



Article

Land Cover and Land Use Change Decreases Net Ecosystem Production in Tropical Peatlands of West Kalimantan, Indonesia

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Abstract: Deforested and converted tropical peat swamp forests are susceptible to fires and are a major source of greenhouse gas (GHG) emissions. However, information on the influence of land-use change (LUC) on the carbon dynamics in these disturbed peat forests is limited. This study aimed to quantify soil respiration (heterotrophic and autotrophic), net primary production (NPP), and net ecosystem production (NEP) in peat swamp forests, partially logged forests, early seral grasslands (deforested peat), and smallholder-oil palm estates (converted peat). Peat swamp forests (PSF) showed similar soil respiration with logged forests (LPSF) and oil palm (OP) estates (37.7 Mg CO₂ ha⁻¹ yr⁻¹, 40.7 Mg CO₂ ha⁻¹ yr⁻¹, and 38.7 Mg CO₂ ha⁻¹ yr⁻¹, respectively), but higher than early seral (ES) grassland sites (30.7 Mg CO₂ ha⁻¹ yr⁻¹). NPP of intact peat forests (13.2 Mg C ha⁻¹ yr⁻¹) was significantly greater than LPSF (11.1 Mg C ha⁻¹ yr⁻¹), ES $(10.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1})$, and OP $(3.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1})$. Peat swamp forests and seral grasslands were net carbon sinks (10.8 Mg CO_2 ha⁻¹ yr⁻¹ and 9.1 CO_2 ha⁻¹ yr⁻¹, respectively). In contrast, logged forests and oil palm estates were net carbon sources; they had negative mean Net Ecosystem Production (NEP) values ($-0.1 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ and $-25.1 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$, respectively). The shift from carbon sinks to sources associated with land-use change was principally due to a decreased Net Primary Production (NPP) rather than increased soil respiration. Conservation of the remaining peat swamp forests and rehabilitation of deforested peatlands are crucial in GHG emission reduction programs.

Keywords: deforestation; forest logging; tropical climate; peat swamp forests; oil palm estate; NEP



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1. Introduction

Around 44 Mha out of all worldwide peatlands (400 Mha) lies in tropical nations, of which about 15 to 21 Mha are in Indonesia [1]. A recent study updated the estimate of the total peatlands in Indonesia that is 13.4 Mha [2]. Tropical peatland ecosystems are among the largest ecosystem carbon (C) stocks on earth, with about 82–92 PgC [3,4], The largest peatland area is on the island of Borneo (\approx 6.8 Mha) [5]. Tropical peatland forests have significantly been affected by deforestation, forest degradation, and land conversion [6,7]. Carbon stocks of tropical peatlands have been estimated to range from 81.7 to 91.9 Pg or about 15–19% of all global peat C stocks (610 Pg) [8]. Peat forests in Indonesia store about 57 Pg C [9]. The degradation is widespread in Indonesia; intact peat swamp forest now only comprises <7% of all peatland areas in Indonesia [7]. Land-use change has shifted carbon dynamics such that the converted peatland landscapes are now net sources of carbon [10].

Factors that govern peat accumulation in the tropical peat swamp forest ecosystem are the diverse vegetation peat-forming communities, the continued supplies of woody organic matters, the inundated environment [11], and the absence of fires. When the conversion

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of tropical peatlands occurs, these first three factors disappear and cause the rate of peat decomposition to become higher than the rate of organic matter supply. A rapid rate of peat oxidation occurs because of sufficient oxygen availability in the aerobic peat layer due to drainage and shortage of organic matter supply due to deforestation and the change of land cover, from the forest into seral grasses and monoculture oil palm estate.

Agriculture and tree estate development and management in peatlands include draining saturated soils necessary to provide suitable growing conditions [12]. Drainage canals decrease the water levels of peatlands, thus increasing aerobic decomposition rates and, therefore, carbon emissions [9]. An increase of drainage depth by 10 cm may increase emissions of about 9 Mg $\rm CO_2$ ha $^{-1}$ yr $^{-1}$ [13]. Another consequence of drainage includes the increased occurrence of peat fires, resulting in the release of significant amounts of $\rm CO_2$, as much as 1400 Mg $\rm CO_2$ ha $^{-1}$ [14,15].

Changes in carbon sequestration and emissions affected by peat forest deforestation and LUC can be quantified by comparing the net ecosystem production (NEP) of different land cover types in the same ecosystem [16,17]. Net ecosystem production (NEP) is defined as the difference between gross primary production (GPP) and ecosystem respiration (ER) [16]. GPP is defined as the gross vegetation uptake of CO_2 utilized for the photosynthesis process [16]. Ecosystem respiration is the total CO_2 that is released from the ecosystem to the atmosphere through autotrophic (vegetation) and heterotrophic (microbial) respiration processes [16,18,19]. Net primary production (NPP) is defined as the difference between GPP and autotrophic respiration [20]. NEP is determined by subtracting heterotrophic respiration from NPP. Few studies have determined NEP in tropical peat forests [15,21]. However, [22,23] reported that the NPP of tropical peat forests was 11.2 Mg C ha⁻¹ yr⁻¹ and 13.2 Mg C ha⁻¹ yr⁻¹, respectively.

Many studies have reported differences in soil respiration due to land use. Soil respiration was higher in intact peat forests (21 Mg C ha⁻¹ yr⁻¹) than oil palm and sago estates (15 Mg C ha⁻¹ yr⁻¹ and 11 Mg C ha⁻¹ yr⁻¹, respectively) in Sarawak, Malaysia [24]. In contrast, it was found that soil respiration of Indonesian oil palm estates was higher (28.4 Mg C ha⁻¹ yr⁻¹) than those in both intact and logged peat forests (16.0 Mg C ha⁻¹ yr⁻¹ and 18.5 Mg C ha⁻¹ yr⁻¹, respectively) [25]. A review by [26] concluded that total soil respiration was more significant in managed peat ecosystems (52.3 Mg CO₂ ha⁻¹ yr⁻¹) than in natural peat forests (35.9 Mg CO₂ ha⁻¹ yr⁻¹). However, in addition to soil emissions, the NPP is needed to determine net greenhouse gas emissions due to land cover change.

