Anthropogenic impacts on lowland tropical peatland biogeochemistry

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Abstract

Tropical peatlands store around one-sixth of the global peatland carbon pool (105gigatonnes), equivalent to 30% of the carbon held in rainforest vegetation. Deforestation, drainage, fire and conversion to agricultural land threaten these ecosystems and their role in carbon sequestration. In this Review, we discuss the biogeochemistry of tropical peatlands and the impacts of ongoing anthropogenic modifications. Extensive peatlands are found in Southeast Asia, the Congo Basin and Amazonia, but their total global area remains unknown owing to inadequate data. Anthropogenic transformations result in high carbon loss and reduced carbon storage, increased greenhouse gas emissions, loss of hydrological integrity and peat subsidence accompanied by an enhanced risk of flooding. Moreover, the resulting nutrient storage and cycling changes necessitate fertilizer inputs to sustain crop production, further disturbing the ecosystem and increasing greenhouse gas emissions. Under a warming climate, these impacts are likely to intensify, with both disturbed and intact peat swamps at risk of losing 20% of current carbon stocks by 2100. Improved measurement and observation of carbon pools and fluxes, along with process-based biogeochemical knowledge, is needed to support management strategies, protect tropical peatland carbon stocks and mitigate greenhouse gas emissions.

Peatlands hold the largest terrestrial pool of organic carbon (C) in the biosphere, storing 600–650gigatonnes (Gt) (refs[1–3]). They also play a part in the cycling of nutrients and the delivery of other ecosystem services, including regulation of the water supply and biodiversity support. Most of the global peatland C stock is in the high northern latitudes (Table 1) and is largely remote from human influence. However, approximately 16% of peatland C (around 105Gt)[1,2] is held in C-dense tropical peatlands, some of which are close to large and growing human populations[4] . The utilization of peatlands for forestry, agriculture and other purposes has converted them from a long-term C sink into an intense source of greenhouse gas emissions, contributing about 5% of global anthropogenic emissions[5] . Mid-latitude and tropical peatlands supply the majority of this total[6,7] and are increasingly acknowledged as critical in the global C cycle and in efforts to combat climate change[8–11]. There is growing understanding and recognition of tropical peatland extent and the consequences of human and climate-driven disturbances, particularly in loss of stored C and enhanced greenhouse gas emissions[11]. Anthropogenic impacts on tropical peatlands span a gradient from minor vegetation modification through to vegetation removal, alteration of hydrology by drainage, and changes in peat physical and biogeochemical properties resulting from land-use conversion and fire. These alterations have been extensive in Southeast Asia, but peatlands in other tropical regions are increasingly exposed to human and climate impacts as a result of socio-economic development, warming temperatures and altered rainfall regimes[8,10]. Avoiding tropical peatland deforestation, drainage, agricultural conversion and fire can halt the transfer of this large C pool to the atmosphere. Ongoing or re-established C sequestration through initiatives to protect and restore peatland ecosystem functions provides a potential low-cost pathway to climate mitigation. Intervention measures to protect intact tropical peatlands alongside rewetting and revegetation of drained peatlands could drive these ecosystems towards a pre-eminent role in natural climate solutions[8–10]. In this Review, we discuss the contributions that tropical peatlands make to biogeochemical cycling and examine how land-use and fire-driven transformations alter biogeochemical processes. Lowland systems are the focus, because they occupy large areas, but we acknowledge the existence of smaller, tropical montane peatlands. We consider the potential impacts of ongoing habitat degradation and a warming climate on the future biogeochemistry of these ecosystems and explore emerging opportunities to protect their C stocks and mitigate greenhouse gas emissions.

Location, formation and vegetation

Tropical peatlands form where high year-round rainfall and humidity combined with low-lying topography and poor drainage have resulted in persistent soil saturation, low oxygen availability and reduced rates of plant litter decomposition (Fig. 1; Table 1). They occupy at least 440,000 km2 , and perhaps more than 600,000km2 if extensive wetlands in South America are confirmed to be peat-forming2,4 , and have a C store that is equivalent to 30% of the C held in rainforest vegetation12. Tropical peatlands have their greatest extent in Southeast Asia2,13–18, Africa1,2,19–24, and Central and South America2,4,25–29 (Table 2). Southeast Asian peatlands were described in scientific accounts from the early twentieth century30, but peatlands across the rest of the tropics have largely only been documented since 2010. Indeed, the world's largest single expanse of tropical peatland in the Congo Basin, covering 146,000km2 (an area larger than England or the island of Java, for example), was only described in 2017 (ref.1). Differences in past and contemporary hydroclimate and geomorphological setting have resulted in variations in peat and C accumulation rates over time. The build-up of most Southeast Asian peatlands occurred throughout the Holocene, although accumulation at some inland sites in Kalimantan, Indonesia, slowed or ceased from around 2,000years ago15. This slowdown has been attributed to strengthening El Niño Southern Oscillation (ENSO) activity that increasingly led to peat oxidation rather than accumulation, owing to increased rainfall seasonality and associated extended periods of drought15. Reduced rates or discontinuities in peat accumulation are evident on other continents; for example, from 1,300 to 400 calendar years before present (cal yr bp) in Amazonian Peru26 and 7,300 to 2,000cal yr bp in the Congo Basin1,24. These slowdowns were probably also driven by hydroclimatic changes (increased rainfall seasonality and/or lower annual rainfall) and an increase in peat decay. In both these latter locations, peat accumulation resumed following the return of wetter site conditions, specifically a higher water table with less seasonal variability. The vegetation of most intact lowland peatlands comprises evergreen trees, palms, or a combination of the two (Fig. 1). Large hardwood species dominate Southeast Asian peatlands31. In Africa and the Americas, there are extensive palm communities (Raphia, Mauritia and Mauritiella spp.)1,32 in addition to hardwood trees, along with open, sedge-dominated vegetation. At the scale of a single peatland, vegetation frequently displays a zonation from shallow to deeper peat based on flooding and nutrient gradients1,25,32,33. This pattern is mirrored by increasing tree stem density, decreasing tree height and decreasing aboveground biomass. At a local scale, distinct plant assemblages occur in response to peat surface microtopography, with wet, sparsely vegetated anaerobic hollows interspersed by moist, aerobic hummocks that support most of the tree growth and that are formed by buttressed tree bases and root systems34–36.

