

**A spatio-temporal analysis on the regime shift of
the below-ground system in degraded logged-over
Bornean tropical rainforests**

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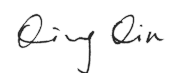
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Abstract

Carbon (C) sequestration in below-ground systems is vital for both the global carbon budget and the productivity of forest ecosystems. In humid tropical regions, high temperatures and precipitation accelerate C turnover, yet a significant portion of total C is stored in the soil, particularly in the protected pool where soil organic matter (SOM) associates with iron (Fe) and/or aluminum (Al) minerals. This association shields SOM from microbial respiration, thereby facilitating long-term soil C sequestration. However, C loss from soil has been widely observed in logged tropical forests, yet the underlying mechanisms remain unclear. This introduces uncertainty in estimating C stocks and poses challenges in comprehending C dynamics in secondary forests, which currently make up the majority of humid tropical rainforests.

This thesis aimed at providing preliminary findings that examine a hypothetical mechanism of soil C loss in degraded tropical rainforests following selective logging. The proposed mechanism involves not only a decline in litter input due to above-ground biomass (AGB) loss, but also a regime shift in soil redox states, which may destruct the association between SOM and soil minerals. Chapter 1 provides a theoretical foundation for this hypothetical mechanism through a review of how logging and degradation in tropical rainforests can disturb C and water cycling. In contrast to the common trend of natural restoration of soil C with time elapsed from logging (Covington et al., 1981), recent studies in humid tropics have identified significant and permanent change in soil C dynamics, specifically increased soil respiration probably originated from sequestered SOM (Mills et al., 2023). Conversely, the alteration of soil redox potential (Eh) has been identified as a significant environmental factor influencing mineral weathering and the subsequent destruction of mineral-organic associations. However, in-situ measurements of Eh have been scarce, and the impact of forest degradation on soil Eh remains unclear.

As such, a case study was conducted in two timber-producing forest reserves located in Malaysian Borneo, where forest patches currently exhibit a range of degradation statuses at landscape scale due to different logging histories. In Chapter 2, I studied the loss of mineral-associated OM after logging in the main rooting zone (e.g., 0–30 cm), and examined a hypothetical mechanism of SOC reduction: first, decrease in AGB limiting OM input; second, decrease in soil redox potential (Eh) leading to the reductive dissolution of short-range-ordered iron (SRO Fe) minerals that destabilize some mineral-associated OM. Thirty-five plots at different degradation levels were investigated for both above- and belowground properties. AGB and tree community composition were employed as indicators of vegetation degradation gradient; multiple physicochemical properties in top-30 cm soils were measured every 10 cm depth. I analysed the relationship between AGB and soil C with the mediator SRO Fe, and investigated the role of soil Eh in linking the changes in AGB and SRO Fe. The results revealed simultaneous decreases in AGB, SRO Fe and soil C in top-30 cm soils, and SRO Fe mediated 43% of the hypothetical causal effect of AGB on soil C in deeper (20–30 cm) soil. Soil Eh decreased with decreasing AGB in a logistic pattern, dropping to a reductive regime ($Eh^7 \leq 0.05V$) when more than half of the AGB was removed from the pristine level. Mean SRO Fe stock in the

reductive soils was significantly lower than that in the oxic soils ($E_h^7 > 0.05$ V), and the loss of SRO Fe corresponds to the decomposition of OM in 10–30 cm soils. I suggest that the reductive shift in soil is caused by the weakened evapotranspiration as destructive selective logging inflicts canopy openness and succession failure. This chapter presents the possibility that forest degradation may reduce the size of protected soil C pool resulting from the loss of soil SRO Fe minerals.

In Chapter 3, I investigated the relationship between canopy damages and topsoil (10 cm) moisture in two logged forests in Malaysian Borneo, simultaneously controlled logging intensity, time elapsed from historical logging, and spatial autocorrelation. Volumetric soil water content (VSWC), canopy height model (CHM), leaf area index (LAI), and historical logging data were collected from 84 transects placed subjectively in 15 sites exhibiting varying canopies. Canopy structure metrics (CSM) was derived from CHM and LAI within a 20-meter buffer for each transect, to which a principal component analysis (PCA) was then applied. The magnitude of canopy structural degradation was indicated by the first principal component (PC1) and analyzed for its impact on VSWC across logging periods, and contrasted with topography. Spatial autocorrelation of VSWC was examined regarding to canopy conditions. A significant increase in VSWC from $0.27 \text{ m}^3 \text{ m}^{-3}$ to over $0.4 \text{ m}^3 \text{ m}^{-3}$ after logging. The immediate increase could be a result of extracting mature individuals of late-successional species holding large biomass, while the persistent wet condition may be due to retarded biomass recovery. In the study area, canopy structure was a stronger predictor of soil moisture than topography. The spatial autocorrelation of soil moisture was significant, while the most degraded canopies presented the largest spatial extent of autocorrelation. This chapter revealed that soil wetting occurs following selective logging in humid tropical forests. This phenomenon is driven by two main factors: reduced transpiration and probably also intercepted evaporation caused by canopy loss. The effect of increased soil evaporative demand resulting from canopy opening is outweighed. Such elevation in soil moisture could disrupt carbon and nitrogen cycling through redox reactions, and its coupling with increased evaporative demand at forest floor could threaten seedling growth and therefore impede succession, which consequently put stress on the overall vulnerability of disturbed tropical rainforests.

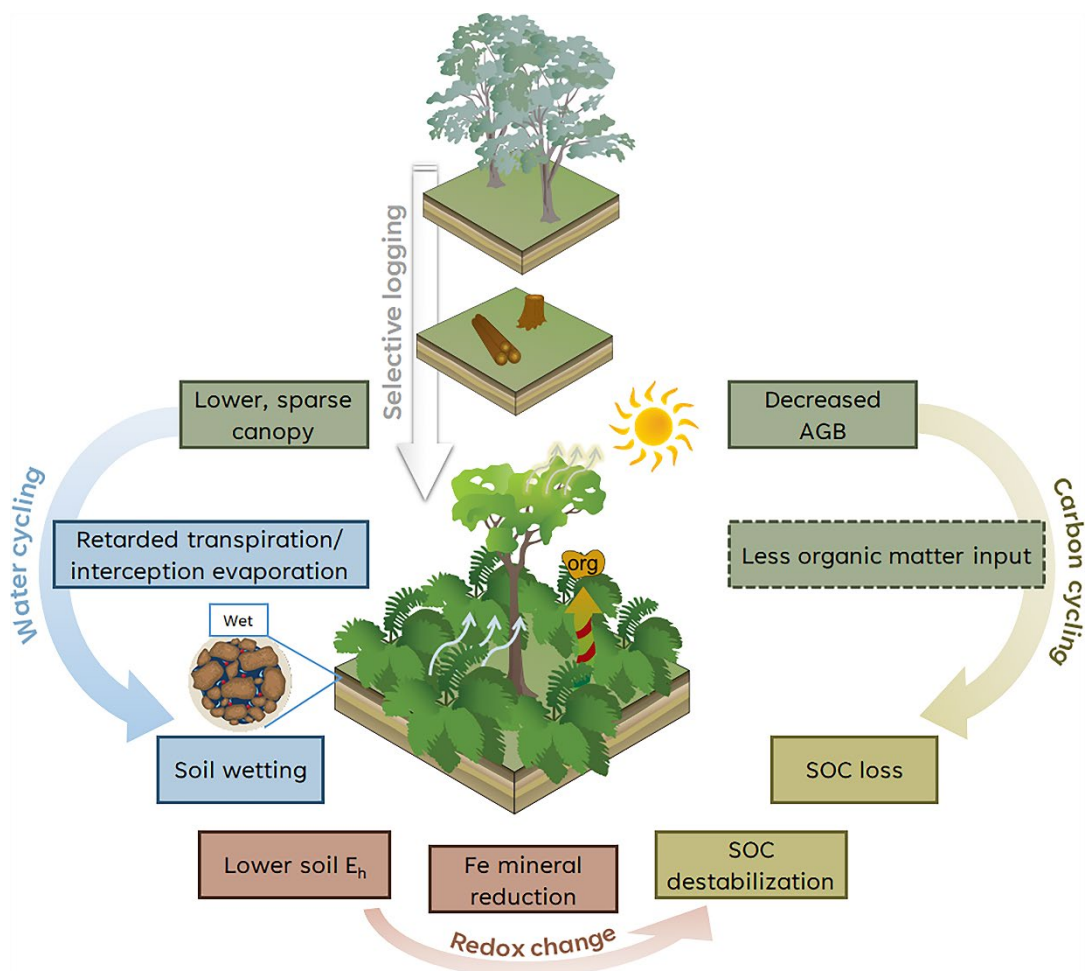
Based on these results, Chapter 4 addressed the implications of soil regime shift for sustainable forest management in timber-producing humid tropical rainforests, as well as the primary limitation of the current thesis. It was concluded that the nonlinear change of the below-ground has occurred and expanded at a spatial scale that may exceed the scale of degraded forests, and may have negative feedbacks in the above-ground regarding forest recovery. On the other hand, measurements of soil and vegetation properties have only provided snapshots of the entire environment. Also, the biotic control on Fe cycling has not been addressed in this thesis, leaving an important area for future research.

List of Abbreviations

ACME	average causal mediation effect	Fe_{dc}	dithionite-citrate extracted iron
ADE	average direct effect	Fe_o	acid-oxidate extracted iron
AIC	Akaike information criterion	ICP	inductively coupled plasma
Al	aluminum	GAM	generalized additive mode
Al_{dc}	dithionite-citrate extracted aluminum	LAI	leaf area index
Al_o	acid-oxidate extracted aluminum	N	nitrogen
AGB	above-ground biomass	NBR	normalized burn ratio
C	carbon	NDVI	normalized difference vegetation index
C/N	carbon:nitrogen ratio	nMDS	non-metric multidimensional scaling
CHM	canopy height model	Ox	acid-oxalate
CSM	canopy structural metrics	OM	organic matter
CL	conventional logging	ORP	oxidation-reduction potential
dbh	diameter at breast height	PCA	principal component analysis
DC	dithionite-citrate	RIL	reduced-impact logging
DEM	digital elevation model	SOM	soil organic matter
DTM	digital terrain model	SRO	short-range-ordered
E_h (E_h⁷)	redox potential (normalized to pH7)	TWI	topographic wetness index
ET	evapotranspiration	UAV	unmanned aerial vehicle
Fe	iron	VPD	vapor pressure deficit

Chapter 1

General introduction



1.1 Forest soils in humid tropics

Soil, as the Earth's outermost layer and a vital natural resource, is a dynamic matrix of minerals, organisms, gases, and water. As a subsystem within the ecosystem, soil interacts with vegetation, animals, water bodies, and air, playing a critical role in regulating the exchange of materials and energy. While the pedogenic processes occur over millions of years, human interventions in terms of land-use and land cover change can lead to rapid and ultimately detrimental changes in soil physical, chemical, and biological characteristics (Brearley and Thomas, 2015). These changes can disrupt the inherent structural and functional integrity of soil systems persistently (Seybold et al., 1999), posing profound risks to the entire ecosystem.

As with other types of soil, forest soils have developed from geological parent materials interacting with climates and organisms. Forest soils are specifically characterized by the presence of deep roots of trees, a significant O horizon (the decomposed litter layer), and recycling of organic matter (OM) and nutrients (Boyle, 2005). In humid tropical regions where water and energy supplies are typically abundant, the primary geomorphological processes influencing soil formation are chemical weathering, mass movements, and fluvial erosion (Gutiérrez, 2005). In particular, the high effective soil moisture (defined as precipitation subtracting potential evapotranspiration; Kramer and Chadwick, 2018) tends to hydrolyze and leach away the silica as well as readily soluble, active cations, while accumulating resistant clays, mainly iron (Fe) and aluminum (Al) oxides, in the B horizon (the subsoil; Hillel, 2008). As such, soils in this region typically exhibit an ABBtC profile: a shallow, porous A horizon with dark, raw and acid OM grades into a yellowish B horizon (a mineral horizon featured by eluvial loss of silicate clay), and the underlying argic Bt horizon has stronger reddish or yellow color than the E horizon (Driessen, 2001; see Fig. 1.1 left for an example). The horizonation is sometimes nondistinctive, and the variation normally correlates with terrain conditions.

Although these acid, strongly weathered soils are nutrient-poor (Sayer et al., 2024), their mineralogy, combined with the OM input from above-ground vegetation through physicochemical bonds to form soil aggregates, contributes significantly to the ecological services that soil provides in the following perspectives:

1. The maintenance of the vast biomass and biodiversity of tropical forests, which is not solely dependent on the subsoil minerals but also the residing soil microbes that decompose OM and acquire nutrients. Soil aggregates are resistant to decay and serve as microhabitats for microorganisms, influencing the microorganisms that live within them and vice versa (Carson et al., 2007; Hillel, 2008);
2. The integral role in water cycling, which includes regulating and partitioning water and solute flow, and conserving water for plant transpiration. Soil aggregate is the basis for soil physical structure (Asano and Wagai, 2014). Soils that have been eroded or compacted are more prone to generating overland flow, exhibiting a reduced infiltration rate, and are susceptible to potential waterlogging (Hillel, 2008; Brearley and Thomas, 2015);
3. Filtering, buffering, degrading, and immobilizing of organic and inorganic materials. For

example, carbon (C) and nitrogen (N) from litter deposits are initially incorporated into microbial biomass and allocated to different byproducts (e.g., enzymes, polysaccharides) or mineralized (*sensu* "microbial filter"). The residuals then interact with soil minerals to form stabilized soil aggregates, which determines long-term C sequestration below ground (Cotrufo et al., 2013).

It can be seen that soil aggregate is the key to all these functional services. As previously stated, pedogenic Fe and Al oxides are essential components in the formation of aggregates in humid tropics (Kirsten et al., 2021), and are also extensively involved in the underlying mechanisms of immediate and persistent alterations in the soil system resulting from human interventions. Therefore, before delving into the details of human disturbances on the above-ground and their potential impact on the below-ground, it is necessary to provide an overview of soil taxonomy and soil aggregation in the study area.

