








Degradation of Southeast Asian tropical peatlands and integrated strategies for their better management and restoration

By Adi Jaya

REVIEW

Degradation of Southeast Asian tropical peatlands and integrated strategies for their better management and restoration

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Abstract

1. About half of the world's tropical peatlands occur in Southeast (SE) Asia, where they serve as a major carbon (C) sink. Nearly 80% of natural peatlands in this region have been deforested and drained, with the majority under plantations and agriculture. This conversion increases peat oxidation which contributes to rapid C loss to the atmosphere as greenhouse gas emissions and increases their vulnerability to fires which generate regional smoke haze that has severe impacts on human health. Attempts at restoring these systems to mitigate environmental problems have had limited success.
2. We review the current understanding of intact and degraded peatlands in SE Asia to help develop a way forward in restoring these ecosystems. As such, we critically examine them in terms of their biodiversity, C storage, hydrology and nutrients, paying attention to both above-ground and below-ground subsystems.
3. We then propose an approach for better management and restoration of degraded peatlands that involves explicit consideration of multiple interacting ecological factors and the involvement of local communities who rely on converted peatlands for their livelihood.
4. We make the case that as processes leading to peatland development involve modification of both above-ground and below-ground subsystems, an integrated approach that explicitly recognizes both subsystems and their interactions is key to successful tropical peatland management and restoration.
5. *Synthesis and applications.* Gaining a better understanding of not just carbon stores and their changes during peat degradation, but also an in-depth understanding of the biota, nutrient dynamics, hydrology and biotic and abiotic feedbacks, is key to developing better solutions for the management and restoration of peatlands in Southeast Asia. Through the application of science- and nature-based solutions

that recognize the interactions among the above-ground and below-ground sub-systems, and taking into account the livelihood needs of local people, we propose a way to mitigate the ongoing environmental damage that is occurring in these iconic and unique ecosystems.

KEYWORDS

above-ground–below-ground, carbon storage, climate change, greenhouse gas emissions, nature-based solutions, restoration, revegetation, rewetting

1 | INTRODUCTION

Peatlands cover an estimated 500,000 km² across the tropics with a C pool of at least 100 Pg (Dargie et al., 2017; Page et al., 2011). About 35%–50% of these peatlands occur in SE Asia (including New Guinea) where they have formed on coastal and sub-coastal lowlands under forest vegetation (Dargie et al., 2017; Gumbrecht et al., 2017; Page et al., 2011). In the past, these peatlands supported the livelihoods of small numbers of indigenous people through fisheries, hunting and the provision of non-timber forest products (Page et al., 2011). In recent decades, however, peat swamp forests have been extensively logged (Langner et al., 2007) and drained for monoculture plantation development of tree crops such as acacia *Acacia* spp. and oil palm *Elaeis guineensis*, as well as for agriculture, at both industrial and smaller scales (Miettinen et al., 2012). As a result, peatland forest cover in SE Asia has declined from 76% to 29% (11.9 to 4.6 Mha) between 1990 and 2015 (Miettinen et al., 2016).

Conversion to plantations or other forms of agriculture results in several long-term changes in the peatland ecosystem. Removal of the original forest cover combined with drainage results in high rates of peat decomposition and carbon dioxide (CO₂) emissions such that the ecosystem switches from a net C sink to a source (Miettinen et al., 2017). Drainage also increases susceptibility to fire which results in additional peat loss and greenhouse gas (GHG) emissions, and is accompanied by extreme episodes of smoke pollution (haze), which seriously impact human health (Marlier et al., 2013; Page et al., 2002). The 2015 fire season alone is estimated to have caused persistent exposure of 69 million people to unhealthy air quality conditions and nearly 12,000 premature deaths (Crippa et al., 2016). Emissions from biological oxidation of drained peat as CO₂ are estimated to be 132–159 Mt/C year with an additional 122 Mt C/year from peat fires (Miettinen et al., 2017), with additional losses of C as methane (CH₄) and dissolved organic carbon (DOC) from drainage channels (Cook et al., 2018; Manning et al., 2019; Moore et al., 2013). Furthermore, peatland subsidence following agricultural conversion and resultant peat oxidation typically occurs at rates of 3–4 cm/year (Evans et al., 2019; Hooijer et al., 2012), which over time will lead to flooding risks as the land surface reaches the gravitational drainage limit.

In addition to causing the loss of C, clearing and degradation of peat swamp forests have a negative impact on regional biodiversity.

By 2015, only 6.4% of peat swamp forests in peninsular Malaysia, Sumatra and Borneo remained in a pristine condition (Miettinen et al., 2016), placing several obligate peat forest species under threat of extinction (Giesen et al., 2018; Thornton et al., 2018). In addition, the habitat quality of remaining areas of forested peatland is being reduced by habitat fragmentation, drainage impacts, fire from surrounding landscape and unsustainable (and often illegal) timber extraction (Miettinen et al., 2016).

In peatlands that have been converted to commercial plantations, current management practices involve maintaining sufficiently low water table depths to enable optimal growth of tree crops while also reducing water-table draw down during dry seasons (Couwenberg & Hooijer, 2013). Water-tables fluctuate according to variation in rainfall, and the magnitude of these fluctuations will be greatest at sites with the lowest water-table depths (Couwenberg & Hooijer, 2013). This leads to frequent drying-wetting cycles that may increase peat loss and subsidence (Hooijer et al., 2012), and increase the risk of fire, during drier months. In addition to peatland under some form of land cover, there is an extensive area (18%–25% of the total, Miettinen et al., 2017; Wijedasa et al., 2018) with a land cover of shrubs and ferns that has resulted from deforestation and regular fires.

In response to extensive fires in 2015, the Indonesian government set up an agency, the BRG (Badan Restorasi Gambut; Peatland Restoration Agency), tasked with restoring degraded peatlands to prevent future fires through peatland rewetting and revegetation, and livelihood revitalization (BRG, 2016). Similar initiatives are being implemented at a range of scales by the private sector (e.g. under Ecosystem Restoration licences) and by a number of conservation and restoration projects (Puspitaloka et al., 2020). However, understanding of the effectiveness of rewetting in reducing peatland subsidence and GHG emissions remains limited (Dohong et al., 2018; Jauhainen et al., 2008; Wilson et al., 2016). Furthermore, little is known about how to most effectively revegetate and restore degraded peatlands, in part because of limited understanding of the ecology of the dominant peatland plant species.

In this review, we discuss the ecology of peatlands in SE Asia, environmental consequences of their conversion and degradation and challenges related to their management and restoration. In doing this, we first consider both intact and degraded peatlands in terms of their resident biota, C and nutrient dynamics, hydrology, and soil organisms and processes. We then use this knowledge to discuss

how to best implement a holistic approach for managing and restoring degraded peatlands that integrates both above-ground and below-ground ecological processes, and that recognizes the need for engagement of local communities. Our underlying goal is to highlight the multiple environmental problems that result from peatland degradation and to propose mitigation approaches using science- and nature-based solutions. This is relevant to enable responsible and sustainable management of peatlands that is under production, and to reverse peatland degradation through ecosystem restoration.

2 | TROPICAL PEATLAND HABITATS AND THEIR DEGRADATION

In their undisturbed intact state, tropical peatlands form a unique habitat in the SE Asian region because of their high water-tables and deep layers of organic matter (OM) which often separate plant root systems from underlying parent materials. Peat swamp forests support a high diversity of biota, some of which are endemic to this ecosystem (Giesen et al., 2018; Posa et al., 2011; Thornton et al., 2018). In pristine conditions, around 45 higher plant species (~3% of the peat swamp forest flora), mainly trees such as *Dyera polyphylla*, *Palaquium cochleariifolium* and *Shorea* spp., are restricted to SE Asian peatlands (Giesen et al., 2018). Many of the tree species that dominate in peatlands have specific adaptations to the waterlogged conditions, for example, by having buttress or stilt roots that provide improved stability, and breathing roots (pneumatophores) that protrude above the peat surface (Page et al., 2006).