Quantification and comparisons of the net emissions and NEP from intact tropical peatland forests with sites logged or converted to agriculture are needed to understand the carbon dynamics and conservation values of these landscapes. We aimed to quantify and determine the differences in NEP in intact peat forest and adjacent, logged forest, degraded sites, and oil palm estates. The primary objectives of this study were to quantify changes in soil CO₂ fluxes and NEP resulting from logging (LPSF), logging and fire (ES), and land conversion to oil palm estates. We hypothesized that logging and land-use changes significantly alter the NEP of tropical peat swamp forests. This is because logging and land conversion may significantly increase heterotrophic respiration by lowering groundwater levels impacted by drainage canals; while decreasing NPP by removals of native trees to peat swamp forest ecosystem.

2. Materials and Methods

2.1. Study Site

The study area was located near Ketapang, West Kalimantan, Indonesia (Figure 1). The sampled peat dome (34,651 ha) was a deep coastal peatland, which the Pawan River borders on the north, Pesaguhan River on the south, hills on the east, and alluvial soils on the west. The two main rivers flow to the Karimata Strait in the Java Sea. Historical data on rainfall near Ketapang averages 2892 mm per year [27], while the annual temperature

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averages 27.3 °C (from 1982 to 2012). The study area has a range of elevation above mean sea level from 10 to 24 m [28].

The peat forests on this dome had been partly disturbed and exploited for timber (subsistence use) since about 1988. At that time, the access to the dome was opened through road building and started the timber exploitation and forest conversion [29]. The forests are composed of typical tree species in peat swamps, including *Aglaia rubiginosa* (*Hirn.*) Pannel, Dactylocladus stenostachys (Oliv.), and Dyera costulata (Hook.f)., Palaquium spp. [23]. Three relatively undisturbed peat swamp forests/PSF and three logged peat swamp forests/LPSF) were selected in this study. Tree canopy of 30 m heights dominates PSF, and that of 15 m dominates the LPSF sites.

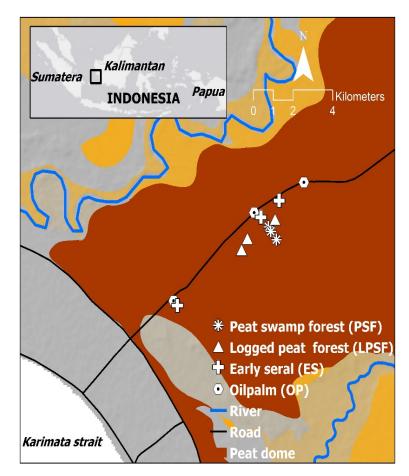


Figure 1. Study sites (white markers) within a deep peat dome near Ketapang, West Kalimantan, Indonesia. Roads (black line) cross-cutting the deep peat dome (dark brown). The peat area was delineated by [30] to represent a dome-shaped peatland between Pawan River on the north and Pesaguhan River on the south. Grey areas represent the non-peat areas. Adapted by permission from [Springer Nature Customer Service Centre GmbH]: [Springer Nature] [Mitigation & Adaptation Strategies for Global Change] (Land cover changes reduce net primary production in tropical coastal peatlands of West Kalimantan, Indonesia, Imam Basuki et al.), [COPYRIGHT] (2018) [23].

In addition to the forests, three early seral dominated by grasses and ferns (ES) and three smallholder oil palm estates (OP) were sampled. The OP estates were in close proximity to the other land cover types. The early seral sites had been logged in the past. They had been burnt several times, enabling ferns (e.g., *Stenochlaena palustris* and *Blechnum indicum*) and grasses (e.g., *Themeda triandra* and *Andropogon gerardii*) [31,32] to dominate. Early seral sites were first formed from the logged forests that were initially logged and burned in 1994 (Table 1). The three sampled oil palm (*Elaeis guineensis*) estates were three, four, and five years old. These estates were established on previously early seral sites that

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had been cleared and canalized around their boundaries. All sites occurred near the center of the peat dome.

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Year	Pre-1988	1988	1994	2010
Process	Subsistent use	Road and logging	Clearing/deforestation	Clearing + burning
Land use/land cover	Intact peat swamp forests (PSF)	Logged peat swamp forests (LPSF)	Early seral (ES)	Smallholder and industrial oil palm estate (OP)
Photos				

2.2. Soil Respiration: Total, Heterotrophic and Autotrophic Respiration

 CO_2 emissions from soils were measured monthly on all land cover types for 15 months beginning August 2014. Two transects of 38.5 m were established at each site to measure soil CO_2 emissions. Twenty-four sampling points were systematically established 3.5 m apart along each transect (Figure 2).

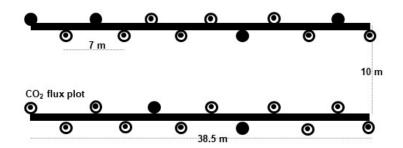


Figure 2. Plot design to measure CO_2 fluxes, soil total (hollow; 18) and heterotrophic (black; 6) respirations in two transects of 38.5 m undisturbed peat swamp forests (PSF; n = 3), partially logged peat forests (LPSF; n = 3), oil palm estate (OP; 3 plots) and early seral (ES; 3 plot) sites.

