






Tropical peatlands and their contribution to the global carbon cycle and climate change

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Abstract

Peatlands are carbon-rich ecosystems that cover 185–423 million hectares (Mha) of the earth's surface. The majority of the world's peatlands are in temperate and boreal zones, whereas tropical ones cover only a total area of 90–170 Mha. However, there are still considerable uncertainties in C stock estimates as well as a lack of information about depth, bulk density and carbon accumulation rates. The incomplete data are notable especially in tropical peatlands located in South America, which are estimated to have the largest area of peatlands in the tropical zone. This paper displays the current state of knowledge surrounding tropical peatlands and their biophysical characteristics, distribution and carbon stock, role in the global climate, the impacts of direct human disturbances on carbon accumulation rates and greenhouse gas (GHG) emissions. Based on the new peat extension and depth data, we estimate that tropical peatlands store 152–288 Gt C, or about half of the global peatland emitted carbon. We discuss the knowledge gaps in research on distribution, depth, C stock and fluxes in these ecosystems which play an important role in the global carbon cycle and risk releasing large quantities of GHGs into the atmosphere (CO₂ and CH₄) when subjected to anthropogenic interferences (e.g., drainage and deforestation). Recent studies show that although climate change has an impact on the carbon fluxes of these ecosystems, the direct anthropogenic disturbance may play a greater role. The future of these systems as carbon sinks will depend on advancing current scientific knowledge and incorporating local understanding to support policies geared toward managing and conserving peatlands in vulnerable regions, such as the Amazon where recent records show increased forest fires and deforestation.

KEYWORDS

carbon cycling, climate change, greenhouse gas emissions, land-use change, tropical peatlands

1 | INTRODUCTION

Peatlands are a type of wetland that form when waterlogged anoxic conditions limit the decomposition and respiration of organic matter (Vitt, 2013) and creates an accumulation of peat. Like most wetlands, peatlands can have dense vegetation cover with lacustrine

characteristics (presence of the water plants), sometimes influenced by river seasonality and dynamics (Lähteenoja et al., 2013), as well as seasonal or annual floods with geomorphological features where water is retained (Finlayson & Milton, 2018; Kelly (Letcher) et al., 2013; Warner & Rubec, 1997). While there is no absolute consensus on what defines peat, most studies have settled on two criteria: soils

that have both an organic matter content of at least 30% (Reiche et al., 2010; Sorensen, 1993), though typically with a higher threshold of 50% (Gumbricht et al., 2017) or 65% (e.g., Dargie et al., 2017), and a minimum depth of 30–40 cm (Dargie et al., 2017; Page & Baird, 2016; Page et al., 2011).

These ecosystems provide unique ecosystem services, such as water storage by regulating the river's discharge, thereby benefiting ecosystems and human communities (Harenda et al., 2018), along with regulating water flow in hydrographic basins, including buffering floods (Joseph, 2005). Moreover, they are fertile fields for agricultural and horticultural production (Rieley et al., 2008), play an important role in sediment, nutrient and carbon (C) retention (Rieley et al., 2008), and are home to a unique biodiversity that includes a variety of endemic species (Wilson et al., 2001).

Peatlands cover a total area of about 185–423 million hectares (Mha) throughout the world (1.2%–2.8% of the earth's total land area; Xu et al., 2018). In the tropical area, zones covered by peat range from 90 to 170 Mha and are located mainly in South America, Southeast Asia and Central Africa (Gumbricht et al., 2017). These systems store large amounts of C (469–694 Giga tons of C; Lähdenoja et al., 2012; Leifeld & Menichetti, 2018; Page et al., 2011; Yu, Fang, et al., 2010; Yu, Loisel, et al., 2010) and act as net sinks of atmospheric carbon dioxide (CO₂). However, they can also act as major sources of greenhouse gas (GHG) emissions, such as CO₂ and methane (CH₄), into the atmosphere (Leifeld & Menichetti, 2018; Roulet, 2012), due to either natural processes such as changes in autotrophic and heterotrophic respiration rates, changes in river paths, droughts and natural fires or anthropogenic interferences including logging, drainage, deforestation, fires, and land-use and land cover (LULC) changes (Hooijer et al., 2010; Leng et al., 2019; Yule et al., 2016).

Changes to the gross C uptake and/or release of these ecosystems can reverse whole-peatlands carbon budget and significantly alter the current and future global climate (Worrall et al., 2011; Wu & Roulet, 2014). In recent years, tropical peatlands have been receiving more attention not only because of their contribution to the global carbon budget and climate change but also because of new estimates of larger peatland areas in the tropics (Dargie et al., 2017; Draper et al., 2014; Gumbricht et al., 2017; Page et al., 2011; Xu et al., 2018). To understand how tropical peatlands contribute to global climate change, it is important to understand their geographic coverage, capacity to store and sequester carbon, and the main factors that drive their degradation (Yu, 2011).

In contrast to temperate peatlands, in which the relationship between climate, ecosystem dynamics and carbon (C) accumulation is well studied, the body of literature on tropical peatlands is mainly concentrated on Southeast Asia (Page et al., 1999; Hartmann & Niklaus, 2012), Peru in South America (Kelly et al., 2017; Lähdenoja et al., 2012; Roucoux et al., 2017; Sorribas et al., 2016) and, to a lesser degree, the Cuvette Centrale basin in Africa (Dargie et al., 2017, 2019). This paper presents an extensive review about tropical peatlands in terms of their biophysical conditions that promotes peat formation (e.g., temperature, rainfall, groundwater, nutrient pool and substrate quality), spatial distribution and carbon stock, as well as

how these ecosystems are affected under different disturbance regimes. Moreover, the paper identifies and discusses knowledge gaps surrounding this highly threatened, yet poorly understood ecosystem in several regions of the tropical area.

2 | PEAT FORMATION PROCESS AND BIOPHYSICAL CHARACTERISTICS OF TROPICAL PEATLANDS

In general, peat is formed when the amount of photosynthetically produced organic matter exceeds the loss of organic matter through fire, decomposition and lateral loss (Hodgkins et al., 2018). Peat formation is led by several factors, such as hydrological dynamics (groundwater, seasonality and river dynamics), climatic characteristics (temperature and precipitation), underlying topography and geology of the area, nutrient pool, chemistry and vegetation dynamics (FAO, 2014; Hapsari et al., 2017; Yu, 2012). Hydrological dynamics are among the main factors that regulate peatlands and control peat formation processes, predominant vegetation, nutrient content, carbon sequestration capacity and decomposition processes (Blodau, 2002; Limpens et al., 2008). In certain peatlands, where water-saturated condition occurs all year around, peat soil profiles identified peat domes that reach depths up to 15 m (Gumbricht et al., 2017).