Peat swamp forests host at least 80 endemic species of fish (Posa et al., 2011), many of which live in the water-filled pores and channels within the peat itself. Additionally, as most of the lowland forests throughout SE Asia have been cleared, existing peat swamp forests serve as refugia for species that have historically used a wider range of forest types (Posa et al., 2011). For instance, pristine peat swamp forests are the most important remaining habitat for the iconic orangutan (Erb et al., 2018; Wich et al., 2008) and for several endangered gibbon species (Cheyne et al., 2008; Quinten et al., 2010). There are also likely to be other animal species that are partially or fully dependent on peat swamp forest habitats; for example, very little is known about their invertebrate and below-ground biota.

Commercial exploitation of peat swamp forests intensified from the 1980s onwards, with the allocation of timber concessions (Dommain et al., 2016). Valuable timber species including ramin (*Gonystylus bancanus*) and meranti (*Shorea* spp.) that were once abundant in intact forests were logged and transported or floated out of the forests using light rail or through a system of constructed canals. The disturbance to the forest canopy from logging and to the peat from canal development has altered the forest microclimate and hydrological conditions by disrupting evapotranspiration processes and lowering groundwater levels. This has left these forests more susceptible to desiccation and potential fires (Field et al., 2009; Langner et al., 2007). Subsequently, from the 1990s, conversion of peat swamp forests to plantation agriculture by drainage and

deforestation accelerated, especially on Sumatra and Kalimantan (Miettinen et al., 2016). During and for some years after the economic downturn of the late 1990s, Indonesia's forests, including peat swamp forests, were subject to high levels of illegal logging, which not only increased loss of forest cover but also the risk of fire (Miettinen et al., 2017).

The transformation of peat swamp forests into either deforested, degraded peatlands or plantation and smallholder agriculture has had significant social, economic, environmental and human health consequences in the region and beyond. These impacts involve the loss of biodiversity, including rare and endangered animal species, for example, flat-headed cat *Prionailurus planiceps*, Sunda clouded leopard *Neofelis diardi*, marbled cat *Pardofelis marmorata*, orangutans *Pongo* spp., fresh-water turtles, large flying fox *Pteropus vampyrus natuna* and several peat swamp fish species (Giam et al., 2012; Posa et al., 2011). In the worst-case scenario, in which the rate of conversion across the region was to reach that of the most rapidly deforested river basin, 77% (79 of 102 species) of the narrowly adapted (stenotopic) fish species are likely to become extinct, a figure that would more than double known extinctions of the world's fresh-water fishes (Giam et al., 2012). They have also led to significant reductions in plant species populations; for example, 8 uncommon and 20 rare species that are restricted to this habitat may be under threat (Giesen et al., 2018). Several economically valuable timber species found in peat swamp forests, including ramin (*Gonystylus* sp.; Barstow & Randi, 2018), and several meranti species (e.g. *Shorea platycarpa*; Ashton, 1998) are listed by IUCN as critically endangered.

The degradation and conversion of peatlands has led to the disruption of natural hydrological functions (Evers et al., 2017), thereby increasing drought severity (Taufik et al., 2020) and fire hazards (Taufik et al., 2019), which, in turn, cause a rapid destabilization of the peatland C store (Baird et al., 2017), as we discuss below. This results in loss of sequestered C to the atmosphere as CO₂, and is accompanied by land subsidence, which increases the risk and duration of flooding, particularly for low-lying, shallow peatlands close to the coastline or rivers (Hooijer et al., 2015). Finally, upon peatland conversion to industrial or smallholder plantations and agriculture, there is an increased migration of human populations to these areas, which creates further pressures on local communities living in and near to pristine forests that rely on these forests for their livelihood (Silvius & Suryadiputra, 2005).

3 | CARBON RELEASE FROM DEGRADED SOUTHEAST ASIAN PEATLANDS

As tropical peatland is a globally important C store, large-scale conversion and degradation generates high C emissions. These are associated with reduced Net Primary Production (NPP; Basuki et al., 2019), drainage-driven peat oxidation and fluvial losses, and losses through combustion of peat by fire (Figure 1). We now discuss how these C losses occur, to better understand how conversion and degradation affect the peatland C cycle.

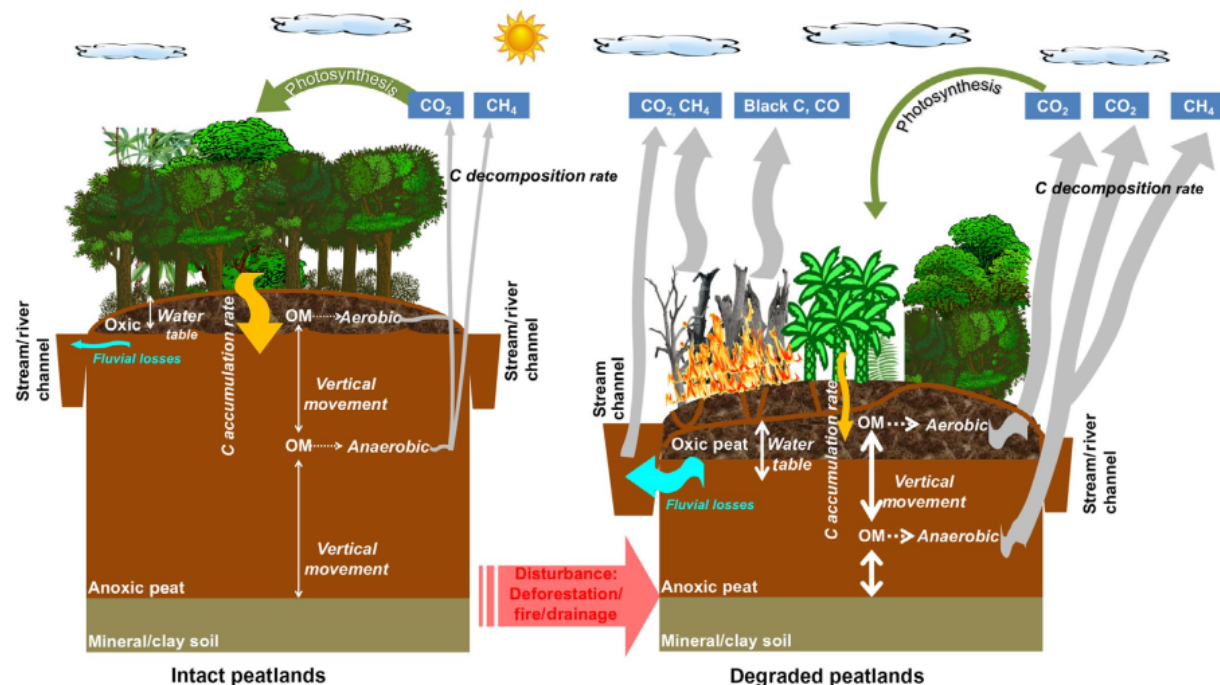


FIGURE 1 Carbon gains and losses from pristine and degraded peatlands. Thickness of arrows indicates relative magnitude of flux in pristine versus degraded peatlands. OM = organic matter; C = Carbon