Land-use changes and impacts

Extensive land-use changes have occurred on Southeast Asian peatlands. In peninsular Malaysia, Borneo and Sumatra, peatland covered by native forest declined from 119,000km2 in 1990 to 46,000km2 in 2015 (with most of this forest disturbed by timber extraction and unlogged forest occupying less than 10,000 km2), while agricultural areas increased from 17,000 km2 to 78,000 km2 over the same time period37. The extent of these changes and the rapid loss of intact peat swamp forest is globally unprecedented. Peatland conversion in Indonesia and Malaysia has been driven by small-scale farmers (43–44%) and industrial plantation companies producing palm oil (39%) and pulp and paper (11–26%)37,38. In addition, an extensive area of deforested and fire-prone peatland is idle with no current economic use37,39. In other tropical regions, peatland utilization is typically limited to lower-impact activities that do not require drainage. These activities include the collection of palm fruits in Amazonia40,41 and the use of forest resources for subsistence livelihoods in the Congo Basin42. There is, however, more extensive agriculture on peatlands in eastern and southern Africa43. Extraction of non-timber forest products, such as wild fruits, can cause ecosystem degradation40, whereas the threat of future land-use changes for remaining intact peatlands is considerable, driven by the potential for timber extraction, agricultural conversion and development of inland oil fields42,44. The consequences of this land-use change are discussed in the following sections.

Hydrological consequences of drainage

Agricultural uses of peatland are often accompanied by drainage measures because dryland crops that cannot tolerate prolonged inundation are grown. In an undrained state, ombrotrophic tropical peatlands (Tables 1,2) have high to very high peat hydraulic conductivity (permeability), similar to gravel45; lower conductivity is noted for peatlands influenced by river flood waters46. Despite their convex, domed surface topography (Table 1) and elevated permeability, intact peatlands are maintained in a saturated or near-saturated condition because of high rainfall and the roughness of the peat surface (hummock– hollow microtopography). In combination, these features ensure high water storage capacity at the peat surface, a low hydraulic gradient, and slow radial water loss towards the edge of the dome18,45. Water storage responds mainly to losses via evapotranspiration from the peat surface and vegetation. Once a peatland has been deforested and drained, the contribution of subsurface flow greatly increases. Forest removal reduces evapotranspirative losses, resulting in increased runoff and flashiness of water-table variations18,45, while drainage reduces peat porosity and water storage capacity47. Accordingly, peatlands converted for agriculture can be over-supplied with water during the wet season, leading to flooding, but under-supplied during the dry season, when there is a risk of water deficit45,48 and fire.

Peat subsidence

The hydrological impacts of peatland conversion are exacerbated by other changes initiated by drainage, namely peat subsidence, which increases the risk of flooding. Subsidence is a function of physical and biological processes, comprising peat compaction following lowering of the water level and peat oxidation above the water level, which stimulates microbial decomposition and the release of C (as carbon dioxide (CO2)) to the atmosphere49,50. Initial subsidence can be rapid, accounting for surface lowering of up to 1m in the first 2 years50. Subsequently, when decomposition is the dominant process, rates are in the range 3–5 cmyr-1 for plantation landscapes in Southeast Asia50–53, with a mean value of 2.2 cm yr–1 across all degraded and converted land covers54. Over time, drainage-driven subsidence changes peat dome morphology and reduces C storage capacity55. The reduction in the mean slope of the dome reduces water flow velocity in the drainage network and increases surface inundation risk during periods of high rainfall56–58. Over time, subsidence will bring the peat surface within reach of river flood levels or coastal high tides, increasing flooding duration and extent and the threat of saline intrusion50,53,59. Unlike in northern peatlands, pumped drainage to maintain low water levels for agricultural production will probably not be feasible in the tropics owing to economic and practical difficulties associated with installing and maintaining infrastructure capable of operating under high rainfall rates and flashy flows. Unless dryland crops are replaced by species adapted to inundation38,60, agriculture on drained tropical peatlands will inevitably end when gravity drainage becomes impossible. A further risk associated with peat subsidence is the eventual exposure of underlying infertile sands or previously waterlogged pyrite-rich marine clays to aerobic conditions61,62. Oxidation of pyrite (iron sulfide) produces sulfuric acid, resulting in severe acidification of peat and drainage waters. The drop in pH (to <pH2.0 in some cases) mobilizes metals into solution, including Al, Fe, Mn and As (ref.63). This drainage water can be toxic for plants, aquatic life and humans64–66, with detrimental impacts on crop production. Although soil amendments (lime or fertilizers) can alleviate toxicity for plants and maintain crop yields, the only way to stop pyrite oxidation is to raise the water table and re-establish anaerobic conditions within the sulfide-rich layer66.

