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Major and persistent shifts in below-ground carbon dynamics and soil respiration following logging in tropical forests

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Abstract

Soil respiration is the largest carbon efflux from the terrestrial ecosystem to the atmosphere, and selective logging influences soil respiration via changes in abiotic (temperature, moisture) and biotic (biomass, productivity, quantity and quality of necromass inputs) drivers. Logged forests are a predominant feature of the tropical forest landscape, their area exceeding that of intact forest. We quantified both total and component (root, mycorrhiza, litter, and soil organic matter, SOM) soil respiration in logged (n = 5) and old-growth (n = 6) forest plots in Malaysian Borneo, a region which is a global hotspot for emission from forest degradation. We constructed a detailed below-ground carbon budget including organic carbon inputs into the system via litterfall and root turnover. Total soil respiration was significantly higher in logged forests than in old-growth forests (14.3 ± 0.23 and 12.7 ± 0.60 Mg C ha^{-1} year^{-1}, respectively, p = 0.037). This was mainly due to the higher SOM respiration in logged forests (55 ± 3.1% of the total respiration in logged forests vs. 50 ± 3.0% in old-growth forests). In old-growth forests, annual SOM respiration was equal to the organic carbon inputs into the soil (difference between SOM respiration and inputs 0.18 Mg C ha^{-1} year^{-1}, with 90% confidence intervals of −0.41 and 0.74 Mg C ha^{-1} year^{-1}), indicating that the system is in equilibrium, while in logged forests SOM respiration exceeded the inputs by 4.2 Mg C ha^{-1} year^{-1} (90% CI of 3.6 and 4.9 Mg C ha^{-1} year^{-1}), indicating that the soil is losing carbon. These results contribute towards understanding the impact of logging on below-ground carbon dynamics, which is one of the key uncertainties in estimating emissions from forest degradation. This study demonstrates how significant perturbation of the below-ground carbon balance, and consequent net soil carbon emissions, can persist for decades after a logging event in tropical forests.

KEYWORDS
autotrophic respiration, belowground carbon allocation, CO_2 flux, harvest, heterotrophic respiration, SAFE Project, selective logging, soil organic matter

1 | INTRODUCTION

Soil respiration of terrestrial ecosystems represents the largest carbon efflux from the ecosystem to the atmosphere, approximately 75–100 Pg C year^{-1} globally (Bond-Lamberty & Thomson, 2010; Schlesinger & Andrews, 2000); this figure is eight to 11 times larger than the global CO_2 emissions from fossil fuels (Le Quéré et al., 2018). Soil respiration is thus one of the key components of the global carbon budget, yet, it remains poorly constrained.

In tropical forest ecosystems, soil respiration accounts for approximately 50% of the total ecosystem respiration (Malhi, 2012). Soil respiration is the sum of heterotrophic respiration by soil microbes and soil fauna, autotrophic respiration by plant roots, and the respiration of mycorrhizal symbionts. Because different soil respiration components originate from different carbon pools, are controlled by different factors, and may respond differently to disturbance, it is important to measure soil respiration at the component scale, in addition to measuring total soil respiration, to gain a better process-level understanding.

Heterotrophic respiration may originate from rhizo-deposits (carbon lost directly from roots), from dead plant remains (leaf, woody and root tissue), and from soil organic matter (SOM; Kuzyakov, 2006). SOM respiration, in turn, may be divided into respiration that either is or is not stimulated by rhizodeposition; the former is referred to as priming effect and the latter as basal respiration. Because fresh carbohydrates are the preferred substrate for soil microbes, heterotrophic respiration derived from the labile carbon pools dominates over the basal SOM respiration (Schimel et al., 1994; Trumbore, 2000). Recalcitrant SOM constitutes only a small fraction of the soil respiration, despite constituting most of the soil carbon stock. In tropical forests <20% of soil respiration is derived from carbon fixed more than one year ago (Trumbore, 2000).

Autotrophic respiration by plant roots typically accounts for 30%–50% of soil respiration in tropical forests (Bond-Lamberty et al., 2004; Chen et al., 2011). It is to be noted, however, that due to method constraints these estimate include, in most cases, mycorrhizal respiration and heterotrophic rhizosphere respiration derived from newly assimilated root exudates and recently dead fine roots and hyphae. Microbial rhizosphere respiration may exceed the rate of actual root respiration (Chen et al., 2006; Kuzyakov, 2002). It has been debated whether mycorrhizal respiration should be considered autotrophic or heterotrophic; mycorrhizal fungi are heterotrophic organisms, but the substrate for mycorrhizal respiration is coming directly from the roots, without entering the litter pool available to decomposers (Hopkins et al., 2013). Autotrophic respiration is strongly linked to plant productivity; in tropical forests about 60% of gross primary productivity is used in plant respiration (Malhi, 2012), of which root respiration constitutes approximately 30% (Anderson-Teixeira et al., 2016; Malhi et al., 2014).

Root respiration and microbial decomposition of rhizo-deposits of living roots are primarily substrate-limited processes and can therefore be strongly driven by photosynthesis and plant production processes (e.g. plant growth and allocation), while the respiration

derived from SOM is mainly process-rate limited and controlled by temperature and moisture (Kuzyakov & Gavrichkova, 2010). Respiration originating from dead plant material is intermediate in this respect.

Greenhouse gas emissions from forest degradation in the tropics account for 1.09 Pg year^{-1}, of which 53% is from timber harvest (Pearson et al., 2017). The prevalent method of timber harvests in native tropical forests is selective logging, wherein a proportion of the largest canopy trees of timber-yielding species is harvested in 20–40 year cycles. Typical logging intensity is 30–50 m^3 ha^{-1} but may vary from 1 to 220 m^3 ha^{-1} (Putz et al., 2012). Infrastructure, such as skid trails, log landing sites and logging roads, and damage to the surrounding vegetation constitute the main sources of carbon emissions, rather than the extracted logs themselves (Pearson et al., 2014).

Empirical data on the effect of selective logging on soil respiration are scarce, and mainly restricted to single-plot studies. The available results from tropical forests do not show a clear trend, with reports of selective logging showing neutral (Adachi et al., 2006; Ishizuka et al., 2005; Takada et al., 2015; Yashiro et al., 2008), negative (Mori et al., 2017) or positive (Saner et al., 2012) effects on total soil respiration. We are not aware of any empirical partitioned soil respiration estimates from selectively logged tropical forests to date. Selective logging reduces the amount of metabolically active tissue, causing a decrease in autotrophic respiration. When the forest starts to recover, its productivity increases to, or possibly beyond, the pre-logging levels (Berry et al., 2010; Blanc et al., 2009; Riutta et al., 2018), and autotrophic respiration follows a similar pattern. Heterotrophic respiration is likely to increase immediately after logging (Huang & Asner, 2010) due to the new inputs of dead organic matter in the form of dead roots, above-ground logging residue, abandoned logs, and trees that died or lost branches and foliage due to collateral damage. Rather than following a monotonic decline, there is typically a second peak in respiration 10–20 years after the disturbance, due to the decay of recalcitrant legacy carbon and elevated post-disturbance mortality (Adachi et al., 2011; Harmon et al., 2011). In addition to carbon losses from necromass, there is also some indication that soil disturbance enhances heterotrophic respiration from the slow, recalcitrant SOM pool (Janssens et al., 2001). Gaps and logging roads, which are typical features in selectively logged forests, have a lower soil respiration rate than the surrounding closed canopy areas due to substrate limitation (Ishizuka et al., 2005; Saner et al., 2009; Takada et al., 2015), which increases the spatial heterogeneity in logged forests.

Below-ground carbon dynamics constitute one of the key uncertainties in monitoring emissions from forest degradation (Vargas et al., 2013). This paper contributes towards filling this knowledge gap, and has two objectives. First, we aimed to quantify total and component (root, mycorrhiza, litter and SOM) soil respiration rates in selectively logged ($n = 5$) and old-growth ($n = 6$) forest plots Malaysian Borneo, a region which is a global hotspot for emission from timber harvest (Pearson et al., 2014). Second, with data on the inputs of organic carbon to the soil via litterfall and root turnover, we aimed to quantify what fraction of these inputs is respired directly from that pool, and consequently what proportion of dead plant

tissues becomes part of SOM and microbial biomass pool. These soil carbon input-output calculations enable us to determine if the soils are sequestering or losing carbon.