In many tropical peatlands, the soil is seasonally flooded mostly by large rivers with high nutrient content and intense sediment deposition. These factors associated to high precipitation patterns and temperatures favor the development of flooded peatlands concomitant of dense tree coverage, with high floristic diversity and high net primary productivity (Gillman et al., 2015) and absence of mosses (Page et al., 1999). On the contrary, in many northern peatlands, the low temperature and low nutrient inputs favors the dominance of the bryophyte genus *Sphagnum* (Clymo, 1987) and a shrub layer is usually well developed with sparse occurrence of large trees (Ingram, 1978; Vitt, 2013).

The peatland vegetation cover described above is an important characteristic that influences the composition and the process of peat formation. Peat in tropical peatlands is mainly formed by woody material and dead branches and roots (Dommain et al., 2015; Gallego-Sala et al., 2018), whereas most of the peat in northern peatlands is formed of *Sphagnum* mosses and sedges. The woody material contains high C:N and lignin:N ratios that degrade slowly (Gandois et al., 2012, 2014). This promotes the release of phenolic components that inhibit decomposition (Wang et al., 2015). These conditions increase the aromatic content in the soil and create a reduced oxidation state in which C remains and recalcitrance is high, despite high temperatures (Hodgkins et al., 2018). Divergent from the peat formation process in northern peatlands, the low soil temperatures, freezing and the acid characteristics of the cell wall of *Sphagnum* species favor the reduction of C oxidative processes even with abundant labile carbohydrates (*Sphagnum*; Clymo, 1984; Vitt, 2013).

In general, there are two types of peatlands: ombrotrophic and minerotrophic (Clymo, 1987), being divided according to the origin

of nutrient input in the system. Ombrotrophic peatlands are influenced exclusively by water from precipitation (no other sources; Bourbonniere, 2009; Takada et al., 2016; Vitt, 2013) while minerotrophic peatlands are typically formed in depressions and floodplains and receive mineral nutrients with incoming surface or groundwater (Bourbonniere, 2009; International Peatland Society (IPS), n.d.; Lhteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lhteenoja, Ruokolainen, Schulman, & Oinonen, 2009; Takada et al., 2016; Vitt, 2013).

At the start of the peat formation, the peatland is initially minerotrophic (Clymo, 1987). As the peat layer grows in height, the dome becomes elevated and the peatland may no longer be affected by the river that feeds into it or by the entry of groundwater, thereby obtaining water exclusively from precipitation and becoming ombrotrophic. At this stage, nutrient and mineral deposits are mainly from atmospheric dry deposition or precipitation, but large amounts of nutrients can also come from dust and air pollution (Ponette-Gonzlez et al., 2016). For instance, according to Swindles et al. (2018), the oldest Peruvian tropical peatlands discovered to date were formed in three stages: first, peat was formed in an abandoned river channel with open water and aquatic plants; then inundated forest swamp was formed and finally the peat dome raised as the peat accumulated.

Many peatlands in tropical region are minerotrophic having been formed from the lateral migration of rivers (Lhteenoja et al., 2012, 2013; Lhteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lhteenoja, Ruokolainen, Schulman, & Oinonen, 2009; Schumann & Joosten, 2008). Most of them are located in river deltas, floodplain areas, abandoned river channels and shallow oxbow lakes (dead arms; Baker et al., 2014; Craft & C.B.T.-C., 2016; Rebelo et al., 2009; Rieley et al., 2008). However, there are examples of ombrotrophic peat bogs in the tropics in South America (Page et al., n.d.; Swindles et al., 2018), Southeast Asia (Page et al., 2006; Wsten et al., 2008) and Africa (Dargie et al., 2017) reported in the literature. In Southeast Asia, different formation processes have been observed and most of the peat is currently ombrotrophic, with some related to ancient sea-level rise and an increase of Holocene precipitation (Dommain et al., 2011). Thus, even at similar latitudes, the mechanisms of peat formation, regulation and carbon accumulation can differ between regions.

3 | DISTRIBUTION AND CARBON STOCK OF TROPICAL PEATLANDS

There is a lot of variation in the published data about the occurrence and distribution of tropical peatlands. Up to a few years ago, Southeast Asia (Indonesia, East Sumatra, Kalimantan, Papua New Guinea, Papua New Guinea and Malaysia) was considered to have the largest peatland C reservoirs in the tropical area (Dargie et al., 2017; Joosten, 2009; Lhteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lhteenoja, Ruokolainen, Schulman, & Oinonen, 2009; Miettinen & Liew, 2010; Miettinen et al., 2016;

Page et al., 2002, 2011); however, large intact peatlands have recently been described in South America (Draper et al., 2014) and Africa (Dargie et al., 2017). For example, Dargie et al. (2017) used field measurements combined with remote sensing data to estimate the extent of a peat complex in the Cuvette Centrale region of the Congo Basin, the largest intact tropical peatland to date at 14.6 (13.2–15.6) Mha. As a result of these recent studies, estimates of tropical peatlands have been revised (see Gumbrecht et al., 2017; Xu et al., 2018) and the total area of tropical peatlands is now considered to cover 90–170 Mha (23%–30% of the total area covered by peatlands throughout the world). This new estimate is two to three