Carbon cycling

Tropical peatlands combine a vegetation cover capable of high biomass productivity with the capacity to transfer a portion of that biomass into long-term ecosystem C storage within the peat67. Carbon enters the system through photosynthesis and leaves it as: CO2 via plant autotrophic respiration (Ra); CO2 via heterotrophic respiration by microbial organisms (Rh), primarily under aerobic conditions; methane (CH4), through anaerobic respiration by methanogenic microorganisms; and as dissolved organic carbon (DOC) and, to a lesser extent, as particulate organic carbon (POC), transported into drainage channels and rivers. Leaching of dissolved CO2 to drainage waters provides an alternative pathway for loss of respired C. Carbon and bicarbonate fluxes tend to be negligible in highly acidic peat drainage waters68, but these waters can be highly over-saturated with CO2, which subsequently degasses to the atmosphere69. The ecosystem will function as a C sink if photosynthetic C input via net primary production (NPP; photosynthesis minus Ra) exceeds the sum of gaseous and fluvial C losses, leading to accumulation of C in living biomass, plant litter and peat. If the peat is saturated, Rh proceeds at a reduced rate under anaerobic conditions, resulting in release of CH4 by methanogenesis. Undecomposed or partially decomposed organic material enters long-term storage in the peat. However, if there is an aerobic layer at the top of the peat column, for example, during periods of reduced rainfall or because of artificial drainage, a larger amount of organic material is exposed to aerobic decomposition, leading to increased loss of C as CO2 to the atmosphere and fluvial C to waterways, and potentially to overall net ecosystem C loss (Fig. 2a). The magnitude of and balance between different peatland C effluxes are primarily linked to abiotic hydrological constraints on peat microbial communities and their respiration pathways, but also to biotic factors. The woody, lignin-rich nature of much of the plant litter supplied to the peat surface confers resistance to microbial decay under anaerobic conditions70–74. However, if the peat is oxygenated, easily degraded fractions, such as cellulose, and more recalcitrant fractions, such as lignin, can both decompose rapidly71. In general, deforestation, drainage and agricultural conversion result in increased aeration, higher peat surface temperatures and increased nutrient inputs (from fertilization), all of which enhance peat decomposition47,50,53,59.

Over the Holocene, tropical peatlands have functioned as net C sinks, with a cooling effect on global climate3,75, despite episodes of reduced C accumulation resulting from changes in hydroclimate. Rates of long-term, average C accumulation since peat initiation are in the range 0.2–0.7 tCha−1 yr−1 for inland and 0.6–1.1 tCha−1 yr−1 for coastal peatlands in Kalimantan and Sumatra, Indonesia15. Carbon accumulation rates are similar in Peruvian peatlands (0.3–1.1tCha−1 yr−1)76. In comparison to lower long-term values for northern peatlands (0.2–0.3 tCha−1 yr−1)77–80, elevated tropical rates can be attributed to high peat swamp forest NPP combined with low rates of Rh, owing to persistent soil saturation and the relative recalcitrance of lignin-rich litter inputs.

Peatland carbon stocks

Current assessments indicate that Southeast Asian peatlands are the most C dense (average 2,775tCha–1)2 . Values are lower for shallower African and South American peatlands (2,000tCha–1 for the Congo Basin1 ; 800 tCha–1 for Peru27). Of an estimated global tropical peat C stock of 105GtC (range 87–136GtC), Southeast Asian peatlands contribute 69GtC (range 66–70GtC) and African peatlands about 34GtC (range 9–52GtC)1,2 . South and Central American peatlands store about 13 Gt C (range 11–14 Gt C) of the 105 Gt estimate, but potentially store up to 100GtC if extensive South American wetlands are proved to be peat-forming1,2,4 . Prior to anthropogenic disturbance, vegetation C density on Southeast Asian peatlands was in the range 27–275tCha–1 (ref.81). For peatlands of the Congo Basin and northeastern Peru, maximal values are 67–124tCha–1 and 80–161 tCha–1, respectively1,32,81,82. Although most C storage occurs belowground, vegetation C plays an essential part in providing the source of organic matter for peat formation and maintaining ecosystem functions to protect the belowground C pool83.

Carbon fluxes

Net ecosystem exchange. Assessments of the contemporary C dynamics of forested tropical peatlands suggest that although some continue to act as C sinks, for others this function has been reduced or lost through some combination of forest disturbance, drainage, climate variability or climate change (Fig. 2b). Data obtained from the eddy covariance technique, which measures the land–atmosphere C flux (net ecosystem exchange (NEE)), have shown a minimally disturbed palm swamp in Peru to be a strong net C sink at the rate of –4.7±1.9 tCha−1 yr−1 (ref.84). A peat swamp forest in Sarawak, Malaysia, also sequestered C, albeit at a lower rate (–1.4±0.5tCha−1 yr−1, where a negative value represents a C sink)85. In contrast, forested peatland sites affected in some capacity by logging (including construction of logging tracks and canals) and regional plantation development in Kalimantan86, Sarawak87 and Sumatra88 were net C sources, with NEE of 1.7–4.2 tCha−1 yr−1. These results suggest that the peatland C balance is highly sensitive to even modest levels of disturbance. In the case of the Sumatran study, C loss was observed during the 2019 ENSO-related dry season88. Nevertheless, the scale of C emission was lower than that from a forest affected by drainage and vegetation disturbance within the same landscape and measured over the same period (4.2±2.4 tCha−1 yr−1 as opposed to 10.8±1.1 tCha−1 yr−1). The scale of increasing C loss along a forest degradation gradient has also been demonstrated in Central Kalimantan. There, emissions increased from 1.7±2.0tCha−1 yr−1 in a lightly drained, selectively logged forest, to 3.2±2.0tCha−1 yr−1 in heavily drained forest and 5.0±0.7 tCha−1 yr−1 in a drained, burned forest86. There have been few published studies using the eddy covariance technique in tropical peatland land covers other than peat swamp forest. These studies focus on oil palm (Elaeis guineensis) plantations in Sarawak, Malaysia (Fig. 2b). A mature plantation had emissions of 9.9±1.6 tCha−1 yr−1 (annual mean water table –0.64±0.07m). In contrast, a peat swamp forest in the same region functioned as a net sink over the same study period (–1.4±0.5tCha−1 yr−1; annual average water table –0.19±0.03m)89. Lower emissions in the range 4.9±0.1 to 6.0±0.1tCha−1 yr−1 were reported for a mature plantation with an unusually shallow annual average water table (–0.26±0.04m)90. However, a much higher emission of 34.7 ± 0.1 to 46.5 ± 0.03 t C ha−1 yr−1 (average annual water table –0.54 ±0.05 m) was measured in a young plantation within a few months of its conversion from forest90. Net C loss from peatland developed for agriculture occurs by reducing C input (lower NPP, biomass removal via harvest, more degradable litter) and increasing C loss via heterotrophic respiration (Rh). Elevated emissions during early stages of plantation development are attributed to high Rh emissions (from the decomposition of both peat and woody debris remaining following deforestation) and low levels of NPP by young palms. While the palm trees are growing, C uptake into biomass will partially offset C loss from the peat. However, this uptake only represents a temporary sink since palm fruits are harvested regularly and the palms themselves are replaced after around 25years, at which point most biomass C will be remineralized to CO2 via decomposition91. Furthermore, a mature plantation contains less C in aboveground biomass than the forest it replaced (typically 40tCha–1 (ref.92), compared to 100–275tCha–1 for peat swamp forest93). In drained systems, radiocarbon measurements on DOC indicate that a substantial proportion of the overall C loss is of older (hundreds to thousands of years) peat, implying destabilization of the long-term C store94–96. Microbial population dynamics strongly influence these C losses through heterotrophic respiration, which is influenced by changes in hydrology (water-table depth and soil moisture). Rh is also affected by the quality (decomposability) and quantity of organic material available for decomposition (litter, peat and root exudates), air and peat temperatures, and peat nutrient status67,97–100 (Box 1). NPP is reduced by forest disturbance and conversion but, as with Rh, might also be sensitive to water-table drawdown, which can decrease the photosynthetic capacity of the vegetation88.