We hypothesised that:

Hypothesis H1 *Compared with old-growth forests, heterotrophic respiration is higher in logged forests because of the larger necromass pool, which is due to both the higher current mortality and legacy of the logging.*

Hypothesis H2 *Mycorrhizal respiration is lower in logged forests due to the lower abundance of ectomycorrhizal Dipterocarp trees (Both et al., 2019; Riutta et al., 2018), which tend to be extracted as timber trees.*

Hypothesis H3 *Given similar root net primary productivity (NPP; Riutta et al., 2018), root respiration does not differ between the forest types.*

Hypothesis H4 *Overall, total soil respiration is higher in logged forests, as the loss of mycorrhiza has a smaller effect on soil respiration than the gain in necromass.*

Hypothesis H5 *In old-growth forests, the SOM carbon pool is in equilibrium, therefore the annual SOM respiration equals the organic carbon inputs into the soil. In logged forests, the system is in disequilibrium due to the pulse of labile carbon at the time of the logging and due to the current higher tree mortality rate.*

2 | MATERIALS AND METHODS

2.1 | Site description

The study sites were located in Malaysian Borneo, in the states of Sabah and Sarawak. The climate in the region is moist tropical, with an annual daily mean temperature of 26.7°C and annual precipitation of 2600–2700 mm (Kumagai & Porporato, 2012; Walsh & Newbery, 1999).

Five plots were in selectively logged forest in the Kalabakan Forest Reserve (SAFE Project Experimental Area, see www.safeproject.net; Ewers et al., 2011) and six plots in old-growth forest (two in Danum Valley Conservation Area, two in Maliau Basin Conservation Area, two in Lambir Hills National Park; Table 1). All plots were 1 ha intensive carbon dynamics monitoring plots, part of the Global Ecosystem Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk; Malhi et al., 2021; Marthews et al., 2014). For a more detailed plot description and a map of the sites see Riutta et al. (2018). The selectively logged plots had been logged two (SAFE-03, SAF-04) or four (SAF-01, SAF-02, SAF-05) times, the plots thus forming a gradient from moderately to heavily logged forest. The first round of logging took place in mid-1970s, followed by one to three repeated rounds between 1990 and early 2000s. The pre-logging biomass of the logged plots was similar to the current biomass of the old-growth plots (Riutta et al., 2018).

TABLE 1 Plot code (as in the ForestPlots database) and field name, location and characteristics of the eleven study plots

Plot code and name	Plot location	Coordinates	Forest type	Soil type; topography	Basal area of trees >10 cm DBH ($m^2\,ha^{-1}$)
SAF-01 B South	Kalabakan Forest Reserve, SAFE Project, Sabah	4.732°, 117.619°	Heavily logged	Clay; mostly flat with a moderate slope on one edge	6.81 ± 1.00
SAF-02 B North	Kalabakan Forest Reserve, SAFE Project, Sabah	4.739°, 117.617°	Heavily logged	Clay; undulating	11.1 ± 1.81
SAF-05 Tower	Kalabakan Forest Reserve, SAFE Project, Sabah	4.739°, 117.617°	Heavily logged	Clay; undulating	13.9 ± 1.70
SAF-03 E	Kalabakan Forest Reserve, SAFE Project, Sabah	4.691°, 117.588°	Moderately logged	Clay; steep slope	19.6 ± 1.88
SAF-04 LF	Kalabakan Forest Reserve, SAFE Project, Sabah	4.765°, 117.700°	Moderately logged	Partly sandy loam, partly clay; flat	19.3 ± 1.70
DAN-04 Danum Carbon 1	Danum Valley Conservation Area, Sabah	4.951°, 117.796°	Old-growth	Clay; steep slope	32.0 ± 3.30
DAN-05 Danum Carbon 2	Danum Valley Conservation Area, Sabah	4.953°, 117.793°	Old-growth	Clay; flat	30.6 ± 3.37
MLA-01 Belian	Maliau Basin Conservation Area, Sabah	4.747°, 116.970°	Old-growth	Clay; undulating	41.6 ± 3.59
MLA-02 Seraya	Maliau Basin Conservation Area, Sabah	4.754°, 116.950°	Old-growth	Clay; moderate slope	34.7 ± 2.74
LAM-07 Lambir Clay	Lambir Hills National Park, Sarawak	4.183°, 114.022°	Old-growth	Clay; valley	31.8 ± 3.85
LAM-06 Lambir Sand	Lambir Hills National Park, Sarawak	4.188°, 114.019°	Old-growth	Sandy loam; undulating with steep slopes	41.1 ± 2.45

For more details of the logging history see Fisher et al. (2011), Pfeifer et al. (2016), Reynolds et al. (2011), and Struebig et al. (2013). The exact location of the plots was chosen randomly, and the logged plots contain old skid trails, log landing sites and logging roads.

In the old-growth plots, the most common tree genera were *Shorea* (Dipterocarpaceae) and *Diospyros* (Ebenaceae) in Danum, *Shorea* and *Parashorea* (Dipterocarpaceae) in Maliau and *Shorea* and *Dryobalanops* (Dipterocarpaceae) in Lambir. In the logged plots, the most common genera were *Macaranga* (Euphorbiaceae), *Shorea* and *Syzygium* (Myrtaceae). The logging had shifted the tree species community towards early successional species, which comprised 29 ± 8.3% of the logged plot basal area. For a more comprehensive description of the species composition, see Both et al. (2019) and Riutta et al. (2018).

The soils are orthic Acrisols or Ultisols in the Sabah plots and hu-mult Utisols or udult Utisols in the Sarawak plots (for a comprehensive description of the soil types see Kho et al., 2013; Marsh & Greer, 1992; Nainar et al., 2015; Tan et al., 2009). The soil characteristics of the plots (three replicates per plot, using the RAINFOR protocols; see Quesada et al., 2010) are shown in Table 2 (see also multivariate analysis in Riutta et al., 2018).

2.2 | Soil respiration measurements

Soil respiration was measured using a static chamber technique. We measured both total soil respiration and respiration partitioned into components, using standardised sampling techniques following the GEM protocol (Malhi et al., 2014; Marthews et al., 2014). Key sampled components include above-ground litter, root + priming + root turnover (in this instance, we define priming respiration as the non-symbiotic respiration originating from rhizodeposition; we will refer to root + priming respiration as root respiration for conciseness), mycorrhizae, and SOM. The SOM pool also includes microbial biomass, but we will refer to it as the SOM pool for conciseness.

Total soil respiration was measured in 25 points per plot, positioned in a 20 × 20 m grid. According to Adachi et al. (2005), a sample size of 19 and 18 was required for estimating soil respiration rate within ±20% of the true mean at the 95% probability level in primary and secondary forest, respectively, in peninsular Malaysia, while Metcalfe et al. (2008) suggested an ideal sample size of 27 ± 6 to estimate the true mean within ±10% at 95% probability in neotropical forests. We used a shallow polyvinyl chloride collar of 11 cm diameter and 10 cm length, which was inserted 5 cm deep into the soil. To estimate the headspace volume as accurately as possible, the exact collar height above the soil surface was measured.

Partitioned respiration was measured in four locations within each plot, close to the plot corners, so the distance between the replicates was approximately 90–95 m. Each partitioning location had a cluster of six collars, approximately 30 cm apart. (Figure 1):

C1: A shallow collar of 10 cm length, inserted 5 cm into soil (same as the total respiration measurement). The respiration estimate from Collar C1 is total respiration, comprising litter, root +root turnover, mycorrhizal, and SOM respiration.

C2: A 35 cm collar, inserted 30 cm into soil, with four circular holes of 5 cm diameter cut on the collar walls and covered with a 35-micron mesh, which excludes roots (and thus also the respiration originating from rhizosphere and from root turnover) but allows the ingrowth of mycorrhiza. The respiration estimate includes litter, mycorrhizal, and SOM respiration.

C3: As Collar C2 but no with holes in the walls, roots and mycorrhiza excluded. The respiration estimate includes litter and SOM respiration.

