Ekardt et al., 2020; Kumar et al., 2020).

Tropical peatlands have demonstrated resilience to perturbations, such as climatic changes, throughout prehistory, but they are also quickly degraded by more intense, short-lived disturbances caused by human activities. Significant gaps remain in our knowledge of peatland processes, particularly around positive and negative feedbacks that act to destabilise or stabilise the system (Page and Baird, 2016). An urgent need exists to understand more about the dynamics and resilience of peatlands, including the most likely drivers that lead to the loss of their peat-forming potential.

Another priority of tropical peatland research is to engage with communities who live in and around these ecosystems and use them for their livelihoods in ways that might have much in common with palaeoanthropocene human-peatland interactions (as in tropical forests, i.e., Roberts et al., 2021, 2018). Engagement with local people is necessary to address socio-ecological, political and economic issues, in addition to scientific questions. More effort is required to understand how to protect and restore peatland ecosystems with respect to not only the engineering challenges, but also the challenges of securing support from all peatland stakeholders. Peatland conservation and restoration may require: measures to protect, or explore collaboratively, alternative local livelihoods; monitoring and regulation of agribusinesses engaged in peatland use and management; and resources, training, legislation and partnerships to enable implementation of the above (Carmenta et al., 2020; Harrison et al., 2020). For effective conservation and restoration, understanding how societies value and care for peatlands is essential (Byg et al., 2020, 2017), in a relationship that may extend deep into prehistory, and the socio-economic and political context in which peatland management decisions are currently made (Dohong et al., 2017) and resolved on the ground (O'Reilly et al., 2020).

4. Conclusion

Review and synthesis of the literature on tropical peatlands provide insights that address the three questions posed in this paper.

Firstly, prior to transformative human activity, the majority of peatlands across lowland Southeast Asia, the Central Congo Basin and Amazonia, shared a common ecology and development trajectory: of forest vegetation in waterlogged conditions resulting in the accumulation of peat carbon. Specific regional and local peatland dynamics differed, for example, the timing of peat initiation and hydrological and vegetation development pathways, determined by the local climatic, geological, hydrological and ecological conditions, and history.

Secondly, palaeoecological records indicate that tropical peat swamp forest ecosystems have persisted through a variety of disturbances: episodes of climatic drying and drought, relatively low-intensity and intermittent burning, and incidences of localised and short-term anthropogenic forest clearance, with the dynamics of disturbance and recovery specific to each locality. Several studies have demonstrated hiatuses in peat accumulation linked to past climatic changes, followed by evidence of renewed peat accumulation (e.g., Anshari et al., 2004; Hubau et al., 2015; Kelly et al., 2017).

Thirdly, peatland ecosystem resilience is not evident where anthropogenic activity has become more intensive, more frequent, and larger in scale in the last c. 200 years (e.g., Cole et al., 2015), demonstrating the onset of transformative human impacts on these ecosystems. More

extensive movement of people into, and intensive use of, peatland areas, along with the use of fire and drainage to manipulate these ecosystems, have led to significant losses of vegetation and carbon, primarily in Indonesia and Malaysia (Girkin et al., in progress). In line with observations from the palaeoanthropocene, however, regional idiosyncrasies still dominate. No one universal type of anthropogenic impact affects all tropical peatlands. This is exemplified by the persistence of largely intact peatlands in the Central Congo and Amazon basins.

Tropical peatlands have accumulated carbon over millenia as a result of waterlogged conditions. These conditions pose challenges for local communities, yet palaeoecological studies indicate that people have interacted with these landscapes throughout the Holocene, and that tropical peatlands have responded dynamically to low-level prehistoric, palaeoanthropocene human activity. Contemporary studies demonstrate the loss of ecosystem function and extent of transformation that is possible in tropical peatlands since industrialised land use conversion began. If these ecosystems, rich in resources of local to global value and vulnerable to irreversible transformation, are to persist, more careful consideration is necessary on how we interact with them, perhaps learning from the deeper palaeoanthropocene period.

Several areas of future research are suggested to address outstanding gaps in knowledge. Firstly, acquisition and analysis of high resolution palaeoecological and palaeoenvironmental records from the under-researched tropical peatland localities, coupled with high resolution radiocarbon dating, will enable us to understand more about natural and anthropogenic processes, and their interactions, in these ecosystems. Secondly, feeding these data into models of peatland ecosystems will help to fill vital knowledge gaps, namely around carbon sequestration and emission dynamics through time. Thirdly, future research should prioritise working collaboratively with people living in and around tropical peatlands, to understand their livelihood needs and aspirations, and explore pathways for sustainable interaction with these invaluable ecosystems.

CRediT authorship contribution statement

LESC and NTG conceived the article. KAH, DH, CMÅ and KHR wrote the first draft. All authors contributed to subsequent revisions of the article.

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.

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Note

This article is the first of a two-part review of *Tropical peatlands in the anthropocene*. The articles have been written together to provide complementary reviews of the past, present and future interactions of people with tropical peatlands, focusing on those in Southeast Asia, Central

Africa and Amazonia. *Tropical peatlands in the anthropocene: lessons from the past* (herein) explores: (i) the state of knowledge on tropical peatland development and ecosystem responses to anthropogenic disturbance in the palaeoanthropocene (the period following the earliest evidence for human presence), using evidence from palaeoecology, and (ii) how past disturbances compare with contemporary levels of anthropogenic disturbance and the insights they provide for predicting future responses and ecosystem resilience. *Tropical peatlands in the anthropocene: the present and the future* (the second article; Girkin et al., in progress) describes: (i) the patterns of human interaction with tropical peatlands in the 20th and early 21st centuries, and (ii) how these impacts could be mitigated in the future. The articles cross-reference each other to indicate where the reader can learn more on themes that are covered more fully in the other.

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