1.1.1 Physicochemical properties of dominant soil (Ultisols) in Bornean lowland rainforests

Malaysian Borneo and Indonesian Kalimantan as a whole is composed of extensive, predominantly low-lying alluvial plains, surrounding the interior uplands (Tan, 2008). The parent materials, Tertiary sandstone and shale, are among the oldest land surfaces, and have been subjected to intense weathering conditions. This area is originally covered by lowland *Dipterocarp* forests (Ohta et al., 1991), and according to the USDA soil taxonomy system of classification, the dominant soil group is Ultisols. Ultisols is an intensely weathered soil developed under warm and humid climates and formed on old erosional or depositional surfaces, such as sedimentary rocks (Ashraf et al., 2018; Fig. 1.2).

The term Ultisols originates from the Latin *ultimus*, suggesting an "ultimate" or extreme condition of leaching (Hillel, 2008). Ultisols have few weatherable minerals left, mainly Fe- and Al-(hydro)oxides. The predominant mineral in soil clays is kaolinite ($\text{Al}_2\text{O}_3 \cdot 2\text{SiO}_2 \cdot 2\text{H}_2\text{O}$), with vermiculite ($[(\text{Mg}, \text{Fe}^{2+}, \text{Fe}^{3+})_3[(\text{Al}, \text{Si})_4\text{O}_{10}](\text{OH})_2 \cdot 4\text{H}_2\text{O}]$) and gibbsite ($\text{Al}(\text{OH})_3$) being secondary in abundance (Ohta et al., 1991). Despite for the high acidity and low permanent charges, the abundance of Al leads to Al toxicity and strong phosphorus (P) sorption that significantly limits plant nutrients (Soong et al., 2020), and low biological activity makes the natural regeneration of Ultisols very slow (Driessen, 2001). The surface soils of Ultisols are generally porous and of high OM under a protective forest cover, with clay content in excess of 30% in the A horizon (particle size $< 2 \mu\text{m}$; Tan, 2008). However, with deforestation, the valuable A horizon degrades and slakes, allowing for the formation of a hard surface crust that promotes erosion (Driessen, 2001).

1.1.2 The formation and stability of soil aggregates in humid tropical forests

Soil aggregation is the process by which soil minerals are arranged around soil organic matter (SOM) through particle associations. The formation of soil aggregates can be conceptualized in a hierarchical order, as proposed by Golchin et al. (1994) and summarized by Six et al. (2004):

1. The formation of macroaggregates (250–2000 μm) around fresh plant residue with clay content and microbial-derived binding agents during decomposition;

2. The decomposition and subsequent fragmentation of coarse OM results in the formation of fine OM, which gradually becomes encrusted with clay particles and microbial products, forming stable microaggregates (<250 μm) as cores of macroaggregates;
3. Breakdown of microaggregates after the depletion of microbial available OM, which ends the production or even triggers the consumption of binding agents;
4. The degradation of binding agents in macroaggregates and the releasement of mineral crusts and microbial byproducts, which will enter the next cycle of macroaggregate formation.

The binding agents, which can be either organic or inorganic, temporary or persistent (Six et al., 2004), play an essential role in the formation and stability of soil aggregates. Biotic binding agents include fungal hyphae and microbial byproducts such as polysaccharides or lipids (Abiven et al., 2007). While in non-arid, oxide-rich soils like Ultisols in humid tropics, the dominant inorganic binding agents are Fe and Al oxides, both are more persistent, and function at micro and macro levels through physical and chemical ways (Six et al., 2004; Wagai et al., 2020). At microscale, positively charged oxides act as a sorbent, facilitating the adsorption of negatively charged OM at mineral surface, coprecipitation with mineral coatings, or adherence to minerals by electrostatic forces (Totsche et al., 2018). At silt-clay scale, surficial oxides of both clay particles and organic colloids physically form the bridge between them (Chen et al., 2020). These interactions contribute to the overall stability and structure of soil aggregates in humid tropical environments.

In turn, the stability and turnover of soil aggregates are governed by those of these binding units, which will be referred to as organo-mineral associations (Totsche et al., 2018). Disruption of either organo-mineral associated OM or minerals can cause aggregate disintegration and triggering turnover. Various biotic factors influence this process, such as the recalcitrance of OM, which depends on its type (e.g., glucose vs. cellulose), and the activity and metabolism of microorganisms (Abiven et al., 2007). Additional abiotic factors include moisture, pH, redox potential, ionic strength, and mechanical load (Totsche et al., 2018).

In the context of deforestation and forest degradation, disturbances in the above-ground vegetation affect the above factors directly or via multiple biogeochemical processes, and the nature and extent of the above-ground disturbances strongly influence responses from the below-ground environment. Some of these responses are immediate or exhibit recoverability, while others result in structural changes and functional loss, both relate to an irreversible changes of soil aggregation (Guariguatta and Ostertag, 2001; Brearley, 2011).

1.2 Degradation of humid tropical forests

Deforestation and forest degradation are the main threats to forest across the globe but distinctly different processes (Sasaki and Putz, 2009). Deforestation is defined as the permanent conversion of forest to other land uses, with a threshold of crown loss of up to

10 or even 30%; forest degradation is more difficult to discern and quantify, but also causes considerable impacts on biodiversity and CO₂ emissions (Sasaki and Putz, 2009). The broad definition of degradation is the reduction in the overall capacity of a forest to supply goods and services including C storage, climate regulation, biodiversity conservation, and wood products, as a result of anthropogenic and environmental changes (FAO, 2005).

It is estimated that more than half of the world's tropical forests are not old-growth, but naturally regenerating secondary forests from human intervention (Poorter et al., 2016). The International Tropical Timber Organization (ITTO) suggested that up to 850 million ha of forests in the tropics could already be degraded (ITTO, 2002), which makes up the majority of global forest degradation (FAO, 2020). Although it is generally acknowledged that disturbed forests will eventually recover to pre-disturbance levels if left long enough, the time taken for it is under debate and varies depending on geographic location, disturbance history, and category (Cole et al., 2014). If disturbances are too large or frequent, the ecosystem might be shifted to a state from which transitions back to the stable state are unlikely (Ghazoul et al., 2015). In other words, if the natural recovery process, which involves a succession of changes in vegetation structure and species composition following a disturbance, ultimately fails to restore the ecosystem to its original state, then there will be a permanent loss of forest ecological services (Ghazoul and Chazdong, 2017).

The indicators employed in degradation assessment may differ between scales (e.g., from stand to landscape level), management purposes, and methodologies (e.g., satellite remote sensing, aerial photography, and plot survey); the quantification also requires a proper reference state, which is typically provided by primary forests (Thompson et al., 2013). The framework of criteria and indicators for defining and delineating areas of degraded forest promoted by Thompson et al. (2013) suggests a minimum set of indicators for five criteria as follows:

1. Growing stock ($\text{m}^3 \text{ ha}^{-1}$ of wood) for the production criteria;
2. Ecosystem state (i.e., area of specific forest type) and fragmentation for the biodiversity criteria;
3. Population density and area affected by invasive species for the unusual disturbances criteria;
4. Area affected by fire and soil erosion for the protective function criteria;
5. C stock (biomass ha^{-1}) for the C storage criteria.

However, it is challenging to achieve a complete and accurate data set to generate all the indicators above for disturbed as well as the referential primary forests, particularly in tropical regions. Therefore, based on the driving factors of degradation in the study region, feasible approaches and the key biogeochemical processes involved in this study, I will be focusing on the practice of timber production and its effects on Bornean lowland tropical rainforests from the perspective of above-ground biomass (AGB) stock and tree community composition.

1.2.1 Timber production as the major driver of forest degradation in Borneo

Borneo located in the Indomalayan region contains six terrestrial ecoregions and covers approximately 75 million ha of land area, where lowland rainforests account for about 43 million ha (WWF, 2001). These forests are distinguished by dominant dipterocarp trees, which possess a high timber stock and are of commercial value (Tan, 2008). Consequently, Borneo is notable for the prevalence of the timber industry (Curran et al., 2004), and currently over half of the total land area is designated as production forests (Aoyagi et al., 2017). Over the 20-year period until early 2000s, timber (including industrial plantation) exports from Borneo alone exceeded all wood exports from tropical Africa and Latin America combined (Cleary et al., 2007). While forestry causes forest degradation, agricultural developments and large-scale forest fires cause extensive deforestation. The study by Curtis et al. (2018) classifying drivers of global forest loss in the period of 2001 to 2015 suggests that forestry, rather than natural disturbances represented by wildfire, contributes more to the temporary tree cover loss in Southeast Asia as a whole.

In most cases, timber extraction in Bornean rainforests employs selective logging. The conventional approach of selective logging (CV) is to harvest large canopy trees of commercial species with an intention to enhance the regrowth of residual small commercial trees and eventually convert the entire stands to commercial species. However, CV practices often ignore logging guidelines and the second and third entries of logging may occur at short time intervals (Edwards et al., 2010), which creates an imbalanced harvest-regrowth condition. In addition, CV results in collateral forest damages, including damage of surrounding trees, alteration of forest microclimate, and disturbance of surficial soil and nutrient cycles (Asner et al., 2004). Now, CV is considered to be responsible for rapid forest degradation in the tropics (Sasaki et al., 2012). These effects can be both immediate and long-lasting on forest ecological and biogeochemical processes, and the high wood production is at the expense of C stock and long-term timber availability (Asner et al., 2004; Sasaki et al., 2012).

Consequently, reduced-impact logging (RIL) has been introduced to safeguard the sustainability of timber resources, environments and societies. RIL is only permitted in areas with slopes between 0 and 25 degrees; the machinery used is a combination of a crawler tractor and a log-fisher, a modified excavator with a long cable, which is used to avoid damage to remnant forests and forest soils; a pre-harvest investigation and planning are required to decide on the target individuals, road alignment, and cutting cycle (Sabah Forest Department, 2014). It is estimated that RIL reduces C emissions by 33% to 46%, while protecting sensitive habitats and maintaining timber yields (Griscom et al., 2019).

1.2.2 Characteristics of degraded timber-producing tropical rainforests in Borneo

The natural vegetation of timber-producing forests in Borneo has been significantly impacted by decades of CV practices prior to the implementation of sustainable forest management with RIL (Sabah Forest Department, 2014). Consequently, there exists a limited amount of intact forest patches and an extensive amount of secondary forest patches, which have undergone different disturbance histories, been at varying stages of

succession, and exhibited varying levels of degradation. These forest patches are dispersed continuously across the landscape in a mosaic formation.

In the literature and industry, the most commonly used indicators evaluating magnitude of forest degradation are associated with AGB and forest structure, including basal area and tree density, while the latter two are significantly correlated with AGB in most cases. Therefore, the magnitude of forest degradation is determined with AGB loss in comparison with a reference forest (i.e. reference level) over a certain period. Previous studies in Borneo have well established that degraded forests possess a smaller amount of AGB, lower basal area, and tree density than intact forests. In Sabah, the above-ground woody biomass in secondary forests is only one-third that of old-growth forests (Riutta et al., 2018), where highly degraded forests are typically with AGB $<100 \text{ Mg ha}^{-1}$, while the well-developed forests are with AGB $\geq 600 \text{ Mg ha}^{-1}$ (Imai et al., 2014).

The loss of AGB is often associated with arrested succession and a shift in tree community composition, particularly in Bornean lowland rainforests with a remarkably high biodiversity (Imai et al., 2014). Degraded secondary forests are composed primarily of pioneer tree species that are fast-growing, low in wood density, tolerant to sunlight, and have high foliar nutrient concentrations (Kerdraon et al., 2020). As the degree of forest degradation increases, the number and abundance of pioneer species increase, while those of shade-tolerant, climax species decrease, both in terms of mature individuals and seedlings (Imai et al., 2014; Aoyagi et al., 2017; Sawada et al., 2022). In some cases, the invasion of ferns and lianas into logged-over forest patches can even impede the initial phase of secondary succession by reducing the recruitment of pioneer species and increasing the mortality of remnant trees (Takeshige et al., 2023).

Canopy height and coverage (or the opposite, canopy openness) are directly related to C stock and are also practical indicators of logging intensities particularly useful at landscape scales. They have direct impacts also on the forest floor and the below-ground system. Sasaki and Putz (2009) proposed a minimum crown cover of 40% and a minimum canopy height of 5 m as thresholds for degradation. However, the impacts of canopy damage on ecosystem services can occur before reaching these thresholds. In the case of selective logging, the upper canopy and/or canopy internal structure can be damaged through the extraction of mature individuals of dominant species, which significantly lowers the foliage amount and average tree height. Additionally, the construction of skid trails, roads, and log landings can lead to canopy fragmentation or even openings (DeArmond et al., 2022). Such changes in the canopy can alter forest functioning in modifying local climate in terms of precipitation interception, thermal buffering, and airflow control (Takahashi et al., 2017; Jucker et al., 2018). Forest microclimates greatly influence soil respiration and nutrient cycling, thereby making canopy structural degradation an important factor in forest regeneration (Santos et al., 2024).

1.3 Below-ground responses to logging and degradation in humid tropical rainforests

Below-ground responses to above-ground vegetation disturbances or degradation have

been extensively studied. A general assumption of recovery has been established for the below-ground system, analogous to the post-disturbance forest restoration assumption (outlined in Section 1.2). For instance, a widely examined and accepted paradigm of soil C dynamics after forest harvesting was promoted by Covington in 1981 (Fig. 1.3). Based on data from hardwood stands in North America, the author described a time-dependent pattern of forest floor OM storage: starting from the value of old stands, then exponentially declined by 50% in the first 20 years after harvest and recovered through logistic growth over the following 40 years (Covington, 1981; Yanai et al., 2003). However, DeArmond et al. (2022) concluded from previous studies in Amazonia that a post-logging soil emission of C and N may last for more than the first 20 years; two recent studies in Malaysian Borneo also noted that soil respiration increased considerably and persistently after logging (Riutta et al., 2021; Mills et al., 2023). The contradictory evidence showed that, despite of the common trend which has been observed and examined in many cases, there may be potential alterations in the biogeochemical process governing the cycling of material and energy in disturbed and/or degraded forest ecosystems. These alterations could explain variations in the below-ground responses to forest harvesting.