TABLE 2 Soil characteristics (0–30 cm depth) of the study plots. Values are mean ± 1 SE within plots and by forest type

Plot code	Sand/Silt/Clay (%)	Bulk density (g cm^{-3})	C (%)	N (%)	P (mg kg^{-1})	K (mg kg^{-1})	eCEC (mmol$^+$ kg^{-1})	pH (H$_2$O)
SAF-01	49, 31, 20	0.79	1.23 ± 0.56	0.14 ± 0.05	273 ± 38.7	73.3 ± 9.6	59.4 ± 3.2	4.3 ± 0.08
SAF-02	44, 36, 20	0.96	0.63 ± 0.38	0.06 ± 0.03	122 ± 4.2	84.3 ± 18.2	51.1 ± 2.2	4.3 ± 0.19
SAF-05	21, 52, 27	0.86	1.87 ± 0.33	0.20 ± 0.04	386 ± 42.5	49.1 ± 1.4	54.7 ± 4.8	4.9 ± 0.25
SAF-03	46, 32, 22	1.03	0.98 ± 0.43	0.10 ± 0.01	158 ± 20.0	79.6 ± 25.2	32.7 ± 6.3	3.8 ± 0.18
SAF-04	66, 25, 9	1.02	2.63 ± 0.97	0.16 ± 0.02	61.5 ± 4.5	26.7 ± 7.3	5.5 ± 1.7	3.7 ± 0.57
DAN-04	34, 42, 24	0.83	0.89 ± 0.12	0.09 ± 0.01	433 ± 81.4	18.7 ± 9.6	63.2 ± 1.6	5.5 ± 0.20
DAN-05	33, 42, 25	1.30	1.00 ± 0.37	0.11 ± 0.02	201 ± 5.9	64.1 ± 3.6	49.2 ± 3.82	4.5 ± 0.23
MLA-01	43, 34, 23	0.99	0.80 ± 0.25	0.08 ± 0.01	149 ± 15.8	71.1 ± 7.6	44.9 ± 7.0	4.0 ± 0.08
MLA-02	36, 44, 20	0.98	1.02 ± 0.22	0.13 ± 0.02	210 ± 11.1	67.3 ± 13.6	46.4 ± 2.3	4.3 ± 0.29
LAM-07	43, 49, 8	1.36	0.95 ± 0.07	0.10 ± 0.02	127 ± NA	64.8 ± 21.3	35.2 ± 6.9	4.4 ± 0.16
LAM-06	69, 19, 12	1.08	0.98 ± 0.08	0.08 ± 0.01	73.4 ± NA	42.2 ± 10.4	30.3 ± 9.1	4.4 ± 0.03
Logged, Mean	45, 35, 20	0.93 ± 0.05	1.47 ± 0.35	0.13 ± 0.02	200 ± 57.9	62.6 ± 10.8	40.7 ± 9.9	4.2 ± 0.21
Old-growth, Mean	43, 38, 19	1.08 ± 0.08	0.94 ± 0.03	0.10 ± 0.01	199 ± 51.1	54.7 ± 8.3	44.9 ± 4.7	4.5 ± 0.21

Litter   No litter

Roots and mycorrhizae

C1   S1   10 cm

Root exclusion

Mycorrhizal growth into collars through four holes of 5 cm diameter covered with 35 micron mesh

C2   S2   35 cm

Root and mycorrhizae exclusion
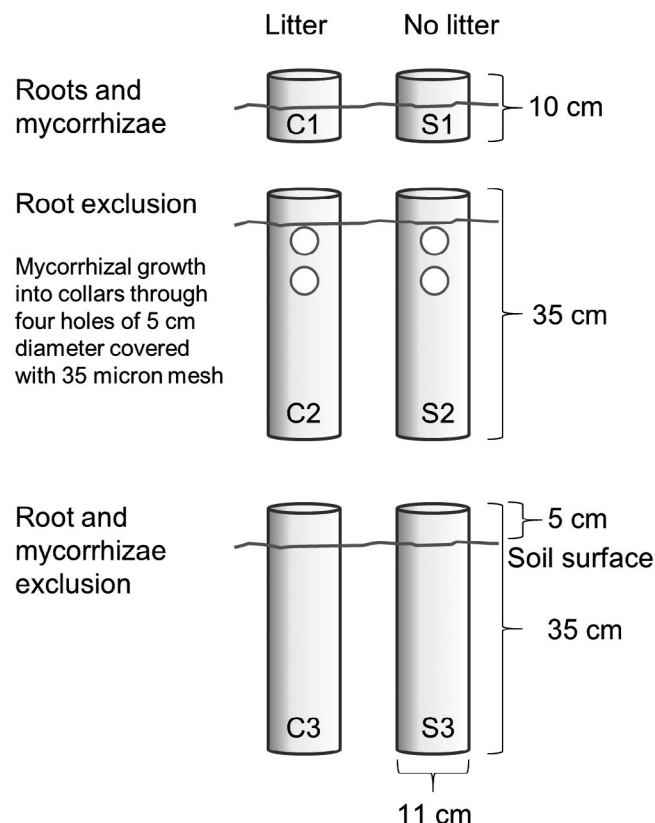
5 cm
Soil surface

C3   S3   35 cm

11 cm

FIGURE 1 Schematic representation of the cluster of six collars for measuring partitioned soil respiration, with treatments for excluding litter, roots and mycorrhizae (see text for details). Each one-hectare plot has four replicate clusters for partitioned respiration measurements

S1, S2 and S3: As collars C1, C2 and C3, respectively, but litter layer removed and litter respiration thus excluded. The soil surface was covered with small, locally collected stones to retain surface moisture and to minimise carbon and nutrient transfer from the recently fallen litter to the soil. New litter that had fallen onto the collars was removed and discarded prior to each respiration measurement. The litter mass loss during the first month of decomposition in this site is approximately 10% (Elias et al., 2020).

To install the deep collars (C2, C3, S2 and S3), a 30 cm deep hole was dug with a post-hole digger. The vertical profile of the excavated soil was maintained as carefully as possible. Roots were removed by hand-searching in the field, the collar was placed into the hole and backfilled with this root-free soil. The collars were allowed to stabilise for eight weeks before the data collection started. In previous studies that use the root removal method, fluxes have been shown to stabilise in under one week (Edwards, 1991; Sapronov & Kuzyakov, 2007). We also conducted a separate experiment to evaluate the disturbance caused by the handling of the soil when removing the roots (File S1). Fluxes did not differ between the handled soil and undisturbed control treatments ($F_{1,151} = 0.2779$, $p = 0.5989$).

Soil respiration was measured every four to 6 weeks, with some occasional longer gaps. The data were collected in 2008–2010 in Lambir, in 2011–2017 in SAFE and in Maliau, and in 2015–2017 in Danum. We used an EGM-4 portable infrared gas analyser (IRGA) and a cylindrical SRC-1 soil respiration chamber (both from PP Systems) of 10.0 cm diameter and 15.0 cm height. A custom-made adapter ring of 3.5 cm height and 11 cm diameter was fitted to the chamber, which matched the diameter of the collars and allowed an air-tight seal of the measurement system (Marthews et al., 2014). The chamber was equipped with a fan to mix the headspace air. Air was circulated with flow rate of 350 ml min^{-1} through the IRGA inlet and outlet ports via 1/8'' tubing. Following a five-second stabilisation period after the chamber placement, CO_2 concentration in the chamber headspace was automatically recorded for 124 s.

2.3 | Calculation of total and component respiration estimates

CO_2 flux was calculated from the change in CO_2 concentration in the chamber headspace as a function of time by fitting a least squares linear regression. The slope of the regression was used as an estimate for the flux. The slope was converted to mass by applying the ideal gas law. The raw data of the SAF, DAN and MLA plots are open access (Riutta et al., 2021).

The flux data distribution was skewed to the right and followed a log-normal distribution (Figure S2.1). Therefore, the values were log-transformed for outlier detection. The log-transformed flux values that were smaller or larger than two standard deviations of the mean were flagged as potential outliers and checked. To be removed from the dataset, the data point had to be an outlier in comparison to both the other collars in the same plot on the same day and the time series of that particular collar. This was to ensure that hotspots or cold spots and atypical days were retained in the dataset and only erroneous measurements removed.

From the partitioned respiration treatment, we calculated estimates for litter layer, root +root turnover, mycorrhizal, and SOM respiration at each partitioned respiration cluster ($n = 4$ per plot), after preforming the outlier removal.