3.1 | Carbon release from peatland conversion and degradation

Following peatland land-use change, oxidation of soil OM that has accumulated over millennia usually leads to a shift in the peatland C balance from a net sink to a net source of atmospheric C (Miettinen et al., 2017). This loss of C currently accounts for approximately 78% of SE Asia's total GHG emissions from managed land cover (i.e. 146 Mt/C year; Cooper et al., 2020; Miettinen et al., 2017). The balance of CO₂ versus CH₄ emissions varies considerably, and is driven by the redox potential of the peat and strongly affected by the long-term position of the water-table (Couwenberg et al., 2010). As such, water-table draw down increases greatly during peat forest degradation and peatland conversion, and has been shown to substantially increase CO₂ fluxes while reducing CH₄ emissions (Cooper et al., 2020; Jauhainen et al., 2005; Wright et al., 2013). For example, eddy covariance measurements have revealed annual CH₄ exchanges over natural peat forest (i.e. $9.1 \pm 0.9 \text{ gm CH}_4 \text{ m}^{-2} \text{ year}^{-1}$) to be twice that from plantations of *Acacia* spp. (i.e. $4.7 \pm 1.5 \text{ gm CH}_4 \text{ m}^{-2} \text{ year}^{-1}$) on converted peatland with a low water table (Deshmukh et al., 2020). Furthermore, a clear diurnal variation in CH₄ exchange has been shown for natural forest (where the groundwater levels was higher) relative to *Acacia* plantations, which could be due to groundwater levels being consistently below the rooting zone in the latter (Deshmukh et al., 2020). Furthermore, in converted and degraded peatland, water saturation of dry peat upon rainfall inundation can actually support higher peat CO₂ release by promoting microbial respiration (Wright et al., 2013). Rainfall could also

promote downward transport of labile C substrates that prime microbial communities to release C from deep peat layers, as has been demonstrated in other soil types (Fontaine et al., 2004; Kuzyakov et al., 2000).

In addition to evapotranspirative losses, water moves through tropical peatlands as subsurface flow within the peat profile and as overland flow (Baird et al., 2017; Kelly et al., 2014). As peatland deforestation and drainage result in conversion of peatland C to particulate organic C (POC) and DOC (Cook et al., 2018; Moore et al., 2011; Rixen et al., 2016), C enters the peatland hydrological system, including peatland canals and rivers. This enhanced C loss arises in a large part through organic material being metabolized by microbial activity (Cook et al., 2018; Moore et al., 2013). The fluvial losses as DOC from disturbed tropical peatlands in Indonesia have been shown to be around 50% greater than those from an adjacent intact peat swamp forest (Moore et al., 2011, 2013) and via CO₂ and CH₄ evasion from water surfaces (Manning et al., 2019), although this is smaller than gaseous C losses from the peat surface (Cooper et al., 2020; Hirano et al., 2012; Moore et al., 2013). In an El Niño year, when a lower discharge than usual is observed, TOC fluxes from oil palm plantation sites were found to be dominated (91%) by DOC and ranged from 34.4 ± 9.7 to $16.3 \text{ g C m}^{-2} \text{ year}^{-1}$ (Cook et al., 2018). In another study, levels of DOC from leaves in a degraded secondary peatland forests in a leaching experiment rose rapidly to levels far higher (up to 1,760 mg/L) than natural levels (74–84 mg/L) in the peat swamp (Yule & Gomez, 2009). More than 50% of the DOC that is lost through fluvial processes is believed to be subsequently mineralized either in rivers or after it enters the sea, where it is emitted

to the atmosphere as CO₂ (Wit et al., 2015). Such losses represent an indirect contribution to GHG emissions, which are currently poorly quantified but may be an underappreciated contributor to the large total amounts of C that eventually reach the atmosphere due to peatland degradation and conversion (Cook et al., 2018).

3.2 | Carbon release following fire events

Undisturbed peat swamp forest is highly fire resistant, because it has a water-table close to the surface of the forest floor for most of the year and a humid microclimate beneath the closed canopy. Over recent decades, however, peatland fires have been substantial in terms of area burnt, severity of combustion and the scale of emissions of greenhouse and trace gases, aerosols and particulates (Huijnen et al., 2016; Page et al., 2002; Stockwell et al., 2016). Across SE Asia, fire has long been used as a cheap, fast and effective means to clear forest debris, regrowth and crop residues. But wherever anthropogenic disturbance has interfered with the natural hydrologic self-regulation of the peatland, drying of the peat surface has transformed a formerly fire-resistant ecosystem into one that can be highly flammable (Page & Hooijer, 2016; reviewed in Evers et al., 2017). In addition, increased human access and activities have escalated the number of both accidental and intentional fire ignitions (Cattaua et al., 2016).

Peatland fires are dominated by smouldering combustion (Hu et al., 2018) that persists for long time periods, and can penetrate from several centimetres to several tens of centimetres below the peat surface depending on moisture conditions (Ballhorn et al., 2009; Page et al., 2002; Simpson et al., 2016). Low oxygen availability at the fire front results in incomplete combustion, meaning that CO₂ release is accompanied by emissions of CH₄ and other toxic gaseous products, such as carbon monoxide, hydrogen cyanide and formaldehyde. Furthermore, high levels of small particulates (PM_{2.5}—particulate matter with diameter less than 2.5 µm) are released, which are injurious to human health (e.g. Kiely et al., 2020; Stockwell et al., 2016; Wiggins et al., 2018). This type of air pollution impacts negatively on livelihoods and economies over great distances because smoke plumes can be transported over tens or even hundreds of kilometres (Marlier et al., 2015). Some of the most severe fires in recent years (e.g. in 1997, 1998, 2006, 2009 and 2015) have occurred in conjunction with El Niño–Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) events (Field et al., 2009; Hong et al., 2008; Reid et al., 2013) which create drought conditions across western Indonesia and Malaysia. Ongoing peatland disturbance has, however, seen fire occurrence becoming decoupled from climate: in 2013, for example, extensive tracts of peatland in central Sumatra burnt during a short, 2-month dry spell in an otherwise wet year (Gaveau et al., 2015). Meteorological drought (low rainfall) leads to hydrological drought (decline in peatland water-table), causing soil moisture deficits and dry litter on the peat surface, which is highly combustible and serves as a fuel layer (Taufik et al., 2017). Hence, human-induced ignition can initiate wildfires

even in non-drought years, and with amplification during drought years (Taufik et al., 2020), with major implications for biogeochemical cycles in peatlands through loss of nutrients bound in organic matter and thus ecosystem nutrient capital.

Fires in SE Asian peatlands are a major source of GHG emissions to the atmosphere, with average annual emissions of around 100 Tg C year according to the Global Fire Emission Database (GFED; www.globalfiredata.org/index.html). Higher emissions occur during extreme fire years: for example, estimates for 2015 range from 227 Tg C (Huijnen et al., 2016) to 510 Tg C (Yin et al., 2016). The greatest uncertainty for estimating emissions is the depth of burn, that is, the volume of combusted peat (Ballhorn et al., 2009) with only a limited number of studies estimating fire fuel consumption (e.g. Simpson et al., 2016). Other studies have indicated significant variability in fire gaseous emissions factors between sampled fires and sites, reporting a 91% variation in CH₄ emissions from peat fires at sites in Malaysia which are likely to be due, at least in part, to differences in peat bulk density (Smith et al., 2018).

In addition to direct emissions, peat fires bring about local environmental impacts, including changes in peat chemistry and microbiology, although again, the research base is limited (but see Dhandapani, Ritz, et al., 2020). Combustion consumes surface peat, which is rich in labile C compounds, and exposes deeper peat layers that are at a more advanced stage of decomposition and contain more recalcitrant compounds (Könönen et al., 2015). The microbial abundance and phosphatase activity in burned peat soils are significantly less than that of unburned soils (Sazawa et al., 2018). In addition, burning and consequent loss of OM lowers the peat surface, bringing it closer to the groundwater level. Some studies have shown that successive fires can reduce the rate of soil respiration (Hirano et al., 2014) and thereby also the rate of peat surface subsidence (Konecny et al., 2016). However, other studies have shown that the loss of vegetation cover may increase mean surface soil temperature, thereby enhancing the rate of peat decomposition (Jauhiainen et al., 2014). In a comparison of fire and non-fire affected peatland in Brunei, no significant decrease in soil respiration at the burnt location was found, although CH₄ effluxes were enhanced in the fire-affected sites, due to a prolonged higher water table which provided more optimal conditions for methanogenesis (Lupascu et al., 2020).

