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Degradation increases peat greenhouse gas emissions in undrained tropical peat swamp forests

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Abstract Tropical peat swamp degradation can modify net peat greenhouse gas (GHG) emissions even without drainage. However, current Intergovernmental Panel on Climate Change (IPCC) guidelines do not provide default emission factors (EF) for anthropogenically-degraded undrained organic soils. We reviewed published field measurements of peat GHG fluxes in undrained undegraded and degraded peat swamp forests in Southeast Asia (SEA) and Latin America and the Caribbean (LAC). Degradation without drainage shifted the peat from a net CO_2 sink to a source in both SEA (− 2.9 ± 1.8 to 4.1 ± 2.0 Mg CO_2–C ha^{-1} yr^{-1}) and LAC (− 4.3 ± 1.8 to 1.4 ± 2.2 Mg CO_2–C ha^{-1} yr^{-1}). It raised peat CH_4 emissions (kg C ha^{-1} yr^{-1}) in SEA (22.1 ± 13.6 to 32.7 ± 7.8) but decreased them in LAC (218.3 ± 54.2 to 165.0 ± 4.5). Degradation increased peat N_2O emissions (kg N ha^{-1} yr^{-1}) in SEA forests (0.9 ± 0.5 to 4.8 ± 2.3) (limited N_2O data). It shifted peat from a net GHG sink to a source in SEA (− 7.9 ± 6.9 to 20.7 ± 7.4 Mg CO_2-equivalent ha^{-1} yr^{-1}) and increased peat GHG emissions in LAC (9.8 ± 9.0 to 24.3 ± 8.2 Mg CO_2-equivalent ha^{-1} yr^{-1}). The large observed increase in net peat GHG emissions in undrained degraded forests compared to undegraded conditions calls for their inclusion as a new class in the IPCC guidelines. As current default IPCC EF for tropical organic soils are based only on data collected in SEA ombrotrophic peatlands, expanded geographic representation and refinement of peat GHG EF by nutrient status are also needed.

Keywords Soil · Land-use change · Emission factor · Southeast Asia · Latin America and the Caribbean

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Introduction

Tropical peat swamp forests play an important role in regulating atmospheric concentrations of greenhouse gases (GHG). They are characterized by permanently or seasonally saturated soils and high litter inputs that exceed rates of organic matter decomposition, leading to substantial soil carbon and nitrogen storage. Drainage and conversion of tropical peat swamp forests to other uses are known to increase net GHG emissions from peat soils (Hergoualc'h and Verchot 2014; Inubushi et al. 2003; Swails et al. 2021). Anthropogenic activities that degrade peat swamp forests such as harvest (e.g., Basuki et al. 2021; Hergoualc'h et al. 2023), grazing (Eusse and Aide 1999), crop cultivation under the canopy (Swails et al. 2021) and fire (Astiani et al. 2018) without deforestation and conversion and regardless of drainage could also potentially exacerbate peat GHG emissions. The types of anthropogenic disturbances in undrained tropical peatlands and their associated impacts on peat GHG emissions are not well characterized, although some studies found substantial differences in GHG emissions between undegraded and degraded sites (Hergoualc'h et al. 2023; Swails et al. 2021; Sánchez et al. 2017).

Drainage of peatlands increases oxygen availability in the soil, which accelerates CO_2 emissions and decreases CH_4 fluxes from peat decomposition (Hergoualc'h and Verchot 2012; Hergoualc'h et al. 2017b; Itoh et al. 2017) while tending to increase N_2O emissions (Pärn et al. 2018). With or without drainage, vegetation disturbance alters C inputs rates, directly impacting peat onsite CO_2 emissions (difference in C inputs from litterfall and root mortality and C outputs from heterotrophic respiration; Drösler et al. 2014; Hergoualc'h and Verchot 2014). In addition changes to litter input quantity and quality can affect nutrient content of substrate for microbial decomposition (Allison and Vitousek 2004; Hobbie 2015; Lugo et al. 1990), potentially influencing heterotrophic respiration (Jauhiainen et al. 2016; Swails et al. 2018) as well as soil CH_4 and N_2O emissions (Hergoualc'h and Verchot 2014). Forest disturbance also modifies its microclimate (Blonder et al. 2018; Both et al. 2017; Marsh et al. 2022), which can affect biogeochemical cycling rates for example, reducing canopy cover increases air temperature potentially enhancing organic matter mineralization (Hoyt et al. 2019), however links between microclimate alteration and decomposition rates in tropical forests are unclear (Both et al. 2017). Tropical peat soils impacted by fire undergo extreme changes, including enrichment with cations (Ca, Mg, Mn, Fe, Na, Zn) (Könönen et al. 2015), which may enhance aerobic decomposition of soil organic matter over the short-term (Astiani et al. 2018; Lupascu et al. 2020). Ash remaining on site after fires raises soil pH, accelerating N loss (Certini 2005). Fire also increases the hydrophobicity of soil organic matter leading to additional nutrient losses due to erosion (Certini 2005). Nutrient content and microbial community in restored tropical peatlands indicate that these ecosystems are still influenced by historical land-use and management for years following restoration (Nurulita et al. 2016). Peat GHG emissions may be elevated in secondary peat swamp forests decades after initial disturbance (Swails et al. 2021).

Countries report their GHG emissions to the UNFCCC (United Nations Framework Convention on Climate Change) using guidelines developed by the Intergovernmental Panel on Climate Change (IPCC). The 2013 Wetland supplement provides in Chap. 2 (Drösler et al. 2014), default Tier 1 emission factors (EF) for drained forest on peat to quantify emissions of CO_2 onsite, N_2O emissions from peat decomposition, and peat CH_4 emissions. Current IPCC guidelines do not provide methodological guidance for anthropogenically degraded organic soils that are undrained, which has implications for national GHG accounting in peat-rich countries where significant extents of undrained peatlands are degraded. For example, in Indonesia, forests subject to selective logging, shifting cultivation, fire, fuelwood collection, and livestock grazing account for 59% of total peat swamp forest area (Indonesian Ministry of Environment & Forestry 2021) with a substantial proportion unaffected by drainage (Dadap et al. 2021). Therefore, EF are needed to estimate peat emissions in undrained forests that are degraded by anthropogenic disturbance. Additionally, the potential influence on GHG fluxes of peat nutrient status (ombrotrophic vs. minerotrophic) (Drewer et al. 2010; Saarnio et al. 2007) and variation in climate (Ribeiro et al. 2021), forest vegetation (Wang et al. 2015), and management practices (Lilleskov et al. 2019) in the tropics calls for refinement of peat GHG EF by nutrient status and expanded geographic representation of the current IPCC default Tier 1 EF based only on data collected in SEA ombrotrophic peatlands.