Litter layer respiration was estimated as the mean of (i) Collar C1 – Collar S1, (ii) Collar C2 – Collar S2, and (iii) Collar C3 – Collar S3 (Figure 1).
Root + root turnover respiration was estimated as the mean of (i) Collar C1 – Collar C2 and (ii) Collar S1 – Collar S2.
Mycorrhizal respiration was estimated as the mean of (i) Collar C2 – Collar C3 and (ii) Collar S2 – Collar S3.
Soil organic matter respiration from the SOM pool was given the value of Collar S3.

Because of the methodology, the litter and root exclusion collars do not receive new inputs of litter or root debris. We assume these fresh inputs would constitute the fast SOM pool (<1 year residence

time, sensu Trumbore, 2000), thus, our SOM respiration estimate represents the respiration of older carbon, fixed ≥1 year ago. The respiration of the labile SOM carbon derived from recent litter and root debris is measured together with litter respiration and root respiration. We do not attempt to separate the 'pure' litter respiration and the litter-derived labile SOM respiration. We do, however, attempt to separate the respiration of living and dead roots. To estimate the respiration derived from the newly dead roots we estimated the inputs of fine and coarse root necromass into the soil using data on root NPP and stocks (Table 3; Kho et al., 2013; Riutta et al., 2018). In old-growth plots, where the biomass stock is in equilibrium, we assumed that the annual fine and coarse root NPP was equal to the annual root mortality. In logged plots, on the other hand, the biomass is increasing, so the disequilibrium between productivity and mortality had to be taken into account. Therefore, we subtracted the mean annual change in fine and coarse root stock from the fine and coarse root NPP, and used this difference as an estimate for the annual root mortality in logged forests. In both forest types, some

proportion of root debris inputs was assumed to be respired within a year ('root turnover respiration'), while the rest would become part of the SOM pool. Based on a decomposition study in Lambir (in the same forest site as our plots LAM-06 and LAM-07), 31% of fine and 49% of coarse newly-dead root mass decays within one year (Ohashi et al., 2019). We multiplied our root necromass input estimates by these proportions to estimate the root turnover respiration. We then estimated living root respiration ('autotrophic', although strictly speaking also includes priming effect of roots on heterotrophic soil respiration) by subtracting the estimated root turnover respiration from the measured root +root turnover respiration. The root turnover respiration estimate was added to the SOM respiration originating from the ≥1-year old soil C pool, to get an estimate of the total SOM respiration. Because of several assumptions in these calculations, we assigned a ±50% uncertainty to the root turnover respiration estimate. For other calculated terms, which were combinations of several measured variables, we estimated the propagated error using standard rules of quadrature (Hughes & Hase, 2010).

TABLE 3 Summary of the auxiliary data for constructing below-ground carbon budget

Variable	Method	Frequency	Spatial replication per plot	References
Soil carbon stock	Soil carbon content and bulk density	Once	3	[a]
Litterfall	Litter traps, collected every 14–30 days	20–100 collection dates per plot, average value used	25	[b,c]
Leaf herbivory	A product of litterfall and herbivory rate measured from leaf photos from litter traps	Litterfall as above; herbivory rate measured in one campaign	25	[b,d]
Canopy NPP, corrected for herbivory	Sum of litterfall and herbivory	Once	25	[b,c,d]
Litter stock	Quadrats of 50 cm × 50 cm	Once	5	
Canopy stock	A product of LAI derived from Li-dar and leaf mass per area derived from leaf traits campaign	Once	Plot-level[1]	[b,d,e]
Woody NPP (stem and coarse roots)	Repeated tree censuses, allometric relationships to estimate above-ground and coarse root biomass from diameter and height	2–4 censuses per plot, average value used	Sum of stems >10 cm diameter within each subplot (25)	[b,c]
Fine root NPP	In-growth cores	5–50 collection dates per plot, average value used	16 (9 in LAM-06 and LAM-07)	[b,c]
Coarse root stock	Tree census, allometric relationship to estimate coarse root biomass from diameter	Once	Sum of >10 cm diameter within each subplot (25)	[b,c,f]
Fine root stock	In-growth cores	1–5 collection dates per plot, average value used	16 (9 in LAM-06 and LAM-07)	[b,c]

Abbreviation: NPP, net primary productivity.

[1]Li-dar-derived leaf area index (LAI) estimate not available for LAM-06 and LAM-07, LAI estimated from hemispherical photos and correction factor applied based on the Li-dar LAI to hemispherical photo LAI ratio in the other old-growth plots.

[a]Quesada et al. (2010), http://www.rainfor.org/en/manuals/in-the-field.

[b]Kho et al. (2013).

[c]Riutta et al. (2018).

[d]Both et al. (2019).

[e]Milodowski et al. (in press).

[f]Niiyama et al. (2010).

2.4 | Constructing a below-ground carbon budget

We constructed a detailed below-ground carbon budget by combining the respiration estimates with the previously published estimates of organic matter stocks and fluxes into the soil (Kho et al., 2013; Riutta et al., 2018), collected over the same time period as the soil respiration data. These methods are summarised in Table 3. For the organic inputs derived from the canopy, we used estimates of canopy NPP, canopy C stock, herbivory and frassfall, litterfall, and litter C stock. For fine and coarse root inputs, we used estimates of fine and coarse root NPP and C stock. In old-growth forests, where the above-ground woody carbon stock was in equilibrium, we assumed that living root C stock was also in equilibrium and root mortality was equal to root NPP. In logged forests, with a growing above-ground woody C stock, we estimated root mortality by subtracting the change in root stock from root NPP (separately for fine and coarse roots). Dead root C pool was not quantified, but we quantified the inputs into (root mortality) and outflows from (root debris decay) that pool. The root debris decay rates were based on the estimates by Ohashi et al. (2019), as described in the previous section.

We estimated the root exudation rate from literature as (i) 6% of total NPP (Finzi et al., 2015), (ii) 59% of root NPP (Abramoff & Finzi, 2016), (iii) 37% of root respiration (calculated from data in Sun et al., 2020), (iv) 0.63 g exudation per g of fine root stock per year (Sun et al., 2017), and (v) 0.50 and 0.18 g exudation per g of arbuscular and ectomycorrhizal host species fine root stock per year, respectively (Sun et al., 2020), weighted by their basal area proportions. The five approaches yielded reasonably similar estimates (0.96, 2.25, 0.80, 2.64, and 1.68 Mg C ha^{-1} year^{-1} for logged forests, and 0.81, 1.36, 1.14, 2.48 and 1.25 Mg C ha^{-1} year^{-1} for old-growth forests). We used the mean of these estimates (1.66 and 1.41 Mg C ha^{-1} for logged and old-growth forests, respectively) in our soil carbon budget, with ±100% uncertainty.

We estimated frassfall as (i) 56% of canopy herbivory (Castagneyrol et al., 2018) and (ii) 2.2% of litterfall (Schowalter et al., 2011). The resulting estimates were 0.19 and 0.07 Mg C ha^{-1} year^{-1} for logged forests and 0.25 and 0.11 Mg C ha^{-1} year^{-1} for old-growth forests. We used the mean of these estimates (0.13 and 0.18 Mg C ha^{-1} year^{-1} for logged and old-growth forests, respectively), with ±100% uncertainty.

Carbon losses by leaching of dissolved organic and inorganic carbon (DOC and DIC) were not included in our soil carbon budget. We compared our soil respiration estimates to reported post-logging DOC and DIC fluxes to assess their importance in the soil carbon budget (see Section 4).

2.5 | Statistical analyses

This paper focused on the spatial variation (within and among plots, and between old-growth and logged forests) rather than on temporal trends. Therefore, all temporal replicates of each soil respiration measurement point were pooled to derive a mean value (untransformed data) for that point, and estimate for each one-hectare plot was calculated as the mean of the spatial replicates (for data distributions see Figure S2.2).

To test whether both total and component respiration rates differed between the logged and old-growth forest plots, we used t-tests, where each one-hectare plot formed one replicate. To test whether proportional contributions to total, such as the relative contribution of soil respiration components (root, mycorrhiza, litter and SOM) to total soil respiration, and the relative contribution of litter and root inputs to total necromass pool, differed between the forest types, we used linear models for compositional data (Pawlowsky-Glahn & Buccianti, 2011), in the R package 'compositions' (van der Boogaart et al., 2014; van der Boogaart, 2008).