4 | CURRENT STATUS OF NUTRIENT DYNAMICS IN SOUTHEAST ASIAN PEATLANDS

Tropical peat swamp forests in SE Asia generally have low nutrient availability especially when peat deposits are deep, as the surface layers become disconnected from the underlying parent material (Page et al., 2006; Wüst & Bustin, 2003). The dome-shaped topography in pristine peat swamps limits inflow of surface water and therefore nutrient input from rivers and streams is restricted to riparian zones (Gandois et al., 2014; Page et al., 2006). Nutrient inputs are low and depend primarily on rainfall, dusts and marine aerosols from outside

the system (Weiss et al., 2002), and litterfall and microbial decomposition of litter inputs and organic materials within the system (Page et al., 1999; Sjögersten et al., 2011; Yule, 2010). Additionally, in peatlands of low nutrient availability, nitrogen (N)-fixing trees (e.g. *Koompassia malaccensis*) can serve as a source of N to the system (Ong et al., 2015). The plant-soil system cycles and retains nutrients near the peat surface, and studies in Malaysia (Too et al., 2018; Wüst & Bustin, 2003) and Indonesia (Lampela et al., 2014; Neuzil et al., 1993; Weiss et al., 2002) have shown nutrients to be highest in the top of the peat profile (0–80 cm) because of biological accumulation (Sulistiyanto, 2005). This decline in nutrient availability with depth, together with shifts in peat redox and substrate quality, contributes to explaining the strong depth-wise declines in microbial activity, and the capacity of the microbial community to mineralize nutrients (Jackson et al., 2009; Too et al., 2018).

In intact peat swamp forests, nutrients are tightly retained, both through being bound in relatively recalcitrant forms and through impairment of nutrient mineralization resulting from the high water table and low oxygen availability (Hoyos-Santillan et al., 2019). When peatlands are drained, logged and converted to agriculture, nutrients become more labile, leading to short-term increases in their availability upon mineralization, followed by longer-term decline in nutrient capital in disturbed, secondary and cleared forest (Dhandapani et al., 2019; Könönen et al., 2015). For example, studies in Malaysia (Dhandapani et al., 2019; Yule & Gomez, 2009) and Indonesia (Könönen et al., 2015) provide evidence that degradation, drainage and conversion of peat swamp forests can lead to decline in major nutrients such as N, P, base cations and micronutrients due to enhanced organic decomposition (Tonks et al., 2017), although some cations can also increase (Könönen et al., 2015). Furthermore, it has been shown that most macronutrients in the top 0–5 cm layer of peat were about 50% lower in the secondary forest than pristine peat swamps, because of reduced leaf litter addition, with P as a notable exception (Dhandapani et al., 2019). Conversion to agriculture also leads to changes in nutrient balances when land management involves inputs of new nutrients, such as additions of mineral (NPK) fertilizers and manure, or the planting of N-fixing trees such as *Acacia* spp. This contributes to nutrient runoff and eutrophication of nearby canals and rivers, and to gaseous losses of nitrogen as nitrous oxide (N₂O) emissions (Jauhiainen et al., 2012). In summary, clearing of peat forest and its degradation or conversion to agriculture leads to nutrient cycling shifting from a system in which nutrients are conserved to a system with greater rates of nutrient turnover and net losses.

5 | CURRENT HYDROLOGICAL MANAGEMENT PRACTICES IN TROPICAL PEATLANDS

Most major crops will not thrive in the waterlogged conditions of natural peat swamps (Andriess, 1988). The two most common commercial peatland crops, oil palm and *Acacia* spp., both require

well-drained peat to provide good yields. Furthermore, high water tables hinder fertilizer application, and interfere with access to planting areas by workers and machinery. Therefore, the strategy for plantation agriculture on peatlands in SE Asia has been to lower the water-table to improve conditions for managing and growing crops. For example, the Roundtable on Sustainable Palm Oil 2012 Best Management Practices for oil palm cultivation recommend that the water table be maintained at a depth of 40–60 cm below the peat surface (Lim et al., 2012). Water regulation is achieved by a hierarchical network of drains (Andriess, 1988; Tay, 1969). This is essentially passive regulation, with the drainage network providing an easy route for water added by precipitation to leave the peatland.

Water management and site preparation in plantations alter the hydraulic properties of the peat. Shrinkage and compaction of surface peat reduce average pore space in the peat matrix and increase peat bulk density of surface peat in the first 1–5 years after drainage (Hooijer et al., 2012; Tonks et al., 2017). Furthermore, lower groundwater levels in drained peatlands lead to changes in the temperature regime of surface peat (Hoyt et al., 2019), and OM decomposition, like most metabolic processes, is affected strongly by temperature (Sjögersten et al., 2018). Specifically, low groundwater levels are associated with larger fluctuations in peat surface temperature and larger diurnal fluctuations in efflux of CO₂ from the peat surface (Hirano et al., 2014; Jauhiainen et al., 2012, 2014). In addition, sites with low water table regimes are more vulnerable to drought event and will release greater amounts of CO₂, CH₄ and DOC compared to pristine peatlands, as a result of enhanced oxidative enzyme activities and microbial respiration (Kwon et al., 2013). The Soil Water Atmospheric Plant (SWAP) hydrological model (Kroes et al., 2017), which is based on two key variables (i.e. drainage resistance which is driven by the density of canals and canal water level), demonstrated that the drainage resistance of drained acacia plantation is less than half that of pristine forest (Taufik et al., 2019, 2020). Therefore, groundwater drains more easily from acacia plantations than from pristine forest, leading to lower groundwater levels and amplification of groundwater drought. The frequency of groundwater drought of transformed peatland is at least three times that of pristine peatland (Taufik et al., 2020).

In tropical peatland hydrological management, 'rewetting' involves measures to reverse the hydrologic effects of drainage for agriculture by blocking the ditches and canals to maintain higher water levels (Jaenicke et al., 2010). The effectiveness of rewetting in reducing peat decomposition has been evaluated by experiments involving either controlled mesocosms or direct hydrological interventions in the field (Jauhiainen et al., 2008), and by modelling approaches (Jaenicke et al., 2010). The outcomes of these studies are, however, inconclusive. Although rewetting can reduce the rate of peat decomposition due to water-saturation and anaerobic conditions, this might be in part offset by fermentation or anaerobic respiration (Cooper et al., 2019). Sites under high water-table regimes (Hirano et al., 2012; Jauhiainen et al., 2005, 2012, 2014) or complete water-saturation upon rewetting (Wilson et al., 2016) are associated with lower surface CO₂ efflux across a variety of land