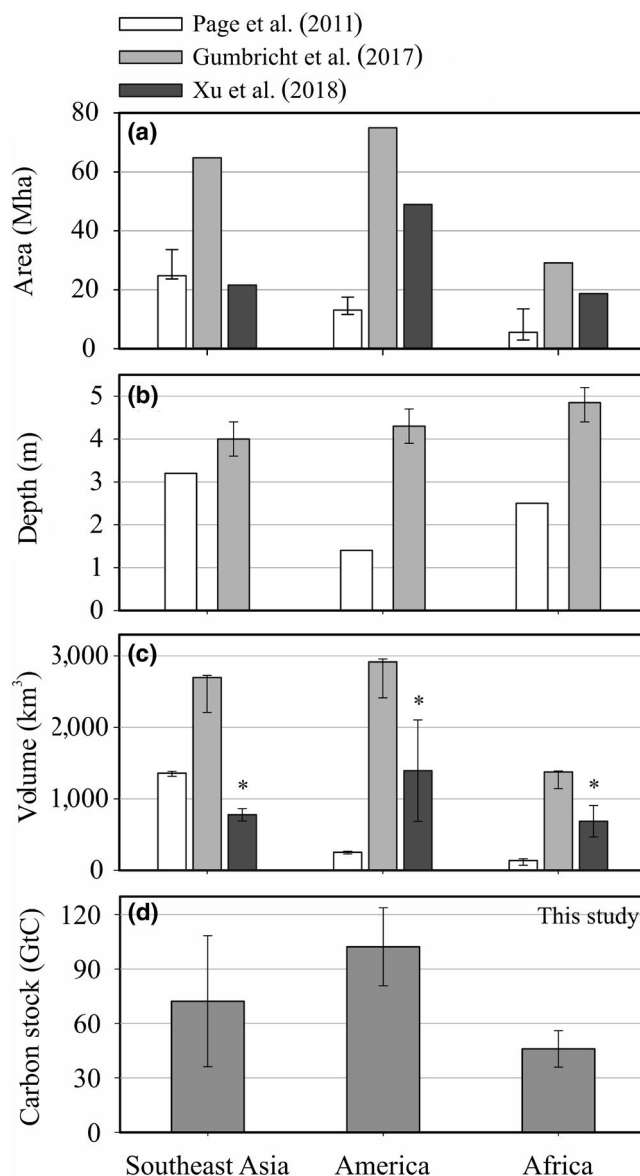


FIGURE 1 Estimated peat area (a), depth (b) and volume (c), presented by Page et al. (2011), Gumbrecht et al. (2017) and Xu et al. (2018) of tropical peatlands. (d) Estimated carbon stock (Gt C) in tropical peatlands. Error bars are minimum and maximum estimates when available. *Values estimated using peatland area from Xu et al. (2018) and mean depth from Gumbrecht et al. (2017) and Page et al. (2011)

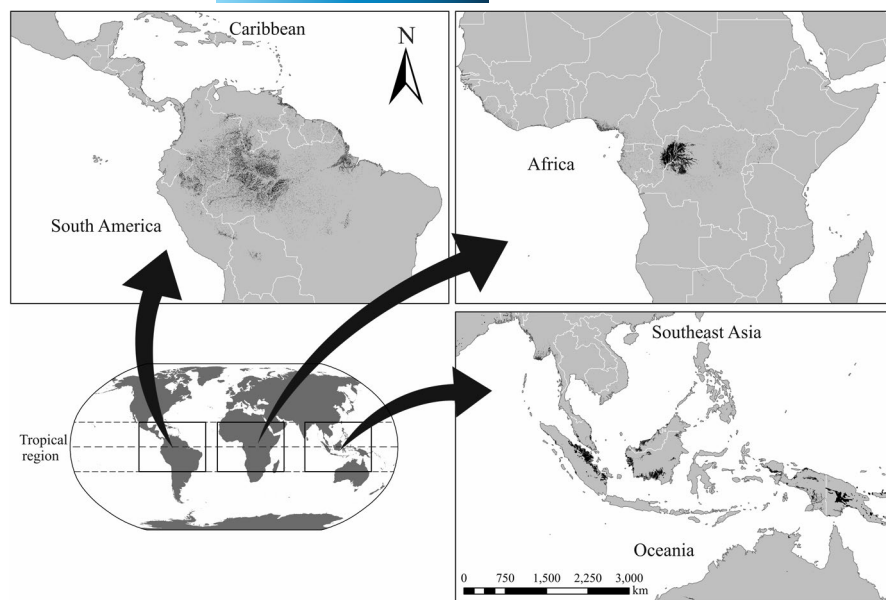


FIGURE 2 Distribution of peatlands in tropical regions. Data from Xu et al. (2018)

times larger than the 56 Mha that Page et al. (2011) reported and which led to new discussions on the physical and chemical factors that define wetlands and peatlands (Figure 1).

The new estimates of total peat cover in the tropics represent a volume of about 3,850–7,268 km³ (estimated using area from Gumbrecht et al., 2017 and Xu et al., 2018, and mean depth from Gumbrecht et al., 2017), which is much higher than the previous estimate of 1,758 km³ (Page et al., 2011; Figure 1). Considering these estimates, the largest reserves of peat are located in Brazil (area and volume of 23 Mha and 900 km³, respectively), Indonesia (14 Mha and 578 km³) and the Democratic Republic of the Congo (9 Mha and 445 km³, Figure 2). It is important to note that in Indonesia there is a longer history of fieldwork and, therefore, a relatively large database of ground-truthing points (Jaenicke et al., 2008), whereas to date there are relatively few published field data from the Congo Basin (Dargie et al., 2017), and even fewer from Brazil (Lähteenoja et al., 2013).

Based on the estimated volume of peat in the tropics and the average carbon content per km³ of peat (Lähteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lähteenoja, Ruokolainen, Schulman, & Oinonen, 2009), we estimated that peat in the tropics stores an equivalent of 152–288 Gt C (Table 1), which is significantly higher than previously reported estimates of 119.2 Gt C (Leifeld & Menichetti, 2018), 104.7 Gt C (Dargie et al., 2017), 90 Gt C (Moore et al., 2013), 88.6 Gt C (Page et al., 2011) and 52 Gt C (Zoltai & Martikainen, 1996). The stock of 152–288 Gt C is equivalent to the amount of C emitted by burning fossil fuels at a rate of 10 Gt C/year for the next 15–30 years (Murdiyarso et al., 2010; Raupach et al., 2013). C emission from fossil fuel in 2014 were 9.8 Gt C (<https://www.globalcarbonproject.org/>). In addition, the mid-range value of our estimated C stock (215 Gt) represents about 25% of the terrestrial carbon pool in the tropics (846.3 Gt C), considering both carbon aboveground (374.9 Gt C, phytomass) and stored in the soil (571.3 Gt C, Scharlemann et al., 2014).

The main explanation for the large range in our new estimate of tropical peatland C stock (152–288 Gt C) is the different

methodological approaches adopted for the estimation of the area. For instance, the numerical model that Gumbrecht et al. (2017) adopted to estimate total area uses a set of factors associated with hydrological modeling, time series of vegetation, soil moisture and hydro-geomorphological data. Xu et al. (2018) considered a wide variety of sources from different authors and regions and applied criteria of relevance, spatial resolution as well as age, and combined these data sources to produce a new amalgamated global map of peatland distribution. For areas where peatland-specific datasets were not available, they estimated peatland extent based on the distribution of histosols derived from the Harmonized World Soil Database v1.2 (HWSD). Page et al. (2011) considered data from national soil inventories from different countries. Data from the latter may not be comparable given the different definitions of peat and inclusion of non-peat organic soils. The new estimates of Gumbrecht et al. (2017) and Xu et al. (2018) suggest that the extent of differing with what was previously reported of what was previously reported (Page et al., 2011).

Peatlands in the tropical zone are found in many countries; however, some regions have large peatland areas and carbon stock. The South American peatlands are estimated to be located mainly in the Rio Negro Basin (Brazil) and Pastaza-Marañón Foreland Basin (PMFB, Peru; Draper et al., 2014; Lähteenoja et al., 2013; Lähteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lähteenoja, Ruokolainen, Schulman, & Oinonen, 2009); however, to date there has been limited ground-truthing of the former (Lähteenoja et al., 2013) and therefore larger uncertainty associated with the extent and volume of Brazilian peatlands. The PMFB alone is estimated to represent a C stock of 3.14 (0.44–8.15) Gt C with 90% of this total contained belowground. The large uncertainty reflects the need for more field data.