Soils are open systems, and soil properties are always responding to external forces and undergoing changes. Some properties respond rapidly (1 to 10^2 years), including OM content, redistribution of salts, clays, and formation or obliteration of mottles; while other properties, like horizons of clay, Fe-humus (i.e., the organo-mineral association), or carbonate accumulation, are considered to change relatively slow (10^2 to 10^3 years; Chadwick and Chorover, 2001). The terms "rapid" and "slow" appear to imply a linear response of soil properties to external forces. However, soil in fact may not respond linearly to environmental forces. It may persist at a stable state with a large range of environmental forcing, but then change abruptly under a small increment in forcing there may be potential alterations in the biogeochemical process governing the cycling of material and energy in disturbed or degraded forest ecosystems. These alterations could lead to variations in the below-ground responses to forest harvesting (Desie et al., 2019). Such nonlinearity has been observed in soil acidification and clay mineral formation process along rainfall and/or temperature gradients, both of which are supposed to be "slow" changes (Vitousek and Chadwick, 2013). This leads to the concept of "pedogenic threshold": soil properties or processes change slowly between thresholds, but rapidly and irreversibly when the threshold is exceeded (Vitousek and Chadwick, 2013).

As been summarized by Chadwick and Chorover (2001), the accumulation of soil properties and their subsequent susceptibility to change is largely influenced by self-enhancing feedback processes that increase a particular property until exhaustion of one or more of the reactants brings about a termination. In the context of selective logging and forest degradation in the humid tropics, such feedbacks can be specified as the disturbed C and water cycles and their influence on soil physicochemical properties and microbial activities.

1.3.1 The disturbed carbon cycle in logged tropical rainforests

Forest ecosystems translocate C from the atmosphere to living organisms, litter, and the

below-ground. The full cycle of C can be divided into (1) the acquisition and release of C in the above-ground, and (2) the sequestration and mineralization of C in the below-ground. The year-round high precipitation and temperature make humid tropical forests highly productive comparing to temperate and boreal forests, and there is a large translocation of C to the below-ground in humid tropics, as well as high rates of C mineralization and recycling (Malhi et al., 1999).

In the above-ground, acquisition of C from the atmosphere is basically through photosynthesis in forest canopies (Malhi, 2012); while the sources of C emission are more diverse, including respiration from living organisms like leaves and stems, as well as from necromass like litterfall and deadwood. On the other hand, C cycling in the below-ground system is regulated by OM input from leaf and wood detritus, soil microbial decomposition, and the stabilization capacity of soil organic matter (SOM; a scheme plot is given in Fig. 1.3A). These factors are intrinsically correlated: the amount and quality of OM input influence soil microbial activity and hence the rate of decomposition (Noordwijk et al., 1997); and the inclusion of OM within soil aggregates reduces their decomposition rate (Six et al., 2000). In addition, recent studies emphasize microbial residues to be a primary regulator for the formation and accrual of SOM (Zhu et al., 2024).

Intact forests are generally regarded as C sinks, while degraded forests continue to be a major source of atmospheric carbon dioxide (CO₂; Mills et al., 2023). The characteristics of degraded forests, as outlined in Section 1.2.2, exert a substantial impact on forest C cycle as a whole. The above-ground woody biomass in secondary forests is significantly lower than that of old-growth forests (Riutta et al., 2018). Greater canopy openness after disturbance and lower tree height during succession increase radiation and precipitation reaching the substory (Jucker et al., 2018), which in turn increases the variation in air and soil temperature, as well as soil water content (Kerdran et al., 2020). Furthermore, the use of heavy machinery and topsoil removal in order to level the ground surface directly and immediately causes soil compaction (DeArmond et al., 2022), which has been found to significantly reduce abundance and diversity of soil microbiota (Hartmann et al., 2014).

As for the below-ground system, these alterations in both biotic and abiotic conditions bring complex effects to the processes that underpin soil C dynamics and storage (a schematic plot is provided in Fig. 1.3B). The majority of case studies have reported significant decrease in SOM content after disturbances (Guariguata and Ostertag, 2001), which can be attributed to modified OM input rates and/or changes in degree of protection of SOM (Noordwijk et al., 1997). Although high temperature and precipitation in this region speed up OM decomposition and thus limit topsoil SOM stabilization (Malhi et al., 1999), C stock in deeper soils (e.g., down to 2-m depth) protected by mineral-organic associations may account for approximately half of the total C accumulated in both above-ground biomass and soil C pools (Wade et al., 2019). A recent study conducted in logged Bornean rainforest concluded that comparing with intact forests, post-logging forests showed significantly elevated soil respiration which is likely to originate from stabilized SOM, although the specific mechanisms are not well-understood (Mills et al., 2023). The loss of protected SOM can be particularly detrimental because SOM stabilizes soil aggregates,

increases the water-holding capacity of soils, serves as an energy source for soil decomposers and nutrient source for plants (Guariguata and Ostertag, 2001).

1.3.2 The disturbed water cycle in logged tropical rainforests

Water cycle in forest ecosystems is comprised of precipitation, evapotranspiration (ET), infiltration, and surface runoff (Goeking et al., 2020). ET is recognized as the most important factor influencing water budget in humid tropical region, as it specifies the total flow of water into the atmosphere, which is composed of two processes: evaporation from canopy-intercepted water, soil, and open water; and transpiration from plants (Pancel and Köhl, 2016; Wei et al., 2017). In the humid tropics, since high rainfall (ranging from 1,500 to 2,500 mm annually) and temperature (exceeding 18°C, which allows for more water vapor in the air) are distributed evenly throughout the year, ET can proceed at its potential rate, which transfers over half of total precipitation to the atmosphere (Malhi et al., 2002; Kumagai et al., 2004; Bonell and Hufschmidt, 2005).

Logging and forest degradation on canopy structure simultaneously affects the three essential fraction of ET, and subsequently soil moisture (Keller et al., 2023). Decreases in tree density and canopy coverage decrease interception and increase throughfall that reaches the forest floor (Keller et al., 2023), which together increases water input to the soil; on the other hand, biomass loss limits transpiration, which decreases plant up-take of soil water content. Although these changes reasonably indicate an increase in soil water content, which has been consistently observed across climate zones (Wiekenkamp et al., 2016; Zhang et al., 2017), recent findings suggest that if canopy loss surpasses a certain threshold, the thermal buffering provided to the substory would be abruptly reduced (Jucker et al., 2018). This will enhance direct evaporative demand of soil (Senior et al., 2010). These two lines of evidence bring opposite effects on ET, making the actual response of soil moisture debatable.

Although it is recognized that the impacts of canopy damages on the forest floor may diminish rapidly as selectively logged forests recover and fill canopy gaps (Asner et al., 2004; Senior et al., 2017), it is important to note that the role these large trees fulfil in local hydrological regimes may not be compensated for within a decadal time span (Lindenmayer et al., 2012). Canopy transpiration basically transports more water than evaporation in humid tropical rainforests, and the whole amount of transpiration depends on the total biomass and the average response of a large number of individuals and species (Granier et al., 1995). Therefore, it is presumable that the disturbed water cycle may persist before a total recovery of forest canopy in terms of both coverage and structure.

1.4 Soil redox potential as a mediator of disturbed carbon and water cycles in degraded humid tropical rainforests

1.4.1 Definition of soil redox states and redox potential

Oxidation-reduction (redox) reactions, mediated by soil microbiota, govern elemental cycling in soil systems. All redox reactions are comprised of two coupled half-reactions (oxidation and reduction) that involve a redox couple (a reducing agent that donates electrons, and its corresponding oxidized form that accepts electrons; examples of common

redox couples are given in Fig. 1.5). The dominant redox reaction defines soil redox state, and the corresponding Gibbs energy of the reaction defines the severity of the state (e.g., weakly, moderately, or strongly; Chadwick and Chorover, 2001).

The kinetics of redox system suggest that potential redox reactions occur progressively along a gradient of decreasing Gibbs energy. That is, the dominant redox reaction shifting to the subsequent one at the point when the oxidizing agent involved in the previous reaction has been depleted, and soil redox state changes in a nonlinear way. Common oxidizing agents present in soil include O_2 , NO_3^- , $Mn(IV)$, $Fe(III)$, and SO_4^{2-} (Chadwick and Chorover, 2001). As each of these reactants is depleted, soil shifts to increasingly reductive states.

The thresholds of redox states can be quantified by redox potential (Eh, V), which represents the free energy available for the electromotive force of the reactions (Zhang et al., 2021), and therefore reveals the tendency of an environment to oxidize or reduce certain compounds (Rowell, 1994). The physical chemistry of redox reactions leads to a numerical relationship between Eh and concentrations of redox couples in soil (Rowell, 1994). In natural soil systems, the lower (anaerobic/anoxic) and upper (aerobic/oxic) boundaries of redox state are determined by the reduction of CO_2 to methane (CH_4) and the presence of oxygen (O_2); and the empirical values for these boundaries are approximately -0.2 V and 0.8 V, respectively (Rowell, 1994; Zhang et al., 2021). However, strict Eh boundaries between the upper and lower limits can hardly be defined (Zhang et al., 2021). Theoretical Eh values for common redox couples are showed in Fig. 1.5, and empirically, 0.4 V indicates the threshold of oxidizing soil, while 0.1 V indicates reducing soil (Barcellos et al., 2018).

1.4.2 Shifts in soil redox regimes driven by moisture dynamics in humid tropical rainforests

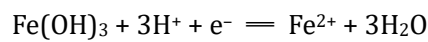
Unlike classically defined anaerobic soils like wetlands, soil redox oscillations in humid tropical rainforest are spatially and temporally heterogeneous (Bhattacharyya et al., 2018). The major reason is the variability in soil moisture, which has long been known to impact soil O_2 concentrations (Hall et al., 2013). In the humid tropics where precipitation is high and frequent, the increased infiltration often correlates with declines in soil O_2 concentration and hence decreased Eh, presumably because moisture limits O_2 diffusion in soil matrix (Hall et al., 2013; Bhattacharyya et al., 2018). On the other hand, as O_2 serves as the most energetically favorable electron acceptor for microbial respiration and redox reaction. While the acid, highly weathered soil (i.e., Ultisols) accumulates only relatively stable Fe and Al oxides, there is a high biogeochemical demand for O_2 in the below-ground (Hall et al., 2013). As a result, elevated soil moisture could have an immediate and significant impact on soil Eh, shifting the soil redox regime from oxic to anoxic by changing soil O_2 concentrations. Field measurements revealed that soil moisture, O_2 concentration, and Eh rapidly responded to precipitation and drought events, although topographic effects, i.e., slope and elevation, affected the significance of changes (Barcellos et al., 2018).

As introduced in Section 1.3.2, logging and forest degradation potentially increase soil

moisture due to less water uptake by plant transpiration, which may also contribute to the shift in soil redox regime. However, at present, no study has provided direct evidence linking the extent of forest degradation with changes in soil moisture and/or Eh, and justifying these changes across space and time.

1.4.3 Temporary and persistent effects of redox regime shift on soil carbon stock

The disturbed C cycle in degraded humid tropical rainforests can be attributed to the loss of SOM (see Section 1.3.1). On the other hand, Fe and Al (hydro)oxides are crucial to stabilize SOM by serving as binding agents, and therefore regulate SOM turnover in humid tropics (see Section 1.1.2). However, Fe minerals have been widely acknowledged to be redox sensitive. Despite for the reductive dissolution of well-ordered, thermodynamically stable Fe(III)-oxide crystals under anoxic conditions:



which destructs Fe-OM association, a preferential dissolution of less-crystalline, short-range-ordered (SRO) Fe minerals have also been observed under fluctuating redox dynamics. Both processes coincided with increased dissolved OM, which is more readily available for microbial utilization (Bonneville et al., 2004; Weber et al., 2006; Bhattacharyya et al., 2018).

Furthermore, in humid tropical soils, the reductive dissolution and structural composition change of Fe minerals can result in a permanent reduction in the capacity of soil C sequestration. This is due to the following reasons:

1. In perhumid tropical regions, descendance dominates soil water movement and results in a rapid leaching of weathering products (Pancel and Köhl, 2016). This indicates that even if soil returns to an oxic state that allows the reduced Fe^{2+} ions to re-oxidize, it will not be able to restore the original level of Fe contents;
2. The SRO Fe minerals are distinguished from larger bulk Fe oxides by their ability to undergo sorptive reactions with organic functional groups. This is due to their greater numbers of valence-unsatisfied hydroxyl groups, which are a consequence of the structural disorder (Mikutta et al., 2005). Consequently, they are the most reactive phase in SOM stabilization, although they are less thermodynamically stable (Bonneville et al., 2004; Coward et al., 2018). Both the preferential loss and transformation to crystalline phases under fluctuating redox environments can permanently reduce SRO Fe mineral contents.

The reduction of soil C sequestration capacity caused indicates a permanent lowered upper limit in below-ground C stock, even with higher C inputs. The conceptual formation of soil C pool in forest ecosystems is composed of "non-protected" and "protected" parts (Six et al., 2002; Fig. 1.6). The non-protected pool mostly consists of recently derived, partially decomposed plant residues that are not associated with soil particles; the protected pool can be further divided into three pools according to the stabilization mechanisms (Six et al., 2002), which continuously convert non-protected soil C into protected form. Soil aggregates, which extensively participate in all three mechanisms (see Section 1.1.2), can be destructed under the soil reductive shift driven by temporarily

increased soil moisture or undergo less effective formation as a result of permanent Fe mineral loss and/or transformation. Above all, degradation in the above-ground can extend to the below-ground through the biogeochemical response involving water and Fe cycling. This provides a potential explanation for the altered C cycle, specifically in relation to sequestered SOM (see Section 1.3.1).

1.5 Aims, approaches, and structure of the present thesis

1.5.1 Overview of the current condition of plant and soil in the study site

This study was based on two forest reserves, Deramakot (5.23°–5.47°N, 117.30°–117.63°E; 55,083 ha) and Tangkulap (5.30°–5.52°N, 117.28°–117.37°E; 27,550 ha), locating in northern Borneo. Borneo supports some of the last remaining intact tropical rainforest in Asia, which has been by far the most affected forest ecosystem globally due to conversion to agricultural lands, oil palm plantations, and selective logging. The region of these two reserves has an elevation range of 20 to 300 meters above sea level, an average daily temperature of 25.5°C, and an annual rainfall exceeding 3,000 mm with little seasonality (Ong et al., 2012). Ultisols is the predominant soil type, and the original vegetation consists of mixed dipterocarp lowland rainforests with *Dipterocarpus* and *Shorea* genera (Imai et al., 2012).