Eighteen points were marked and selected to measure total soil respiration (autotrophic and heterotrophic sources) and 6 for only heterotrophic respiration. Heterotrophic respiration was accomplished by trenching the perimeter of the plots to a 50 cm depth to cut existing roots. A 200 cm circular circumference of the root barrier was established in the trenched plot [33,34]. The inside trench wall was covered with a very fine mesh aluminum screening, and the trench was backfilled to minimize disturbance. Soil CO₂ measurement was done a month after setting up the trenches to provide time for the cut roots to be decomposed. When plants were found growing within the trenched plot, they were removed to avoid root growth affecting the soil's CO₂ emissions. A boardwalk was constructed on each transect to prevent disturbance on the peat surface while measurements were taking place. Autotrophic respiration was calculated by subtracting the heterotrophic to the total soil respiration.

Soil CO_2 respiration was measured using a portable infrared gas analyzer EGM-4 (PP Systems, USA) connected to the peat surface with a closed soil respiration chamber. The CO_2 emissions (mg m⁻² h⁻¹) were calculated from the linear change with time of gas concentration [35]. Soil CO_2 concentrations were automatically recorded every 4.5-s interval for about two minutes. In each site, the respiration measurements were taken

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between 3 pm until 6 pm. Due to the remote and difficult access, only one or two sites could be measured in a day to have similar timing of sampling in all sites.

2.3. Net Primary Production and Net Ecosystem Production

Net primary production (NPP) was measured and quantified for all sample sites of different cover types. The NPP of both aboveground and belowground was quantified [23]. The annual sum of tree growth and litterfall was quantified as aboveground production, while the yearly growth of roots was quantified as belowground production.

In each forested sample site (PSF and LPSF), six plots, six of a 10 m radius circle area, were set up 30 m in the distance along a line transect (total length 150 m; adapted from [5,36]). All trees in each plot were measured for their tree diameter at breast height (DBH) to be later extrapolated using our tree diameter growth model. A total of 120 trees, 20 in each forested site (three PSF and LPSF sites) were randomly chosen in 35×10 m² plots, located 10 m to the 150 m transect. At each site, to create a diameter growth model, tree growth was measured monthly for a year through the installation of tree bands (dendrometer), 1.3 m aboveground (DBH) [37]. In addition, the litterfall accumulation rate was measured using six litterfall traps positioned every 7 m apart along the 35 m transect. Each trap has an area of about 0.23 m² and was set up a meter above ground and tied to surrounding trees or wooden poles. Litterfall samples were gathered twice during the wet season (November and December 2015) and four times during dry seasons of two consecutive years (September and October of 2014 and 2015). Samples of litterfall were packed in plastic bags and transported to the laboratory at Bogor Agricultural University, Bogor, Indonesia. After those samples were dried at 60 °C to constant mass and weighed, the C content was then measured using a LECO Analyzer (dry combustion method/induction furnace). Chimner and Ewel [22] reported that branch fall production was estimated as 9.89% of the litterfall annual production. Root: shoot ratio in terrestrial biomass [38] was used to estimate the coarse root production, as its ratio to the aboveground biomass of all the forests trees. 12% of the overall annual production of tree, coarse root, and litterfall was used to estimate fine root production [22]. Annual NPP of all trees in PSF and LPSF was thus calculated as a sum of the aboveground and belowground NPP, which captured the annual production of tree growth, coarse and fine root growth, as well as litter and branch fall accumulation.

NPP in oil palm estate was assessed through six 10 m radius plots located 30 m apart along a 150 m transect in each sample site (similar to those in the intact and logged forests). The height of the base of their young leaves of all oil palm trees was measured at all OP sites and re-measured two years later. Annual height growth of oil palm trees was calculated by subtracting the initial tree height from the tree height at Year 2, then dividing by two. Annual biomass growth for OP trees was estimated using an allometric equation [39], which was developed in Sumatera and Borneo islands from harvested oil palm trees <1 to 8 m in height on peatlands [39]. About 75.3% of frond production, which is 68.8% of the tree biomass growth, was used to estimate the pruned frond biomass, and about 71.7% of root production, which is 14.2% of the tree biomass growth, was used to estimate dead root biomass [40]. The dead root and pruned frond production were summed to quantify the annual NPP of OP sites. As the oil palm estates were less than five years old, the contribution of fruit to the total NPP was neglected.

Early seral sites (ES) were measured for their NPP through transect of squared plot design. In each ES site, six 1 $\rm m^2$ plots were established at 7 m intervals along a 35m transect. All aboveground standing herbaceous biomass and litterfall were harvested in a 1 $\rm m^2$ plot at the six locations on each site. These ES plots were burned in September 2014, which enabled us to measure the annual aboveground NPP of ES after a year. Standing mass and litterfall were sampled using destructive sampling. Those masses were packed, weighed, and sub-sampled before transporting to the laboratory. In the laboratory, those samples were dried at 60 $^{\circ}$ C to constant mass, weighed, and processed with a LECO Analyzer to measure the carbon concentration. We used 110% of total leaf and litterfall to estimate the

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annual production of root [41]. The Annual NPP of ES was estimated as the sum of whole leaf, litterfall, and root production.

A conversion factor of 0.47 [5] was used to convert biomass to C mass. Then, C mass was reported as CO_2 (C- CO_2) by multiplying C values by 3.67, the molecular ratio of CO_2 to C.

NEP is the difference between NPP and heterotrophic respiration [16]. NPP and respiration values were transformed into the same unit, Mg $\rm CO_2$ ha $^{-1}$ yr $^{-1}$, then NEP was calculated by subtracting the heterotrophic respiration value to the NPP. It should be noted that this study did not measure carbon fluxes in the form of methane, aquatic components, and respiration from big woody debris. Thus, the NEP value in this study only represents a part of the total NEP from those studied land use and cover types.