Peat surface CO2 flux.

In the absence of NEE measurements using the eddy covariance technique, Rh emission rates can enable the comparison of peat surface C effluxes from intact ecosystems with those under other land uses. Rh CO2 fluxes from undisturbed peat swamp forest typically range between 9.0 and 14.0tCO2-Cha–1 yr–1. For example, Rh fluxes of 9.5±0.3 tCO2-Cha–1 yr–1 and 13.8 ± 1.0 t CO2-C ha–1 yr-1 have been reported from Kalimantan, Indonesia99,101, with similar values of 8.9±4.8 and 9.9±1.75tCO2-Cha–1 yr–1 from Sarawak, Malaysia102,103. These values compare to Rh emissions from historically logged forest of 5.1 ± 1.7 tCO2-Cha–1 yr–1 from North Selangor, Malaysia104. A lack of studies of Rh CO2 fluxes from peatlands in the Congo Basin and South America limit comparisons. However, a study from an undisturbed forested peatland in Panama105 measured a flux of 4.0±1.2 tCO2-Cha–1 yr–1, indicating that fluxes from ombrotrophic peatlands in Central America are likely to be of the same order of magnitude. Drainage of peat swamps results in increased aerobic microbial activity, which is associated with higher decomposition of organic matter and accompanying increased Rh emissions of CO2 from the peat surface106. This increase is further amplified by a higher intensity of land use, for example, from diverse cropping systems to intensively managed monoculture plantations107,108, with higher Rh fluxes in plantations109. Rh CO2 fluxes reported for agricultural peatlands in Southeast Asia are generally within the range 14–20tCO2-Cha–1 yr–1 (ref.110). There is a robust correlation between long-term water-table depth and Rh emissions110–114, as well as time since conversion104. For an annual average water-table depth of –0.70m (representative of drainage depths in many agricultural peatlands), an Rh value of 17±3tCO2-Cha–1 yr–1, based on a modelled relationship between water table and C loss, has been proposed110. This value is comparable to IPCC Tier 1 emission factors of 11 (5.6–17) and 20 (16–24)tCO2-Cha–1 yr–1 for plantations of oil palm and Acacia (the main species grown for pulpwood), respectively115. Modelled relationships between water table and C loss for plantations110 indicate that the Rh flux rate increases by 0.25tCO2-Cha–1 yr–1 with every centimetre of increase in water-table depth. A similar study113 based on eddy covariance data suggests a net CO2 emission of around 10tCO2-Cha–1 yr–1 for a mean annual water-table depth of –0.70m and an increase of 0.16tCO2-Cha–1 yr–1 for each centimetre of increase in water-table depth. The increased peat surface temperature of deforested peatland and the application of fertilizers also influence the rate of Rh emissions116,117. At an agricultural peatland in Kalimantan, shading resulted in 33% and 66% lower CO2 emissions from unfertilized and fertilized plots, respectively; under unshaded conditions, fertilizer application increased emissions by 58%116.

Methane flux.