However, the current forest patches vary from near-pristine to highly degraded due to different logging histories. The first recorded timber production was in 1956 for Deramakot and 1970 for Tangkulap, both were conventional, high-impact selective logging (Ong et al., 2012). In 1995, RIL was introduced to Deramakot as an improved method of selective logging, which then contributed to maintaining forest intactness and now Deramakot holds higher biomass and a more pristine-like tree community composition (Kitayama et al., 2018). Contrarily, Tangkulap was under CV until 2002, which formed extensive, severely degraded forest patches (Kitayama et al., 2018). All logging activities have been suspended in Tangkulap since 2003, yet highly degraded forests (fern thickets and liana-laden forests) still cover 35.1% of entire Tangkulap after two decades of logging (Takeshige et al., 2022). The extensive and varied forest patches exhibiting a range of succession and/or degradation statuses distributed at the landscape scale make the two reserves an ideal site to conduct this study.

1.5.2 Application of remote sensing techniques in forest research

The evolution of remote sensing techniques has facilitated global forest research in up-scaling, historical disturbance detection and evaluation, and forest trait studies. Estimating disturbance history and intensity can be challenging even at stand level in many tropical timber-producing forests due to the inaccuracy of harvest records. Remote sensing data analysis based on the medium resolution Landsat image archive can provide information at pixel and landscape levels. These images offer continuous observations at a 30-m spatial resolution dating back to 1972. By using commonly used temporal segmentation algorithms such as LandTrendr (Kennedy et al., 2010) and visualization tools like TimeSync (Cohen et al., 2010), annual-based Landsat image time series can help identify and monitor

vegetation disturbances and reestablishment (Frazier et al., 2015). In the context of forest harvesting, several spectral indices have been adapted for quantifying disturbance and the following regeneration status (Gao et al., 2020). Among a good deal of vegetation indices, normalized burn ratio (NBR) and its change over time have been linked to forest structural properties and are suitable for tracking forest recovery (Frazier et al., 2018).

Meanwhile, the application of unmanned aerial vehicle (UAV) providing high-resolution optical images or point cloud data has become popular in forest studies relating to vegetation traits at finer spatial resolution in smaller spatial extents (Alonzo et al., 2018). UAV can fly near canopies and acquire extremely high-resolution images, which enables the identification of features at individual level (Onishi and Ise, 2021). A previous study conducted in the same study area employed UAV images as a ground truth for the classification of forests at different degradation levels (Takeshige et al., 2022).

1.5.3 Research questions and study designs

It has been demonstrated that the mechanistic understanding of the below-ground responses to logging-induced forest degradation in humid tropical timber-producing rainforests, particularly with regard to soil C loss, is lacking. The objective of this thesis is to provide preliminary answers to this question. Basing on the soil C sequestration mechanism based on organo-mineral association, I hypothesized that a regime shift occurs in the below-ground redox states from oxic to anoxic, which is most likely caused by weakened ET and consequently increased soil moisture under forest degradation. The reductive shift triggers dissolution of soil Fe oxides, results in the destruction of soil aggregates and improves microbial accessibility of SOM protected by the association with minerals. Together with limited input of OM in degraded forests, soil C stock decreases immediately after logging, while the capacity for soil carbon sequestration may be permanently lost due to the irreversible loss of active Fe minerals.

This research employs a multidisciplinary approach, involving field and/or laboratory measurements of soil properties and microclimate, drone survey, and Landsat time series analyses. The specific questions addressed in subsequent chapters are listed below:

Chapter 2: How do soil C, Fe and Al minerals, and Eh change along a forest degradation gradient? Will there be a nonlinear relationship between the indicator of above-ground degradation and soil redox regime?

Chapter 3: How does soil moisture change under different forest degradation status, and how would other factors, including time elapsed from disturbance, topography and spatial autocorrelation, affect such change?

Questions posed in Chapter 2 were addressed by stand-level research, where forest degradation gradient was represented by a chrono-sequence method. Questions posed in Chapter 3 were initially addressed by stand-level research, while sampling sites were grouped according to disturbance period, larger at spatial extent, and explored for the spatial pattern (autocorrelation) that would enable scaling up. The findings of Chapters 2 and 3 were employed in Chapter 4 to demonstrate the spatial extent and pattern of the below-ground environment regime shift at the landscape scale.

Figures

A



B



Fig. 1.1 Soil profile in pristine (left) and highly degraded (right) forest patches. (A) 0 to 0.2 m depth; (B) 0 to 1 m depth. Photo by Imai, N. and Qin, Q.

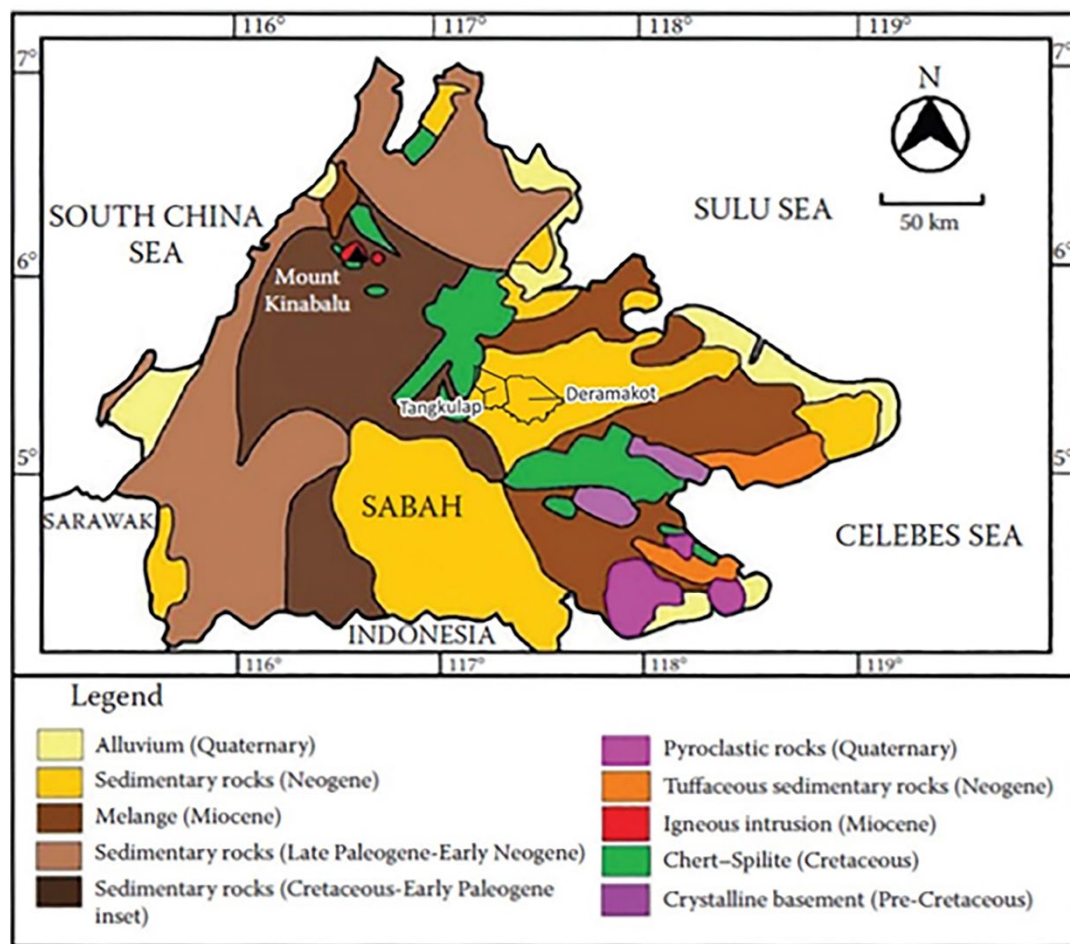


Fig. 1.2 Geological map of Sabah and locality of the study area (Tangkulap Forest Reserve and Deramakot Forest Reserve), quoted and changed from Fig. 2.4, Ashark et al., 2018.

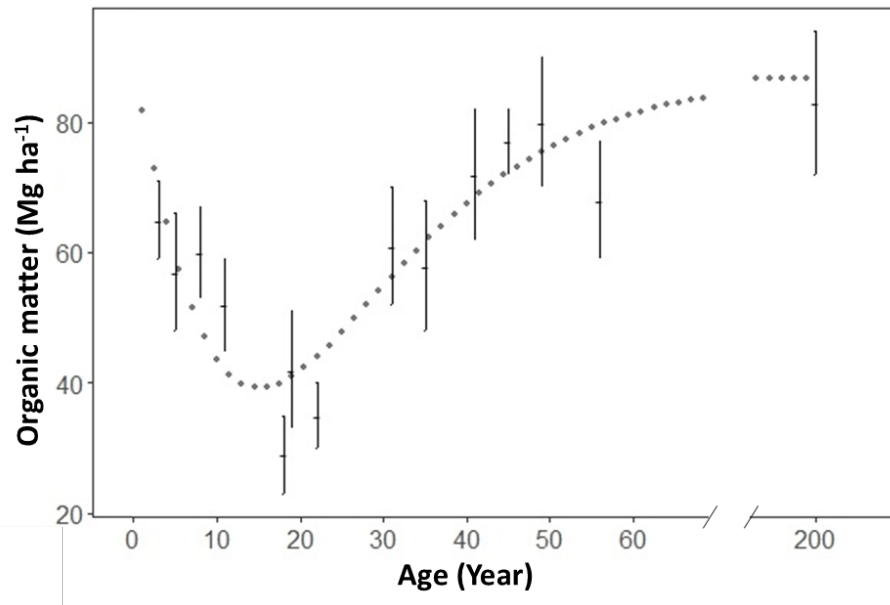


Fig. 1.3 Covington's (1981) measurement and empirical curve fit, quoted and changed from Fig. 1, Covington, 1981. Data are mean and 95% confidence interval ($n = 30$ per year). Curve is least squares fit of a gamma function ($Y = -5.25X^{1.24}e^{-0.0649X^{1.063}} + 86.75$)

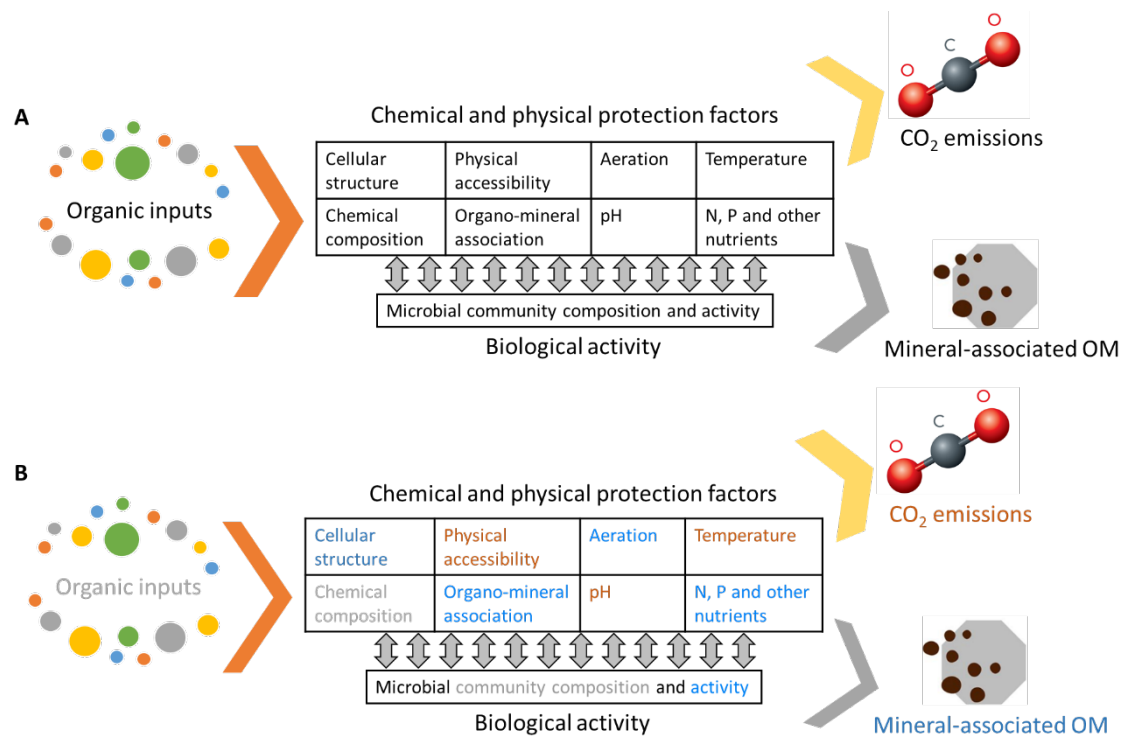


Fig. 1.4 Schematic illustration of factors influencing the rate of decomposition (CO₂ release) of OM inputs. Quoted and changed from Fig. 2., Noordwijk et al., 1997. (A) the status of an intact forest; (B) altered factors in a disturbed/degraded forest. Comparing to the status of intact forests, factors that are expected to increase are indicated in orange, those that are expected to decrease are indicated in blue, and those that are uncertain are indicated in grey.