In this paper we investigated peat GHG fluxes in undrained undegraded and degraded tropical peat swamp forests using observational data reported in the literature. We present peat CH_4, N_2O and onsite CO_2 EF for undegraded and degraded forests in Southeast Asia (SEA) and Latin America and the Caribbean (LAC) and explore environmental variables controlling peat GHG fluxes. We address the following questions: (1) How do tropical peat EF (onsite CO_2, CH_4, N_2O) and environmental variables differ between forest conditions (undegraded vs. degraded) and regions (SEA vs. LAC)? (2) Which environmental variables control peat GHG fluxes in these ecosystems? (3) How do the magnitudes of net peat GHG budgets and relative contributions of each EF (onsite CO_2, CH_4, N_2O) vary according to forest conditions and regions? (4) What are research needs for further refinement of EF for undrained anthropogenically degraded tropical peat forests?

Methods

Data collection, calculation, and presentation

We compiled a database from international peer-reviewed publications (Table 1) of soil respiration and peat CH_4 and N_2O fluxes and controlling environmental variables in undrained peat swamp forests that were undegraded (UF) or degraded (UFDeg). The locations of study sites are displayed in Fig. 1. Undrained undegraded and degraded forests were identified based on study site descriptions provided in the publications included in our synthesis. We

Table 1 Data sources for calculation of annual peat GHG fluxes and C inputs to peat in undrained undegraded (UF) and degraded (UFDeg) peat swamp forests of Southeast Asia (SEA) and Latin America and the Caribbean (LAC)

	SEA				LAC			
	UF	n	UFDeg	n	UF	n	UFDeg	n
Root mortality	2, 30	5	2, 5	2	7	7	2	
Total soil respiration	1, *18*, 34, 35	4	1, 2, 10, 14, 17, *19*, 21, 24, 32, 34	12	*13*, 15, 36	5	*13*	2
Methane	6, 33, 34	3	3, 10, 14, 16, 17, 19, 21, 23, 28, 34	12	9, 12, 15, 36	6	12	2
Nitrous oxide	6, 33, 34	3	10, 16, 20, 12, 25, 34	6	12	1	12	2

Studies partitioning total soil respiration into autotrophic and heterotrophic components are italicized. For all fluxes, n represents the number of replicate sites

Sources: 1, Basuki et al. 2021); 2, Brady (1997); 3, Busman et al. (2023) ; 4, Chimner & Ewel (2005); 5, Chimner & Ewel (2004); 6, Deshmukh et al. (2021); 7, Dezzeo et al. (2021); 8, Eusse & Aide (1999); 9, Griffis et al. (2020); 10, Hadi et al. (2005); 11, Harrison et al. (2007); 12, Hergoualc'h et al. (2020); 13, Hergoualc'h et al. (2023); 14, Hirano et al. (2009); 15, Hoyos-Santillan et al. (2019); 16, Inubushi et al. (2003) ; 17, Inubushi et al. (1998); 18, Ishida et al. (2001); 19, Ishikura et al. (2019); 20, Jauhiainen et al. (2012); 21, Lau et al. (2022); 22, Mata et al. (2012) ; 23, Melling et al. (2005a, 2005b); 25, Melling et al. (2007); 26, Ong et al. (2015); 27, Rahajoe et al. (2000); 28, Sakabe et al. (2018); 29, Saragi-Sasmito et al. (2019); 30, Shimamura & Momose (2005); 31, Sulistiyanto et al. (2004); 32, Sundari et al. (2012); 33, Swails et al. (2023); 34, Swails et al. (2021); 35, Vijayanathan et al. (2021); 36, Wright et al. (2013)

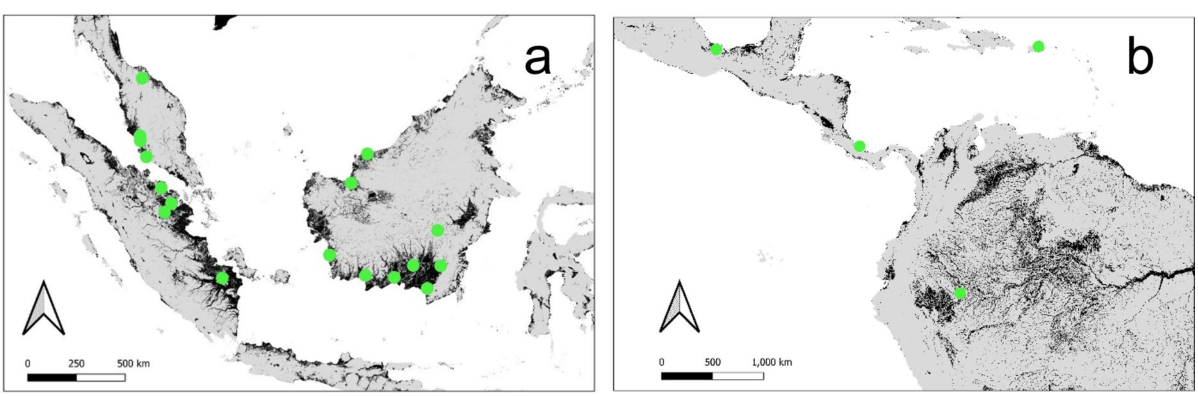

Fig. 1 Study locations (green circles) and peatland extent (black areas, Gumbricht et al. 2017) in Southeast Asia (n = 17) (**a**) and Latin America and the Caribbean (n = 4) (**b**). Study locations in Thailand and Micronesia are not shown (n = 2). There were no data for African peat swamp forests

assumed that degraded sites were undrained if drainage or altered hydrology were not mentioned in the site description. Degraded sites included actively and previously logged forests as well as secondary forest regrowth following partial clearing for cultivation of crops under a reduced canopy (Table S1). Degraded palm swamp forests in Peru were subject to felling of *Mauritia flexuosa* palms for fruit collection, in addition to timber harvest (Hergoualc'h et al. 2020, 2023). All degraded sites were considered to be in an active or recovery stage of degradation as they had been monitored less than 50 years after anthropogenic disturbance. Indeed the time for degraded tropical forests to recover biomass and soil carbon stocks to the level of undisturbed forests is around a century (Martin et al. 2013).