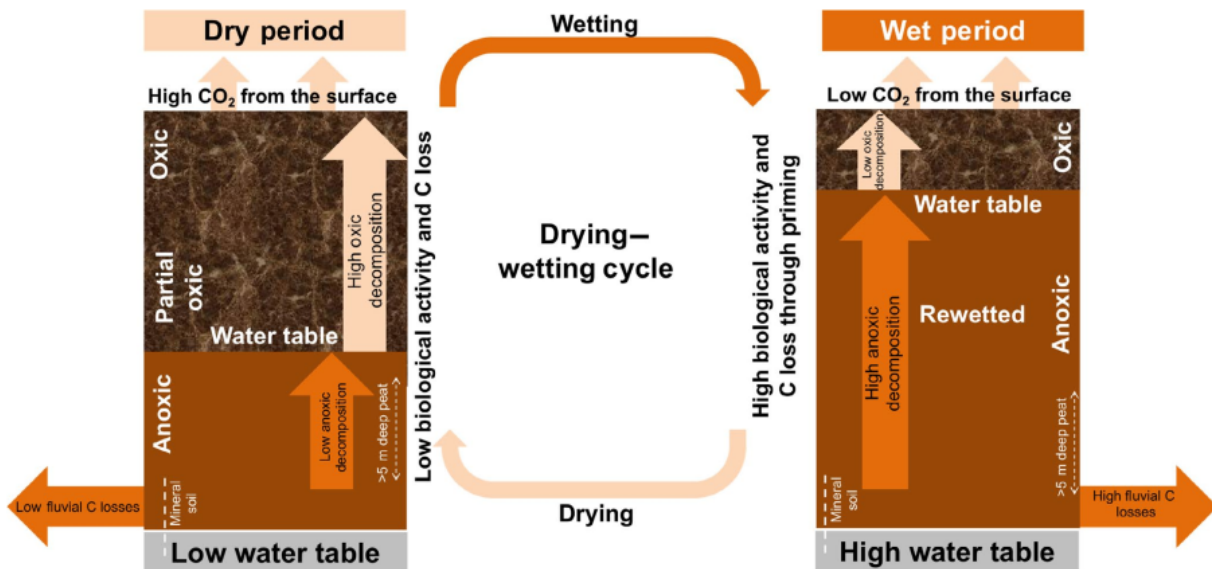


FIGURE 2 Carbon fluxes in the dry versus wet period in managed or degraded peatlands. In these peatlands, there are continual wetting–drying cycles that drive temporal variation in the water table and therefore the processes that lead to carbon loss from the peatlands

uses. Conversely, while subsidence rates (associated with peat decomposition) slow down, they do not necessarily halt completely, when water tables are at or above the peat surface (Couwenberg & Hooijer, 2013). This suggests that even with rewetting decomposition may still continue in the water-saturated zone through anaerobic respiration, with C being lost either through fluvial networks (Cook et al., 2018; Gandois et al., 2014; Moore et al., 2013) or as CH_4 (Deshmukh et al., 2020). Though not well studied in peat, it is likely that drying–wetting cycles can stimulate microbial activity by priming (described earlier) and therefore continued decomposition of organic C (Fontaine et al., 2004; Kuzyakov et al., 2000; Figure 2). Finally, litterfall contributes to the open pore structure of surface peat during its formation, and in plantations or degraded peatlands there are reduced litter inputs which leads to loss of this pore structure (Tonks et al., 2017); and this can hamper hydrological recovery even if peat is rewetted. In total, because of the persistent effects of drainage on its structure and chemistry, a rewetted peatland cannot be expected to behave like a natural peatland in its hydrology, soil ecology or gas exchange.

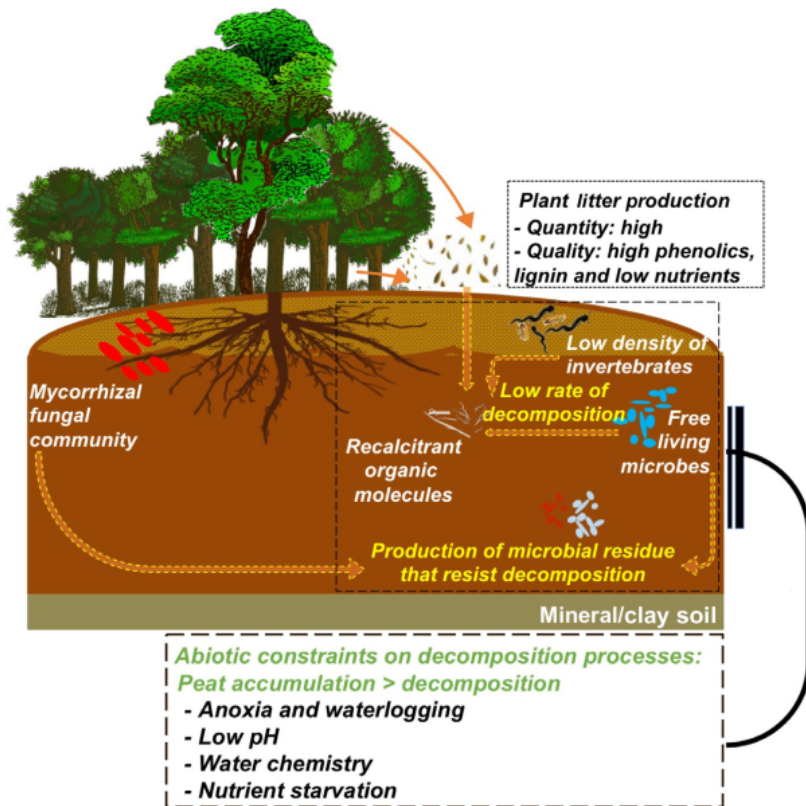
6 | BELOW-GROUND BIOTA AND PEATLAND FUNCTIONING

Accumulation of peat occurs due to production of OM from plants exceeding loss of OM through decomposition (Figure 3). The low OM decomposition rates in tropical peatlands are likely mostly due to unfavourable conditions for decomposers, including low pH, anoxia and low nutrient availability (Jackson et al., 2009; Page et al., 1999). Slow rates of decomposition are also likely driven by low quality of litter inputs through dominant plants producing leaf, root

and wood litter that is high in tannins and lignin and low in nutrients (Yule, 2010; Yule & Gomez, 2009). Upon drainage and deforestation, decomposer processes are promoted by a lower water table and greater oxygen availability, which leads to more CO_2 release and thus loss of peat and greater subsidence (Furukawa et al., 2005; Hirano et al., 2012; Jauhiainen et al., 2005). However, the ecology of the below-ground biota in tropical peatlands and its role in ecosystem functioning, or in contributing to peat loss and land subsidence following peatland conversion, is poorly understood.

Decomposition in all ecosystems is carried out by prokaryotic microbes and fungi, with their activity then modulated by soil fauna. In intact peat swamp forests, the prokaryotic community is dominated by taxa characteristic of acidic, waterlogged conditions such as Proteobacteria, Acidobacteria, Verrucomicrobia and Planctomycetes (Kanokratana et al., 2011; Liu et al., 2020; Mishra et al., 2014). The highest prokaryotic diversity occurs near the peat surface (Ong et al., 2015; Too et al., 2018) and decreases sharply with depth due to anoxia and lack of fresh organic inputs; at depth, Acidobacteria and Crenarchaeota become the dominant bacterial and archaeal taxa, respectively (Jackson et al., 2009). With depth, there is also an increased abundance of anaerobic methanogenic bacteria (notably Methanobacteriaceae) and methanotrophic bacteria (notably Methylocystaceae) which are favoured by persistently saturated conditions (Finn et al., 2020). Conversion of pristine conditions to drained secondary forest has been shown to cause large changes in prokaryotic communities, for example by favouring Gram-positive bacteria over Gram-negative bacteria, which contribute to increased aerobic (vs. anaerobic) microbial activity and therefore more than doubled emissions of CO_2 (factor of 2.15; Dhandapani et al., 2019). The relative abundance of Gram-positive bacteria, and associated aerobic microbial activity, is further increased by a higher

FIGURE 3 Mechanisms by which peat accumulates in intact, non-degraded peatlands. These include high production of low-quality litter, low densities of decomposer microbes and invertebrates, low soil biological activity, recalcitrant fungal residues and abiotic constraints. Several of these mechanisms may be impaired during peatland degradation which in turn prevents carbon from accumulating, but appropriate management or restoration of peatlands may reverse this impairment



1 intensity of peat land use, for example from diverse cropping systems to monoculture oil palm plantations (Dhandapani et al., 2020). Although we have an unclear understanding about the mechanistic basis by which changes in the structure of the peatland microbiome lead to shifts in its functioning during peat forest clearing, conversion and land-use intensification, the available evidence reveals a strong shift towards aerobic prokaryotic communities which likely contribute to rapid loss of peat.