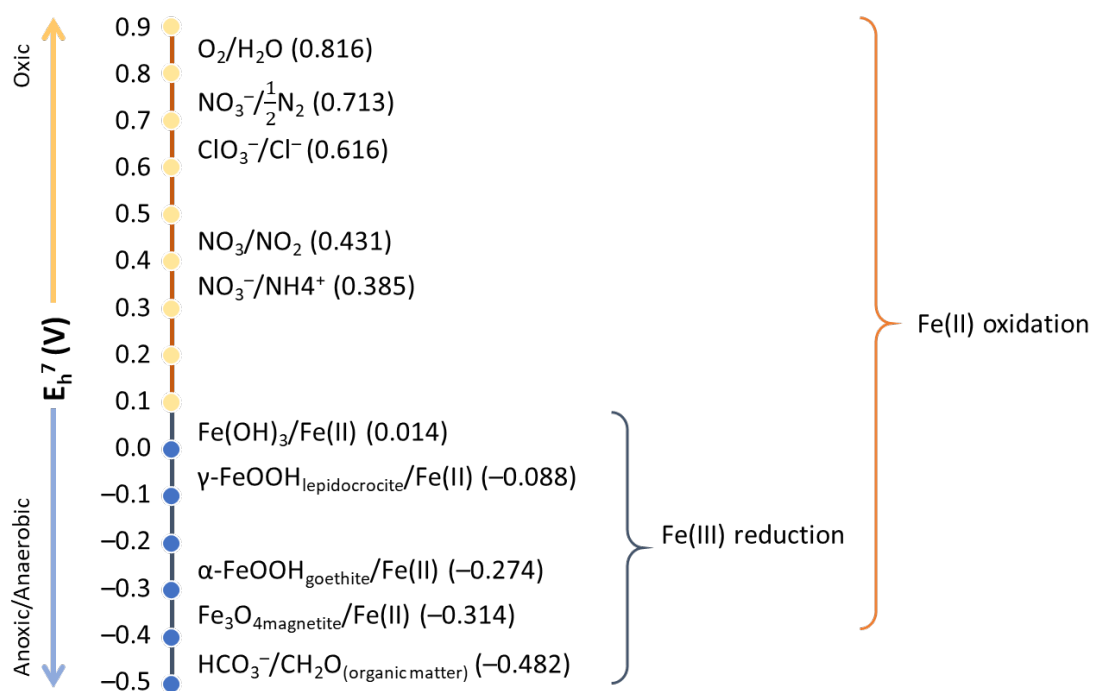


Fig. 1.5 Theoretical E_h^7 (V) values for reduction-oxidation couples that are significant to (microbially mediated) iron redox cycling, quoted and changed from Fig. 2, Weber et al., 2006.

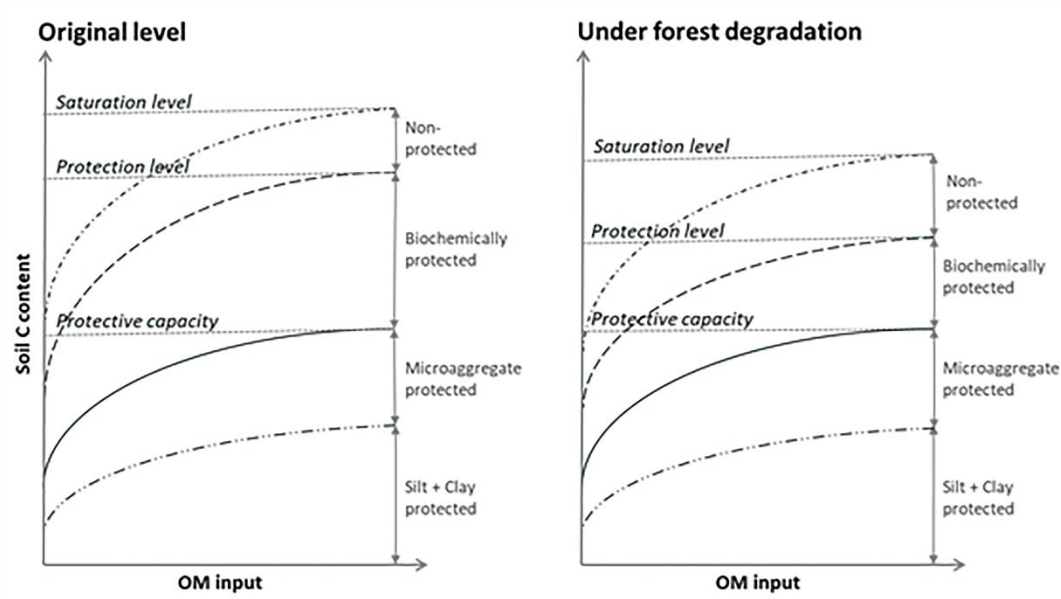


Fig. 1.6 Schematic illustrations of total soil C contents stabilized by different mechanisms, quoted and changed from Fig. 1, Six et al., 2002. Left: the original level; right: after disturbances and presents resilience loss. The scheme after disturbances (right) is based on my hypothesis.

Chapter 2

Soil redox potential as a potential mediator of soil carbon loss in logged Bornean lowland tropical rainforests

Based on publication

Qin, Q., Wagai, R., Aoyagi, R., Titin, J. & Kitayama, K. Destructive selective logging in tropical forests causes soil carbon loss through forest degradation and soil redox change. *For. Ecol. Manag.* **551**, 121555 (2024) doi: 10.1016/j.foreco.2023.121555.

Abstract

Soil organic carbon (SOC) stock in tropical forests can be reduced significantly after logging, not only due to lowered above ground biomass (AGB) and consequentially reduced organic matter (OM) input, but also consumption on sequestered soil C protected by OM-mineral association. In this chapter, I studied the loss of mineral-associated OM after logging in the main rooting zone (e.g., 0–30 cm), and examined a hypothetical twofold underlying mechanism of SOC reduction: first, decrease in AGB limiting OM input; second, decrease in soil redox potential (Eh) leading to the reductive dissolution of short-range-ordered iron (SRO Fe) minerals that destabilize some mineral-associated OM. Thirty-five plots at different degradation levels were investigated for both above- and belowground properties. AGB and tree community composition were employed as indicators of vegetation degradation gradient; multiple physicochemical properties in top-30 cm soils were measured every 10 cm depth. I analysed the relationship between AGB and soil C with the mediator SRO Fe, and investigated the role of soil Eh in linking the changes in AGB and SRO Fe. The results revealed simultaneous decreases in AGB, SRO Fe and soil C in top-30 cm soils, and SRO Fe mediated 43% of the hypothetical causal effect of AGB on soil C in deeper (20–30 cm) soil. Soil Eh decreased with decreasing AGB in a logistic pattern, dropping to a reductive regime ($Eh^7 \leq 0.05V$) when more than half of the AGB was removed from the pristine level. Mean SRO Fe stock in the reductive soils was significantly lower than that in the oxic soils ($Eh^7 > 0.05 V$), and the loss of SRO Fe correspond to the decomposition of OM in 10–30 cm soils. I suggest that the reductive shift in soil is caused by the weakened evapotranspiration as destructive selective logging inflicts canopy openness and succession failure. This chapter presents the possibility that forest degradation may reduce the size of protected soil C pool resulting from the loss of soil SRO Fe minerals.

Keywords: *Selective logging; Forest degradation; Soil carbon stock; Short-range-ordered Fe minerals; Soil redox*

2.1 Introduction

Soil carbon (C) pool is recognized as the largest pool of terrestrial organic C in the biosphere, in particular the forest soils, which retain about two-thirds of total forest C stock (Nave et al., 2010). Even in wet tropics, where C turnover is accelerated by high temperature and precipitation, previous studies estimated that soil stores 30–68% of the total C stock (Pan et al., 2011; Wade et al., 2019). In turn, soil C serves as a principal source of energy for nutrient cycling and hence sustains forest productivity (Gao et al., 2013). The capacity of the below-ground system to sink and sustain C is therefore crucial for forest ecosystems and global C cycle.

Conceptually, soil C pool of a forest ecosystem is composed of two parts: an 'unprotected C pool', which mostly consists of recently derived, partially decomposed plant residues that are not associated with soil particles; and a protected C pool, commonly known as 'stabilized' soil organic matter (SOM; Six et al., 2002). The stabilization mechanism of SOM, which is a combination of physical, chemical and microbial processes, continuously converts unprotected soil C into protected forms. Compared to unprotected C, stabilized SOM is better protected from potential C loss by respiration, erosion, or leaching (Sollins et al., 1996). Long-term experiments also reported that higher C inputs did not further increase soil C stock, suggesting that the stabilization or sequestration ability of C inputs is critical for soil C stock levels (Gao et al., 2013).

As deforestation and forest degradation proceed in tropical forests (Hansen et al., 2013), soil C pool also responds to vegetation change in a complicated way. The impacts of forest conversion on soil have been studied from various perspectives, and it has been recognized that soil structure and chemical properties change immediately after deforestation, among which the decrease of SOM is observed and emphasized in multiple studies (Guariguata and Ostertag, 2001). In the tropics, selective logging is one of the major drivers of forest degradation (Bousfield et al., 2023). Previous studies have reported that the removal of marketable, mature climax tree species by intensive selective logging directly affected canopy structure (e.g., smaller mean canopy size, lower mean canopy height, and reduced canopy complexity), and would further influence soil C efflux in the remnant forest stands via changes in temperature, moisture, biomass and necromass inputs (Riutta et al., 2020; Teixeira et al., 2020; Milodowski et al., 2021). A recent study conducted in Malaysian Borneo found that in logged forests, C-flux from OM degradation exceeded the C-input from litterfall and root turnover (Riutta et al., 2020). Together, the evidence suggests that forest conversion consumes not only the 'unprotected C pool' but also protected (stabilized) SOM, although the mechanism of the latter is not fully understood.

Current understanding suggests that SOM stability and storage are principally determined by soil mineral (or clay plus silt content) via OM-mineral associations, including adsorption and coprecipitation at molecular scales, and aggregation at larger scales (Rasmussen et al., 2018; Wagai et al., 2020). In wet tropical forest soils, iron (Fe) secondary minerals have been widely studied for their dominant abundance and extensive participation in SOM stabilization. Particularly, due to their high specific surface area and various binding sites, the short-range-ordered minerals (SRO minerals, e.g., ferrihydrite

and nanocrystalline goethite) have been defined as more reactive than larger bulk oxides (Bonneville et al., 2004; Han et al., 2019). These features make SRO Fe minerals efficient in SOM stabilization but sensitive to reduction/oxidation (i.e., redox) dynamics and more microbially reducible (Yang et al., 2015; Bhattacharyya et al., 2018; Coward et al., 2018).

Confront with lower plant area, degraded canopy structure and damages to the understory, logged forests are expected to be constrained in leaf area and therefore transpiration. In the prehumid rainfall regime, such reduced transpiration associated with forest-structural changes must cause a stagnant or fluctuating water condition in the remnant forest stands, which then affects soil redox potential (E_h) and creates hot moments for Fe mineral reduction (Barcellos et al., 2018). Previous studies using field measurements, incubation and simulation methods have showed that active Fe minerals and Fe-OM interactions are sensitive to redox effects in tropical soils (Bhattacharyya et al., 2018; Barcellos et al., 2018; Calabrese and Porporato, 2019). However, there is an inadequacy of data on whether and how such a mechanism works under conditions of forest degradation.

In this chapter, I tackle a key question of my thesis, i.e., how selective logging impacts SOC stock in lowland tropical forests. For this purpose, data were collected from both above and below ground, including tree census, in-situ redox potential measurement, and soil sampling under different forest degradation statuses at two timber-producing forest reserves in Malaysian Borneo (Fig. 2.2.1). I investigated relationship between soil physicochemical properties and vegetation status, then examined how the relationship would vary along depths. Also, noting that the unprotected and protected soil C pools can be influenced simultaneously after deforestation and are thus not mutually exclusive, I made a quantitative assessment of the two processes using a mediation analysis as will be explained in Section 2.2.6.

It is hypothesized that SOC declines with increasing magnitude of degradation in remnant logged-over forests via a twofold mechanism: Firstly, the decline of AGB in degraded forests decreases the supply of OM (i.e., litterfall) to soils, and hence the amount of OM input; secondly, the decrease of soil E_h resulting from forest degradation consequentially causes the reduction of SRO Fe minerals, destabilizes SOM and hence decreases SOC. The former directly relates with the decline of unprotected soil C pool, while the latter is more pertinent to that of protected soil C pool.

2.2 Materials and methods

2.2.1 Site overview

This research is based on two adjacent forest reserves, Deramakot and Tangkulap, covering an area of 826.8 km² in north Borneo (Fig. 2.2.1). The altitude of the two reserves ranges from 20 to 300 m asl; the mean daily temperature is about 25.5°C; and the annual precipitation is about 3,098 mm and aseasonal (Ong et al., 2012). The typical humid equatorial climate promotes the formation of sedimentary, highly weathered Ultisols in this area.

The primary vegetation of the two forest reserves is lowland mixed dipterocarp forest. After decades of timber production, this area is currently covered by forest patches varying

from near-pristine to highly degraded, covered by ferns and/or vines. Different logging applications were considered the major reason for the variance in current vegetation status (Takeshige et al., 2022), which had been discussed as conventional logging and reduced-impact logging in the literature. Both methods select marketable, mature individuals of dipterocarp trees, yet the former neglects seeding regeneration and causes damage to surrounding vegetation and surface soil when opening skid trails (Burivalova et al., 2014; Imai et al., 2014). Both reserves experienced conventional, destructive selective logging dating back to 1956 in Deramakot and 1970s in Tangkulap (Sabah Forestry Department, 2014). In Tangkulap, however, such extensive conventional logging continued until 2002, leaving behind expanded, severely degraded vegetation patches even after two decades of regrowth (Kitayama et al., 2018). In contrast, reduced-impact logging was introduced to Deramakot in 1995, which requires pre-harvest inventory and planning that mitigate damage to forest reproduction. This contributed to a higher AGB and a more pristine-like tree community composition in Deramakot in comparison with Tangkulap (Imai et al., 2014; Kitayama et al., 2018).

2.2.2 Sampling plot allocation

A total of 35 study plots at various degradation statuses were sampled in 2020 (Fig. 2.2.1). I defined plot areas as either a 20-m diameter circle or a 30 m × 30 m square; any two plots were set apart at a minimum center distance of 30 m. To avoid sampling bias, I followed the stratified random sampling design described by Imai et al., 2014. An annual mosaic of the year 2020 was generated from Landsat 8 Top-of-Atmosphere (TOA) reflectance product using median value of Band 7 (the second short wave infrared band), then classified into 6 categories with Jenks natural breaks method to stratify the data set. The top 5 categories approximately represented an ascending degradation status from pristine forest to highly-degraded (category 6 represented bare soil and was therefore removed from sampling), and 7 sampling plots were assigned to each. As such, the category number could be used as an ordinal variable in the subsequent statistical analyses. Detailed categorical descriptions are listed in Table S1. To minimize the effects of human factors (e.g., edge effect of roads) and spatial autocorrelation, plots in categories 1 through 4 were located 100 m from car-accessible roads (several category 5 plots were next to abandoned skid trails originally for bulldozers), and all plots were centered at least 30 m apart.