Our analysis included only data collected using an experimental design which adequately covers spatiotemporal variability of GHG fluxes. Studies with a minimum of three spatial replicates per site, monitored at a minimum frequency of every two months over a period of at least one year were considered to meet this requirement. Whenever the fluxes were reported per unit hour or day, these were extrapolated to a full 365-day year. We considered each site as a replicate and computed a single mean annual value for multi-year studies.

To explore drivers of variation in soil GHG fluxes in undrained peat swamp forests, we investigated relationships among total soil respiration, peat CH_4 and N_2O fluxes and concurrently measured controlling environmental variables (rainfall, air and soil temperature, water table level, soil pH, C:N ratio, cation exchange capacity, base saturation, mineral N content, and peat minerotrophy or ombrotrophy status as defined by its Ca:Mg ratio, Lahteenoja et al. 2009). We classified peat with Ca:Mg ratio exceeding that of rainwater i.e. 6 (Berner and Berner 1996 in Weiss et al. 2002) as minerotrophic as this indicates minerotrophic Ca input from incoming surface or ground water in addition to atmospheric deposition (Weiss et al. 1997, 2002; Muller et al. 2006).

Following the IPCC guidelines (Drösler et al. 2014), onsite peat CO_2 emission or uptake was calculated as the difference in C outputs from soil heterotrophic respiration and C inputs from litterfall and root mortality. We excluded offsite CO_2 emissions via waterborne C losses as these are minimal in undrained peat swamp forests (Moore et al. 2013). Root exudates represent an important but uncertain onsite C input to soil (Jones et al. 2004), and they are excluded from peat onsite CO_2 budgets by the IPCC. Following Hergoualc'h and Verchot (2011), litterfall observations restricted to fine litter [all apart from the studies by Hergoualc'h et al. (2023) and Ong et al. (2015)] were corrected to include large-branch fall as 30% of total C inputs (from litterfall, root production, and large branch-fall), as observed by Chimner and Ewel (2005). Annual root mortality was assumed to equal annual root production in some instances (Brady 1997; Chimner and Ewel 2004; Shimamura and Momose 2005), which is reasonable for understanding soil C dynamics over short timescales (Hertel et al. 2009). In the case of studies that did not measure litterfall and/or root mortality, we applied the average rates calculated for undrained undegraded and degraded forests in SEA and LAC. Among field studies measuring heterotrophic respiration with the trenching method, we considered only experimental designs with trenches dug to a depth at which no coarse roots are observed (approximately 1 m deep, Hergoualc'h et al. 2017b). For studies that measured only total soil respiration, heterotrophic respiration was calculated using the average partitioning ratios for undrained undegraded and degraded forests in SEA and LAC (Table S2).

All CH_4 emission data were from chamber-based measurements except the studies of Deshmukh et al. (2021), Griffis et al. (2020), and Sakabe et al. (2018) where fluxes were measured by eddy covariance. The fluxes measured by Deshmukh et al. (2021) were reduced by 10% to exclude tree-mediated CH_4 emissions (Sjögersten et al. 2020). Emissions of CH_4 by Griffis et al. (2020) and Sakabe et al. (2018) were similar to soil chambers CH_4 fluxes measured at the same locations by Hergoualc'h et al. (2020) and Hirano et al. (2009), respectively, indicating a minor contribution of trees to ecosystem-scale CH_4 flux.

We calculated net onsite peat GHG budgets as the balance of onsite peat CO_2 emission or uptake rate and the N_2O and CH_4 emission rates. The annual CH_4 and N_2O fluxes were converted to CO_2-equivalent considering global warming potentials (GWP) with climate-carbon feedbacks over a 20-year time horizon (86 kg CO_2-equivalent kg^{-1} CH_4 for CH_4 and 268 kg CO_2-equivalent kg^{-1} N_2O for N_2O) and over a 100-year time horizon (34 kg CO_2-equivalent kg^{-1} CH_4 for CH_4 and 298 kg CO_2-equivalent kg^{-1} N_2O

for N_2O)(Myhre et al. 2013). Though a 100-year time horizon is the convention for national GHG inventories, a 20-year horizon is more appropriate for evaluating impacts of forest degradation that typically occur over 20 to 30 years in the tropics. Additionally, a 20-year time horizon is more closely aligned with the urgent need to reduce emissions to meet temperature goals under the Paris Agreement (Abernethy and Jackson 2022). We calculated the relative contribution of each gas to net peat GHG budgets considering the absolute values of emissions and uptakes in CO_2-equivalents.

Statistics

Statistical analysis was performed using R (V4.0.5) software with a probability threshold of 0.05 to determine significance. Uncertainties are reported as standard errors. The normality of residuals distribution for total soil respiration, peat CH_4 and N_2O fluxes, and controlling environmental variables was tested using the Shapiro–Wilk test. GHG fluxes and environmental variables were compared between regions (SEA vs. LAC) and between forest conditions (undegraded vs. degraded) in SEA by the t test or Mann–Whitney U test, depending on the normality of residuals distribution and availability of sufficient data points for a statistical test. No test was performed to compare forest condition in LAC due to the limited number of sites. Differences in annual precipitation between SEA and LAC were evaluated by comparing mean values at sites across the two regions regardless of forest condition. We assessed differences in water table seasonality between the two regions and between forest conditions by comparing the average difference in mean water table levels during the three shallowest and the three deepest consecutive months. Seasonality was determined per site where monthly water table level was available (data from Busman et al. 2023; Melling et al. 2005a, b, 2007; Swails et al. 2021, 2023 for SEA, and Hergoualc'h et al. 2020, 2023; Wright et al. 2013 for LAC) and the site-level seasonality values were averaged to calculate a mean value across forest conditions in each region and per condition across regions for comparison. Relationships between annual GHG fluxes and environmental variables were developed applying linear and curvilinear univariate regression to site-level values, and to mean forest condition values in each region ($n=4$). For significant relationships, we selected the regression form that explained the most variation in the independent variable. We considered each site as a replicate to calculate the standard error of fluxes per forest condition and region. Gaussian error propagation was used for propagating uncertainties in calculations of peat CO_2–C and GHG budgets (Lo 2005).