2.4. Soil Parameters

Environmental factors were measured during soil respiration measurements. Water table depth was measured in 6 water wells at each site. The wells were perforated PVC tubes (10 cm diameter) and inserted to depths of 2 m into the peat. The water level was measured once a month, at the same time as CO_2 flux measurements. Soil temperature at 10 cm depth was measured using a temperature probe sensor in soils adjacent to the CO_2 flux measurement points (i.e., 24 points per site).

2.5. Statistical Analyses

Data distribution among land uses, seasonal rainfall, biomass sources, and primary production sources were tested for their normality using Saphiro-Wilks and Kolmogorov-Smirnov tests. When the data were normally distributed, mean values of CO₂ flux and NEP among land cover types were tested for their differences with analysis of variance (ANOVA). A least significant difference (LSD) test was performed to determine which means were significantly different during ANOVA. When non-normally distributed data were found, the Kruskal-Wallis H test was used. Diameter at breast height data of 120 forest trees was used to model tree growth (biomass gain) using regression analyses. Statistical analyses were conducted using IBM SPSS software version 20.

3. Results

3.1. Annual Ecosystem Respiration

Heterotrophic respiration was significantly different among the land cover types. It was lower in ES sites than in LPSF sites by 10 Mg CO₂ ha⁻¹ yr⁻¹ and lower than in OP sites by 8 Mg CO₂ ha⁻¹ yr⁻¹ (p < 0.05) (Table 2 and Figure 3). Similarly, total soil respiration in ES (40.8 Mg CO₂ ha⁻¹ yr⁻¹) was significantly lower (p < 0.05) than in PSF (48.5 Mg CO₂ ha⁻¹ yr⁻¹), LPSF (50.2 Mg CO₂ ha⁻¹ yr⁻¹), and OP (47.5 Mg CO₂ ha⁻¹ yr⁻¹). All land cover types were similar in their autotrophic respiration, ranging from 9.3 to 10.8 Mg CO₂ ha⁻¹ yr⁻¹. In addition, we found a very weak effect of environmental factors such as soil temperature and groundwater level ($r^2 = 0.05$) on respiration (heterotrophic and total soil).

Table 2. Heterotrophic, autotrophic, and total respiration, water table depth, and mean soil temperature in intact forest, logged peat forest, early seral, and oil palm estate are reported as mean \pm one standard error. Different lower-case letters represent the statistically significant difference (p < 0.05) on a variable among land use types.

Scheme	Heterotrophic Respiration	Autotrophic Respiration	Total Soil Respiration	Water Table Depth	Soil Temperature
		$-Mg CO_2 ha^{-1} yr^{-1}$	cm	°C	
Peat swamp forest 1	40.0 ± 5.8	5.9 ± 2.9	45.9 ± 5.5	44.3 ± 10.4	27.1 ± 0.1
Peat swamp forest 2	40.1 ± 5.3	13.9 ± 4.1	54.0 ± 5.7	48.4 ± 10.4	27.3 ± 0.2
Peat swamp forest 3	32.9 ± 4.5	12.8 ± 2.3	45.6 ± 4.3	45.3 ± 10.1	27.2 ± 0.3
Peat swamp forest mean $(n = 3)$	37.7 ± 2.4 a	10.8 ± 2.5 a	48.5 ± 2.7 a	46 ± 20.1 a	27.2 \pm 0.4 $^{\mathrm{a}}$

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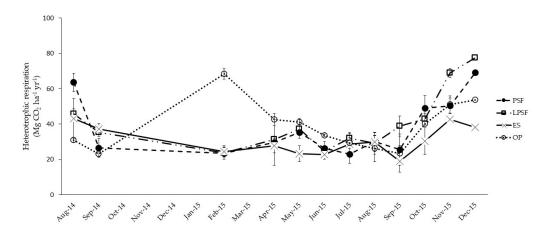
Scheme	Heterotrophic Respiration	Autotrophic Respiration	Total Soil Respiration	Water Table Depth	Soil Temperature
	-	-Mg $\mathrm{CO_2}\ \mathrm{ha^{-1}\ yr^{-1}}$		cm	°C
Logged peat swamp forest 1	43.0 ± 5.4	10.9 ± 4.6	53.9 ± 5.3	39.9 ± 10.5	27 ± 0.2
Logged peat swamp forest 2	39.6 ± 5.1	6.1 ± 4.2	45.6 ± 4.9	34.0 ± 9.9	26.8 ± 0.2
Logged peat swamp forest 3	39.4 ± 4.3	11.6 ± 3.4	51.0 ± 5.4	45.1 ± 10.6	27.3 ± 0.3
Logged peat swamp forest mean $(n = 3)$	$40.7\pm1.2~^{\rm a}$	9.5 ± 1.7 a	$50.2\pm2.4^{\text{ a}}$	$39.7\pm20.3~^{a}$	$27\pm0.5~^{a}$
Early seral 1	26.0 ± 2.5	14.9 ± 4.1	39.6 ± 4.3	59.8 ± 13	30.5 ± 0.5
Early seral 2	31.3 ± 4.0	6.1 ± 1.2	37.5 ± 4.2	40.4 ± 12.5	29.1 ± 0.3
Early seral 3	34.6 ± 2.0	10.7 ± 5.8	45.3 ± 5.8	50.7 ± 9.9	28.9 ± 0.3
Early seral mean $(n = 3)$	$30.7\pm2.5^{\ \mathrm{b}}$	10.6 ± 2.5 a	40.8 ± 2.3 b	$50.3\pm23.5~^{a}$	$29.5\pm0.8^{\text{ b}}$
Oil palm estate 1	42.2 ± 7.0	8.6 ± 5.4	49.3 ± 4.3	88.4 ± 10.3	31.5 ± 0.3
Oil palm estate 2	38.5 ± 3.3	5.9 ± 3.2	44.4 ± 3.5	74.4 ± 9.1	30 ± 0.3
Oil palm estate 3	35.4 ± 3.6	13.3 ± 6.0	48.7 ± 4.9	72.2 ± 9.3	30 ± 0.4

 9.3 ± 2.2^{a}

 38.7 ± 2.0 a

Oil palm estate mean (n = 3)

Table 2. Cont.