In Africa, peatlands occur in many countries, but extensive peatlands are located in the Rugezi Marsh in Rwanda, the Okavango Delta in Botswana, the Sudd catchment in Sudan and in particular the Congo basin (Grundling & Grootjans, 2018). The Cuvette Centrale

TABLE 1 Tropical peatland carbon stock (Gt C) showing mean values and/or (range) if available

System/location	Land cover	Carbon stock (Gt C)	Reference
Tropical Asia		68.9 (66.6–70.4)	Page et al. (2011)
Central Kalimantan, South Sumatra and West Papua	Peat swamp forest	55 ± 10	Jaenicke et al. (2008)
Indonesia	Native Forest	23.2	Dommain et al. (2014)
Indonesia	Native vegetation and impacted areas	30	Rudiyanto et al. (2015)
Indonesia	Native vegetation and impacted areas	57.4	Page et al. (2011)
Malaysia	Native vegetation and impacted areas	9.1	Page et al. (2011)
Southeast Asia	Native vegetation and impacted areas	172	Sjögersten et al. (2014)
Southeast Asia	Native Forest	65	Dommain et al. (2011)
Southeast Asia	Native vegetation and impacted areas	20	Dommain et al. (2011, 2014)
Tropical America		12.7 (11.5–13.4)	Page et al. (2011)
Peru (Pastaza-Marañon)	Native Forest	3.14 (0.4–8.1)	Baker (2014)
Peru (Pastaza-Marañon)	Native Forest	3.12 (0.8–9.5)	Lähteenoja et al. (2012)
Tropical Africa		6.9 (3.5–8.1)	Page et al. (2011)
Cuvette Centrale, Congo	Native Forest	30.6 (6.3–46.8)	Dargie et al. (2017)
Global scenario		(469–694)	Page et al. (2011); Yu, Fang, et al. (2010); Yu, Loisel, et al. (2010)
Tropical undisturbed		(139–251)	Miettinen and Liew (2010); Zoltai (1996)
Tropical disturbed		(13–37)	Kurnianto et al. (2015); Zoltai and Martikainen (1996)
Tropical		(152–288)	This study
Non-tropical		(387–394)	Gorham (1991); Immirzi and Maltby (1993); Page et al. (2011)

wetland of the Congo basin is estimated to contain a C stock of 30.6 (6.3–46.8) Gt C (Bwangoy et al., 2010; Dargie et al., 2017; Table 1). Again, note the large uncertainty range, which is a reflection of the fact that this estimate is based on a relatively sparse set of field measurements (Dargie et al., 2017). Peatlands have also been reported in southern Africa, mainly along the eastern coast (Mozambique Coastal Plain) and in the central plateau (Grundlin and Gloor, 2005; McWethy et al., 2016).

The total area covered by peatlands in Southeast Asia is roughly 21 Mha (Xu et al., 2018). Most of these peatlands are in Indonesia (15 Mha), Malaysia (2.2 Mha), Thailand (40,000 ha) and, to a lesser extent, Vietnam, Brunei and the Philippines. A recent estimate put the peat C store in Indonesia alone at 28.1 (13.6–40.5) Gt C (Warren et al., 2017). Unlike other large tropical peat reservoirs in the world that are either untouched or have had little alteration, peatlands in Southeast Asia have faced intense anthropogenic disturbances since the 1970s, when permission was granted to use these extensive areas for commercial purposes.

Due to the current large uncertainties around carbon stocks in tropical peatlands, it is notorious that with the advance of knowledge in the identification of tropical peatlands (mainly extension and depth) resulted in significantly higher estimates for carbon stocks in the tropical zones. For South America and Africa, the large uncertainty reflects the need for more field data (Dargie et al., 2017).

Peatlands in relatively remote African and Amazonian regions currently face low human intervention, however as anthropogenic activities, such as commercial agriculture, exploitation of waters for hydropower (in Andes), forestry (including deforestation), construction of impoundments, roads and ports, and gas exploration in peatlands increase, so does the degradation of these ecosystems (Baker et al., 2014; Lähteenoja, Ruokolainen, Schulman, & Alvarez, 2009; Lähteenoja, Ruokolainen, Schulman, & Oinonen, 2009; Roucoux et al., 2017). Therefore, decreasing uncertainties about area, and C stock in such remote regions is crucial to estimate the true C accumulation potential of these peatlands and to prevent future impact of human activities that peatlands may face mainly in South America and Africa.

4 | TROPICAL PEATLAND CARBON ACCUMULATION, CLIMATE CHANGE AND THE GLOBAL CARBON CYCLE

The carbon accumulation rates in undisturbed tropical peatlands range from 24 to 300 g C m⁻² year⁻¹ (Table 2), while for boreal and temperate undisturbed peatlands they are generally lower (vary from 2 to 271 g C m⁻² year⁻¹, Olefeldt et al., 2012; Renou-Wilson et al., 2019). Although substantial variation occurs depending on

TABLE 2 Carbon accumulation rates ($\text{g C m}^{-2} \text{ year}^{-1}$) from tropical peatlands and from non-tropical peatlands (for comparison) showing mean values and/or (range) if available. Positive values are carbon accumulation and negative values are carbon loss