To test whether carbon inputs into and respiration rates from different pools (e.g. litterfall and litter respiration) were in equilibrium, we used a paired t-test, where the carbon input and respiration in each plot formed a pair. We further quantified the uncertainty in the soil carbon equilibrium estimate (whether SOM respiration rate is equal to the organic carbon inputs into the soil; Hypothesis 5) with bootstrap simulations for each individual 1-ha plot to create 90% confidence intervals for the estimates. We used the empirical data of total soil respiration, litterfall, and fine and coarse root mortality (n = 25 per plot for each variable). We created 1000 bootstrapped datasets (the size of which is 25) for each variable, by plot. To simulate the proportion of SOM respiration out of total respiration, and the proportion of litterfall, and fine and coarse root debris that would become part of the SOM pool (litter and root debris inputs that were not respired within 1 year), we generated a beta distribution for each of these proportional variables, the parameters of which were calculated using the observed mean proportions by plot and assuming that standard deviation was 50% of the mean.

The estimates of the SOM respiration, and litter, fine and coarse root debris inputs into SOM were then calculated by multiplying the 1000 bootstrapped empirical estimates of total soil respiration, litterfall, and fine and coarse root mortality by the proportions drawn randomly from the corresponding beta distributions. Total organic inputs into SOM was the sum of litter, and fine and coarse root debris inputs. The difference between total inputs into SOM and SOM respiration determined whether the SOM pool was in equilibrium. The results were assessed by individual 1 ha plots (1000 values per plot) and by calculating the mean by forest type (logged forest, n = 5 plots and old-growth forest, n = 6 plots) 1000 times from the bootstrapped plot-level data. All statistical analyses were done in R (R Core Team, 2019).

We also carried out a supplementary analysis on which factors controlled spatial variation in soil respiration at the scale of the individual respiration collar and at the scale of the 1-ha plot. The methods and results are described in File S3.

3 | RESULTS

3.1 | Total and component respiration in logged and old-growth forests

Logged forests had 13% higher total soil respiration rate than old-growth forests ($t_{6.44}$ = 2.615, p = 0.037), 14.3 ± 0.23 and 12.7 ± 0.60 Mg C ha^{-1} year^{-1}, respectively (Figure 2). The within-plot spatial variation was higher in logged forests (within-plot coefficient of variation 25%–54% in logged plots and 16%–40% in old-growth plots) but the between-plot variation was higher in old-growth forests (CV of 3.6% for logged plots and 12% for old-growth plots).

Total respiration was first partitioned into components that can be directly estimated by comparing the different collar types (Figure 1), namely litter respiration, root + root turnover respiration, mycorrhizal respiration, and SOM respiration (Figure 3). Measured SOM respiration was 22% higher ($t_{6.44}$ = 2.990, p = 0.015) in logged forests than in old-growth forests, 7.8 ± 0.32 and 6.3 ± 0.39 Mg C ha^{-1} year^{-1}, respectively. Litter respiration ($t_{7.93}$ = 1.760, p = 0.015), root + root turnover respiration ($t_{4.14}$ = −0.038, p = 0.9714), and mycorrhizal respiration ($t_{9.00}$ = −1.032, p = 0.329) did not differ between forest types. We further partitioned the data into root (autotrophic) and root turnover (heterotrophic) respiration (Figure 3). The new estimate for root respiration (1.33 ± 0.71 and
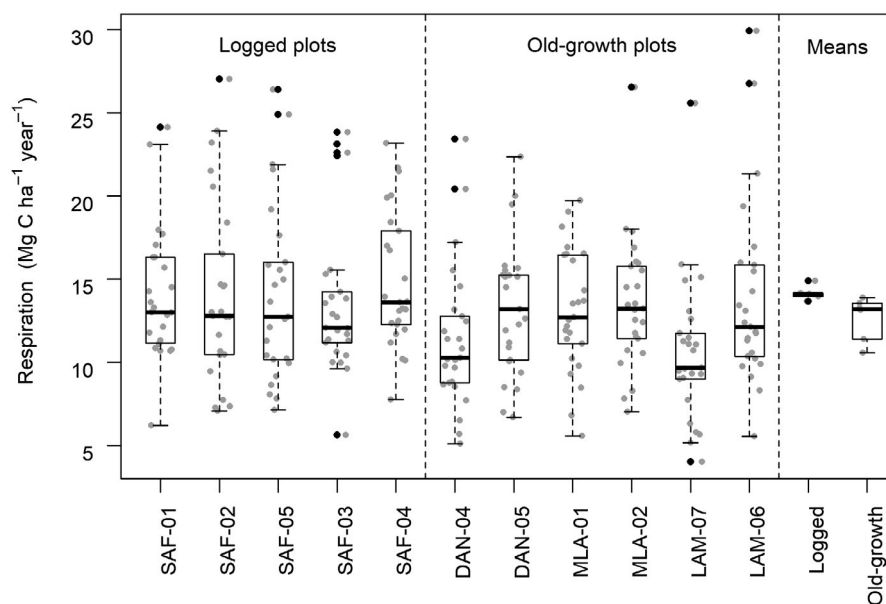
FIGURE 2 Total soil respiration in the individual plots and by forest type (logged and old-growth; significantly different, $t_{6.44}$ = 2.615, p = 0.037). For individual plots, the data represents the temporally averaged values of each spatial replicate (grey dots, n = 25 per plot). For the forest types, the data represents the variation among individual plots (grey dots, n = 5 in logged forest, n = 6 in old-growth forest)
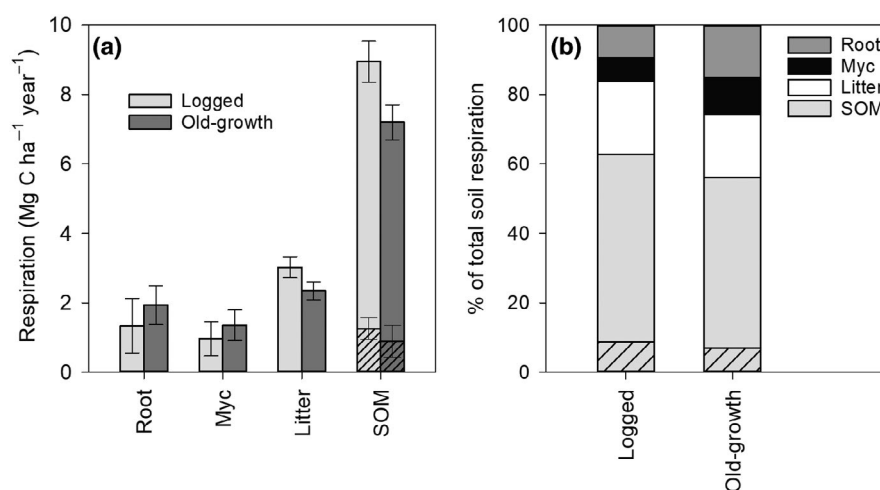

FIGURE 3 Soil respiration partitioned into root, mycorrhizal (Myc), litter, and soil organic matter (SOM) respiration in logged and old-growth forest. (a) Mean ± 1 SE for each respiration component by forest type (only SOM respiration significantly different, $t_{6.44}$ = 2.990, p = 0.015) and (b) the proportional contribution of the components to total soil respiration (significantly different between forest types, $F_{1,9}$ = 32.47, p < 0.001). Note that root and litter respiration also include their priming effects. The initial measured root respiration also included root turnover respiration, which was subtracted (see text) and added to SOM respiration (its contribution to SOM shown as hatched bars)

1.72 ± 0.59 Mg C ha^{-1} year^{-1} in logged and old-growth forests, respectively), was approximately 54% (logged) and 34% (old-growth) lower after subtracting the estimate for the root turnover respiration (1.25 ± 0.45 and 0.89 ± 0.32 Mg C ha^{-1} year^{-1} in logged and old-growth forests, respectively). Neither the revised root respiration estimate ($t_{4.27}$ = −0.609, p = 0.574) nor the root turnover respiration estimate ($t_{4.58}$ = 1.431, p = 0.217) differed between the forest types.