 47.5 ± 1.6 a

 $78.3 \pm 19.1^{\text{ b}}$

 $30.5 \pm 0.8^{\ b}$

Figure 3. Heterotrophic respiration trend from August 2014 to December 2015 in PSF (black circle), LPSF (square hollow), ES (cross), and OP (hollow circle). Dry months are represented by data from August, September, and October (5 months). Wet months are represented by data from February to July and November to December (7 months). Error bars show \pm standard error (SE) of the heterotrophic respiration data.

Autotrophic respiration during wet months (4.7 and 3.2 Mg $\rm CO_2~ha^{-1}~yr^{-1}$) was significantly lower (p < 0.05) than dry months (16.3 and 17.8 Mg $\rm CO_2~ha^{-1}~yr^{-1}$) in LPSF and OP, respectively (Table 3). In contrast, heterotrophic respiration during wet months (45.7 Mg $\rm CO_2~ha^{-1}~yr^{-1}$) was significantly higher than in dry months (28.8 Mg $\rm CO_2~ha^{-1}~yr^{-1}$) in the oil palm estates (p = 0.001).

During wet months, total soil respiration in oil palm estates was the highest among land cover types (48.9 Mg CO₂ ha⁻¹ yr⁻¹). In this period, the heterotrophic respiration in PSF (36.7 Mg CO₂ ha⁻¹ yr⁻¹) was significantly lower than OP (45.7 Mg CO₂ ha⁻¹ yr⁻¹; p < 0.01). The total and heterotrophic respiration of ES (38.8 and 29.7 Mg CO₂ ha⁻¹ yr⁻¹) were also significantly lower than OP (48.9 and 45.7 Mg CO₂ ha⁻¹ yr⁻¹; p < 0.05).

During dry months, total soil respiration in forests ranged from 53.4 to 54.7 Mg CO₂ ha⁻¹ yr⁻¹ and was higher than in non-forest sites that ranged from 43.5 to 45.5 Mg CO₂ ha⁻¹ yr⁻¹. In this period, heterotrophic respiration of OP (28.8 Mg CO₂ ha⁻¹ yr⁻¹) was lower than LPSF (38.4 Mg CO₂ ha⁻¹ yr⁻¹; p = 0.006) and PSF (39.0 Mg CO₂ ha⁻¹ yr⁻¹; p = 0.09).

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Table 3. Heterotrophic, autotrophic, and total respiration during dry and wet months in intact forest, logged peat forest, early seral, and oil palm estate. Data are mean \pm one standard error.

	Soil Respiration						
	Dry Months (August to October)			Wet Months (November to July)			
Site	Heterotrophic	Autotrophic	Total	Heterotrophic	Autotrophic	Total	
Peat swamp forest 1	41.2 ± 6.3	9.9 ± 4.2	51.1 ± 6.5	39.2 ± 5.9	3.0 ± 1.1	42.2 ± 5.0	
Peat swamp forest 2	40.2 ± 5.3	18.9 ± 5.1	59.2 ± 7.4	40.1 ± 5.6	10.2 ± 3.2	50.3 ± 4.6	
Peat swamp forest 3	35.5 ± 4.2	14.5 ± 3.5	50.0 ± 3.5	31.0 ± 4.9	11.5 ± 1.2	42.5 ± 4.9	
Peat swamp forest mean	39.0 ± 10.1	14.4 ± 8.3	53.4 ± 11.5	36.7 ± 10.8	8.3 ± 4.5	45.0 ± 9.4	
Logged peat swamp forest 1	42.4 ± 2.9	17.9 ± 6.3	60.2 ± 5.3	43.5 ± 7.0	5.9 ± 2.5	49.4 ± 5.3	
Logged peat swamp forest 2	36.7 ± 2.4	14.3 ± 4.5	51.0 ± 5.7	41.6 ± 6.6	0.2 ± 3.2	41.8 ± 4.4	
Logged peat swamp forest 3	36.2 ± 2.1	16.8 ± 5.0	53.0 ± 6.8	41.7 ± 5.4	7.9 ± 1.1	49.5 ± 4.7	
Logged peat swamp forest mean	38.4 ± 4.9	16.3 ± 9.9	54.7 ± 11.3	42.2 ± 12.1	4.7 ± 5.0	46.9 ± 9.4	
Early seral 1	27.5 ± 3.3	13.6 ± 6.2	37.9 ± 5.8	25.0 ± 2.1	15.9 ± 2.1	40.9 ± 3.4	
Early seral 2	30.8 ± 4.8	8.4 ± 1.2	39.2 ± 4.9	31.8 ± 3.6	4.5 ± 1.1	36.2 ± 4.1	
Early seral 3	37.6 ± 2.1	15.8 ± 9.1	53.4 ± 8.3	32.4 ± 1.9	7.0 ± 2.0	39.4 ± 2.7	
Early seral mean	31.9 ± 7.1	12.6 ± 12	43.5 ± 12.7	29.7 ± 5.4	9.1 ± 4.5	38.8 ± 6.6	
Oil palm estate 1	30.1 ± 2.1	18.7 ± 4.3	45.3 ± 3.6	50.8 ± 8.3	1.4 ± 5.4	52.2 ± 4.8	
Oil palm estate 2	31.1 ± 3.0	10.4 ± 4.3	41.5 ± 4.7	43.8 ± 2.6	2.7 ± 2.0	46.5 ± 2.5	
Oil palm estate 3	25.3 ± 2.9	24.4 ± 7.0	49.7 ± 7.8	42.6 ± 2.5	5.4 ± 4.2	48.0 ± 2.1	
Oil palm estate mean	28.8 ± 5.2	17.8 ± 10.5	45.5 ± 10.6	45.7 ± 10.1	3.2 ± 7.9	48.9 ± 6.5	

3.2. Net Primary Production in Intact and Logged Peat Swamp Forests

The NPP of intact peat forests (13.2 Mg C ha⁻¹ yr⁻¹) was significantly greater than any other cover type (p = 0.05; [23]). The ecosystem NPP of LPSF was 11.1 Mg C ha⁻¹ yr⁻¹, compared to 10.8 Mg C ha⁻¹ yr⁻¹ for ES and 3.7 Mg C ha⁻¹ yr⁻¹ for OP (Figure 4).