System/location	Land cover	Carbon accumulation rates ($\text{g C m}^{-2} \text{ year}^{-1}$)	Reference
Tropical Asia			
Central Kalimantan	Native Forest	22.3 (6.5–121.4)	Page et al. (2004)
Central Kalimantan	Native Forest	31.3 (16.6–73.2)	Dommain et al. (2011)
Central Sumatra, Indonesia	Secondary peat swamp forest	55	Hapsari et al. (2017)
Indonesia	Native Forest	72	Dommain et al. (2015)
Indonesia	Native Forest	94	Page et al. (2004)
Brunei (Borneo)	Peat swamp forest (mangrove forest)	300	Dommain et al. (2015)
Brunei (Borneo)	Peat swamp forest (<i>Shorea albida</i>)	50	Dommain et al. (2015)
Kalimantan Central	Drained peatlands and forest	85	Page et al. (2004)
Kalimantan, Indonesia	Peat swamp forest	94.3	Page et al. (2004)
Malaysia	Rain forest	(79–147)	Kosugi et al. (2008)
Riau, Sumatra	Native Forest	81 ± 1.4	Neuzil (1997)
Sarawak, Malaysia	Undrained peat swamp forest	8.46 ± 0.51	Wong et al. (2020)
Sarawak, Malaysia	Relatively disturbed secondary peat swamp forest	4.17 ± 0.69	Wong et al. (2020)
Sarawak, Malaysia	Oil palm plantation	2.19 ± 0.21	Wong et al. (2020)
Southeast Asia	Native forest	(30–270)	Page et al. (2004)
Southeast Asia	Drained affected peat swamp forest	(–499 to –174)	Rieley et al. (2008)
West Kalimantan	Drained peatlands and forest	(74–85)	Neuzil (1997)
Tropical America			
Amazonia	Amazonian forests without El Niño event	–100	Saleska et al. (2003)
Amazonia	Amazonian forests with El Niño event	(100–200)	Saleska et al. (2003)
Amazonian peatlands	Forested peatland	(26–195)	Lähteenoja et al. (2009)
Costa Rica	Fragments of Yollillo (<i>Raphia</i>)	(250–260)	Mitsch et al. (2010)
French Guiana	Pristine tropical rain forest	–138	Bonal et al. (2008)
Peru (Pastaza-Marañon)	Native Forest	52 ± 22 (36–85)	Lähteenoja et al. (2009)
Peru (Pastaza-Marañon)	Native Forest	(28–108)	Lähteenoja et al. (2012)
Cayambre-Coca	Peatlands in the Andes Mountains	51.1	Chimner and Ewel (2005)
Tropical Africa			
Cuvette Centrale, Congo	Native Forest	23.9 ± 5.8 (18.3–33.1)	Dargie et al. (2017)
Kenya	Tropical papyrus peatland	160	Jones and Humphries (2002)
Burundi	Buyongwe Swamp	125	Pajunen (1996)
Burundi	Ndurumu Swamp	65	Pajunen (1996)
Rwanda	Cyili Swamp	113	Pajunen (1996)
Rwanda	Gishoma Swamp	(86–106)	Pajunen (1996)
Rwanda	Mashya Bog	91	Pajunen (1996)
Rwanda	Cyabaralika Swamp	33	Pajunen (1996)
Rwanda	Kiguhu Swamp	31	Pajunen (1996)
Global scenario			
Tropical undisturbed		(24–300)	Chimner (2004); Kurnianto et al. (2015)
Tropical disturbed		(–499 to –174)	Rieley et al. (2008)
Non-tropical		(–248 to 271)	Olefeldt et al. (2012); Renou-Wilson et al. (2019); Roulet et al. (2007)

peatland type, hydrology, vegetation type and peat formation (Craft et al., 2008; Sjögersten et al., 2014), C accumulation rates are, with a few exceptions, greater in the tropics and decrease with latitude (Sjögersten et al., 2014). Additionally, the carbon accumulation rates in undisturbed tropical peatlands are generally much higher than in intact old-growth tropical forests, commonly over mineral soils, in Africa and Amazonia (40–91 and 0–47 g C m⁻² year⁻¹, respectively; Hubau et al., 2020).

The accumulation rates depend on the balance between carbon uptake by vegetation and carbon emitted to the atmosphere and lost to adjacent terrestrial or aquatic system. CO₂ emission vary greatly in tropical peatlands (250 and 13,841 g C m⁻² year⁻¹; Table 3) and tend to be greater than in non-tropical systems (411 ± 128 g C m⁻² year⁻¹; Bubier et al., 2003; Clair et al., 2002; Crow & Wieder, 2005; Mäkiranta et al., 2009; Silvola et al., 1996). Estimated fluxes of CH₄ from peatlands are typically several orders of magnitude lower than those for CO₂ (Table 3). CH₄ emissions are indeed undetectable in some peatlands and an uptake from the atmosphere might occur instead (Sjögersten et al., 2014). Previous studies have estimated that undisturbed temperate and boreal environments emit moderate to high level of CH₄ (-7.1 to 2,088.6 g C m⁻² year⁻¹; Inubushi et al., 2003; Martikainen et al., 1995; Melling et al., 2005; Mitsch et al., 2010; Turetsky et al., 2014), whereas CH₄ emissions from undisturbed tropical peatlands have been estimated at moderate range of -9.2 to 110.6 g C m⁻² year⁻¹ (Table 3).

Methane formation is driven by methanogenic microorganisms activity (anaerobic decomposers) that degrades organic matter slowly in an anoxic environment (Mitsch et al., 2010). A peatland's capacity to emit less CH₄ appears to be a complex mechanism developed over several thousands of years, given that formerly human-disturbed restored peatlands in temperate systems with well-established vegetation and carbon stock have CH₄ emissions about 150% higher than older peatlands (Renou-Wilson et al., 2019). This fact suggests that to maintain low CH₄ emissions and higher carbon sequestration rates, it is important to not only invest in actions that seek to recover impacted areas but also to ensure that ecosystems are protected.

In the absence of direct human disturbance, many tropical peat deposits are actively accumulating carbon or are in steady states (Dargie et al., 2017; Fatoyinbo, 2017). However, climate change may significantly impact peatlands, and this relationship is poorly understood, particularly in the case of tropical peatlands, and thus the fate of peatlands under future change remains uncertain (Frey & Smith, 2005; Gallego-Sala et al., 2018; Hapsari et al., 2017; Hirano et al., 2012; Hodgkins et al., 2018; Rieley et al., 2008). The effect of climate change will depend mainly on how temperature, total precipitation, sea level and frequency of extreme events will change in a specific region and how they will affect hydrology, vegetation composition and, consequently, primary production, substrate quality, decomposition process, lateral carbon fluxes and C accumulation rates of peatlands.

Some recent work, using Dynamic Global Vegetation Models (DGVMs) indicated, for Northern Hemisphere peatlands, a carbon

sink twice as big than the 1861–2005 mean under two climate scenarios (defined by the RCPs 2.6 and 6.0), even though rapid climate change (under RCP8.5) might impact negatively the extent of northern peatlands, and the capacity of these areas to act as a carbon sink (Chaudhary et al., 2020; Qiu et al., 2020). As well, some models have predicted continued peat accumulation through to 2100 (Gallego-Sala et al., 2018; Spahni et al., 2013), while most models agree that there will be substantial losses over the next centuries (Avis et al., 2011; Gallego-Sala et al., 2018; Ise et al., 2008), and some models have predicted that loss to start before 2100 (Avis et al., 2011; Ise et al., 2008). Few pan-tropic modeling, studies have been undertaken (Gallego-Sala et al., 2018; Treat et al., 2019) largely due to the sparsity of available data on tropical peatlands that is needed for model parametrization and validation. Climate models for the western Amazon predict increasing precipitation and river discharge over the century (Duffy et al., 2015; Sorribas et al., 2016; Zulkafli et al., 2016), whereas the opposite is predicted for the Eastern Amazon (Duffy et al., 2015; Sorribas et al., 2016), meaning that Brazilian peatlands are likely to be more vulnerable than those in Peru. However, a recent modeling study in the PMFB in Peru predicted that temperature increases would offset any positive effect of increased precipitation on peat accumulation by the end of the century through an increase in decomposition, that is, Peruvian peatlands will cease peat accumulation despite increases in precipitation (Wang et al., 2018). Likewise, in the Congo Basin, there is a clear consensus that temperature will increase under all future scenarios while precipitation is predicted to increase under high emission scenarios and remain relatively unchanged under low emission scenarios (Haensler et al., 2013) and, therefore, Congolese peatlands may also be vulnerable to future climate change. Likewise, studies in Southeast Asian peatlands, many of which are already degraded from deforestation and drainage, have been shown that additional carbon emission could also occur if dry seasons are extended or are more severe due to future climate change (Warren et al., 2017).