Results

Peat GHG fluxes and environmental variables

Mean peat GHG fluxes and environmental variables are presented per region and forest condition in Table 2. Average annual soil respiration tended to be greater in degraded than undegraded forests for both regions, and tended to be greater in SEA than LAC for both forest conditions. In SEA there was a tendency towards higher CH_4 fluxes in degraded than undegraded forests, while in LAC the opposite was true. The average annual soil CH_4 emission was 5 times higher in LAC than SEA in undegraded forests ($p=0.04$), with a similar trend in degraded forests. Average annual peat N_2O fluxes in SEA tended to be higher in degraded than undegraded forests, and the difference was marginally significant ($p=0.08$). N_2O emissions in LAC degraded and undegraded forests are not compared because differences in N_2O fluxes between forest conditions were linked to soil moisture fluctuations that were unrelated to degradation (Hergoualc'h et al. 2020).

Average annual water table level was higher in degraded than undegraded forests in SEA ($p=0.02$), with a comparable trend in LAC. Water level tended to be higher in LAC where it was above the soil surface than in SEA where it was below the soil surface, regardless of forest condition. The difference in water level between the two regions was significant in undegraded forests ($p=0.002$). This trend might be explained by the 10% greater annual precipitation at LAC sites (2772 ± 58 mm) than SEA sites (2539 ± 88 mm) ($p=0.01$). Additionally water table level seasonality tended to be greater in SEA forests (36.0 ± 8.1 cm) than LAC forests (25.1 ± 10.7) though difference between the two regions was unsignificant. Across regions water table level seasonality was similar in degraded (31.3 ± 8.3 cm) and undegraded forests (31.6 ± 11.1 cm). There were not sufficient data

Table 2 Average total soil respiration (SR), and soil CH_4 and fluxes, water table level (WT), air temperature (Ta), and soil temperature (Ts), pH, C:N ratio, mineral N content (NH_4^+ andNO_3^-,NO_3^-/NH_4^++NO_3^-), cation exchange capacity (CEC), base saturation (Base Sat), and calcium to magnesium ratio (Ca:Mg) in undrained undegraded (UF) and degraded (UFDeg) peat swamp forests of Southeast Asia (SEA) and Latin America and the Caribbean (LAC)

	SEA		LAC	
	UF	UFDeg	UF	UFDeg
SR (Mg CO_2–C ha^{-1} yr^{-1})	10.4 ± 1.8 (4)	15.1 ± 2.0 (12)	7.9 ± 1.3 (5)	8.3 ± 1.8 (2)
CH_4 (kg C ha^{-1} yr^{-1})	22.1 ± 13.6 (3) a	32.7 ± 7.8 (12)	218.3 ± 54.2 (6) b	165.0 ± 4.5 (2)
N_2O (kg N ha^{-1} yr^{-1})	0.9 ± 0.5 (3)	4.8 ± 2.3 (6)	1.3 (1)	0.8 ± 0.3 (2)
WT (cm)	− 31.3 ± 4.5 (5) a, β	− 14.8 ± 3.9 (13) α	0.1 ± 1.2 (4) b	6.5 ± 0.4 (2)
Ta (°C)	27.8 ± 0.4 (4)	27.4 ± 0.5 (11)	27.1 ± 0.9 (4)	30.5 ± 0.6 (2)
Ts (°C)	26.7 ± 0.4 (5)	26.1 ± 0.2 (8)	25.9 (1)	25.5 ± 0.1 (2)
pH	3.6 ± 0.2 (5)	3.6 ± 0.1 (10)	4.6 ± 0.4 (4)	–
C:N	30.7 ± 6.3 (4)	30.7 ± 1.6 (10)	24.5 ± 4.1 (3)	15.0 ± 1.1 (2)
NH_4^+ (mg N kg d.m.$^{-1}$)	1,521.3 ± 1155.5 (2)	145.2 ± 75.9 (7)	997.8 (1)	662.7 ± 265.9 (2)
NO_3^- (mg N kg d.m.$^{-1}$)	4.0 ± 1.9 (2)	22.7 ± 11.5 (8)	2.8 (1)	2.9 ± 0.2 (2)
NO_3/(NH_4^+/NO_3^-)	0.009 ± 0.009 (2)	0.117 ± 0.079 (7)	0.003 (1)	0.005 ± 0.002 (2)
CEC (cmol + kg^{-1})	50.3 ± 47.8 (2)	55.7 ± 11.6 (8)	70.9 (1)	69.6 ± 1.1 (2)
Base Sat (%)	24.8 ± 9.2 (2)	30.7 ± 8.8 (6)	44.8 (1)	48.8 ± 13.5 (2)
Ca:Mg	3.7 ± 1.6 (2)	1.6 ± 0.3 (4)	6.3 ± 4.3 (3)	14.1 ± 0.6 (2)

Means ± standard error (n) are presented for undegraded and degraded forests

Latin letters (a, b) indicate significant differences between regions within a forest condition. Greek letters (α, β) denote significant differences between forest conditions within a region, respectively. No letters are displayed in the absence of a significant difference. Negative WT values indicate water table level below the soil surface

for statistical comparison of forest conditions within regions. LAC sites had predominantly minerotrophic peat while all SEA sites were ombrotrophic peatlands. Other variables were homogeneous across regions and not affected by degradation.