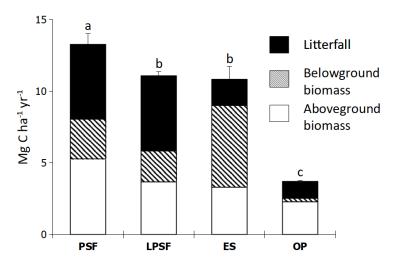


Figure 4. Primary production of belowground biomass, aboveground biomass and litterfall (NPP) in intact and logged peat forest, early seral sites (ES), and oil palm estates (OP). Production of biomass and litterfall (NPP) reported as a mean value. Error bars show \pm standard error (SE) of the production. PSF represents intact peat forests, and LPSF means partially logged forests. Lower case letters represent statistical significance in production. Adapted by permission from [Springer Nature Customer Service Centre GmbH]: [Springer Nature)] [Mitigation & Adaptation Strategies for Global Change] (Land cover changes reduce net primary production in tropical coastal peatlands of West Kalimantan, Indonesia, Imam Basuki et al.), [COPYRIGHT] (2018) [23].

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3.3. Net Ecosystem Production

The mean NEP of intact forests was $10.8~{\rm Mg~CO_2~ha^{-1}~yr^{-1}}$ ($2.94~{\rm Mg~C~ha^{-1}~yr^{-1}}$). In contrast, oil palm estates were significant sources of greenhouse gas emissions. The NEP of oil palm was $-25.1~{\rm Mg~CO_2~ha^{-1}~yr^{-1}}$ ($-6.85~{\rm Mg~C~ha^{-1}~yr^{-1}}$). Logged forests were also sources of greenhouse gas emissions with a slightly negative NEP ($-0.1~{\rm Mg~CO_2~ha^{-1}~yr^{-1}}$). The difference in NEP between intact forest and oil palm was $35.9~{\rm Mg~CO_2~ha^{-1}~yr^{-1}}$, and between intact and logged forest was $10.9~{\rm Mg~CO_2~ha^{-1}~yr^{-1}}$.

The NEP of logged forests and oil palm estates was significantly lower than PSF (Table 4) (p = 0.056 and 0.001), but not ES (p = 0.8). NEP was significantly correlated with the NPP (r = 0.95), but not with the heterotrophic respiration (r = 0.08; Figure 5).

Table 4. Net primary production (NPP), net ecosystem production (NEP), and heterotrophic respiration in intact and logged peat forest, early seral, and oil palm estate were reported as mean \pm SE whenever possible.

Site	Total NPP	Heterotrophic Respiration	NEP
		–Mg $\mathrm{CO_2}$ ha $^{-1}$ yr $^{-1}$ —	
Peat swamp forest 1	50.4	40.0 ± 5.8	10.4
Peat swamp forest 2	42.4	40.1 ± 5.3	2.3
Peat swamp forest 3	52.8	32.9 ± 4.5	19.9
Peat swamp forest mean	48.5 ± 2.8	37.7 ± 2.4	10.8 ± 5.1
Logged peat swamp forest 1	38.8	43.0 ± 5.4	-4.2
Logged peat swamp forest 2	40.7	39.6 ± 5.1	1.1
Logged peat swamp forest 3	42.2	39.4 ± 4.3	2.8
Logged peat swamp forest mean	40.6 ± 1.0	40.7 ± 1.2	-0.1 ± 2.1
Early seral 1	31.3 ± 12.8	26 ± 2.5	5.3
Early seral 2	48.1 ± 19.7	31.3 ± 4.0	16.8
Early seral 3	39.9 ± 16.3	34.6 ± 2.0	5.3
Early seral mean	39.8 ± 4.9	30.7 ± 2.5	9.1 ± 3.8
Oil palm estate 1	14.1 ± 1.4	42.2 ± 7.0	-28.1
Oil palm estate 2	13.4 ± 3.5	38.5 ± 3.3	-25.1
Oil palm estate 3	13.4 ± 1.0	35.4 ± 3.6	-22.0
Oil palm estate mean	13.6 ± 0.2	38.7 ± 2.0	-25.1 ± 1.8

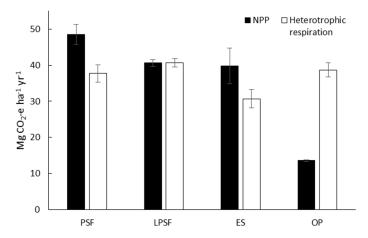


Figure 5. The net primary production and heterotrophic respiration rates in intact (PSF), logged peat forests (LPSF), early seral communities (ES), and oil palm estates (OP). Vertical bars are one standard error of NPP and respiration.

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3.4. Soil Parameters

Depth to the water table and soil temperatures varied between land cover types (Table 5). There was a lower water table at the OP sites than others, likely due to trenching and canals nearby. The mean annual water table depth in OP was 78.3 cm in contrast to the <50 cm depth for the water levels in other cover types (PSF, LPSF, and ES). The seasonal differences in water table depth in OP between dry season (August to October) and wet season (November to July) were lower than other ecosystems (p < 0.05).