Heterotrophic respiration, consisting of litter, root turnover and SOM respiration, was higher in logged forests than in old-growth forests ($t_{8.70}$ = 4.62, p = 0.001; Figure 3). In both forest types, heterotrophic respiration dominated over autotrophic respiration, accounting for 85 ± 4.7% and 76 ± 5.7% of the total respiration in logged and old-growth forests, respectively (difference of the proportions between forest types marginally significant, $F_{1,9}$ = 4.73, p = 0.058). The overall relative contribution of the respiration components, namely
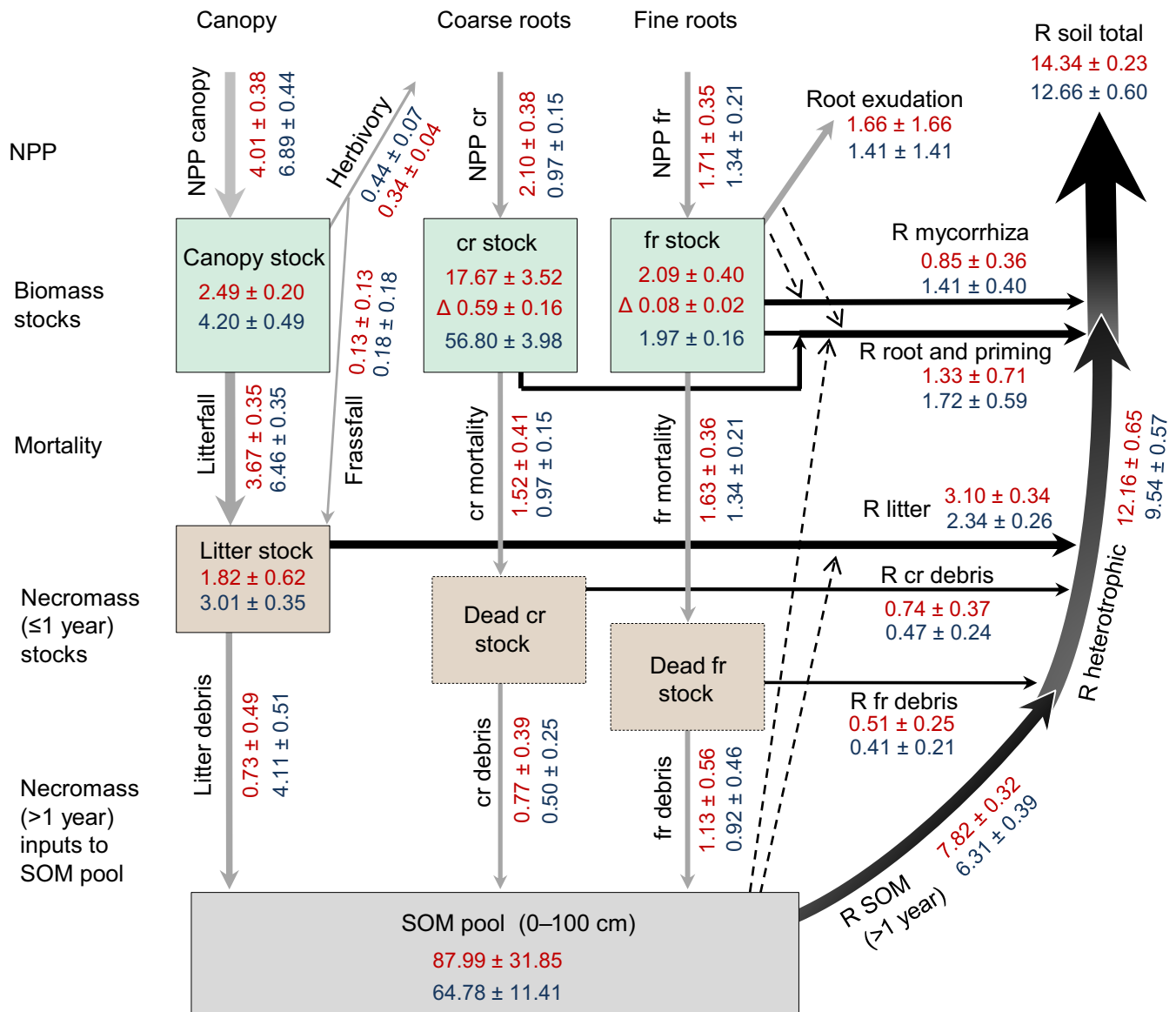
FIGURE 4 Diagram of the stocks (boxes) and fluxes (arrows) that contribute to total soil respiration. The values are mean ± 1 SE in logged (red, n = 5) and old-growth (blue, n = 6) plots. Black arrows denote the respiration components (CO_2 fluxes) and the grey arrows denote the flows of organic carbon. The dotted black arrows represent the priming effect, where the presence of litter or roots increases the respiration from the SOM (soil organic matter) pool. Priming effect was not separately quantified in this study but included as part of the litter or root respiration. The fr (fine root) and cr (coarse root) debris respiration refers to the respiration of newly dead (<1 year) roots. The inputs into the SOM pool refer to debris greater than 1 year of age, i.e. the litter and root debris that was not respired from the litter layer or from the dead root stock within 1 year. Similarly, the SOM respiration does not include the respiration of more recent than one-year old matter. In logged forest, root biomass stocks are not in equilibrium, thus the estimate of the annual change is included (Δ stock). Coarse and fine root necromass stocks were not quantified. The units in the figure are Mg C ha^{-1} and Mg C ha^{-1} year^{-1} for stocks and fluxes, respectively. cr, coarse roots; fr, fine roots; NPP, net primary productivity; R, respiration; SOM, soil organic matter

litter (22 ± 2.4% in logged forests; 18 ± 2.2% in old-growth forests), root (9.1 ± 4.9%; 14 ± 4.7%), mycorrhizal (5.9 ± 1.1%; 11 ± 3.2%), root turnover (8.7 ± 3.2%; 7.0 ± 2.6%) and SOM (55 ± 2.4%; 50 ± 3.9%) respiration, differed between forest types ($F_{1,9}$ = 32.47, p < 0.001).

Heterotrophic respiration from the fast carbon pools, namely from the litter layer and from the newly (<1 year) dead fine and coarse roots ('root turnover respiration') was higher in logged forests ($t_{8.96}$ = 3.44, p = 0.007), totalling 4.35 ± 0.56 and 3.23 ± 0.41 Mg C ha^{-1} year^{-1} in logged and old-growth forests, respectively (Figures 3 and 4). The relative contribution of these fast pools and the SOM pool to heterotrophic respiration was similar in both forest types (34 ± 4.6% of heterotrophic respiration from fast pool and 66 ± 5.7% from SOM pool in logged forests, 36 ± 4.7% from fast pool and 64 ± 4.3% from SOM pool in old-growth forests; $F_{1,9}$ = 4636, p = 0.513).

3.2 | Below-ground carbon budget

Using previously published data on carbon stocks, productivity and turnover (Kho et al., 2013; Riutta et al., 2018), we compared the carbon inflows into and outflows from the various carbon pools in the form of organic carbon or CO_2 (Figure 4) including a careful estimation of compounding errors. Figure 4 shows the means by forest type, plot level values are available in Riutta et al. (2021).

Total necromass inputs in the form of litterfall, and fine and coarse root mortality, were similar between forest types ($t_{6.17}$ = −1.90, p = 0.104), but the proportional contribution of inputs from litterfall (73 ± 6.4% in old-growth forests, 55 ± 8.9% in logged forests) and from root mortality (27 ± 14% in old-growth forests, 45 ± 11% in logged forests) differed ($F_{1,9}$ = 16.24, p = 0.003; Figure 4). In old-growth forests, litterfall exceeded litter layer respiration (t_5 = 7.04, p < 0.001), with only 36 ± 4.8% of the annual litterfall released to the atmosphere directly as litter respiration. In logged forests, most of the litterfall (84 ± 12%) was respired directly from the litter layer, with no difference between annual litterfall and litter layer respiration (t_4 = 1.02, p = 0.184). Heterotrophic respiration originating from root debris was not directly measured but was estimated as 31% (fine) and 49% (coarse) of root mortality in both forest types (Ohashi et al., 2019).