Conversely, there is evidence to suggest that tropical peats may be more resistant to temperature changes. Hodgkins et al. (2018) observed that the higher aromatic content of tropical peat compared to the peat located at higher latitudes creates both a reduced oxidation state and higher recalcitrance, which prevents carbon release, even at high temperatures. In many peatlands in the northern hemisphere, deep peat has also high recalcitrance characteristics, which means that despite the expected temperature increases from climate change, the deep peat will probably remain stable, suggesting that these carbon stocks may be preserved in the face of climate change given their similar characteristics to tropical peat. Although there may only be a direct relationship between temperature and decomposition in high recalcitrant peat, it is recognized that changes in precipitation can alter the natural hydrology of these environments and enhance the degradation processes of recalcitrant peat (Chimner & Ewel, 2005).

In summary, many peatland areas are projected to stop accumulating peat by the end of the century and beyond, thus creating a positive climate feedback loop where further warming means C losses and,

TABLE 3 Estimates of soil emission of CO₂ and CH₄ from peatlands (g C m⁻² year⁻¹) showing mean values and/or (range) if available

		(g C m ⁻² year ⁻¹)		
System/location	Land cover	CO ₂ ^a	CH ₄ ^b	Reference
Tropical Asia				
Malaysia	Forested peatland		0.02 (−0.05 to 0.10)	Melling et al. (2005)
Thailand	Forest peatland		9.81 ± 23.6 (1.7–110.4)	Ueda et al. (2000)
Central Kalimantan	Peat swamp forest floor	3,493 ± 316	1.36 ± 0.57	Jauhiainen et al. (2004)
Indonesia	Peat swamp forest floor		1.35	Jauhiainen et al. (2004)
Indonesia	Poorly drained forest	174 ± 203		Hirano et al. (2012)
Indonesia	Drained forest	328 ± 204		Hirano et al. (2012)
Indonesia	Burnt and drained forest	499 ± 72		Hirano et al. (2012)
Indonesia	Tropical peatlands (including rice)		(4.4–19.3)	Hadi et al. (2005)
Kalimantan, Indonesia	Forested peatland	2,777 ± 8,322		Hirano et al. (2009)
Kalimantan, Indonesia	Secondary forest	4,494	1.66	Hadi et al. (2005)
Kalimantan, Indonesia	Secondary forest	3,460 (1,603–35,522)	4.4 (0–29)	Hadi et al. (2005)
Kalimantan, Indonesia	Forested peatland	3,495 ± 315 (438–4,818)	1.4 ± 5.7 (−0.09 to 3.1)	Jauhiainen et al. (2004)
Kalimantan, Indonesia	Forested peatland		9.6 ± 5.3	Inubushi et al. (1998)
Malaysia	Forested peatland	3,889		Murayama and Bakar (1996)
Micronesia	Forested peatland	3,469 ± 315 (2,978–3,522)		Chimner (2004)
Sarawak, Malásia	Sago	(552–2,146)		Melling et al. (2005)
Sarawak, Malásia	Oil palm	(403–29,334)		Melling et al. (2005)
Sarawak, Malaysia	Forest ecosystem	(876–4,669)		Melling et al. (2005)
South Kalimantan	Secondary forest	1,200 ± 430	1.2 ± 0.4	Inubushi et al. (2003)
South Kalimantan	Secondary forest peatland to paddy field	(1,200–1,500)	(1.2–1.9)	Inubushi et al. (2003)
South Kalimantan	Changing land-use from Secondary forest to upland tended	(1,000–2,000)	(1.2–0.6)	Inubushi et al. (2003)
South Kalimantan	Abandoned upland crops field	990 ± 110	0.6 ± 0.7	Inubushi et al. (2003)
South Kalimantan	Abandoned paddy fields	1,540 ± 290	1.9 ± 0.5	Inubushi et al. (2003)
Southeast Asia	Secondary Native Forest	3,460	4.4	Hadi et al. (2005)
Southeast Asia	Secondary forest	3,500	0.5	Hadi et al. (2005)
Southeast Asia	Forest ecosystem	2,100		Melling et al. (2005)
Southeast Asia	Lowland peatlands	250	1.09	Couwenberg et al. (2010)
Southeast Asia	Undrained peat swamp forest	3,892 ± 304	1.36 ± 0.57	Rieley et al. (2008)
Southeast Asia	Drained uncultivated agricultural land	1,928 ± 526	0.12 ± 0.09	Rieley et al. (2008)
Southeast Asia	Drained affected peat swamp forest	4,000 ± 1,091	1.3 ± 0.98	Rieley et al. (2008)
Southeast Asia	Burned areas	2,900		Hadi et al. (2005)
Southeast Asia	Converting peat swamp forests into oil palm	5,940		Murdiyarso et al. (2010)
Southeast Asia	Paddy field	1,389	19.6	Radjaguguk (1997)
Southeast Asia	Rice-soybean rotation field	2,019	2.6	Bouwman (1990)
Southeast Asia	Paddy field	1,400	1.4	Hadi et al. (2005)
Southeast Asia	Rice-soybean rotation field	2,000		Hadi et al. (2005)
Southeast Asia	Oil palm	1,500		Melling et al. (2005)

(Continues)

TABLE 3 (Continued)