Table 5. Water table depth and soil temperature (means \pm SE) of intact peat forest (PSF), logged peat forest (LPSF), early seral (ES), and oil palm (OP) during wet and dry months and annually. Superscripted letters denote a significant difference (p < 0.05) when testing between land cover types.

Site	Water Table Depth Level (cm)			Soil Temperature (°C)		
	Dry Months	Wet Months	Annual	Dry Months	Wet Months	Annual
Peat swamp forest	81 ± 13	21 ± 8	46 ± 6 a	27.3 ± 0.5	27.1 ± 0.3	27.2 ± 0.1 a
Logged peat swamp forest	74 ± 13	15 ± 9	40 ± 6 a	27.0 ± 0.5	27.1 ± 0.6	$27.0\pm0.1~^{\rm a}$
Early seral	84 ± 21	26 ± 13	50 ± 7 a	30.0 ± 0.8	28.8 ± 0.8	$29.5 \pm 0.2^{\text{ b}}$
Oil palm estate	105 ± 15	60 ± 13	$78\pm6^{ m \ b}$	30.6 ± 0.8	30.3 ± 0.8	30.5 \pm 1.6 $^{\rm c}$

The OP and ES sites were open and had limited shade; thus, more sunlight reached the peat soil surface. The mean soil temperature on these two ecosystems was $30.5\,^{\circ}$ C and $29.5\,^{\circ}$ C, respectively, and higher than the soil temperature at PSF and LPSF ($27.2\,^{\circ}$ C and $27.0\,^{\circ}$ C, respectively). Seasonal differences in soil temperature in ES between the dry and wet seasons were significantly higher than in other ecosystems (p < 0.05).

4. Discussion

4.1. How Land Use Change Affects Soil Respiration in Tropical Peatland Ecosystems

Total soil respiration in the different peatland cover types ranged from 40 to 50 Mg $\rm CO_2~ha^{-1}~yr^{-1}$, and heterotrophic respiration ranged from 31 to 41 Mg $\rm CO_2~ha^{-1}~yr^{-1}$ (Table 1). Similar total soil and heterotrophic respiration were measured in the intact forests, logged forests, and oil palm estates (p > 0.05). However, significantly lower total soil and heterotrophic respiration were found in early seral than intact forests (p < 0.05). We suspect that the lower heterotrophic respiration in early seral sites may be due to the loss of significant soil microbial populations and the decline of labile - non-recalcitrant forms of organic carbon as a result of repeated fires and losses of dissolved organic carbon in early seral ecosystems [42].

Soil respiration (48.5 Mg CO₂ ha⁻¹ yr⁻¹) of the intact forests in this study was similar to that reported in a review of South East Asia peatlands [43] but slightly lower than studies from Sumatera, Indonesia (59 Mg CO₂ ha⁻¹ yr⁻¹; [25]), South Kalimantan, Indonesia (55 Mg CO₂ ha⁻¹ yr⁻¹; [21]) and Sarawak, Malaysia (77 Mg CO₂ ha⁻¹ yr⁻¹; [24]). The total soil respiration of logged forest (50.2 Mg CO₂ ha⁻¹ yr⁻¹) in our study area was much lower than those reported from a logged forest in Sumatera (68 Mg CO₂ ha⁻¹ yr⁻¹; [25]). The differences in soil respiration in these logged forests may vary in the definition of logged forests. In this study, logged forests were only partially logged by local communities (often for domestic uses) and impacted by a 3-m wide and 2-m deep canal to the north (>0.5 km in the distance) and an 8-m wide and 1-m deep canal to the east (4.5 km in the distance). In contrast, other studies measured respiration where drainage canals are denser, and the entire large overstory had been removed.

Soil respiration in our early seral sites (30 Mg CO_2 ha⁻¹ yr⁻¹) was also lower than bare land sites in Sumatera (60 Mg CO_2 ha⁻¹ yr⁻¹; [44]). Similarly, our soil respiration in the sampled oil palm estates (47.5 Mg CO_2 ha⁻¹ yr⁻¹) was lower than studies in Sarawak, Malaysia (55 Mg CO_2 ha⁻¹ yr⁻¹; [24]) and Sumatera, Indonesia (104 Mg CO_2 ha⁻¹ yr⁻¹; [25]). However, the value was similar to a study in Kalimantan, Indonesia (44 Mg CO_2 ha⁻¹ yr⁻¹; [21]). Those differences may have been affected by the use of different methodologies in measur-

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ing the soil respiration (portable EGM vs. gas sampling), as well as the inherent differences in land use, peat-soil characteristics [45,46] latitude, and groundwater table [47]. These results suggest that soil respiration of tropical peat forests is highly variable, site-specific, and likely high in annual variation [48].

In comparison with other ecosystems, heterotrophic respiration of intact peat forest in this study was lower than upland tropical rain forests (138 Mg CO₂ ha⁻¹ yr⁻¹; [17]), logged peat forests in Jambi (68 Mg CO₂ ha⁻¹ yr⁻¹; [25]), and oil palm estate in Jambi (104 Mg CO₂ ha⁻¹ yr⁻¹; [25]) and Sarawak (55 Mg CO₂ ha⁻¹ yr⁻¹; [24]). Heterotrophic respiration in peat forests was also higher than other wetlands such as mangrove forests in Australia (20 Mg CO₂ ha⁻¹ yr⁻¹; [49]) and Thailand (8 Mg CO₂ ha⁻¹ yr⁻¹; [17,50]).

The land cover type had no impact on heterotrophic respiration in tropical peat forests landscapes [21,47]. However, other studies have found that land cover change in tropical peat forests decreases [24] or increases heterotrophic respiration [25]. Rather than affecting heterotrophic respiration, we found that land-use change affects carbon dynamics principally through decreased carbon sequestration rates (NPP).