Across regions and regardless of degradation, average annual soil respiration increased with increasing soil ratio of NO_3^- to total mineral N (NO_3^-/NH_4^+ +NO_3^-) considering mean forest condition values in each region (Fig. 2). The relationship between soil respiration and mineral N considering site-level values was also significant ($p<0.05$). Peat CH_4 fluxes increased as average annual water table levels rose closer to the soil surface (Fig. 3). The link between CH_4 and water table across forest conditions and regions was driven by the relationship in SEA forests where the average annual water table level remained at or below the soil surface. There was no relationship between CH_4 and ground water levels in LAC, where the average annual water table tended to be at or above the soil surface and there was large variation in rates of annual emissions of CH_4 among sites. N_2O fluxes increased with increasing soil pH across forest

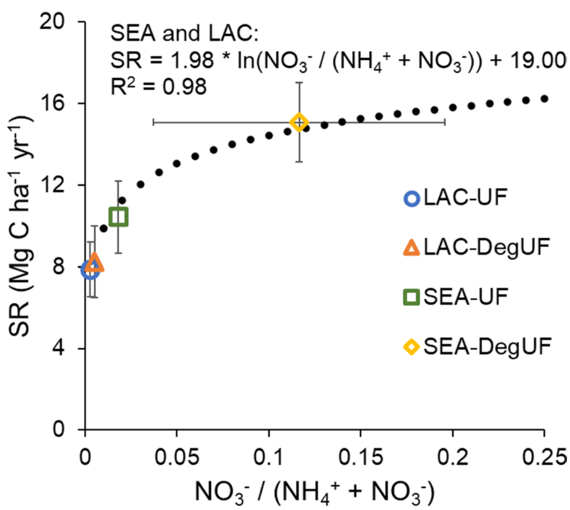

Fig. 2 Relationship between total soil respiration (SR) and $NO_3^-(NH_4^+/NO_3^-)$ ratio in undrained undegraded and degraded peat swamp forests (UF and UFDeg, respectively) in Southeast Asia (SEA) and Latin America and the Caribbean (LAC). Data points and error bars represent the mean per forest condition in each region and associated standard error. Regression was performed on 4 data points and relationship is significant at $p<0.05$

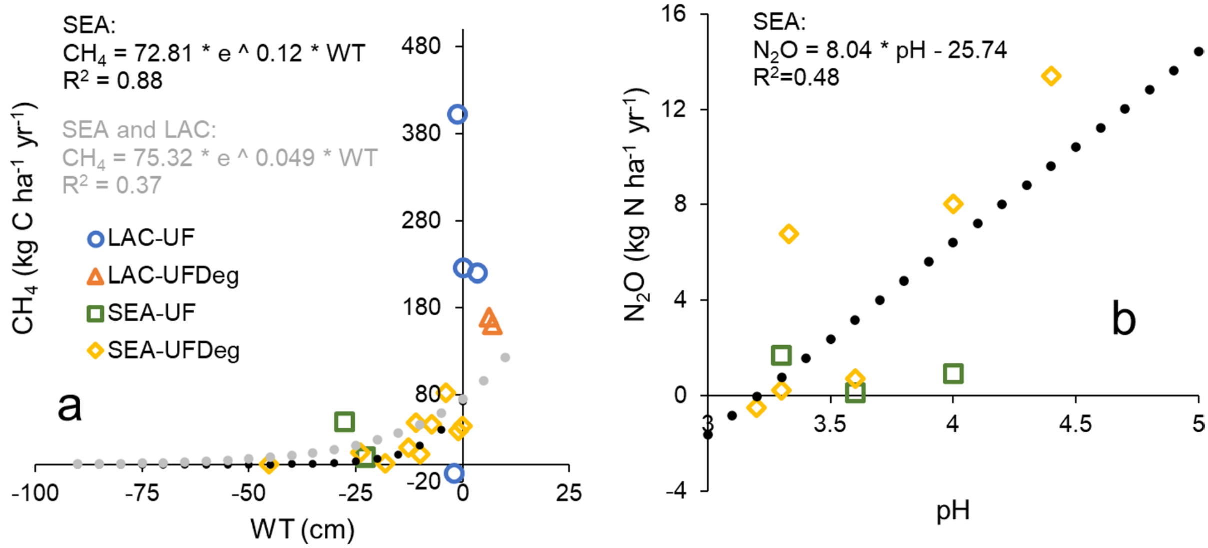

Fig. 3 Relationships between average annual soil CH_4 fluxes and water table level (WT) (**a**) and soil N_2O fluxes and peat pH (**b**) in undrained undegraded and degraded peat swamp forests (UF and UFDeg, respectively) in Southeast Asia (SEA) and Latin America and the Caribbean (LAC). Data points represent the measured value at a site. Relationships are significant at $p < 0.05$. There was no relationship between average annual soil CH_4 fluxes and WT in LAC

conditions in SEA (Fig. 3) (soil pH was not available for LAC sites). However, with limited data the specific parameters of the correlation are not definitive. In SEA variation in annual emissions of N_2O were very small in undegraded forests as compared to degraded conditions.

Peat GHG budget

Annual peat onsite CO_2 and net GHG budgets are summarized in Table 3. In both regions, the peat was a net CO_2 sink in undegraded forest and a source in degraded forest, owing to elevated heterotrophic respiration and reduced C inputs to the peat under degraded conditions. Considering 20-year GWP of non-CO_2 emissions, In SEA undegraded forests peat emissions of CH_4 and N_2O were offset by the uptake of CO_2, while LAC undegraded forests were a net GHG source, owing to large emissions of CH_4. Increased net peat GHG emissions in degraded forests as compared to undegraded conditions were driven by changes in the peat CO_2 balance for both regions. In SEA, enhancement of peat CH_4 and N_2O fluxes in degraded compared to undegraded forests made additional contributions to increased net peat GHG emissions. The peat GHG budget in SEA forests was dominated by CO_2 (79% and 72% in undegraded and degraded forests, respectively) while in LAC CH_4 fluxes accounted for > 50% peat GHG budget regardless of forest condition. N_2O emissions comprised 1% of the peat GHG budget in LAC forests, and contributed more substantially in SEA (4% and 10% for undegraded and degraded conditions, respectively).

Considering 100-year GWP of CH_4 and N_2O, net peat GHG emissions were reduced across forest conditions and regions compared to budgets based on 20-year GWP. In LAC, with high CH_4 emisions, undegraded swamp forests were a net GHG source when considering the 20-yr GWP of CH_4 (86 kg CO_2-equivalent kg^{-1} CH_4, Myhre et al. 2013) and a sink when using methane's 100-year GWP value (34 kg CO_2-equivalent kg^{-1} CH_4, Myhre et al. 2013).