Intact tropical peatlands support their own communities of saprophytic fungi, but very little is known about their composition or roles in ecosystem processes. A handful of studies have explored how fungal communities may be changed upon conversion and clearance of tropical peatlands. For example, studies in Malaysia have shown that the diversity within each of several fungal groups (Ascomycetes, Basidiomycetes, Chytridiomycota and Zygomycota) can be reduced through land conversion from peat swamp forests to oil palm plantation (Kusai et al., 2018; Shuhada et al., 2017). Similarly, cellulolytic and viable fungal communities were shown to be reduced upon peatland conversion from forest to paddy-soybean rotation and paddy field in Indonesia (Hadi et al., 2001). In another study in Indonesia, higher fungal species richness was found in natural peat swamps than in degraded peat soil, with Ascomycota as the most abundant phylum, followed by Basidiomycota, Zygomycota and Glomeromycota (Talukder & Sun, 2019). Furthermore, pathotrophic fungi (e.g. *Metarhizium* and *Pestalotiopsis*) can greatly increase in abundance in degraded peatlands, suggesting the potential of

land conversion to increase the likelihood of plant diseases (Liu et al., 2020). A recurrent theme in these studies is a reduction of diversity of fungal communities upon conversion, but we know little about how the remaining community contributes to decomposition processes, or whether those fungi that are favoured by conversion are better capable of decomposing peat, thereby contributing to loss of peat and its subsidence.

Mycorrhizal fungi play a key role in the formation of OM, both as decomposers and through the accumulation of their necromass (Clemmensen et al., 2013), and with the necromass of ectomycorrhizal (EcM) fungi contributing more to OM formation than that of arbuscular mycorrhizal (AM) fungi (Averill et al., 2014). Southeast Asian peatlands are often dominated by trees of the *Dipterocarpaceae* which potentially support EcM and a variety of other families that all support AM. However, only three studies have explored the mycorrhizal status of trees in intact peat swamp forests in SE Asia, and they all report significant colonization of tree or seedling roots by both EcM (Moyersoen et al., 2001; Mulyani et al., 2014) and AM (Tawarayama et al., 2003). As such, Moyersoen et al. (2001) found no difference in the relative basal area abundance of EcM trees, the proportion of EcM roots in monoliths or fractional colonization of EcM roots, between peat forest and adjacent heath forest in Brunei, despite the very high water table in the peat forest. The extent to which accumulation of necromass of EcM associated with *Dipterocarps* contributes to the build-up of peat, in the manner shown for other EM-dominated ecosystems at higher latitudes

(Clemmensen et al., 2013), is unknown. When intact peat swamp forests undergo drainage and deforestation, mycorrhizal fungi will be lost along with their host trees, but the extent to which this may contribute to the loss of OM and subsidence of peat remains unexplored.

While the below-ground fauna mediate the decomposition processes carried out by bacteria and fungi, we know virtually nothing about the ecology or role of most of this fauna in tropical peat swamp forests. However, termites, which are major decomposers in most tropical and subtropical forests (Eggleton et al., 1996), have been investigated in SE Asian peatlands in a handful of studies. These have shown that while termite densities are often high in intact peat swamp forests, their diversity is typically low (Bourguignon et al., 2018; Neoh et al., 2016; Vaessen et al., 2011), suggesting that a limited number of taxa are adapted to an ecosystem with a persistently high water table. It has also been shown that conversion of peatlands and intensification of their management leads to termite diversity declining further, with the lowest diversity in plantations of oil palm, rubber and *Acacia* (Hidayat et al., 2018; Vaessen et al., 2011). Conversely, a study from peat swamp forests in Brunei showed that selective logging without drainage had limited impact on termite species richness, suggesting that peatland conversion is likely to alter the termite community only when it involves changes to the water table and a loss of forest cover (Bourguignon et al., 2018). Burning of degraded peatlands leads to further losses of termite species but particular genera (*Coptotermes*, *Schedorhinotermes* and *Parrhinotermes*) are adapted for surviving fire and dominate in the post-fire environment when most other termites have been lost (Neoh et al., 2016). The contribution of termites to decomposition processes remains unexplored, and it is unknown as to whether and how those taxa that do remain after peatland degradation, contribute to peat decomposition, losses and subsidence.

7 | ABOVE-GROUND AND BELOW-GROUND APPROACHES FOR IMPROVED RESTORATION AND SOCIO-ECONOMIC OUTCOMES

Protection of the remaining peat swamp forests across the SE Asian region has to be given the highest possible priority in any conservation activity, given their essential role in protecting large C stocks and hosting forest biodiversity while also mitigating GHG emissions and fire risk (Evers et al., 2017; Page et al., 2009; Vernimmen et al., 2020). Land-use planning and policies need to take into account the gamut of valuable and often irrecoverable ecosystem services that are provided by tropical peatlands in their natural state (Uda et al., 2017; Wijedasa et al., 2016), and the high costs and challenges associated with ecosystem restoration (Budiharta et al., 2018). Within private concession lands, companies are pledging to a 'No Deforestation, No Peat, No Exploitation (NDPE)' policies while also applying the High Conservation Value (HCV) and High Carbon Storage (HCS) approach to determine which areas of high C density should be excised from

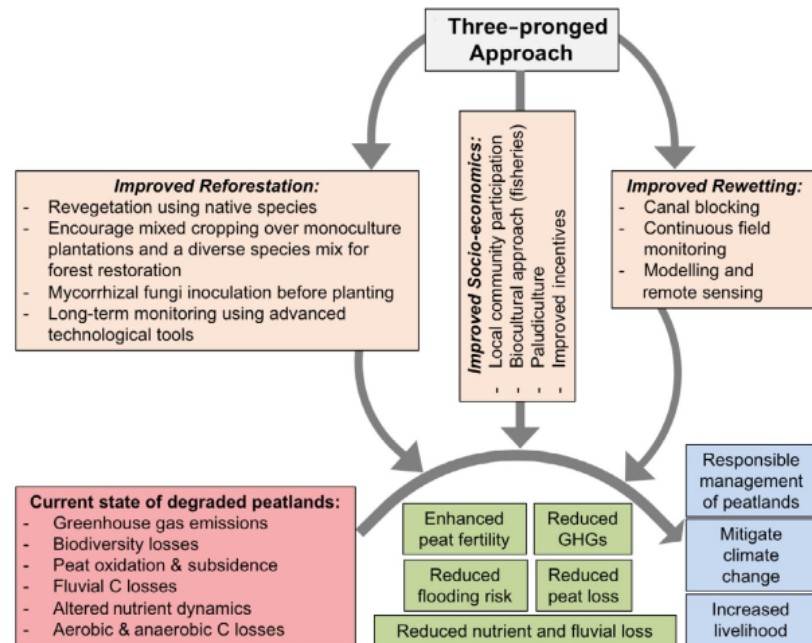
their concession or set aside for protection (HCSA, 2019; Padfield et al., 2016). Some companies have moved further to undertake active rehabilitation of degraded peatland and peat swamp forest, for example under Ecosystem Restoration Concession licences in Indonesia (Harrison et al., 2020). Nevertheless, extensive areas of degraded peat swamp forest and deforested peatland have no formal protection or restoration mandate despite them making a globally significant contribution to land-based greenhouse gas emissions (Cooper et al., 2020; Miettinen et al., 2017; Wijedasa et al., 2018).

7.1 | Restoration efforts that recognize above-ground and below-ground ecological principles

In the past two decades, a growing number of mostly small-scale peatland restoration initiatives have been attempted in SE Asia, notably in Indonesia (Dohong et al., 2018). In response to extensive forest and peatland fires in 2015, Indonesia aimed to restore 2 million hectares of peatlands (Republic of Indonesia, 2016). Restoration initiatives usually involve a combination of rewetting and revegetation to re-establish the water-saturated and forested conditions that more closely resemble the natural peatland environment and that can mitigate the ongoing release of C from peat oxidation and fires, as well as the loss of biodiversity (Evans et al., 2014; Wijedasa et al., 2018). They may also involve revitalization activities to promote suitable alternative livelihood options for local communities (Harrison et al., 2020). However, peatland restoration initiatives are challenging (Harrison et al., 2020; Zeng et al., 2020), and face a high risk of failure when their outcomes are poorly defined (Puspitaloka et al., 2020), socio-economic factors are not adequately considered (Zeng et al., 2020), and efforts to rewet and revegetate peatlands are uncoordinated (Giesen & Sari, 2018). Here, we discuss current solutions and the issues involved in implementing them, and propose an integrated, multidisciplinary approach to the restoration of these unique environments which focuses on combining ecological knowledge of the above-ground and below-ground peatland ecosystem, with consideration of the socio-economics of land use and management (Figure 4).