Diffusive fluxes of CH4 from the surface of tropical peatlands in Southeast Asia are lower than CO2 fluxes but are still important given the high global warming potential of CH4 (ref.11). Fluxes are highly variable within tropical peatlands83. For example, in Indonesia (Kalimantan and Sumatra), diffusive fluxes from peat surfaces in undisturbed forest range between 10±4 and 68±7kgCH4-Cha–1 yr–1 (refs99,118), with fluxes of similar magnitude (43 ± 40 to 85 ± 5 kgCH4-Cha–1 yr-1) measured in Sarawak, Malaysia102–119. Greater CH4 effluxes have been reported from Terengganu, Malaysia, with 151±100 kgCH4-Cha–1 yr–1 measured in undisturbed forest106 and 328±230kgCH4-Cha–1 yr–1 in logged forest in North Selangor, Malaysia, albeit during the wet season when a high water level resulted in a greater peat surface CH4 flux104. As well as peat surface emissions, the stems of some tree species can provide a flux pathway for CH4 (refs120,121). A short study in a Central Kalimantan peat swamp forest during the wet season measured tree stem fluxes that were estimated to be responsible for 62–87% of total ecosystem methane flux121. CH4 fluxes are generally higher but more variable among vegetation types in South and Central America. Emissions of 226 ± 51 kgCH4-Cha–1 yr–1 are reported from intact palm swamp in Peru, with a decline in emissions to 161±66kgCH4-Cha–1 yr–1 at sites affected by palm fruit and timber harvesting, but with high variability between years122. From the same region, evidence of variability both seasonally and among forest types is reported, with fluxes in the range 109 ± 37 to 190±58kg CH4-Cha–1 yr-1 (ref.123). Emissions from palm and mixed forests in Panama are higher at 262±39 and 210 ± 39 kg CH4-C ha–1 yr-1 (ref.124), respectively. As in Southeast Asian peatlands, the stems of some tree species can provide a flux pathway for CH4, with high emissions from Mauritia flexuosa125. Elevated peat surface CH4 emissions from some sites are probably linked to high temperatures126 and large inputs of labile C, for example, as root exudates127,128 from productive vegetation83. Lower emissions might be connected to either high rates of CH4 oxidation in the peat surface layers and in the rhizosphere linked to root oxygen release, which can convert 80–90% of the CH4 produced in the peat profile71,124,129; or to lower substrate quality for methanogenesis if the peat has undergone considerable decay127,130,131. Peatland drainage and agricultural conversion result in reduced peat surface CH4 emissions127. Annual fluxes from drained and plantation areas in Southeast Asia are between 1 and 4kgCH4-Cha–1 yr–1 (refs118,132), and with the potential for the peat surface to act as a small CH4 sink during periods of water-table drawdown102,118. However, the release of water rich in DOC can result in increased CO2 and CH4 emissions from drainage canals, rivers and coastal areas (Fig. 2a). For example, CH4 emissions from drainage ditches have been suggested to negate approximately 10% of the reduction in emissions of CH4 effluxes from drained peatlands133, while canal and river water with high DOC and POC content is linked to elevated CH4 fluxes from coastal lagoons134. Annual fluxes of 35±39kgCH4-Cha–1 yr–1 were measured from an Acacia plantation in Sumatra by eddy covariance. These fluxes were around half of the emissions from nearby forest, a disparity that was attributed to emissions from the canal network118. Similarly, a flux of 61±18kgCH4-Cha−1 yr−1 was reported for an oil palm plantation in Sarawak, with canals the dominant source117. These observations are consistent with the IPCC Tier 1 emission factor for ditch and canal emissions from tropical peat plantations of 1694 (449–2,939)kgCH4-Cha–1 yr–1 (expressed per hectare of water surface115 rather than total plantation surface area), based on a small number of direct measurements135.

Fluvial carbon.

DOC comprises the largest component of fluvial C loss from tropical peatlands, most of which is exported to the sea. This loss is estimated to be around 0.6tCha–1 yr–1 from intact forested peatlands, rising to 0.9 tCha–1 yr–1 from drained areas94,115,136. The IPCC methodology assumes that 90% of DOC export is ultimately mineralized to CO2. Research in the Malacca Strait supports this assumption, suggesting that 80–95% of organic matter exported from coastal peatlands of

Sumatra is mineralized and degassed from the Sunda Shelf before reaching the open ocean137. Although a component of the land–ocean DOC flux, and subsequent CO2 efflux, is natural, additional export following drainage contributes indirectly to CO2 emissions from drained tropical peatlands. The large amount of DOC discharged to the ocean94,138,139 can also result in anoxia, because decomposition processes result in depletion of oxygen from the water column and seafloor sediments140 and in changes to the coastal water pH137, with impacts for marine life, including coral formation.

Future vulnerability.

By 2015, agricultural conversion of Southeast Asian peatlands had resulted in a shift away from long-term C sequestration to an estimated emission from peat oxidation alone of 535MtCO2 yr–1, equivalent to approximately 1.5% of global annual emissions from fossil fuels and industry141. The estimated total emission from peat oxidation between 1990 and 2015 was 9,200MtCO2 (ref.141). Furthermore, the legacy of historical peatland clearances that occurred before 2010 is predicted to contribute a further 4,400–11,500MtCO2 emissions over the period 2010–2130 (ref.38). An expert assessment of the future vulnerability of all tropical peatlands has indicated that around 20% of current C stocks may be lost by 2100 through a combination of higher temperatures, negative moisture balance, fires and sea level rise142. CO2 fertilization as a result of rising levels of atmospheric CO2, as well as regional deposition of N and other nutrients, could increase forest NPP143,144, potentially enhancing peat C sequestration rates through enhanced C influx. However, changes in precipitation could negate these effects145,146. Key drivers affecting the soil processes that cause CO2 and CH4 emissions are moisture-related, including the position of the water table, suggesting that future changes in hydroclimate could substantially affect the capacity of intact peatlands to sequester C86,88, as well as altering emissions regardless of land cover122. The projected intensification of wet and dry seasons in Southeast Asia147 and forecasts for the northwestern Amazon of warmer temperatures and increased precipitation148,149 are likely to affect peatland C cycling in these areas150. There is potential for El Nino events to intensify in future decades151, resulting in extended droughts across Southeast Asia and the Congo Basin152. Regardless, ongoing climatic warming means that the impact of each new drought event will become more severe152. Given that peat accumulation rates are more sensitive to rainfall during the dry season than the wet season14, there are escalating risks of reduced peat accumulation rates. There are also indications that increased temperatures could increase emissions of CO2 and CH4, again regardless of land cover116,124,126,130,153. Although tropical peatlands have shown resilience through past episodes of hydroclimatic variability, the magnitude of current and future anthropogenic disturbances could exceed their adaptive capacity154, and it is clear that land-use changes will increase their vulnerability to climate extremes88. Peatlands in the Amazon and Congo basins will become progressively more vulnerable to a combination of climate and land-use pressures if their accessibility and susceptibility to deforestation and other disturbances increase44.