System/location	Land cover	(g C m ⁻² year ⁻¹)		Reference
		CO ₂ ^a	CH ₄ ^b	
Southeast Asia	Sago	1,100		Melling et al. (2005)
Southeast Asia	Cultivation of palm oil (<i>Elaeis guineensis</i>)	5,940		Murdiyarso et al. (2010)
Southeast Asia	Rice crops (Mega Rice Project)	2,178		Hadi et al. (2005)
Southeast Asia	Rice crops	1,389	26.6	Hadi et al. (2005)
Southeast Asia	Agricultural Soils	2,019	1.7	Hadi et al. (2005)
Southeast Asia	Horticulture	1,500	1.9	Inubushi et al. (2003)
Southeast Asia	Cultures with nitrogen fertilization (<i>Acacia</i> sp e <i>Metroxylon</i> sagu)	2,130	2.6	Couwenberg et al. (2010)
Southeast Asia	Clear felled recovering peat Swamp forest	3,400 ± 927	2 ± 1.5	Rieley et al. (2008)
Sumatra, Indonesia	Forested peatland	3,329 ± 481.8	7.8 ± 4.2	Furukawa et al. (2005)
Sumatra, Indonesia	Forested peatland	2,435 ± 140	10.6 ± 11.9	Furukawa et al. (2005)
Sumatra, Indonesia	Forested peatland	3,294 ± 937	6.7 ± 2.4	Furukawa et al. (2005)
Sumatra, Indonesia	Natural swamp forest drained more than 5 years	267		Jauhainen et al. (2012)
Tropical America				
Bocas del Toro, Panama	Forested peatland (<i>Raphia</i> sp.)	1,857 (96–14,839)	(1.1–110.6)	Wright et al. (2011)
Bocas del Toro, Panama	Forested peatland (<i>Camposperma</i> sp.)	2,085 (543–7,017)	(–7.7 to 31.8)	Wright et al. (2011)
Bocas del Toro, Panama	Open peatland (<i>Cyperus</i> sp.)	1,269 (61–8,322)	(–9.3 to 27.2)	Wright et al. (2011)
Ka'au, Hawaii	Montane swamp	1,112.5 ± 412		Chimner (2004)
Mauim, Hawaii	Montane peatland	2,497 ± 657		Chimner (2004)
Orinoco Llanos, Venezuela	Palm peatland	263 (149–473)		Bracho and San José (1990)
Brazil (Lowlands in São Paulo state)	Pastureland (dry season and wet season)	3,210	(–5.2 to 4.0)	Ribeiro et al. (2018)
Brazil (Lowlands in São Paulo state)	Native forest (dry season and wet season)	2,174	(–3.1 to 4.2)	Ribeiro et al. (2018)
Brazil (Lowlands in São Paulo state)	Irrigated rice crop (dry season and wet season)	2,074	3.1	Ribeiro et al. (2018)
Global scenario				
Tropical undisturbed		(250–13,841)	(–9.3 to 110.6)	Chimner (2004); Kurnianto et al. (2015)
Tropical disturbed		(263–29,334)	(1.9–26.6)	Kurnianto et al. (2015); Zoltai and Martikainen (1996)
Non-tropical		411 ± 128	35.1 ± 2.6 (–7.1 to 2,088.6)	Lund et al. (2010)

^aValues of CO₂ emission are from autotrophic and heterotrophic respiration and do not consider primary production.

^bPositive values of soil emission mean carbon emission and negative mean carbon uptake.

in turn, greater radiative forcing (Gallego-Sala et al., 2018). However, across the entire tropics, and particularly the Amazon and Congo basins, further field data are required to better parameterize and validate models so that we can improve projections of the future C balance in tropical peatlands, which at the moment remain highly uncertain.

Although climate change (such as changes to temperatures and precipitation) has an impact on the dynamics of these ecosystems, direct anthropogenic changes (LULC changes, drainage and deforestation) currently play a greater role. Therefore, understanding the impact of direct anthropogenic changes on these ecosystems can

help us understand whether tropical peatlands are a net sink or net source in the global carbon cycle.

5 | DIRECT HUMAN DISTURBANCES AND THEIR IMPACTS ON CARBON ACCUMULATION RATES AND GHG EMISSIONS IN TROPICAL PEATLANDS

Anthropogenic activities, such as logging, drainage, deforestation, fires and the conversion of native forests to agricultural lands, have been rapidly increasing in peatlands since the 1990s (Hooijer et al., 2010), particularly in developing countries, and have put these ecosystems at risk (Swindles et al., 2018). Although most of the scientific literature on the degradation processes of tropical peatlands focuses on Southeast Asia (Hapsari et al., 2017; Hirano et al., 2009, 2012; Inubushi et al., 2003; Könönen et al., 2015; Rieley et al., 2008), the degradation of large areas of peat and the impacts that may alter their natural conditions have also been documented in both South America and Africa (Baker et al., 2014; Dargie et al., 2017, 2019; Roucoux et al., 2017; Swindles et al., 2018).

In Southeast Asia, domestic and international demand for agricultural and forest products and services has put pressure on tropical peatlands and, by 2010, it was estimated that only 36% of the original peatland area in the Southeast Asia was covered by primary and secondary peat swamp forest (Aziz et al., 2017; Miettinen et al., 2012). In the Indonesian regions of Sumatra and Kalimantan, the two regions of Indonesia with the greatest impacts, only 6% were pristine peat swamp forests (Miettinen et al., 2012). To meet the high demand of agricultural products, the peatlands have been subjected to deforestation (Hirano et al., 2012), widespread drainage (Fatoyinbo, 2017) and recurrent fires (Page et al., 2002). Page et al. (2011) argue that, on the one hand, expansion of agriculture and forestry in the region has provided opportunities to industries and businesses, yet on the other hand it has also had negative environmental impacts. Between 2000 and 2010, Southeast Asia has had the highest annual rate of deforestation (rate of 2.2%) among all tropical humid regions in the world. This deforestation has resulted in the loss of 11 Mha of native forests and has led to significant changes in natural ecosystem dynamics, mainly related to carbon balance (Miettinen & Liew, 2010). Netzer et al. (2013) projected land-use and emissions from peatlands between 2010 and 2050 across Indonesia, Malaysia and in Papua New Guinea and found that under the "business as usual" scenario, in which total production of oil palm will increase without peatland protection measures, the average annual CO₂ emissions would almost double between 2020 and 2050 (from 264 to 424 Tg CO₂/year). In contrast, restoring the peat to native forest vegetation (restoration scenario) would bring annual emissions close to zero.

In Africa, increased economic development could have a negative impact on peatlands through hydrocarbon exploration, logging, plantations and other forms of disturbance that significantly damage these ecosystems, although they are still intact today (Dargie et al., 2019). Additionally, land-use changes occur as a result of

multiple complex and interacting environmental, economic and political factors, which can accelerate the negative impacts of human activities. In Cuvette Centrale region in Congo, rivers are the main transport network and there are relatively few roads. This, along with the large distance from any international port and low population densities, is among the reasons why the Congo basin peatlands have so far been spared from more severe degradation typical for Southeast Asian peatlands. Although limited in number, roads have already been constructed across some of the peatland areas of the Cuvette Centrale. No studies have yet considered the specific impacts of these roads on the peat properties, hydrology or vegetation; however, the observed swamp forest death following road construction suggests that roads could be having a negative impact on the wetlands of the region (Dargie et al., 2017). The low level of human intervention in the Cuvette Centrale peatlands at present suggests that there is still time to protect the peatlands in a largely intact state, possibly by encouraging funding for mitigation of land-use change (Dargie et al., 2019).

In South America, large areas of undisturbed peatlands are increasingly facing a range of threats, including hydroelectricity (river damming) projects, road and railway projects (Finer & Orta-Martínez, 2010; Gutiérrez-Vélez et al., 2011), ore, gas, and oil exploration, logging and drainage for agriculture (Baker et al., 2014; Roucoux et al., 2017). Over exploitation of the palm fruit (*Mauritia flexuosa*—commonly found in wetlands) is also an increasing concern (Kahn & Mejia, 1990; Lilleskov et al., 2019). In contrast with the better-known but highly degraded and at-risk peatlands of Southeast Asia (Miettinen et al., 2012), many peatlands in South America remain largely intact and the threat of destruction from direct human impacts is comparatively low (Baker et al., 2014).