4.2. Effect of Land Use Change on Net Ecosystem Production

The relatively high NEP in the ES sites was related to lower heterotrophic respiration coupled with a relatively high belowground NPP (Table 4). We estimated the carbon losses from peat forest conversion to early seral may reach an estimated 4259 Mg $\rm CO_2$ e ha⁻¹ over 25 years, which includes incidences of numerous peat fires [4]. Combining these data, early seral sites are significant net sources of greenhouse gasses (120 Mg $\rm CO_2$ e ha⁻¹ yr⁻¹).

Compared to other wetlands, the NEP of peat forests in this study was lower than that of tropical mangroves [50–53] but higher than the Siberian peat forests [54] (Figure 6). The high NEP of mangrove ecosystems has been attributed to its high NPP due to its nutrient-rich ecosystem and low heterotrophic respiration due to saturated soil within a tidal environment [17,53]. The low NEP of Siberian peat forests has been attributed to a limited growing season [55]. These findings are similar to our conclusion that the rate of NPP is the primary driver of NEP and that the changes in land use affect NPP to a greater extent than respiration.

In contrast with the NEP reported for peat oil palm estates in Malaysia [56], we found that oil palm estates of our study sites are significant sources of greenhouse gases NEP = $-25.1 \, \text{Mg CO}_2$ e ha⁻¹ yr⁻¹). The palm estates of our study had a lower annual NPP (13.6 Mg CO₂ e ha⁻¹ yr⁻¹) than that reported in [56] (44 Mg CO₂ e ha⁻¹ yr⁻¹). This difference may be due to methodological differences.

We estimated that land cover change in peat forest landscapes to logged forests, early seral sites, and oil palm estates result in net emissions of about 10.9, 1.7, and 35.9 Mg $\rm CO_2$ e ha⁻¹ yr⁻¹, respectively. These results are lower than current IPCC default values for emission from drained peat on forest land, grassland, and oil palm estate (19.4, 35.2, and 36.7 Mg $\rm CO_2$ ha⁻¹ yr⁻¹) [57]. However, these differences are likely related to different methodologies since our NEP includes peat decomposition (respiration) and NPP. The IPCC values represent either historical (peat subsidence approach) or present ($\rm CO_2$ fluxes) sources, excluding peat fires' impacts [57].

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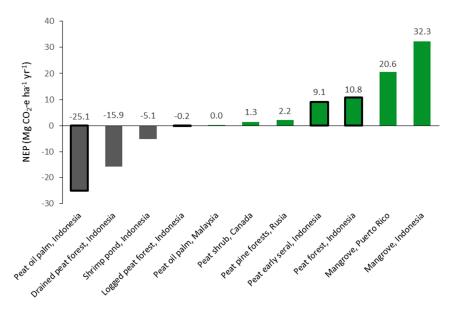


Figure 6. Net ecosystem production among wetland ecosystems. Data for mangrove are from [51,53]. Shrimp pond is from [53]. Peat oil palm is from [56] and this study. Peat pine forest and drained peat forests are from [54,58]. Peat shrub is from [59]. Peat forest, logged peat forest, oil palm, and early seral are from this study (bordered with black line).

4.3. Implications for Tropical Peatland Management

Tropical peat swamp forests sequester carbon because their high annual NPP exceeds their respiration rates. Degradation and conversion (land-use changes) of peat swamp forests significantly affected NPP. [10] stated that tropical peatland landscapes in Indonesia are now net sources of carbon as there is four times more degraded peat forest than the intact forest. Intact peat swamp forests now only comprise <7% of all peatland areas in Indonesia's main islands [7].

In 2015 there were more than three million hectares of oil palm estates and almost one million hectares of degraded grasslands/early seral (ES) in South East Asia [7]. Using our estimates of oil palm's NEP ($-25.1~\rm Mg~CO_2~ha^{-1}~yr^{-1}$), the 3 million ha of oil palm will emit significant amounts of CO₂ into the atmosphere, as much as 75 Tg CO₂ yr⁻¹. In addition, our results from the NEP of early seral sites (9.1 Mg CO₂ ha⁻¹ yr⁻¹) suggest that allowing grasses and ferns to regrow and cover the peat surface under 3 million ha of OP trees could reduce the emissions by about 27 Tg CO₂ yr⁻¹.

Most ignitions in peatland landscapes are from humans and in contrast to early seral sites and logged forests, rarely are fuels dry enough to burn in natural forests [60]. However, our results show that land-use change significantly lowered the water table and increased soil temperatures, thus increasing fire susceptibility [61]. Fire is a significant threat to the production of peatland ecosystems. A single event of uncontrolled peat fire may emit as much as 416 Mg $\rm CO_2$ ha⁻¹ [62]. This is a value equivalent to the NEP of peat forests for almost four decades.

Logging and conversion to early seral communities and oil palm estate reduce potential carbon sequestration by 10.9, 1.7, and 35.9 Mg CO₂ ha⁻¹ yr⁻¹, respectively. These are the differences in NEP between intact peat forest (10.8 Mg CO₂ ha⁻¹ yr⁻¹) and each of logged peat forest (-0.1 Mg CO₂ ha⁻¹ yr⁻¹), early seral (9.1 Mg CO₂ ha⁻¹ yr⁻¹), and oil palm (-25.1 Mg CO₂ ha⁻¹ yr⁻¹). Logging and conversion of peat swamp forests have shifted the ecosystem from a carbon sink to a carbon emitter. The large carbon stocks and emissions arising from the land cover change in tropical peat forests and other ecosystem services of intact peat forests suggest that their conservation and restoration are of local and global importance for mitigating climate change.

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