We assumed that the fraction of the litter or root debris inputs which was not respired directly from that pool (from litter layer or dead root stock) became part of the SOM pool (Figure 4). Thus, in old-growth forests, 62 ± 8.8% of the litterfall entered the SOM pool, while in logged forests the litter inputs to the SOM pool were smaller ($t_{8.99}$ = −4.39, p = 0.002), only 17 ± 11% of the litterfall. The inputs of root debris into the SOM pool were similar in both forest types ($t_{4.81}$ = 1.22, p = 0.280). The sum of all carbon inputs into the SOM pool were higher ($t_{7.58}$ = −2.72, p = 0.028) in old-growth forests (5.53 ± 0.73 Mg C ha^{-1} year^{-1}) than in logged forests (2.63 ± 0.84 Mg C ha^{-1} year^{-1}), due to the higher litter inputs. In old-growth forests, the sum of inputs into the SOM pool did not differ (t_5 = −0.96, p = 0.381) from the SOM respiration rate (6.31 ± 0.39 Mg C ha^{-1} year^{-1}), indicating that the soil carbon pool

was in equilibrium. In logged forests, on the other hand, the sum of the inputs into SOM pool was smaller (t_4 = −5.22, p = 0.006) than SOM respiration rate (7.82 ± 0.32 Mg C ha^{-1} year^{-1}), indicating net loss of soil carbon. Plot-level bootstrap simulations (1000 replicates) of the difference between inputs to SOM and SOM respiration, accounting for uncertainty in the estimates, confirmed the parametric tests: in old-growth forests 90% confidence intervals included zero, both for the mean of the plots and within each plot, while in logged forests the differences was negative (loss of soil carbon) in all cases (Figure 5; Figure S4.1).

Root carbon use efficiency (CUE), which equals root NPP/(root NPP + root respiration), was similar ($t_{5.42}$ = 2.20, p = 0.075) in old-growth forests (0.57 ± 0.23) and logged forests (0.76 ± 0.46). When mycorrhizal respiration was considered as part of the root carbon expenditure, CUE was lower ($t_{7.32}$ = −2.87, p = 0.023) in old-growth forests (0.44 ± 0.22) than in logged forests (0.64 ± 0.47).
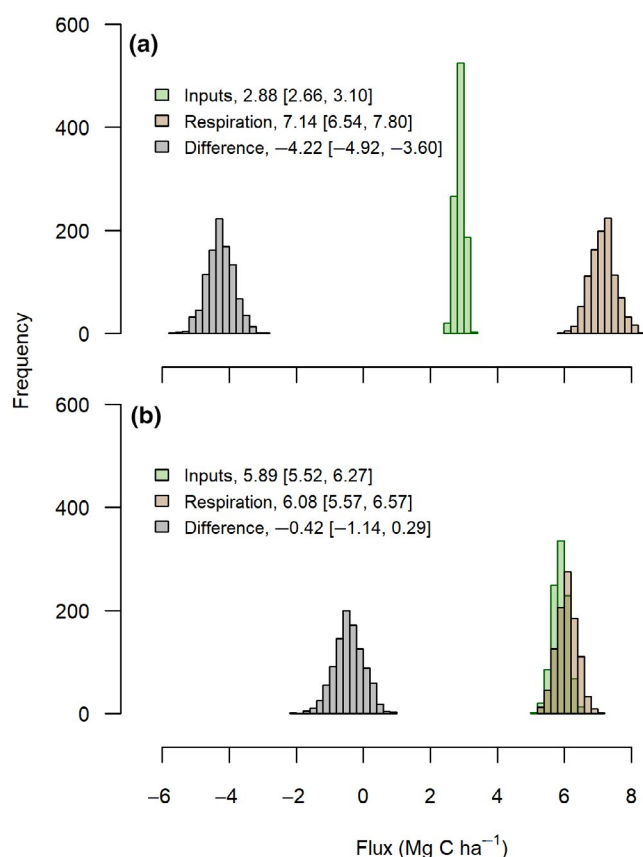

FIGURE 5 Frequency histogram of the 1000 bootstrapped mean estimates of organic carbon inputs into the soil organic matter (SOM) from litter layer and root turnover (green bars), soil organic matter respiration (brown bars), and the difference between the inputs and SOM respiration (grey bars) in (a) logged forest and (b) old-growth forest. The values in the figure legends denote the mean and the 90% confidence intervals. The data for each plot (n = 5 for logged forest, n = 6 for old-growth forest, see Figure S4.1) was bootstrapped 1000 times, and the mean by forest type was calculated for each run. SOM pool is in equilibrium if the difference between the inputs and SOM respiration equals zero. SOM pool is losing carbon if SOM respiration exceeds the inputs

4 | DISCUSSION

4.1 | Total soil respiration is higher in logged forests due to higher heterotrophic respiration

Total soil respiration in our study (14.3 ± 0.23 and 12.7 ± 0.60 Mg C ha^{-1} year^{-1} in logged and old-growth forests, respectively) is slightly below the average (16.8 Mg C ha^{-1} year^{-1}) but well in line with the estimates from other tropical and sub-tropical sites summarised by Rubio and Detto (2017), which range from 6.04 Mg C ha^{-1} year^{-1} in old-growth evergreen monsoon forest in China to 43.52 Mg C ha^{-1} year^{-1} in subtropical wet forest in Puerto Rico. In accordance with our hypothesis, logged forests had a higher total respiration rate than old-growth forests, due to the higher heterotrophic respiration. This, in turn, was mainly due to the higher SOM respiration. There was some indication that litter respiration was higher as well, but the difference between the forest types was not significant. Previous studies on the effect of selective logging on total soil respiration in tropical forests range from negative (Mori et al., 2017), neutral (Adachi et al., 2006; Ishizuka et al., 2005; Takada et al., 2015; Yashiro et al., 2008) to positive (Saner et al., 2012). Similarly inconsistent results have been reported on the effect of silvicultural thinning on soil respiration in temperate and boreal zones (e.g. Concilio et al., 2005; Epron et al., 2004; Saynes et al., 2012; Son et al., 2004; Tang et al., 2005). Based on a meta-analysis of 53 publications, soil respiration is higher in early stages (≤2 years after thinning) but not in later stages of recovery (Zhang et al., 2018), but the site-specific variation is large. Heterotrophic respiration, or its proportional contribution to total respiration, typically increases after thinning (Cheng et al., 2015; Lei et al., 2018; Templeton et al., 2015), indicating that reduction in stand density and basal area cause a shift from autotrophic towards heterotrophic respiration.

Higher SOM respiration may be the result from both decaying coarse roots and other logging residue originating from the time of the logging event and higher inputs of more recently dead roots and above-ground parts arising from the higher mortality rate in logged forests: twenty stems >10 cm DBH ha^{-1} year^{-1} in the logged plots compared with two stems >10 cm DBH ha^{-1} year^{-1} in the old-growth plots (T. Riutta et al., unpublished data; see also Pearson et al., 2014; Shenkin et al., 2015). In addition to the decomposition of the recent organic inputs, the decomposition of the old soil carbon may also be accelerated following soil disturbance, due to nitrogen release and soil aeration (Janssens et al., 2001). In our study, the difference in SOM respiration was fairly modest (22% or 1.38 ± 0.54 Mg C ha^{-1} year^{-1} higher in logged forests compared with old-growth forests). Nevertheless, considering that in South East Asia and in other tropical regions the area of human disturbed forests now exceeds that of intact forests (Bryan et al., 2013; Potapov et al., 2008), even small differences between forest types may have considerable effects on regional or biome-scale carbon budgets.

We did not observe differences in root respiration between the forest types, which also agreed with our hypothesis. The hypothesis was based on an earlier study on the same plots, which demonstrated similar total NPP and root NPP in logged and old-growth forests (Riutta et al., 2018). Because autotrophic respiration is strongly linked to productivity (Hogberg et al., 2001; Kuzyakov, 2006), we expected root respiration also to be similar. It is to be noted, however, that both fine root NPP and allocation of total NPP to fine roots (approximately 11%) in these sites (Riutta et al., 2018), and in Asia in general (Malhi et al., 2011 and references therein), is very low compared to tropical forests worldwide, therefore, root respiration was also expected to be small. Consequently, the estimate of the contribution of root respiration to total soil respiration in our study has a relatively low signal to noise ratio.