Nutrient cycling

Tropical peatlands are predominantly ombrotrophic systems; they are inherently acidic (pH3.0–4.5) and have low nutrient availability2,155. Minerotrophic systems, which include some peatlands in Peruvian Amazonia, exhibit greater diversity, ranging from strongly to mildly acidic (pH3.8–6.1) and with nutrient levels reflecting the degree of influence by river flood regimes156,157. Typical peat surface nutrient concentrations for forested peatlands in Southeast Asia are in the range 100–2,400µgg–1 for Ca, and 300–700µgg–1 for Mg (refs155,158,159). In comparison, Ca and Mg concentrations in surface peats of minerotrophic Amazonian peatlands can exceed 10,000µgg–1 and 2,700µgg–1, respectively156.

Nutrient availability

Nutrient availability in ombrotrophic peatlands depends on wet and dry inputs in rainfall, dusts and marine aerosols from outside the system155, whereas microbial decomposition of organic materials within the system contributes to nutrient stocks159–161. Nitrogen-fixing trees can also serve as a source of N (refs162–165), although N fixation is likely to be inefficient under low-pH conditions. Surface peat N contents are typically in the range 1–2% for ombrotrophic peatlands155,158,159 and 2–2.5% for minerotrophic peatlands156. Forested peatlands in Malaysia164,166, Indonesia155,158,165,167 and Panama168 have the highest plant nutrient concentrations (N, P, Ca, Mg, K) in the upper peat profile. Concentrations are 50 or 100 times higher to a depth of 200 cm because of biological accumulation in plant roots and litter. This bioaccumulation layer is deep compared to northern peatlands, where only the upper 40 cm shows nutrient enrichment169–171, and is attributable to the greater rooting depth of tree-dominated vegetation. Below the bioaccumulation zone there is a rapid decrease in nutrient concentrations into the deeper peat155,158. In intact peat swamps, nutrients are strongly retained within near-surface organic matter as they are bound in relatively recalcitrant forms following initial litter decay172, and because microbial nutrient mineralization is slowed by anoxia71. The decrease in nutrient availability with vertical depth, together with shifts to anaerobic conditions and lower substrate quality, results in strong depthwise declines in the capacity of the microbial community to mineralize and recycle nutrients166,173. Microtopography also influences nutrient availability: litter and surface peat from hummocks (which support most tree growth) have higher nutrient concentrations than hollows158, stressing the importance of efficient recycling between the peat and the vegetation.

N2O

The availability of inorganic N for plant uptake is limited in undrained peatlands owing to slow microbial N mineralization and low nitrification but high denitrification activities under acidic, anaerobic conditions (Fig. 2a). These conditions limit emissions of the greenhouse gas nitrous oxide (N2O) from the peat surface174. Drainage promotes mineralization of organic N to ammonium (NH4 +), which can be nitrified to nitrate (NO3 −)175,176, while also producing partially oxidized conditions conducive to production of N2O (refs177,178). With a few exceptions104, N2O emissions from intact peatlands tend to be low, with some variation reflecting the sensitivity of N2O formation to substrate supply (addition of plant litter) and moisture levels. At two peatlands in Panama, the average cumulative N2O emissions were 1.0 ± 0.3 and 11.5±0.7kgN2O-Nha–1 yr–1 in hardwood and palm swamp forests, respectively124. Comparable low emissions have been reported from intact peatlands in Peru at 1.3±0.6kgN2O-Nha–1 yr–1 (ref.122), and at 0.6±0.1 and 0.4kgN2O-Nha–1 yr–1 in Central Kalimantan and Riau, Indonesia, respectively88,179.

Land-use change impacts on nutrients

Conversion of peat swamp forest to other land covers involves loss of the nutrient stock within the forest biomass, reduced plant litter inputs and longer-term changes in nutrient availability and cycling. Following drainage, the increased rate of organic matter decomposition results in nutrient release, providing a source of nutrients such as P and K for crops and tree stands49. Initial increases in availability can, however, be followed by longer-term decline in nutrient capital as a result of leaching and nutrient export into water courses180. Agricultural practices typically involve inputs of soil ameliorants such as lime to raise the pH along with manure181 and/or inorganic (NPK) fertilizers to provide additional nutrients, or the planting of N-fixing trees such as Acacia spp. Without fertilization, macro-nutrients rapidly become limiting, particularly where there is a high crop off-take, for example of fresh fruit bunches from oil palm plantations182,183 or whole trees in shortrotation pulp and paper plantations49. Fertilizer use can result in nutrient runoff184, eutrophication of waterways140 and enhanced emissions of N2O from the peat surface179. N2O emissions increase following fertilization, but temporal variability is high and influenced both by agricultural practices and fertilizer application rates185. For example, conversion of palm swamp forest to rice agriculture (with high water tables but no fertilizer addition) in Panama led to only a modest increase in N2O fluxes from 3.3±0.4 to 5.0±0.8kgN2O-Nha–1 yr–1, respectively186. However, fertilized sites can have N2O emissions more than 20 times higher than unfertilized sites, with 178±218 and 8±16kgN2O-Nha–1 yr-1, respectively132,187. In addition, peat surfaces receiving inputs of fresh organic matter, such as oil palm fronds, emit more N2O (ref.188). In summary, clearing of peat forest and its conversion to agriculture leads to nutrient cycling shifts from a system in which nutrients are conserved to a system with greater rates of nutrient turnover and net losses, including enhanced emissions of N2O.