A key component of any peatland restoration activity is hydrological restoration (Figure 4), which has a primary aim of obstructing or limiting water flow to raise water levels in canals and ditches, and thereby rewet the adjacent peatland (Dohong et al., 2018). Several projects have evaluated different approaches to dam construction in terms of their cost, and life span, and susceptibility to damage by hydraulic forces, decay and vandalism (Dohong et al., 2018; Page et al., 2009; Ritzema et al., 2014). Evaluating the extent to which canal blocking is effective in raising the water table in the peat itself is difficult, because it requires assessment of how much drier the peatland would have been, had the canals not been blocked or were blocked differently, against the background of fluctuations (Reid et al., 2012) and long-term trends in rainfall (Dommain et al., 2011). The effects of canal blocking on peatland water levels have been studied using field measurements (Jauhiainen et al., 2008; Ritzema

FIGURE 4 A three-pronged approach to better management and restoration of degraded peatlands which incorporates reforestation, rewetting and socio-economic consideration



et al., 2014), remote sensing (Jaenicke et al., 2011) and modelling approaches (Jaenicke et al., 2010). However, none of these methods in isolation can directly estimate the benefits of canal blocking because changes in water levels are complicated by fluctuating inputs from rainfall, and because models require data for parameterization and validation (Jaenicke et al., 2010). Further limitations stem from attempts to correlate remotely sensed soil moisture information (e.g. derived from radar sensors) with groundwater levels, because soil moisture may change rapidly in response to rainfall without reflecting a longer-term change in the peatland water table (FAO, 2020). There is, therefore, a need for improved approaches that integrate data from field monitoring, modelling and remote sensing to evaluate the benefits of rewetting (Figure 4) and to better understand seasonal fluctuations, which are a key driver of below-ground processes, including microbial functions involved in C and nutrient cycling.

For improved reforestation efforts, both above-ground and below-ground ecological principles can be exploited to meet the overall goal for effective restoration of degraded tropical peatlands (Figure 4). Restoring closed-canopy forest vegetation on degraded peatland has the potential to deliver a number of benefits: enhanced biodiversity, a supply of plant litter to the uppermost peat, stabilization of microclimate (e.g. increased humidity and lower maximum surface temperatures) and reduced fire risk due to increased moisture levels in both surface and below-ground fire fuels. In less disturbed peatlands, revegetation may rely solely on natural regeneration, but on more degraded sites enrichment planting is needed (Giesen & Sari, 2018), though this is constrained by the species-specific survivorship of planted seedlings (Lampela et al., 2017; Nuyim, 2005). A major barrier to natural regeneration is the distance from the existing forest edge, with increasing distance reducing the

potential for seed dispersal by birds and mammals but also negatively influencing microclimate, hydrology, nutrient availability and fire frequency (Blackham et al., 2014; Graham et al., 2017; Wijedasa et al., 2020). Even where natural regeneration does occur near the forest edge, limited seed dispersal may warrant tree planting at greater distances, for example, beyond 500 m (Wijedasa et al., 2020). Enrichment plantings at greater distances from the forest edge pose challenges, however, because young trees are exposed to extremes of temperature, drought and flooding, and there is competition from the existing plant community which often consists of a dense cover of light-tolerant weedy ferns, sedges and shrubs.

To date, interventions to restore tree cover on degraded peatlands have been relatively small scale and have met with varied success. Frequently, the emphasis has been on initial tree planting rather than on long-term monitoring, and often with a focus on the number of trees planted rather than the number that survive (Harrison et al., 2020). But it is only through ongoing monitoring that we can gain valuable information on restoration effectiveness across a range of sites and conditions. Ideally, site monitoring data will include plant species composition and biomass, tree species survivorship and other key variables that can provide knowledge of changes in site hydrology, C and nutrient cycling over time. A major gap in understanding is how the choice of plant species for restoration impacts on peatland ecosystem functioning, and how the functional traits of different plant species used during restoration impact on the quality of above-ground and below-ground litter inputs to the peat, C and nutrient fluxes in the peat profile, and mitigation of C loss from the peat. In addition, peat swamp forest trees appear to allocate relatively large proportions of their biomass into root systems, which make an important contribution to below-ground peat accumulation (Brady, 1997; Lampela et al., 2014). Relatively little is

known about differences among peat swamp tree species in root biomass allocation or rates of decomposition of their root, stem and leaf litter. More knowledge on these topics would be useful in identifying tree species for restoration programmes that have the potential to make the greatest contribution to below-ground litter inputs and hence to C accumulation under suitable hydrological conditions.

The below-ground soil biota is a key driver of ecosystem restoration because of its role in regulating the build-up of OM, and the establishment of vegetation (Kardol & Wardle, 2010). Our understanding of the role that the peatland microbiota plays in restoration efforts remains limited, but some work suggests that mixed cropping can support a high microbial diversity that is associated with reduced peat oxidation when compared with monocultures (Dhandapani, Girkin, et al., 2020; Mishra et al., 2014). This suggests that the diverse microbiota associated with more diverse plant communities may reduce peat oxidation and thus C loss and subsidence during restoration, implying that the C balance could be improved by mixed cropping a wider range of tree species within existing plantations, and encouraging a diverse mix of tree species in forest restoration (Figure 4). Furthermore, there have been a handful of studies that have shown how mycorrhizal fungi and their inocula may stimulate the growth and establishment of tree species on degraded peatland (e.g. Mulyani et al., 2014; Tawaraya et al., 2003; Yuwati & Putri, 2020). For example, inoculation of *Shorea balangeran* seedlings with EcM fungi (*Strobilomyces*, *Calvatia*, *Boletus* and *Scleroderma*) has positive effects on their early growth when planted into peatland (Turjaman et al., 2011). Furthermore, some studies have shown beneficial effects of inoculation by AM fungi (*Glomus* spp.) upon transplantation of *D. polyphylla* (Graham et al., 2013) and *Shorea balangeran* (Yuwati & Putri, 2020) into peatland. Such studies point to the importance of understanding the mycorrhizal associations of plant species being targeted for restoration, and of knowing which fungal inoculants are most likely to contribute to their success. Overall, there is a strong need for research to better understand the role of the peat microbiome and linkages between above-ground and below-ground biota in both mitigating peat loss and enabling vegetation establishment during restoration of tropical peatlands, as has been shown for other environments (Kardol & Wardle, 2010).

7.2 | Restoration efforts for livelihoods and improved socio-economic outcomes

One approach to the restoration of peatlands, especially peatlands which are in use by local communities for their livelihoods, entails cultivation at high or high (near or at surface) water tables, that is, paludiculture, or the sustainable production of biomass on wet and rewetted peatlands' (Wichtmann & Joosten, 2007). The concept of paludiculture (Figure 4) is loosely defined and encompasses various aspects that are relevant for restoration, such as the type of ecosystem services provided (e.g. mitigation of greenhouse gases), the hydrological condition of the peat and the source of vegetation for cultivation (Tan, Lupascu, et al., 2020). Increasing efforts are being

made to identify suitable approaches for high water table agriculture on tropical peatlands which integrate environmental and socio-economic goals, but this is a field that is much less developed for tropical than for temperate environments (Tan, Lupascu, et al., 2020). A number of timber species and non-timber commodities, such as jelutong *D. polyphylla*, sago *Metroxylon sagu*, nypa *Nypa fruticans*, illipe nut *Shorea macrophylla* and candle nut (*Aleurites moluccanus*), have been proposed as candidate paludiculture species to support livelihoods of communities during the restoration of degraded peatlands (Giesen & Sari, 2018; Widayati et al., 2016). While some of these crops (e.g. sago) are able to withstand varying degrees of peat rewetting, others that are in use in peat-livelihood projects are dryland crops (e.g. pineapple and coffee) which still require peat drainage. Current economic returns from candidate high water level crops are lower than those from conventional drainage-based crops such as oil palm *E. guineensis*; Tan, Lupascu, et al., 2020), which makes the switch for local communities to paludiculture challenging (Giesen & Sari, 2018). In addition, there has been a lack of market development for paludiculture crops beyond general statements that certain crops could have some future economic value.