Topography was more difficult to control in a timber production reserve. The designated conservation area, where intact forest was present, was typically higher and steeper, and thus could be a confounding factor for logging effects on vegetation and soil properties. To represent the influence from local topography, I collected elevation and slope data from the NASA SRTM Digital Elevation Model (DEM) at 30 m spatial resolution, and adapted the topographic water index (TWI) as an indicator of terrain driven variation in soil moisture (Kopecký et al., 2021; see Table S5 for detailed calculation and summarized statistics). These variables were considered when examining vegetation-soil relationships.

Each soil-collecting point was approximately centered in each plot. Steep slopes were avoided.

2.2.3 Vegetation survey and data analysis

To realize a quantitative and more precise assessment of forest degradation, I used plot-level census data from field surveys conducted in 2018 and 2019 (Sawada et al., 2022; Takeshige et al., 2023), including tree number, taxonomic information at genus level, and diameter at breast height (dbh). To correctly represent canopy status, individuals with dbh < 10 cm were excluded from the dataset. Making use of the census data, I estimated the plot-level AGB as a summation of all trees in each plot. Lacking tree height information, I used the allometric equation proposed by Chave et al. (2014):

$$\text{AGB (kg)} = \exp[-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(\text{dbh}) - 0.0299[\ln(\text{dbh})]^2]$$

for tree AGB estimation, where ρ stands for wood density (g cm^{-3}) and E is a measure of environment stress estimated from site coordinates, defined by cumulative water deficit, temperature and precipitation seasonality (Chave et al., 2014). Specific ρ values were obtained from the Global Wood Density Database (Zanne et al., 2009). Plot-level mean wood densities were assigned to individuals with no wood density data. Biomass in ferns or vines were ignored. The calculation was performed using the BIOMASS package of R (Réjou-Méchain et al., 2017).

The first axis value generated by a non-metric multidimensional scaling (nMDS) analysis was used as an indicator of plot-level tree community composition, i.e., the 'intactness' index. Previous studies have suggested that in a 2-axis nMDS analysis based on Chao's distance, values of the first axis varied linearly with both AGB and community composition at genus level, and are thus been capable of assessing the extent of forest degradation (Chao et al., 2005; Imai et al., 2014). In this study, to balance information loss and index robustness, I used the first axis values of plots from a three-axis nMDS analysis to represent plot-level intactness, and found that these values highly corresponded with vegetation category number and AGB (stress = 0.17, Fig. S2.2.1A). The calculation was performed using the vegan package of R (Oksanen et al., 2017).

2.2.4 Soil sampling and chemical analysis

One soil core down to 50 cm depth was collected with a 3.5 cm diameter corer in each plot and divided into 10-cm depth increments (i.e., five consecutive 3.5 cm diameter×10 cm depth soil cores for each plot). I chose depth-increment sampling over horizon-based sampling due to thin O horizon and indistinct A/B horizon boundary as well as variability in horizonation across plots.

Initial soil characteristics, including gravimetric moisture content, soil pH (H_2O) and bulk density were measured within 2 weeks after collection. Undecomposed plant debris (twigs <1 cm girth, leaf and other fractions ≤ 1 cm, excluded dead roots or woody debris from fallen stems) was randomly collected from each plot to estimate characteristics of standing litter at the time of collection. Dried samples were ground and sieved to 2 mm after removal of roots and stones. Total C and N concentrations were measured by dry combustion method using an N-C analyzer (CHNS-O Analyzer, Thermo Fisher Scientific, Tokyo, JP).

Samples from depths of 0–10, 10–20, and 20–30 cm were extracted with acid-oxalate (Ox) reagent following the standard protocol. This method dissolves organically complexed, non- and semi-crystalline metals, and also SRO inorganic forms of Fe and Al like allophane and imogolite (Ross and Wang, 1993). Finely ground soil samples of 0.25 g each were extracted with 10 mL of 0.2 M acidified sodium oxalate solution (pH = 3.0), shaken at 150 rpm for 4 h in the dark, followed by centrifugation at 1,500g for 30 min at a room temperature. After standing for 30 min, 5 mL supernatant was pipetted and subjected to suction filtration with a 0.45 µm pore size membrane. The concentration of oxalate-extractable Fe and Al (hereafter referred to as Fe₀ and Al₀) was measured by inductively coupled plasma spectroscopy (ICPS-7510, Shimadzu, Kyoto, JP). Measurement was compared with the results obtained by another lab using two reference samples (Fe₀ concentrations were about 3 mg g⁻¹ and 9 mg g⁻¹, and Al₀ concentration were 1.7 mg g⁻¹ and 4.2 mg g⁻¹). My values tended to be higher by 40%, probably due to difference in centrifugal force and filtration conditions, as selective dissolution techniques were known to be susceptible to extraction conditions and especially filtration (Schuppli et al, 1983; Rennert, 2018), which influenced the amount of material that remained suspended in this case.

Thirty-three samples from depth 20–30 cm depth were also extracted with dithionite-citrate (DC) reagent, which releases Fe oxide phases of any crystallinity and OM-mineral complexes and coprecipitated Al phases (Nitzsche et al., 2022). For each sample, 0.5 g of finely ground soil was extracted by 25 mL of 0.68 M sodium citrate solution to which 0.4 g of dithionite was added. The suspensions were shaken at 150 rpm overnight at room temperature, then centrifuged at 3,000 g for 30 min at 5°C. 0.2 mL supernatant was pipetted after standing for 30 min, then measured for DC-extractable Fe and Al (Fe_{DC} and Al_{DC}) in the same way as Ox extraction. Extraction on 21 out of 33 samples was replicated to assess extraction precision, and correlation indices was 0.87 for Fe_{DC} and 0.77 for Al_{DC}.

2.2.5 Soil redox measurement

Thirty-three of the 35 plots were revisited in 2022 and measured for Eh. For each plot, 3 sampling points were randomly selected while covering within-plot variances (i.e., variance of terrain, species and canopy condition). At each sampling point, three platinum electrodes were inserted vertically down to 10, 20, 30 cm depth of the soil, respectively. No design was made to control the possible influence from recent rainfall events. The Eh reading was collected after a minimum standing time of one hour using a HORIBA D-50 pH/ORP meter. The Eh readings represented the voltage difference between the platinum and standard calomel reference electrodes. At each depth, three Eh readings were averaged and normalized to pH7 (Eh⁷) according to the equation (Rowell, 2014):

$$Eh^7 = Eh - 0.177 (7 - \text{soil pH})$$

to approximate the average redox condition at plot level. I used pH values measured for each identical plot in 2020.

2.2.6 Statistical analyses

Significant differences in the means of above- and below-ground properties related to C,

nitrogen (N), Eh⁷, and Fe and Al minerals between predefined forest categories were tested with ANOVA. A post-hoc test (Tukey's honest significant difference test) was then applied to identify the different group(s) if ANOVA results showed significance. I investigated the relationship between soil C as dependent variable and AGB, intactness, Fe₀ and Al₀ as independent variables with interaction terms using a multivariate linear regression analysis, followed by an AIC-based, two-direction stepwise model selection. Depth was included as an ordinal variable in the model to integrate possible depth-dependent interactions.

For interaction term(s) that were included in the selected model, I conducted a mediation analysis to test the hypothetical causal chain in which one independent variable affects one mediator variable or more intermediary variables which could in turn affect the dependent variable. In this case, soil C would always be taken as the dependent variable. As long as I preconceived the disturbances on above ground vegetation as the initiating factor, AGB would be taken as the independent variable, and the other variable in the interaction term as mediator. Estimates and 95% confidence intervals of average causal mediation effects (ACME; the indirect effect of AGB on soil C via mediators), average direct effects (ADE; the direct effect of AGB on soil C) and the total effect (Total; the direct and indirect effect of AGB on soil C) were generated from bootstrapping procedures with 1,000 simulations. The R package 'mediation' was used for mediation analysis (Tingley et al., 2014).

Samples were grouped into oxic and reductive groups using Eh⁷ = 0.05V as a threshold. This threshold was defined empirically from the starting point that Fe minerals act as electron acceptors in redox reactions as well as anaerobic respiration (Weber et al., 2006; Barcellos et al., 2018; Zhang et al., 2020). A full multivariate logistic model was constructed that included AGB, TWI, pH, ordinal variable depth and their interaction terms independent variables to predict whether the redox status was oxic or reductive. Variables that did not significantly reduce residual standard error were dropped with Chi-square test. The 95% confidential interval of prediction was estimated from 10,000 simulations using the R package 'propagate' (Spiess, 2018).

Mean AGB and Fe₀ stocks in top–30 cm soils were compared between the oxic vs. reductive groups with a t-test. The correlation between Eh⁷ and Fe₀ concentration was further analyzed at every 10 cm depth with 95% confidence ellipses. Also, taking C/N ratio as an indicator of SOM quality (i.e., increasing C/N ratio indicates less decomposed SOM with a short turnover time), I analyzed the correlation between C/N ratio and Fe₀ concentration with 95% confidence ellipses. Considering the inadequacy of sample size, all estimation of confidence ellipses was based on a multivariate t-distribution. All data analyses were performed using R version 4.2.2 (R Core Team 2022).

2.3 Results

2.3.1 Significant variation of above and-below ground properties existed among vegetation categories

Summary statistics for top–30 cm soil properties and vegetation categories were listed

in Table 2.1. As for the above ground, average AGB for categories 1 and 2 (intact and least degraded forests) exceeded 400 Mg ha⁻¹, but dropped to about 1/7 for category 5 (most degraded forest). In addition, intactness also decreased significantly in categories 4 and 5, indicating that the degradation of above ground vegetation was not only happened in terms of AGB loss but also tree-community composition change.

As for the below ground, soil C and N stock, pH, Eh⁷, Fe₀ and Al₀ stocks showed significant differences among vegetation categories. In more degraded categories, soil Eh⁷, C, N and SRO Fe stocks decreased significantly while pH increased. Using the empirical value of 0.05 V as the threshold for oxic and reductive conditions, the upper 30 cm soils in category 1 and 2 belonged to oxic and those in category 4 and 5 to reductive. Al₀ stock was significantly higher only in category 2 and showed a considerable variation in the most degraded vegetation (category 5).

The correlation between C/N ratio and degradation gradient was more depth dependent. Litter and surface soil (0–10 cm) C/N showed no difference between vegetation categories, but in 20–30 cm soil, C/N ratio increased significantly in more degraded vegetation. It is also inferable that in more degraded vegetation, C/N ratio decreased more drastically from surficial to deeper soils.

An increase in average bulk density was observed in 0–50 cm soils along the degradation gradient from vegetation category of 1 to 5. However, the change was not statistically significant. Fe_{DC} concentration did not vary significantly among vegetation categories, but the minimum value was observed in category 1, i.e., pristine forests.

2.3.2 Effects of AGB and Fe₀ concentration on soil C concentration in top-30 cm soil

The results of the selected multivariate linear model predicting soil C in top-30 cm are showed in Table 2.2 (for which intactness was not included as it was highly collineated with AGB, see Fig. S2.2.1A). In the model explained over 60% of soil C variation, both AGB and Fe₀ concentration had positive association with soil C. As an ordinal variable, depth was also significantly related to soil C. However, the predictive power of selected model differed between depths. Predicted and observed values were plotted in pairs in Fig. 2.2A and 2B, where a larger standard residual can be seen in the top–10 cm soil.

The selected interaction term (AGB:Fe₀) was further analyzed with mediation analysis. I examined the direct and indirect effects of AGB on soil C mediated by Fe₀ at every 10 cm soil (Fig. S2.2). Estimation and confidence intervals of three types of hypothetical causal effects were plotted in Fig. 2.2C, where an interval above 0 indicated statistical significance. ACME, here representing the effect of AGB on soil C via Fe₀, increased in deeper soils and was significant in 20–30 cm, and its proportion in Total (the proportion of the total effect of AGB on soil C that is via Fe₀) showed that the effect of AGB on soil C was about 43% mediated by Fe₀ at this depth.

2.3.3 AGB and Fe₀ stock differed significantly between oxic and reductive soil groups, and C/N ratio correlated with Fe₀ loss in deeper soils

The selected models predicting Eh⁷ are listed in Table 2.3. Only AGB was found to be a significant predictor variable. Depth and TWI did not significantly reduce model residual

deviation, suggesting that E_h^7 did not vary significantly among depths in top–30 cm soils, and the local soil moisture along this degradation gradient was driven primarily by vegetation rather than terrain factors (Table S2.4).

Fig. 2.3A illustrated the logistic relationship between AGB and E_h^7 . Note that the regression line represented the predicted probability of a soil sample being oxic (i.e., taking the value of 1) but was scaled to the range of E_h^7 (–0.08 to 0.58 V) in Fig. 2.3A. In top–30 cm soils, E_h^7 decreased (i.e., soil switched to a reductive status) at an accelerating rate as AGB decreased before reaching a threshold around 200 Mg ha^{–1}. To be specific, in pristine-like, high-AGB forests (i.e., category 1 or 2, Fig. 2.1), disturbances that removed about half of the original AGB promoted E_h^7 declination in top–30 cm soils. On the other side, restoration of AGB in highly degraded areas, in this study 9.64 Mg ha^{–1} marked the lowest observation, may not necessarily raise E_h^7 to an oxic regime unless AGB approached the threshold at around 200 Mg ha^{–1}.

Fig. 2.3B showed the relationship between E_h^7 and Fe₀ concentration in the two redox groups. In the oxic group, E_h^7 and Fe₀ concentration showed moderate correlation only in 20–30 cm soil (Pearson's $r = 0.48$), while no significant correlation was found at any depth in the reductive group; and more notably, Fe₀ concentration varied widely within a small range of E_h^7 in the reductive group (Fe₀: 0.18 to 6.48 mg g^{–1}; E_h^7 : –0.08 to 0.05 V), which probably reflecting effects from parent materials but the lowest concentration at each depth was always found in the reductive group.