Fire impacts on biogeochemistry

Peatland fires comprise flaming fires that consume aboveground fuels, and lower-temperature ground fires that burn down into the peat and persist for weeks or months until extinguished by rising water tables at the start of the wet season189. Low oxygen availability for sub-surface fires gives rise to smouldering combustion, which produces high emissions of small particulates (PM2.5)190, and a range of volatile organic compounds191–193 and gases (CO, CH4 and CO2). Tropical peat fires emit higher amounts of gases per unit mass of dry fuel burned than fires on northern peatlands, possibly owing to a higher peat fuel C content190. They are also a source of metal emissions and there is evidence that tropical peat fires contribute to atmospheric loadings of heavy metals (Cd, Co, Cu, Mn, Ni, Pb, Ti and Zn) at concentrations that can be carcinogenic and exceed WHO air quality guideline values194–197 (Fig. 3). The closed vegetation canopy and high peat moisture content in an intact peatland ensure a low risk of ignition198 with little likelihood of fires burning into the saturated peat. Since the 1980s, however, peat fires in Indonesia have escalated in extent and frequency199 — only 3% of peat swamp forests in Sumatra and Kalimantan are now considered to be fire-resistant198. This step change can be attributed to forest disturbance and drainage, which increase the availability of dry, combustible fuels, and to growing levels of human access and land-use activities on peatlands, which provide fire ignition sources. Fire severity and duration intensify during periods of prolonged drought associated with ENSO and Indian Ocean Dipole weather events200–204. In 1997, ENSO-related fires released between 810 and 2,570MtC from Indonesian peatlands alone, with the most severe fires located in disturbed peat landscapes205. Since then, fires have become a near-annual event, but with extent and severity increasing with dry-season intensity and length206,207. Fire-driven modifications of peat substrates include changes in physical properties, such as increased bulk density180,208, and peat chemistry changes, such as preferential removal and alteration of organic components (Fig. 3). Burned peat has an increased content of resistant organic compounds (aliphatic and aromatic hydrocarbons), contrasting with unburned samples, which have a greater diversity of labile constituents180,209. Fire also modifies peat pH and the availability of plant nutrient elements, particularly in the immediate aftermath of fire and prior to vegetation recovery. Surface peat at recently burned sites in Southeast Asia had an increase in pH and, owing to N-volatilization during combustion, a lower N content209,210. A study in Selangor, Malaysia211, reported an immediate post-fire increase in surface peat pH (approximately from pH4 to 6) and increases in macro-nutrients (excluding N) and C/N ratios. This effect can, however, be transitory. For example, there was a post-fire shift in porewater pH (pH3.0, unburned site; pH3.5, burned site) in Brunei208 but no change in peat C/N ratios some 14 months after the fire. This observation was attributed to rapid regrowth of secondary vegetation and the addition of fresh litter, and therefore N, to the peat surface. Post-fire flooding can occur, which is attributable to peat combustion. Combustion brings the peat surface closer to the wet-season water table, lowers transpiration rates due to loss of vegetation and reduces peat water storage capacity due to increased bulk density180,208,212. For example, a high water table at a post-fire site in Brunei resulted in near-doubling of peat surface CH_4 emissions compared to intact peat swamp forest (7.8 ± 2.2 versus 4.0 ± 2.0 $mgCH_4$ m^{-2} per hour, respectively)208. Post-fire increases in CH_4 and CO_2 emissions were also noted in the immediate aftermath of a fire in Selangor, Malaysia211. After 5 months, CO_2 emissions returned to pre-fire levels, but CH_4 emissions remained high. Fire-disturbed peatlands can also be a substantial source of CH_4 owing to a change in plant cover. On burned peatland in Brunei, secondary vegetation dominated by sedges (Scleria spp.) provided a plant-mediated flux pathway for 159 ± 96 $kgCH_4$ ha^{-1} per year, comprising 70–80% of total ecosystem CH_4 flux213. A positive relationship between increased peat bulk density and fire-produced CH_4 emissions has also been identified192, probably because increased bulk density maintains a slower fire spread rate, thereby limiting oxygen availability at the fire front214. Forest recovery following a fire can be slow215 owing to lower availability of nutrients and labile C, both of which also reduce the diversity and size of microbial communities216. In Central Kalimantan, post-fire vegetation is limited to a few pioneer tree species and ferns217. Compared with unburned sites, the abundance of bacteria is reduced by 99% at the peat surface and by 63% in subsurface peat (30–50cm), with little change over a 3-year post-fire period218. In mineral soils219, there are post-fire reductions in mycorrhizal communities, which are important for N and P acquisition by vegetation. This reduction could hinder regeneration in tropical peatlands, as many peat swamp trees form mycorrhizal associations. Short- and longer-term effects of fire on the diversity and activity of most peat biota have not been established, but as with tropical mineral soils, fire probably has a negative impact220.