We acknowledge the methodological shortcoming in our partitioned respiration measurements, wherein the root exclusion treatment excludes not only living roots, but also new inputs of dead roots into the system, thus representing respiration in the absence of living and recently died roots. Consequently, the initial estimate for root respiration, if calculated simply as the difference between the root inclusion and root exclusion treatments, includes both autotrophic respiration of living roots and heterotrophic respiration originating from root turnover. We attempted to separate the root turnover respiration from root respiration, which reduced our root respiration estimate by 34% in old-growth forests and by 54% in logged forests, although due to several assumptions involved, we assigned a large, arbitrary ±50% uncertainty to the root turnover respiration estimate. The root turnover respiration estimate was added to the heterotrophic respiration estimate. Due to this correction for the root turnover respiration, we report a larger heterotrophic proportion (85 ± 4.7% and 76 ± 5.7% with and without root turnover correction in logged forests, 76 ± 3.6% and 68 ± 5.2% in old-growth forests) than previous studies in tropical forests. A meta-analysis by Subke et al. (2006) report a tropical average of 48% for the heterotrophic respiration proportion, with 95% confidence intervals of 38% and 58%. However, in a Dipterocarp-dominated dry forest in Thailand, heterotrophic respiration accounted for 66 ± 4% of the total soil respiration, not corrected for the root turnover term (Hanpattanakit et al., 2015), which is in perfect agreement with our uncorrected estimate for old-growth forests, and reflects the low carbon allocation to roots in Asian sites (Malhi et al., 2011). While the methodological limitation of root removal or trenching-based root respiration estimates containing heterotrophic root turnover respiration has been acknowledged in other studies (e.g. Hanson et al., 2000; Subke et al., 2006), we are not aware of this typically being corrected for.

Contrary to our hypothesis, mycorrhizal respiration was similar in both forest types (slightly, but not significantly lower in logged forests), despite the lower basal area of the ectomycorrhizal dipterocarp trees in the logged plots. There was some indication that mycorrhizal respiration was reduced in logged plots, but due to the low signal to noise ratio the difference was not significant. Microbial studies in the same sites showed that mycelial hyphal productivity was not affected by logging, suggesting that the fungal community functioning may be relatively resilient (Robinson et al., 2020).

Ectomycorrhizal fungal richness, abundance and diversity, on the other hand, was significantly reduced by logging, while arbuscular mycorrhizal fungal community did not differ between the forest types (D. Elias et al., unpublished manuscript).

4.2 | SOM pool is in disequilibrium in logged forest

By combining soil respiration data with NPP estimates, we were able to quantify the inputs of organic carbon into and the outflows of organic carbon or CO_2 from the different carbon pools. Based on our estimates, SOM respiration in logged forests exceeds the carbon inputs from litter and root debris into soil (90% confidence intervals did not include zero in any of the logged plots; Figure S4.1). This indicates that logged forest soil is losing carbon at a rate of 5.18 ± 1.11 Mg C ha^{-1} year^{-1}, which is 5.9 ± 4.0% per year of the mean logged forest soil carbon stock. This estimated 5.9% loss is very similar to an earlier estimate of 5% in a simulation study on the impacts of logging in Borneo (Pinard & Cropper, 2000). The most recent meta-analysis on the effect of harvesting on forest soil C stocks, examining 945 studies, reported a decrease of 11%, with the greatest losses occurring in the O horizon (30% loss) and deep soil (60–100 cm, 18% loss; James & Harrison, 2016), which is consistent with our findings that logged plots are losing soil carbon.

The source of this carbon could be either the logging legacy carbon, which is being released, or the loss of the old soil carbon, or a combination of both. There are no direct measurements of the amount of the logging residue at the time of logging or its decay available from our site, but we created a simple model of probable inputs and decay rates (File S5). Even with large uncertainties in the model parameter values, the simulation results suggest that ten years after the logging >90% (with 90% confidence intervals of 73% and 100%) of the logging residue has decayed and the remaining fraction is probably contributing less than 2% to the heterotrophic soil respiration. Therefore, this points towards the source of the current excess respired carbon being the current higher tree mortality (mostly short-lived pioneers that colonised the logging gaps) and the loss of old soil carbon. If we assume a simple exponential decay model, with $Stock_t = Stock_0 \times \exp(-0.059t)$, where $Stock_t$ is the carbon stock at time t, $Stock_0$ is the current soil carbon pool, t is time in years and the exponent 0.059 is the proportion of the soil C stock lost annually, it will take an average of five more years (thus, in total approximately 15 years since logging) for mean logged forest soil carbon pool to reach the mean old-growth forest soil carbon pool. This assessment of the fate of the soil carbon stock is, however, only a ballpark estimate, due to the large variability in the current logged forest soil carbon stock, uncertainty in the soil carbon loss rate, and uncertainty in the assumption that the carbon loss rate is constant over time and can be described with a single exponential model. Previous studies on sites of 35%–100% of biomass removed show that soil carbon stocks are highest immediately after logging due to inputs from logging debris and dead roots, but then drop below pre-logging levels, with the decrease continuing for decades or even centuries (Dean et al., 2017; Diochon et al., 2009; Gillman et al., 1985; Kawaguchi & Yoda, 1985). In contrast to logged forests, old-growth forest soil carbon inputs, on the other hand, very closely matched the SOM respiration in our study (90% confidence intervals included zero in all old-growth plots; Figure S4.1), indicating that the old-growth forest soil C stock is in equilibrium. This finding of the equilibrium in old-growth forests also increases confidence in our overall approach.

According to our estimates, annual litterfall considerably exceeds annual respiration from the litter layer in old-growth forests, indicating that a large fraction (62 ± 3.0%) of the litterfall becomes part of the SOM pool, presumably part of the active SOM pool (sensu Trumbore et al., 1995, turnover time of 1–3 years). In logged forests, on the other hand, comparison between litterfall and litter layer respiration indicated that only 17 ± 10% of the annual litterfall becomes part of the SOM pool. Our results suggest that litter-derived SOM contributes more to SOM respiration in old-growth forests than in logged forests, while root debris inputs and old soil organic carbon are the main sources of the SOM respiration in logged forests.

Our below-ground carbon budget did not include carbon losses from the leaching of DOC and DIC. In mineral soil forest ecosystems, these fluxes are typically small, approximately 2% of the annual soil respiration and <1% of the annual net ecosystem carbon balance (Gielen et al., 2011; Kindler et al., 2011; Peichl et al., 2014). Logging operations result in a short-term pulse of leaching from the organic horizon (Kreutzweiser et al., 2008; Laudon et al., 2009; Morris, 2009; Piirainen et al., 2002), but a large part of these outputs are retained in the mineral soil horizons (Fujii et al., 2009; Piirainen et al., 2002). In the medium term, DOC fluxes may be lower in logged forests than in old-growth forests (Lajtha & Jones, 2018; Morris, 2009), although this depends on the quantity of the remaining woody debris after logging (Lajtha & Jones, 2018). Therefore, the sites in our study probably lost some soil carbon via leaching at the time of logging, which we did not account for, but DOC and DIC fluxes were not likely to constitute a large part of the soil carbon budget, or to differ considerably between logged and old-growth plots during the data collection period.

In summary, these are, to the best of our knowledge, the first estimates for component-scale soil respiration from logged tropical forests, and the first full description of the below-ground carbon cycle. Our results show that logging increases heterotrophic respiration, mainly from the soil organic carbon pool. Comparison between organic carbon inputs into the soil and carbon loss via soil respiration indicates that while old-growth forest soils are in equilibrium, logged forest soils are losing carbon. Carbon losses from soil may offset the carbon uptake of the recovering tree stands. Given that the area of human-disturbed tropical forests now exceeds that of intact tropical forests and that below-ground processes constitute one of the largest uncertainties in monitoring emissions from forest degradation, quantitative estimates and process-level understanding of the soil carbon cycle in disturbed forests are crucial.

DATA AVAILABILITY STATEMENT

Soil respiration data from the SAF-01, SAF-02, SAF-03, SAF-04, SAF-05, DAN-04, DAN-05, MLA-01 and MLA-02 plots in will be openly available in Zenodo, at https://doi.org/10.5281/zenodo.3266770. Soil respiration data from the LAM-06 and LAM-07, and the auxiliary data from all the plots will be available from the corresponding author upon reasonable request. Plot-level estimates of the components of the below-ground carbon cycle presented in Figure 4 are available for all plots in Zenodo, at https://doi.org/10.5281/zenodo.3266770.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.