Discussion

Peat onsite CO_2 emission and uptake

Our synthesis suggests that anthropogenic disturbance in undrained tropical peat forests alters the peat CO_2 sink function primarily by increasing CO_2 outputs from heterotrophic respiration, transforming

Table 3 Peat onsite CO_2 and net GHG budgets for undrained undegraded (UF) and degraded (UFDeg) peat swamp forests in Southeast Asia (SEA) and Latin America and the Caribbean (LAC)

	SEA		LAC	
	Undegraded	Degraded	Undegraded	Degraded
Mg CO_2-C ha^{-1} yr^{-1}				
Litterfall	6.7 ± 0.6 (9)	6.9 ± 0.6 (8)	5.6 ± 0.7 (2)	4.7 ± 1.5 (3)
Root mortality	2.0 ± 1.5 (5)	1.2 ± 1.0 (2)	3.4 (1)	1.7 ± 0.2 (2)
Total peat C inputs	8.6 ± 1.7 (9)	8.1 ± 1.2 (8)	9.0 ± 0.7 (2)	6.4 ± 1.5 (3)
Heterotrophic respiration	5.7 ± 1.0 (4)	12.2 ± 1.6 (15)	4.7 ± 1.9 (5)	7.9 ± 1.8 (2)
Peat onsite CO_2–C budget	**− 2.9 ± 1.8 (12)**	**4.1 ± 2.0 (19)**	**− 4.3 ± 1.8 (6)**	**1.4 ± 2.2 (3)**
Mg CO_2eq ha^{-1} yr^{-1}				
CO_2	− 10.8 ± 6.7 (12)	15.0 ± 7.2 (19)	− 15.8 ± 6.5 (6)	5.1 ± 8.2 (3)
20-Year GWP				
CH_4	2.5 ± 1.6 (3)	3.8 ± 0.9 (12)	25.0 ± 6.2 (6)	18.9 ± 0.5 (2)
N_2O	0.9 ± 0.5 (3)	2.0 ± 1.0 (6)	0.5 (1)	0.3 ± 0.1 (2)
Peat GHG budget	**− 7.9 ± 6.9 (13)**	**20.7 ± 7.4 (22)**	**9.7 ± 9.0 (8)**	**24.4 ± 8.2 (4)**
(% CO_2, CH_4, N_2O)	(80, 16, 4)	(72, 18, 10)	(38, 61, 1)	(21, 78, 1)
100-Year GWP				
CH_4	1.0 ± 0.6 (3)	1.5 ± 0.4 (12)	9.9 ± 2.5 (6)	7.5 ± 0.2 (2)
N_2O	0.4 ± 0.2 (3)	2.2 ± 1.1 (6)	0.6 (1)	0.4 ± 0.1 (2)
Peat GHG budget	**− 9.3 ± 6.8 (13)**	**18.7 ± 7.3 (22)**	**− 5.3 ± 7.0 (8)**	**12.9 ± 8.2 (4)**
(% CO_2, CH_4, N_2O)	(90, 7, 3)	(82, 6, 12)	(65, 33, 2)	(45, 52, 3)

Onsite CO_2 budgets were calculated as the difference of mean annual C outputs from heterotrophic soil respiration and mean annual C inputs from litterfall and root mortality. The number of sites is indicated in parentheses. 20-yr GWP values are used to convert CH_4 and N_2O into CO_2-equivalent. Negative values indicate an emission reduction or removal

the peat into a net CO_2 source even without alleviation of oxygen constraints on aerobic respiration by drainage. Peat onsite CO_2 emissions (Mg CO_2–C ha^{-1} yr^{-1}) in SEA and LAC degraded forests (4.1 ± 2.0 and 1.4 ± 2.2, respectively) were correspondingly 77% and 26% of the default IPCC EF for drained tropical peat forests (5.3) (Drösler et al. 2014). Without EF for undrained degraded forests, anthropogenic emissions from these ecosystems are either unaccounted, or the lack of disaggregation of degraded forests by drainage status, as in the Indonesian Forest Reference Emission Level (Budiharto et al. 2022), may overestimate peat onsite CO_2 emissions, particularly in the case of the Indonesian EF (8.8 Mg C ha^{-1} yr^{-1}, Novita et al. 2021b). Moreover, the latter Tier 2 EF is an overestimate of onsite CO_2 emissions as it was based solely on heterotrophic respiration regardless of litter C inputs.

Mean annual total peat C inputs from litterfall and root mortality (Mg CO_2–C ha^{-1} yr^{-1}) in undegraded forests, which were similar in the two regions (8.6–9.0), were comparable to an average for undrained SEA peat forests (8.9 ± 1.4, Hergoualc'h and Verchot 2014) and slightly higher than a global estimate for tropical flooded forests on organic soils (8.0, Sjögersten et al. 2014). In both regions degradation tended to decrease total litter C inputs (6.4–8.1), but the impact of anthropogenic disturbance was inconsistent among sites in SEA where forests were impacted by different types of activities (logging, agroforestry) and were in different stages of recovery following disturbance (Table S1). For example, litter C inputs were higher in an Indonesian secondary peat swamp forest compared to a paired primary forest site in Central Kalimantan (Swails et al. 2021) but lower in previously logged than pristine forests in Sumatra (Brady 1997). LAC degraded forests were represented by a single location and disturbance type (cutting of *M. flexuosa* palms and timber harvest) (Table S1), therefore degradation-induced reduction in litter C inputs would need to be further evaluated. Consistent with our finding of variation in site-specific impacts of degradation on litter C inputs in peat swamp forests, litterfall in secondary tropical forests on mineral soils may be similar (Bambi et al. 2022; Burghouts et al. 1992; Herbohn and Congdon 1993), reduced (Riutta et al. 2021; Villela et al. 2006), or enhanced (Aryal et al. 2015; Ostertag et al. 2008) when compared to intact forests.

Total soil respiration (Mg CO_2–C ha^{-1} yr^{-1}) in undegraded SEA forests (10.4 ± 1.8) was in the range of earlier findings for undegraded peat swamp forests of the region (12.9 ± 2.1, Hergoualc'h and Verchot 2014). Likewise, total soil respiration in SEA degraded forests (15.1 ± 2.0) was similar to an average for degraded forests in the region (13.0 ± 1.5 Mg CO_2–C ha^{-1} yr^{-1}, Hergoualc'h and Verchot 2014), despite the fact that the earlier study disregarded drainage status. On the other hand, total soil respiration in LAC undegraded and degraded forests (7.9 ± 1.3 and 8.3 ± 1.8, respectively) was lower compared to SEA and slightly lower than a global estimate for wetlands on organic soils that included forest and non-forest ecosystems (8.8 ± 2.2, Sjögersten et al. 2014). The relationship between total soil respiration and the peat nitrate (NO_3^-) content (Fig. 2) links enhancement of soil respiration rate across forest conditions and regions to increased nitrate availability in the soil. Mineral N can stimulate respiration of both roots and microbial populations (Zhou et al. 2014), and enhancement of tropical peat soil respiration rates have previously been linked to increased soil nutrient content in field (Hergoualc'h and Verchot 2014; Sjögersten et al. 2011) and ex situ observations (Jauhiainen et al. 2016; Swails et al. 2018). Although NH_4^+ was abundant in soils (Table 2), it can form complexes with organic matter making it less available to plants and microbes (McNevin et al. 1999; Nommick 1965; Witter and Kirchmann 1989), while NO_3^- is relatively mobile in soil solutions (e.g., Bray 1954; Johnson and Cole 1980; Vitousek et al. 1982).