In general, the degradation process of tropical peatlands begins with the felling of natural vegetation, which reduces the amount of biomass in the system (Könönen et al., 2016), and promotes an increase in C oxidation rates and a reduction of soil moisture because of the increased incidence of direct radiation (Dargie et al., 2019; Jauhainen et al., 2012). However, to a lesser extent, a reduction in vegetation can also lead to increase in soil moisture due to the decrease in transpiration (Porporato et al., 2001). After the deforestation process, the peatlands are artificially drained to reduce groundwater levels to plant perennial and rotating crops (Dargie et al., 2019) are not adapted to the naturally flooded environment. Next, aerial biomass crops are produced, which reduce the ecosystem carbon uptake because the soil no longer has the environmental conditions of peatlands to accumulate carbon, and the carbon accumulated by the crop primary production is removed from the system through the harvest (Roucoux et al., 2017).

The most recent studies on GHG soil emissions from natural and impacted environments show that tropical peatlands have high CO₂ emissions in drained environments used for agricultural production and in recovering areas (Leifeld & Menichetti, 2018). Although non-impacted forests emit C through soil respiration, on average emissions are lower due to the maintenance of natural soil moisture conditions and groundwater levels.

In Indonesia, the carbon lost in peatlands after LULC changes has averaged approximately 60 Mg ha⁻¹ year⁻¹ over 25 years of interference (Murdiyarso et al., 2010). This loss is, in part, due to the absence of vegetation in impacted and/or drained peatlands, given that in undisturbed peatlands C sequestration from vegetation cover offsets C emissions from the soil. In Southeast Asia, it is estimated that in 2006 CO₂ emissions from organic matter decomposition in drained peat soil were equivalent to 1%–3% of all global CO₂ emissions from burning fossil fuels (~630 Mt), and that 82% of these emissions were from Indonesian peatlands (Hooijer et al., 2010). Other studies have pointed to even higher emission rates associated with peat decomposition in Indonesia, reaching about 8% of global emissions from burning fossil fuels (2,000 Mt/year of CO₂, Rieley et al., 2008). Moreover, major events were reported in 1997 and 2015, in which widespread forest and peatland fires burned large areas of the Southeast Asia (Huijnen et al., 2016; Page et al., 2002), especially Indonesia, releasing large amounts of carbon in the land-based atmosphere, mainly in the form of CO₂, CO and CH₄. With an average emission rate of 11.3 Tg CO₂/day during these events, emissions exceeded the European Union's (EU28) fossil fuel CO₂ release rate of 8.9 Tg CO₂/day (Huijnen et al., 2016).

Methane fluxes also change as a result of human disturbance (Reay et al., 2018). The conversion of peatland forests to areas of intensive cultivation, along with significant inputs of nitrogen fertilizers, may alter the natural dynamics of methane and nitrous oxide emissions (Tian et al., 2015). Rice crops in Indonesia have shown very significant CH₄ emissions after being converted from peatland forests (Table 3) because the production of CH₄ by methanogenic microorganisms is boosted by both the ever-flooded system and the use of nitrogen fertilizers (Conrad, 2002). Emissions from these crops may be about 20-fold greater than emissions from natural areas. Nitrous oxide emissions in Indonesia have been shown to increase substantially with land-use change and the introduction of agricultural activities in peatlands (Oktarita et al., 2017). Nitrous oxide emissions from *Elaeis guineensis* (oil palm) monocultures in Indonesia were reported by Hadi et al. (2005) at 9.1 g C m⁻² year⁻¹, higher than those reported by Inubushi et al. (2003) in native peat forests, 1.25 g C m⁻² year⁻¹.

In addition to GHG emissions, drainage enables organic matter to be transported to adjacent watercourses in the form of dissolved organic carbon (DOC), particulate organic matter and dissolved inorganic matter. For instance, Baum et al. (2007) suggest that Indonesian rivers, particularly those receiving effluents drained from peatlands, transfer large amounts of carbon, in the form of DOC, to the oceans (21 Tg/year) and that this accounts for approximately 10% of global riverine DOC inputs into the ocean (Rieley et al., 2008).

Roucoux et al. (2017) examined the services provided by large, intact tropical peatlands, the factors threatening them, and opportunities to conserve them, and cite that, although their contribution from tropical peatlands to climate regulation on the planet is evident, their importance is weakly articulated within existing conservation agendas, mainly because they are poorly described and mapped

and are frequently unrecognized by local agencies and institutions. Fortunately, in Amazonia, Africa and New Guinea, tropical peatland ecosystems are also widespread and often much less intensively exploited. Many can be described as intact at the landscape scale; their hydrology is unaffected by human activity and their vegetation cover is not fragmented or substantially degraded.

6 | FINAL REMARKS

Tropical peatlands are different from boreal and temperate peatlands, particularly their climatic settings, peat matter formation and vegetation coverage. They cover 90–170 Mha which represents 23%–30% of the total area covered by peatlands throughout the world. Bringing together the most up-to-date estimates of peatland area, peat depth, peat volume and peat carbon content, we estimate that tropical peatlands store 152–288 Gt of carbon, which is significantly higher than the previously reported values. The large uncertainty in these estimates is related to methodological approach and the sparse field data on depth and C content, mainly in South America and Africa. Despite tropical peatlands covering a smaller area and storing less carbon than non-tropical peatlands, carbon accumulation rates are greater in the tropics and decrease with latitude, which gives tropical peatlands the important role of accumulating carbon emitted by human activities now and in the future.

Climate change is a threat to peatlands, but at local and regional levels, direct human interventions have played a more important role in impairing the capacity of peatlands to sequester carbon. In the tropical zone, the carbon sequestration rate of peatlands in Southeast Asia has changed from 79 to 300 (uptake) to (–499) to (–174) g C m⁻² year⁻¹ (emission) after direct human interference. Integrated development and management mechanisms supported by strong policies and meaningful incentives can balance this scenario and contribute to more effective measures.

The Amazon region potentially holds the largest natural peatland across the tropics. However, the factors that contribute to tropical peatland degradation are only well understood for Southeast Asian peatlands. To date, very few studies have addressed the impacts of peatland degradation in South America and in Africa. Thus, advancing to fill the current scientific knowledge gaps and incorporating local understanding is crucial for supporting policies geared toward managing and conserving undisturbed peatlands in these regions. Furthermore, understanding and mapping peatlands in Brazil by encouraging research projects can enhance the current knowledge about the potential of these system to uptake and store carbon, and can encourage actions aimed to protect peatlands in this region. Due to the high level of conservation and the expected high capacity of carbon accumulation, the Amazon region peatlands are particularly important in the context of climate change mitigation.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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