Given the large numbers of people now living in or adjacent to peatland in SE Asia, it is increasingly recognized that the participation of local communities in peatland restoration needs to be embraced as an integral part of the process (Graham et al., 2017; Page et al., 2009), whether for governmental land or for concessions. This involves engagement of stakeholders at all stages of defining and addressing the peatland management 'problem', including exploration, goal setting, planning and monitoring phases, to anticipate whether environmental interventions such as restoration programmes could be culturally insensitive or negatively impact livelihoods (Stringer et al., 2006). Failure to understand the relevance and use of peatlands and the exclusion (or superficial inclusion) of local communities in peatland restoration plans can result in resistance by communities. This occurred, for example, in Central Kalimantan, where dams constructed for peatland restoration obstructed transport in canals by resident communities (Dohong, 2016; Page et al., 2009). It is therefore crucial to consider the lived experience of local communities and their interactions with peatlands, as well as the cultural and socio-economic factors that predispose local communities to aspire to restoring degraded peatlands (Puspitaloka et al., 2020; Uda et al., 2020).

Despite a growing body of work on identifying best practices for peatland hydrology and revegetation, there has been a lack of attention on the social dimensions for peatland restoration (Puspitaloka et al., 2020). However, these social dimensions encompass the definition of what peatland restoration means for different actors involved in the process of managing restoration projects, and how restoration activities are defined, executed and sustained for the long term (Uda et al., 2020; Ward et al., 2020). Adopting a biocultural approach (Figure 4) that can assist with integrating these social dimensions by placing emphasis on local values and traditions (Thornton et al., 2020). For example, fisheries are a critical resource for communities living by the edge of peat rivers, but their value

extends beyond the utilitarian, with cultural and spiritual values of catching, consuming and selling fish all requiring consideration in the design and implementation of effective restoration strategies (Thornton et al., 2020).

Restoration of degraded tropical peatlands will necessarily require long time periods, given the need to restore both a closed-canopy forest and the key below-ground processes involved in C sequestration and storage (Harrison et al., 2020). These long time periods reflect the slow growth and high longevity tropical peatland tree species (King et al., 2005; Lieberman et al., 1985) and lengthy (but currently undefined) time periods may be required for the restoration of below-ground microbial processes. These extended time periods are, however, incompatible with the current pace of ecosystem degradation and, in particular, fire events which are occurring on tropical peatlands with increasing frequency (Vettrita & Cochrane, 2019). Average fire-return intervals are shorter over non-forest peat areas, which are the primary targets for replanting and reforestation (Adrianto et al., 2019). A single fire event in a peatland with unregulated drainage can result in an average burn depth of anywhere between 17 and 50 cm (Ballhorn et al., 2009; Konecny et al., 2016; Page et al., 2002), which, even assuming that suitable conditions for peat formation could be re-established, would require several centuries for the lost peat layer to re-accumulate (Harrison et al., 2020). Any restoration strategy for tropical peatlands must therefore incorporate fire prevention alongside rewetting, revegetation and the promotion of appropriate livelihood strategies. Multiple social drivers at the root of the tropical peatland fire phenomenon (Santika et al., 2020; Sze et al., 2019; Tan, Carrasco, et al., 2020) and in order to limit fire occurrence, holistic restoration strategies will be needed to maintain and enhance any remaining natural forest cover and condition while also develop alternative non-burning methods for land management, raise public awareness and promote behavioural change (Harrison et al., 2020).

Our three-pronged approach (Figure 4) emphasizes that the restoration of degraded tropical peatland ecosystems will benefit from an integrated, multidisciplinary approach that involves contributions from researchers and practitioners with expertise in hydrology, microbial ecology, soil science, plant ecology, fire ecology and social sciences, among other topics. Developing these types of collaborative activities will require an in-depth understanding of the ecological and social challenges that need to be faced as well as the types of interventions and science required to address them. It will also involve gaining the support of local communities, with the recognition that these communities are diverse in culture, traditions and land-use history, have varied abilities to cope with peatland degradation and fires, and differ in their capacity and willingness to be involved in peatland restoration. Community willingness may be limited if the costs (both financial and societal) of adopting new land management practices remain unclear and the benefits poorly understood. As such, communities that have relied on oil palm cultivation will find it challenging to participate in peatland restoration since rewetting may entail lower productivity and

financial return for their crops (Ward et al., 2020). This may require active exploration of viable economic alternatives (Tan, Lupascu, et al., 2020), including monetary or business incentives for farmers to commit to more sustainable practices (Figure 4). Most importantly, there is a pressing need to encourage research that involves and has a buy-in from multiple stakeholders and different actors (NGOs, government agencies or private sector, local people) to work towards a common goal of peatland restoration and achieve the benefits that restoration may deliver (Puspitaloka et al., 2020) in terms of increased livelihood, carbon sequestration and responsible management of peatlands (Figure 4).

8 | CONCLUSIONS AND FUTURE DIRECTIONS

We have reviewed current understanding of the intact and degraded peatlands in SE Asia, and critically examined them in terms of their biodiversity, C storage, hydrology, nutrients and the below-ground subsystem. We have then proposed an integrated approach for better management and restoration of degraded peatlands, which involves explicit consideration of multiple interacting ecological factors, and that addresses the involvement of local communities who rely on converted peatlands for their livelihood. In doing this, we emphasize that as processes leading to peatland formation involve several mechanisms that take place in both above-ground and below-ground subsystems, an integrated approach that explicitly recognizes both subsystems and the interactions between them is key for any attempt to successfully manage and restore these ecosystems.

Finally, we highlight some critical research and management needs that, if addressed, would provide much needed information on how to better restore degraded peatlands. First, we need better knowledge of the above-ground and below-ground processes that lead to C accumulation in intact peatlands so that we can understand how to reduce further peat loss in degraded peatlands and how to re-establish the appropriate living machinery (e.g. tree species composition) to maximize peat accumulation during peatland restoration. Second, hydrological and revegetation initiatives aimed at restoration have to some extent been undertaken in isolation. Integration is needed among these initiatives to deliver more robust science and nature-based solutions that take account of the linked ecological and hydrological processes that underpin restoration efforts. Third, in-depth research is required on the functional role of below-ground biota in peatlands, their role in C and nutrient cycling, and their effects on and feedbacks with the plant community. Fourth, we highlight that there is a need for all relevant stakeholders including governmental bodies and local communities to be actively engaged in the development and implementation of any attempts at improved restoration and rehabilitation of these ecosystems. And finally, adopting an integrated management and restoration approach to tropical peatlands is highly relevant to attempting to meet the targets set by the 2030

United Nations Agenda for Sustainable Development and the Paris Agreement on climate change.

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AUTHORS' CONTRIBUTIONS

S.M., D.A.W. and S.E.P. conceived the idea of the manuscript; S.M. wrote the draft of the manuscript in close consultation with D.A.W. and S.E.P. All other authors contributed input and text on topics that most closely aligned with their area of expertise and provided inputs for improving manuscript drafts.

DATA AVAILABILITY STATEMENT


This review was completed entirely using published sources, all of which are cited within the manuscript.

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