The observed trend towards increased total soil respiration rate in degraded forests as compared to undegraded conditions across the two regions could be due to enhancement of heterotrophic and/or autotrophic respiration rates. However, degradation increased the contribution of heterotrophic respiration to total respiration in both SEA and LAC forests (Table S2), based on limited data, suggesting either a decline of autotrophic activity, an enhancement of heterotrophic activity, or both. For example, lowered autotrophic respiration in degraded forests compared to undegraded conditions was associated with a decline in root biomass in paired LAC palm swamp forests, with increased magnitude of total soil respiration attributed to elevation of heterotrophic respiration (Dezzeo et al. 2021; Hergoualc'h et al. 2023). Stimulation of heterotrophic respiration can result from increased quantity of soil C and/or nutrient inputs (Chambers et al. 2000; Wilcke et al. 2005) which in disturbed forests can be caused by increased necromass (Carlson et al. 2017; Palace et al. 2007; Rozak et al. 2018) and decreased litter C:N ratio associated with alteration of species composition (Uriarte et al. 2015). Coarse litter decomposition could be a significant driver of heterotrophic respiration in LAC palm-dominated swamp forests, particularly in degraded sites where the quantity of downed woody debris was increased by palm cutting (Bhomia et al. 2019). Such enhancement can last for decades, as observed by Riutta et al. (2021) in previously logged upland tropical rainforests in Indonesia. Acceleration of soil organic matter decomposition in degraded tropical forests leading to increased soil CO_2 efflux has also been linked to alteration of microbial community composition (Zhou et al. 2018) though no data were from tropical peat swamp forests. Further investigations are needed to clarify links among vegetation disturbance, soil chemistry, and CO_2 emissions from peat decomposition in degraded undrained forests.

Peat CH_4 fluxes

Mean annual peat CH_4 fluxes tended to be greater in degraded than undegraded conditions in SEA, while the opposite was true in LAC based on observations at one single location in Peru (Hergoualc'h et al. 2020). The tendency towards higher CH_4 emissions in degraded than undegraded conditions in SEA may be explained by an increase in mean annual water table level in the disturbed forests compared to intact sites (Table 2). Evapotranspiration, a major determinant of water table level in tropical peatlands, is decreased by vegetation loss (Hirano et al. 2015). Selective harvest can raise the water table level by as much as 20 cm in drained boreal peatland forests (Leppä et al. 2020). The activity of methanotrophs is mainly limited by oxygen availability (Le Mer and Roger 2001), thus higher water table levels favor methane production and CH_4 fluxes increased across forest conditions and regions when mean annual water table level was closer or above the soil surface (Fig. 3).

However, the opposite trends in the impact of degradation on peat CH_4 emissions in the two regions, and the low explanatory power of water table level, suggest either additional controls on methanogenesis or a more nuanced, non-monotonic impact of water level. Turetsky et al. (2014) noted that deeper inundation, as at the LAC degraded sites, can inhibit CH_4

emissions for several reasons—limited diffusion through deeper water, enhanced oxidation in deeper water, especially if flowing, and reduced labile C inputs. Plant residues are known to be a major substrate for methanogens (Le Mer and Roger 2001) and microbial decomposition in wetlands often correlates well with carbon quality index (Bridgham et al. 2013).

In SEA CH_4 fluxes (kg C ha^{-1} yr^{-1}) in degraded forests (32.7 ± 7.8) were elevated compared to the previous estimate by Hergoualc'h and Verchot (2014) of 28.6 ± 9.7 (n = 8) and relatively lower in undegraded sites (22.1 ± 13.6). In LAC, where wetlands contribute a third of global wetland emissions of methane as determined by satellite observations (Stavert et al. 2022), annual fluxes of CH_4 (165.0 ± 4.5 and 218.3 ± 54.2 kg C ha^{-1} yr^{-1} in degraded and undegraded forests, respectively) tended to be an order of magnitude higher compared to SEA (Table 2) but lower than a global estimate for tropical wetlands (401 ± 17, Sjögersten et al. 2014). In addition to lower annual precipitation, at SEA sites precipitation was typically reduced during a period of 4–7 months (Ali et al. 2006; Hirano et al. 2007; Ishikura et al. 2019) while at LAC sites the dry season is shorter (2 months, Griffis et al. 2020) or there is no pronounced dry season (Wright et al. 2013). Diminished seasonality of water table levels in LAC may reflect differences in distribution of rainfall throughout the year, as well as differences in watershed hydrology between SEA and LAC sites. The difference in peat CH_4 emissions between SEA and LAC sites irrespective of forest condition highlights a key challenge to the development of globally relevant soil EF for tropical peatlands.

Peat N_2O fluxes

Peat N_2O fluxes (kg N ha^{-1} yr^{-1}) in SEA undegraded forests (0.9 ± 0.5) tended to be lower than previously estimated for undrained forests (2.7 ± 1.9, n = 7, Hergoualc'h and Verchot 2014) while in degraded forests they were higher (4.8 ± 2.3). In LAC mean annual N_2O fluxes across forest conditions (1.0 ± 0.2), based on measurements from three sites at a single location in Peru (Hergoualc'h et al. 2020), tended to be similar to fluxes from undegraded forests in SEA.