Based on soil redox regime, I then compared AGB and Fe₀ stock in top–30 cm soils (Fig. 2.3C). Average AGB of the reductive group was below 200 Mg ha^{–1}, significantly lower than the oxic group which was nearly 400 Mg ha^{–1}. Simultaneously, the reductive group had a lower Fe₀ stock at every 10 cm depth and in the top–30 cm gross. T-test on Fe₀ stock at every 10 cm depth showed that the difference between oxic/reductive groups was significant in 0–10 and 10–20 cm soil ($p < 0.01$ and $p < 0.05$, respectively, data not showed) but nonsignificant in 20–30 cm soil.

Fig. 2.3D showed that the correlation between C/N ratio and Fe₀ concentration differed between oxic/reductive groups at each 10 cm depth. No significant correlation was observed between the two variables in the oxic group, but in the reductive group, there were significant positive correlations in 10–20 cm and 20–30 cm soils (Pearson's $r = 0.76$ and 0.95 , respectively). However, in addition to the distinctly different correlation pattern, the ellipses of the two groups overlapped to a large extent in the 20–30 cm soil, indicating that the average Fe₀ concentration and the C/N ratio may not be significantly different at this depth.

2.4. Discussion

In this chapter, I observed simultaneous decreases of intactness and AGB in the above ground, and SRO Fe, C and N stocks in the below ground (Fig. 2.1). These results supported my hypothesis on the logging-induced SOC loss: decrease in AGB, significantly limiting plant-derived OM inputs; and decrease in SRO Fe oxides, destabilizing some mineral-associated SOM. Mediation analysis revealed that the two pathways are indeed not mutually

exclusive. Lower AGB was always related to lower SRO Fe concentration in top–30 cm soils (Fig. S2.2), and 43% of the hypothetical causal effect of AGB loss on SOC decline is mediated by SRO Fe in deeper soils (Fig. 2.2C), where SOC stocks are believed to have a longer turnover time due to mineral protection (Wade et al., 2019).

Decreasing soil E_h^7 , the direct factor of SRO Fe mineral reduction, corresponds to AGB loss according to the result of a logistic analysis (Fig. 2.3A). When AGB is as high as pristine forests, soil remains in the oxic regime down to 30 cm depth, then declines rapidly as AGB falls to about 200 Mg ha⁻¹, and finally shifts to the reductive regime when over half of AGB is removed from the pristine level (Fig. 2.3A). This 'reductive shift' in logged forests (which can be identified by significantly lower AGB) substantially reduces SRO Fe minerals in top–30 cm soils (Fig. 2.3B, 3C). In the reductive regime, the loss of SRO Fe varied considerably compared to the equilibrium status in oxic regime (Fig. 2.3C), revealing a combined effect of parent material and redox change in logged forests. Nevertheless, in reductive soils, increasing SRO Fe loss appears to leave behind more microbially-processed SOM characterized with low C/N ratio (Fig. 2.3D).

Note that although AGB was found to be the single predictive variable in the selected model (Table 2.3), its collinearity with intactness (Fig. S2.2.1A) implies that AGB loss is accompanied by changes in tree-community composition and, more specifically, the functional traits of trees in logged forests. From this perspective, the different investment strategies of dominant and pioneer species are thought to drive soil E_h^7 through evapotranspiration, thereby controlling soil moisture and water movement between horizons. Overall, these results demonstrate how selective logging may affect key processes of SOC sequestration in tropical timber-producing forests, and further indicate the impact of vegetation degradation on soil C pools on a decadal time scale.

2.4.1 Reduced canopy, recruitment and rooting weaken evapotranspiration and hence reduce soil E_h^7

In the humid tropics, soil redox dynamics have been observed to vary with effective moisture which is defined as precipitation minus potential evapotranspiration (Hall et al., 2012; Barcellos et al., 2018; Kramer et al., 2018). Characterized with high precipitation (annual average exceeds 3,000 mm) with minor seasonality, maintaining evapotranspiration is crucial to a balanced soil water budget in my study area. The logistic relationship observed between soil E_h^7 and AGB revealed a different, unbalanced pattern of water redistribution, most likely a result of suppressed transpiration due to forest degradation.

Vegetation structural attributes, including density and canopy roughness, strongly influence canopy transpiration (Jucker et al., 2018). Previous study has found that during succession after logging, pioneer species tend to invest more resources in woody structure rather than expanding the crown (Mills et al., 2023), which inevitably leads to a shrinking leaf area index and therefore weakens transpiration. In addition, there has been insufficient recruitment of climax species in degraded forests (Takeshige et al., 2022), which also has an impact on crown size. Sawada et al. (2022) studied the size distribution of *Shorea* trees, the dominant genus in lowland dipterocarp forest and canopy layer in Deramakot and

Tangkulap Forest Reserves. A remarkably decreasing number and proportion of *Shorea* seedlings was observed in degraded forests, indicating a failure of continuous succession and hence the formation of a well-developed canopy layer.

In addition to the reduced canopy size, I also found less root amount and shallower rooting in degraded forests (personal observation, Qin). From two soil profiles down to 1 m depth randomly selected in plots belong to vegetation categories 1 through 5, the maximum root depth extending to about 60 cm depth and no more than 20 cm depth, respectively. Roots play an instrumental role in soil aggregate formation, as growing roots physically alter soil minerals, root-associated microorganisms release weathering agents that mobilize essential soil nutrients, and below-ground rhizodeposition can directly associate with soil minerals (Witzgall et al., 2024). Reduced root contents have directly limit the formation of mineral-associated SOM. In turn, the destruction of aggregates reduces soil macropores and infiltration rate. Increasing soil bulk density in more degraded forests implies fewer pores and root channels in 0–50 cm soils, which may have a great impact on the vertical movement of water between horizons, limiting infiltration in upper layers and raising water table. In a decadal timespan, the combined effect of reduced canopy and rooting may lead to the prolonged reductive condition in top–30 cm soils.

2.4.2 Soil redox condition shapes SRO Fe mineral reduction

As increased effective soil moisture creates a waterlogged, O₂-depleted condition (and other low-valence metal ions, mainly be removed in the early stages of soil weathering), Fe (hydr)oxides act as electron acceptors in anaerobic respiration and/or redox reactions. The conventional kinetic expectation is that the most reactive, SRO Fe solid phases are preferentially dissolved in a reductive dissolution-dominated environment (Thompson et al., 2011) and could be eluted or leached under a humid climate. This process influences both the amount and horizontal distribution of SRO Fe in the soil profile, which may explain the mostly significant decrease of SRO Fe stock in surficial soil (Fig. 2.3C) that receives direct influence from above ground disturbances.

Despite leaching in stagnant soil environment, SRO Fe minerals could also be transformed into more thermodynamically stable phases, i.e., increased crystallinity, under a fluctuating oxic environment (Bhattacharyya et al., 2018). Considering the fact that Fe_{DC} showed nonsignificant difference along degradation gradient and the range of pH is overall acidic (Fig. 2.1), thermodynamic transformation of SRO Fe minerals probably occurs in some soils in the reductive group as well.

In both processes, the OM-mineral association between SOM and SRO Fe minerals can be destructed, and the sorbed OM becomes more soluble to be released as dissolved SOC which is susceptible to microbial respiration. In at least the top-30 cm soils, SRO Fe mineral contents are lost in either way and the same applies to soil C sequestration capacity, i.e., the size of 'protected C pool'.

2.4.3 The long-term effect of SRO Fe mineral loss on soil C pool in degraded tropical forests

Although C chemistry of the studied litter and soils is unclear, a higher C/N ratio is

recognized to represent more undecomposed, plant-derived OM with low degrees of microbial alteration (Nitzsche et al., 2022). The nonsignificant difference of C/N ratio along degradation gradient in litter and 0–10 cm soil implies a surficial-concentrated distribution of fresh, less microbial decomposed OM in humid tropic soils (Fig. 2.1). While in deeper soil, increasing loss of SRO Fe is significantly correlated with lower C/N ratio under a reductive condition (Fig. 2.3D). These two lines of evidence together imply consumption of the less degraded SOM resulting from (1) lower OM input as AGB decreases, which limits substrate for soil microbes (Jiang et al., 2022), and (2) increased reducibility of protected SOM under reductive conditions because of the destruction of OM-mineral association. It provides a viable explanation for previous studies conducted in logged lowland tropical forests, where C loss from old SOM has been found to be the major source of net C emissions at a decadal time scale (Dean et al., 2017; Riutta et al., 2020; Mills et al., 2021).

The current structural change in soil C pools could be long-lasting since the reformation of SRO Fe minerals is hardly predictable on an ecological time scale, implying that SOC stocks may not return to the baseline level even with successful AGB restoration after decades. I therefore propose the necessity to adapt reduced-impact logging methods for the purpose of soil C pool conservation as well. Indeed, when comparing data from intact forests or undergo reduced-impact logging, i.e., categories 1 and 2, I observed only subtle differences in terms of AGB, intactness, soil C, N content, redox potential and SRO Fe minerals (Fig. 2.1). This evidence reconfirms the effectiveness of reduced-impact logging methods for sustainable forest management not only in the above ground but also in the soil environment, both of which are crucial for maintaining C sequestration in tropical timber-producing forests (Imai et al., 2009; Mori et al., 2018).

2.5 Conclusion

In this chapter, I demonstrated that in tropical timber producing forests, soil C stock decline is induced by a twofold mechanism of AGB loss and SRO Fe minerals reduction. The former limits OM input to the 'unprotected C pool', while the latter destabilizes the protected SOM that constitutes the "protected C pool". Specifically, in deeper soils, SRO Fe mineral mediates up to 40% of SOC loss associated with AGB reduction in logged tropical rainforests in North Borneo (Fig. 2.2C). It is the soil redox shift that links the two mechanisms, which can largely be explained by the reduced evapotranspiration resulting from forest degradation. I highlight that SRO Fe mineral loss can be long-lasting, thus limiting soil C sequestration capacity, which further indicates that even with replenishment of OM input through vegetation recovery, soil C stocks may not regain their original size or structural composition. The results have implications for current understanding of ecosystem models simulating SOM dynamics and management of timber production in the tropics.

Tables

Table 2.1 Summary of the measured characteristics of each vegetation category and soil properties in top–30 cm (n = 35). Showed are Mean (S.D.)

Characteristics	Vegetation categories				
	1	2	3	4	5
Intactness	0.17 ^a (0.07)	0.16 ^{ab} (0.05)	0.08 ^b (0.09)	–0.06 ^c (0.07)	–0.37 ^d (0.12)
AGB (Mg ha ^{–1})	458.02 ^a (87.48)	409.59 ^a (125.66)	275.10 ^b (66.77)	254.07 ^b (97.42)	55.85 ^c (42.02)
Soil C stock ^(a) (kg m ^{–2} , 0–50 cm)	42.11 ^a (5.70)	40.19 ^a (6.71)	36.05 ^a (10.21)	41.02 ^a (8.30)	25.38 ^b (13.15)
Soil N stock ^(a) (kg m ^{–2} , 0–50 cm)	4.09 ^{ab} (0.38)	4.52 ^a (0.18)	4.00 ^a (0.83)	3.59 ^{bc} (0.61)	3.05 ^c (1.03)
Litter C/N	37.62 (9.20)	30.75 (2.90)	35.78 (6.03)	35.50 (4.33)	37.67 (9.57)
Surficial soil C/N (0–10 cm)	12.32 (1.43)	11.24 (1.88)	11.08 (1.61)	13.56 (3.73)	12.85 (2.91)
Deeper soil C/N (20–30 cm)	10.12 ^a (2.38)	8.05 ^{ab} (0.94)	7.48 ^b (1.24)	8.85 ^{ab} (2.09)	6.13 ^b (3.38)
Bulk density ^(b) (g cm ^{–3} , 0–50 cm)	0.74 (0.13)	0.78 (0.07)	0.79 (0.17)	0.82 (0.06)	0.92 (0.08)
pH ^(b)	4.75 ^{ab} (0.15)	4.71 ^a (0.16)	4.94 ^b (0.22)	4.89 ^{ab} (0.55)	5.46 ^c (0.14)
Eh ⁷ ^(b) (V, n = 33)	0.51 ^a (0.05)	0.44 ^a (0.07)	0.20 ^b (0.07)	0.02 ^c (0.08)	–0.03 ^c (0.02)
Fe_o stock (mg cm ^{–2})	98.17 ^{ab} (33.62)	132.46 ^a (27.83)	90.12 ^b (19.03)	65.25 ^c (17.37)	60.40 ^{bc} (47.95)
Al_o stock (mg cm ^{–2})	60.35 ^{ac} (20.53)	84.55 ^b (7.69)	55.43 ^{ac} (9.69)	51.63 ^{ac} (18.38)	71.56 ^{abc} (35.70)
Fe _{DC} (mg g ^{–1} , n = 33, 20–30 cm)	14.74 (3.37)	20.77 (4.66)	26.13 (12.98)	19.69 (4.81)	26.08 (11.40)

* Characteristics marked in bold: means that are significantly different between vegetation categories suggested by the results of ANOVA ($p < 0.05$). A post-hoc test (Tukey's honest significant difference test) was then applied to identify the different group(s). AGB: above-ground biomass. Eh⁷: redox potential normalized at pH=7. Fe_o and Al_o: oxalate-extractable Fe and Al, here representing short-range-ordered Fe and Al. Fe_{DC}: dithionite-citrate extracted Fe, here representing total Fe.

^(a) Sum of five measurements every 10 cm depth of 0–50 cm soil.

^(b) Average of five measurements every 10 cm depth of 0–50 cm soil.

Table 2.2 Multivariate linear equation predicting soil C concentration (n = 91)

Estimated		C concentration (Response variable, mg g ⁻¹)
		Selected model*** (df = 85)
		$g(C) = f(AGB, Fe_o, interaction\ term, depth)$
AGB (Mg ha ⁻¹)		0.03**
Fe _o (mg g ⁻¹)		1.61**
depth ^(a)	depth1	-10.32***
	depth2	-12.66***
Interaction	AGB:Fe _o	<-0.01*
Intercept		11.08***
AIC		292.26
Adj. R ²		0.61

* AGB: above-ground biomass. Fe_o: oxalate-extractable Fe, here representing short-range-ordered Fe.

Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot$ $p < 0.05$; n.s. $p > 0.05$.