Management opportunities and challenges

Tropical peatlands contain the largest amount of irrecoverable C of global ecosystems; specifically, C that is vulnerable to release from land-use change but irrecoverable on timescales relevant to mitigate climate impacts8 . Avoiding further loss or degradation of intact tropical peatlands is, therefore, a relatively low-cost pathway for protecting their C stocks and achieving climate goals. The vulnerabilities of tropical peatlands to increased C loss and greenhouse gas emissions are often directly linked to land management, with substantial opportunities for reducing emissions by altering practices. Therefore, the highest management priority should be the enhanced protection of intact peat swamp forests, as many continue to function as net C sinks. This level of safeguarding is critical for forested peatlands in Southeast Asia, where the C sink function is increasingly susceptible to land-use change impacts, fire and climatic variability142, mirroring similar vulnerabilities observed for the region's mineral soil forests221. For peat swamp forests affected by logging, drainage and fire, measures need to be developed and implemented, at scale, to enhance and restore hydrological and ecological integrity109,222. The potential for reduced greenhouse gas emissions will depend upon the degree of prior ecosystem modification and the effectiveness of rehabilitation strategies, especially where actions to raise water levels conflict with livelihood aspirations217,223 (Fig. 4a). The role of peat biogeochemistry and microbiology in successful strategies for ecosystem restoration are areas requiring further investigation109. There is also a clear need for robust and ethical mechanisms to finance activities that reduce emissions224, with successful interventions likely to be those co-produced with local people. For agricultural peatlands where ecosystem rehabilitation to pre-drainage conditions is not socially or economically feasible, options need to be identified to reduce greenhouse gas emissions, fire risk and peat subsidence. Where technically feasible and socially acceptable, raising water levels closer to the peat surface could reduce CO_2 emissions while maintaining agricultural production and livelihoods53,113 (Fig. 4a). This approach is not without its challenges; it will require improved water control and conservation measures to avoid wet-season flooding and dry-season drawdown. There is also a trade-off between reduced emissions and reduced nutrient availability from peat decomposition, which can require additional inputs of macronutrients to maintain crop production (Fig. 4b). Control of N fertilization to optimize yield while reducing N2O emissions will require particular consideration. It is not inevitable that mitigation measures will lead to reductions in economic productivity, but appropriate financial compensation is clearly needed in situations where local populations incur a loss to deliver the wider societal benefit of climate change mitigation. A further option for agricultural peatlands is to develop economically competitive crop species with low fertilization requirements suitable for sites where it is socially acceptable and technically feasible to maintain the highest (near-surface) water levels. Whilst greatly limiting CO2 and N2O emissions (Fig. 4a), this approach — often referred to as swamp cultivation or paludiculture60,225–227 — excludes dryland crop cultivation and thus remains among the future management challenges for tropical peatlands58. There is an increasing body of knowledge on suitable native species that could be grown to provide an economic return, but there remain uncertainties regarding their performance, as well as markets for products227. There are also knowledge gaps regarding the extent to which swamp cultivation can mitigate peat C loss, although initial research in Europe indicates that a near-neutral site C balance can be achieved228.

Summary and future perspectives

Tropical peatlands are globally important C stores. Genuinely intact systems continue to function as a net C sink with a cooling effect on global climate. However, around 60% of tropical peatlands have been subject to anthropogenic alterations10, specifically deforestation, drainage, fire and agriculture. These changes have transformed tropical peatlands that were previously a long term C store into a major source of greenhouse gas emissions. In our judgement, no other terrestrial ecosystem, and certainly none with such high and vulnerable C stocks, has undergone such dramatic degradation and loss over a comparably short period. Additional consequences of anthropogenic transformations include shifts in nutrient cycling, including enhanced N2O emissions; extensive wildfires, particularly on Southeast Asian peatlands, with accompanying episodes of fire-driven air pollution; and increased flood risk resulting from peat subsidence. In recognition of these adverse consequences, various initiatives are emerging to safeguard or rehabilitate the key functions of tropical peatlands. These initiatives mostly focus on protecting ecosystem C storage and mitigating climate change. For degraded peatlands, re-establishing peat formation through restoration of hydrology and vegetation cover could lead to CO2 uptake rates as high as the natural baseline, or potentially even higher as biomass and litter C pools rebuild, thereby contributing to reducing net emissions. Compared to mid- and high-latitude peatlands, there remain substantial knowledge gaps and uncertainties in tropical peatland science. These areas are priorities for further research that will not only enhance our understanding of biogeochemical processes but will also support more effective strategies for ecosystem management and restoration. Despite their contemporary importance in global climate regulation, basic information on the C stocks of tropical peatlands is deficient, even for the better studied Southeast Asian peatlands. The uncertainties associated with estimates of peatland C density derive mostly from limited data on peat thickness, which can generally only be obtained from ground-based surveys229. Continued field investigations are central to improving knowledge of peatland extent and thickness, with satellite data sets and airborne technologies (such as light detection and ranging (LIDAR) and electromagnetic) playing an increasing part in supplementing and extending field-derived information22,230–233. Given the ongoing reduction of peatland C stocks as a result of land-use change and fire, particularly in Southeast Asia141, combined field and remote-sensing surveys are also necessary to monitor C stock changes over time. The biogeochemical consequences of drainage and agricultural conversion of tropical peatlands are well established, particularly in terms of enhanced rates of C loss. Given the scale of contemporary and potential future greenhouse gas emissions from these ecosystems, their current omission from Earth system models142 could result in under-accounting of peatland-mediated climate feedbacks and their contribution to radiative forcing. Incorporating tropical peatlands into process-based modelling will, however, require improved and accurate information, not only about C stocks but also about C fluxes at improved spatial and temporal scales. Studies using the eddy covariance technique are beginning to provide longer-term data sets that enable investigation of ecosystem responses to changes in climate and land management and their relative controls on C dynamics. These data are only currently available from a few peatlands and across limited land covers in Southeast Asia. If extended to other land covers and to peatlands in South America and Central Africa, an eddy covariance flux tower network could become increasingly essential to providing an improved understanding of the resilience or vulnerability of tropical peatland C stocks to changing environmental conditions and the key controls on greenhouse gas exchange rates. To date, drainage and agricultural conversion of tropical peatlands has been most extensive in Southeast Asia. Mitigating greenhouse gas emissions in these landscapes, while also limiting subsidence, will require raised water tables, reduced fertilization and an increase in mixed as opposed to monoculture cropping (Fig. 4b). There are, however, key knowledge gaps around the biogeochemical and microbiological implications of land management. Improved process-level understanding could underpin strategies to reduce C loss from drained peatlands109. The development of swamp cultivation methods could become increasingly relevant for Southeast Asian peatlands as subsidence increases the duration of flooding, thereby requiring alternative economic land uses under high water levels57. Filling the knowledge gaps on tropical peatland biogeochemistry will build an improved evidence base on the vital contribution that responsible management of these C-dense ecosystems can make to reducing greenhouse gas emissions and to maintaining or restoring C sequestration and storage. Tropical peatlands can undoubtedly make an important contribution to nature-based climate solutions, but these efforts will only be effective if they are underpinned by a sound understanding of peatland biogeochemistry.