Changes in pH have been identified as a significant driver of changes to soil microbial communities (Shi et al. 2011) and N_2O production by soils was linked to pH in SEA forests (p = 0.02, Fig. 3). Where nitrification is the main N_2O-forming process, emissions tend to increase as the pH increases (Sahrawat 1982; Granli and Bockman 1996) via its influence on microbial community structure (Jiang et al. 2015). However, the driver of the trend towards increased N_2O emissions in degraded undrained SEA forests compared to undegraded conditions was not clear. Variation in N_2O production by tropical peat soils is related to changes in nitrogen availability (van Lent et al. 2015), and soil N inputs could be increased in secondary forest from enhanced litter inputs (Aryal et al. 2015), lower litter C:N ratio (Yang and Luo 2011; Zou et al. 2021), or both, promoting higher N_2O production rates. Though there was a small increase in aboveground litter inputs in SEA degraded forests compared to undegraded conditions, root mortality decreased with degradation leading to lowered total litter inputs (Table 3). The associated trends towards higher peat N_2O emissions and increased soil NO_3^- content and $NO_3^-(NH_4^+/NO_3^-)$ in degraded compared to undegraded conditions in SEA (Table 2) suggests higher N_2O emissions from soils may be related to NO_3^- substrate-induced enhancement of denitrification rather than total mineral N (NH_4^+ and NO_3^-) availability per se. Vegetation species composition can also influence soil N_2O fluxes in tropical forests (Soper et al. 2018), and changes to species assemblages at degraded sites compared to paired undegraded sites were noted by studies in both regions (Basuki et al. 2021; Bhomia et al. 2019; Novita et al. 2021a). However, variation in N_2O fluxes at LAC degraded sites were linked to differences in soil moisture unassociated with degradation (Hergoualc'h et al. 2020) and the relationship between increased soil N_2O fluxes and species composition in degraded SEA sites is unclear.

Emission factors for undrained degraded tropical peat swamp forests

Although drainage is widely considered the dominant driver of increased soil GHG emissions in tropical peatlands (Couwenberg et al. 2010; Prananto et al. 2020), vegetation and soil processes are tightly linked. Our results indicated enhancement of peat GHG emissions in disturbed peat swamp forests even without lowering of the water table. In SEA, the net peat GHG emissions budget (Mg CO_2-equivalent ha^{-1} yr^{-1}) in undrained degraded forests (20.7 ± 7.4) was similar to that for drained tropical peat forests computed as the sum of default peat onsite CO_2 and CH_4 and N_2O IPCC EF expressed in CO_2 equivalents (21.7, using a 20-year GWP) and a drastic shift from net peat GHG uptake by undegraded forest in the region (− 7.9 ± 6.9). The net peat GHG budget in LAC undrained degraded forests (24.3 ± 8.2) was greater, albeit marginally, than the IPCC drained forest default, which is based on measurements of Indonesian ombrotrophic peats.

Across forest conditions and regions, peat C fluxes as methane were small compared to CO_2 uptake and emission and when expressed on a Mg C ha^{-1} yr^{-1} basis undegraded sites were a net peat C sink. Although the IPCC encourages countries to report their GHG based on 100-year GWP, Abernethy and Jackson (2022) recommend using a shorter time-horizon GWP to better address challenges to achieving temperature goals under the Paris Agreement. Independently of GWP time horizon both SEA and LAC degraded peat swamp forests were net C sources and net GHG sources (Table 3).

Given the differences in peat GHG fluxes across forest conditions and regions, refinement of tropical peat GHG emission factors for undrained degraded forests is required to improve accuracy of country peat GHG emissions inventories. Countries are encouraged to develop Tier 2 (regional) EF for GHG inventories, given that differences in environmental controls on peat GHG fluxes (e.g., management practices, soils and vegetation properties, geologic and geomorphological differences, etc.) may drive differences in net peat GHG emissions. While data from a few arbitrary locations may not be representative of a given region, our synthesis does highlight bias in data availability among regions and its implications. For example, substantial differences in peat CH_4 flux rates between the SEA and LAC forests in this study suggest that application of Tier 1 default EF based on SEA peatlands may underestimate soil emissions of CH_4 in LAC forests. Further investigations of links between vegetation disturbance and changes in organic matter dynamics, soil nutrient cycling, and peat GHG emissions are needed to identify appropriate proxies for differentiating undrained degraded forest. We were limited in our analysis to disturbance types and controlling variables of soil GHG fluxes measured in the studies included in our synthesis; additional exploration of the influence of fire, rainfall history, and vegetation density on peat GHG budgets is needed. Considering the large influence of soil respiration partitioning ratios on estimates of heterotrophic respiration, investigations of the contribution of heterotrophic and autotrophic respiration to total soil respiration in undegraded and degraded forests are critical. Additional measurements that adequately cover spatial and temporal variability in peat GHG fluxes are particularly needed in minerotrophic peats, and Africa is strongly underrepresented in studies of tropical peat GHG fluxes. A substantial proportion of studies in tropical peatlands do not contribute towards reducing uncertainty in annual peat GHG fluxes due to low monitoring frequency and duration. Out of the 39 studies we reviewed on total soil respiration and peat CH_4 and N_2O fluxes in undrained tropical peat swamp forests, 16 (or 41% of the total) were excluded because they did not meet our criteria (see Methods) for measurement frequency or study duration.

Anthropogenic disturbance in undrained tropical peat swamp forests is widespread geographically (Hergoualc'h et al. 2017a; Miettinen et al. 2016) and therefore a major threat to ecosystem function globally, though the total area of undrained degraded peat swamp forests in the tropics is uncertain. Degradation without drainage is an important category of anthropogenic disturbance of peat swamp forests in Southeast Asia, where an estimated 74% of degraded peat swamp forests are hydrologically intact based on mapping of drainage canals (Dadap et al. 2021). Further investigation is needed to determine the extent of tropical peat swamp forest degradation with and without drainage in South America and Africa. Technologies for remote sensing of water table levels (Burden et al. 2020; Swails et al. 2019) and vegetation disturbance (Miettinen et al. 2012; Miettinen and Liew 2010; Hergoualc'h et al. 2017a) in forested peatlands offer potential methods for quantifying the extent of undrained degraded peat swamp forests over large scales. The observed increases in peat GHG emissions in undrained degraded tropical peat swamp forest as compared to undegraded conditions call for their inclusion as a new class in the IPCC guidelines to support countries in their development of GHG inventories.

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Author contributions Literature search and data analysis were performed by ES. The first draft of the manuscript was written by ES and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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