^(a) The ordinal variable depth was labelled as follow: *depth0*: 0–10cm, labeled as 0; *depth1*: 10–20cm, labeled as 1; *depth2*: 20–30cm, labeled as 2.

^(b) For the original full model, see supplementary Table S2.2.2.

Table 2.3 Multivariate logistic equation model that significantly predicted soil redox regime (n = 91)

Estimated	Eh ⁷ (Response variable, binomial)
	Selected model ^{***}
	$g(\text{redox regime}) = \text{logit}(\text{AGB})$
AGB (Mg ha ⁻¹)	0.02 ^{***}
Intercept	-4.28 ^{***}
Residual standard error	0.82 (df = 89)
AIC	64.49

* AGB: above-ground biomass.

Significance codes: ^{***} $p < 0.001$; ^{**} $p < 0.01$; ^{*} $p < 0.05$; [·] $p < 0.05$; ^{n.s.} $p > 0.05$.

^(a) The ordinal variable depths were labelled with numbers. *Depth0*: 0–10cm, labeled as 0; *depth1*: 10–20cm, labeled as 1; *depth2*: 20–30cm, labeled as 2.

^(b) For the original full model, see supplementary Table S2.2.4.

Figures

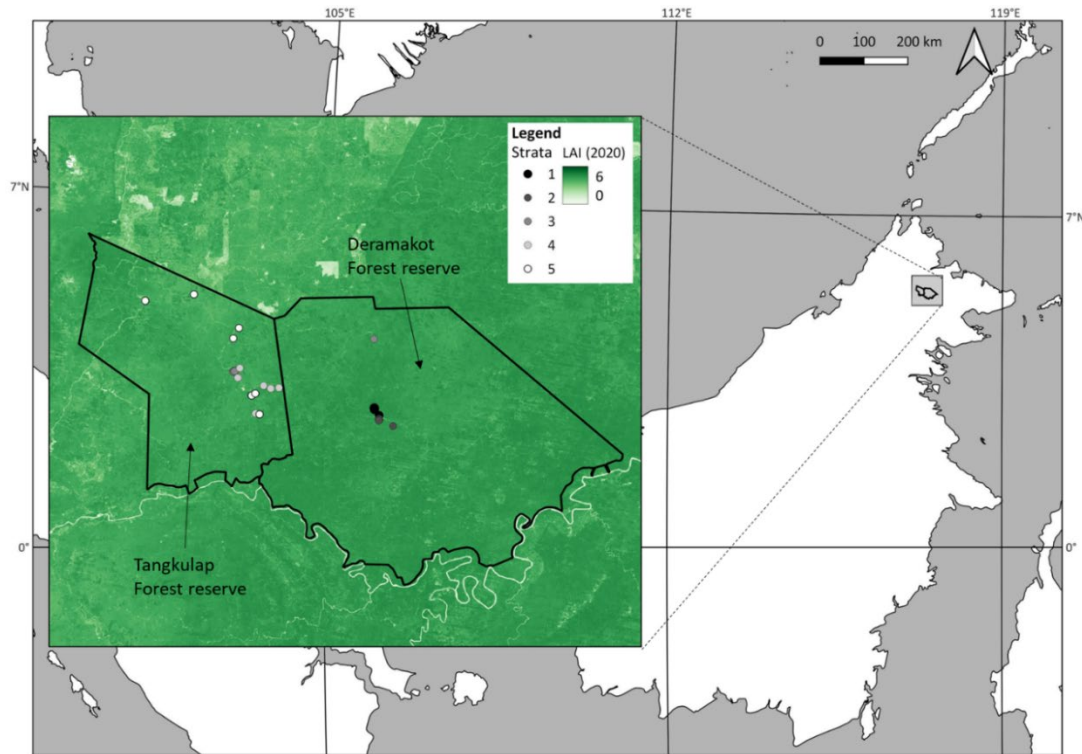


Fig. 2.1 Locality of the two study sites; Deramakot Forest Reserve, and Tangkulap Forest Reserve, Sabah, Malaysia. Points indicate sampling plots ($n = 35$), which are stratified by Landsat 7 Band 7 (shortwave infrared reflectance) to five strata (1-5), corresponding to vegetation categories of increasing degrees of forest degradation (1 = pristine, 5 most degraded). Leaf Area Index (LAI) was calculated from an annual mosaic Landsat image of the year 2020 following the equation: $LAI = 0.57 \times e^{2.33 \times NDVI}$, where NDVI (Normalized Difference Vegetation Index) was calculated as the normalized difference between Landsat Band 4 (red) and Band 5 (near-infrared). Derived LAIs indicate the study area is highly heterogeneous in above-ground vegetation due to past logging.

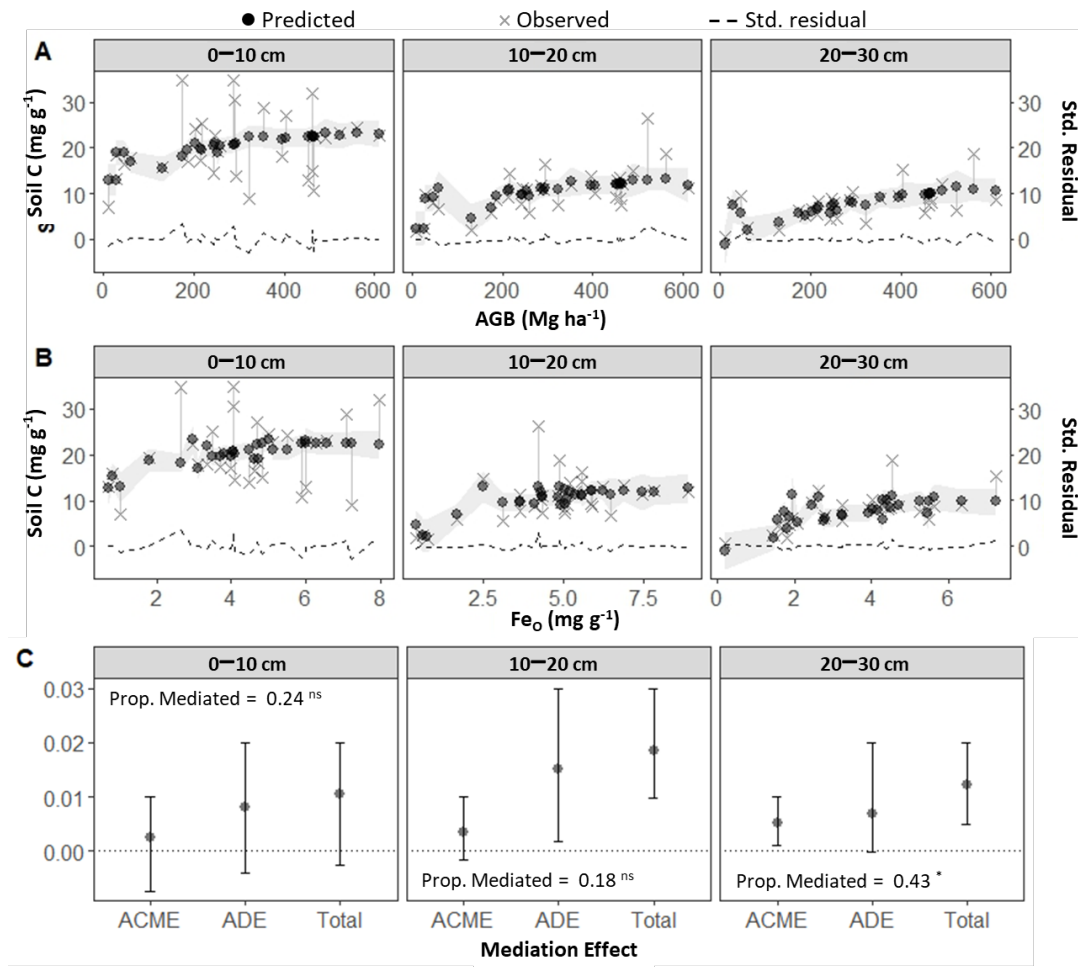


Fig. 2.2 (A) and (B) Multivariate linear regression analysis ($n = 33$) on the top–30 cm soils, equation listed in Table 2.2. Crosses represented observed values, black circles represented predicted values, grey lines linked pairs of observation and prediction. Shadows represented 95% confidence interval. Dashed lines represent standard residuals. (C) Mediation analysis ($n = 33$) on the top–30 cm soils, for scheme plot see Fig. S2.2.2, for simulation results see Table S2.3. Points and error bars represented the estimated mean and 95% confidence interval, respectively. A confidence interval exceeding 0 suggests statistical significance. *ACME*: average causal mediation effects (effect of AGB on soil C via Fe₀), *ADE*: average direct effects (effect of AGB on soil C not via Fe₀), *Total*: sum of ACME and ADE (the effect of AGB on soil C via and not via Fe₀), *Prop. Mediated*: the proportion of ACME in Total.

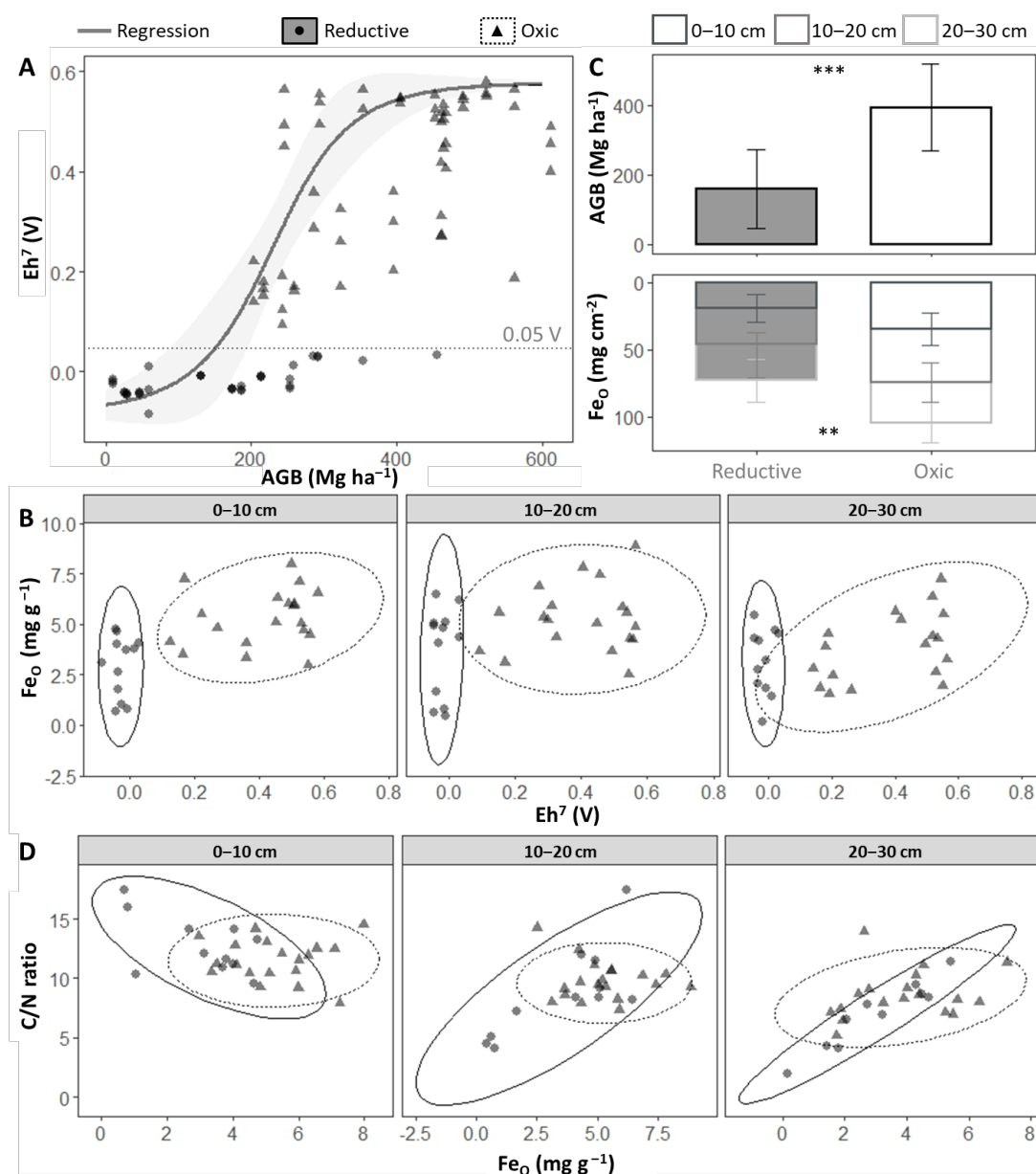


Fig. 2.3 (A) Logistic model fitted to soil redox of top–30 cm soils ($n = 91$, 0 for $Eh^7 < 0.5$, 1 for $Eh^7 > 0.5$), as coefficient summarized in Table 2.3. Points represent actual Eh^7 values, even though logistic curves were result of fitting to oxidic (1) vs. reduced (0). Shadows represented 95% confidential interval. Dashed line marked the threshold $Eh^7 = 0.05\ V$. (B) 95% confidence ellipse of Eh^7 and Fe concentration in oxidic/reductive groups, top–30 cm soils. (C) AGB and Fe_0 stock in top–30 cm soils every 10 cm depth in oxidic/reductive groups. AGB and the gross stock of Fe_0 in top–30 cm soils were compared between the two groups with t-test ($p < 0.01$). (D) 95% confidence ellipse of Fe_0 concentration and C/N ratio (concentration based) in oxidic/reductive soil groups, top–30 cm soils.

Supplementary**Table S2.1** Classification and description of the level of forest degradation for sampling plots (RIL: reduced-impact selective logging; CL: conventional selective logging)

Category	Description
1	No logging evidence, has >4 big trees (>60 cm dbh). <i>Dipterocarps</i> individuals exist.
2	Fewer big trees than class 1, <i>Dipterocarps</i> individuals exist. Experienced RIL.
3	A few big trees and several pioneer species individuals exist (<i>Macaranga</i> , <i>Neolamarckia</i> , etc.). Experienced CL.
4	No big trees and more pioneer species exist. Gaps in the canopy. Experienced CL.
5	Few or no pioneer species and open canopy, mostly covered by fern thickets. Experienced CL.

Table S2.2 Full multivariate linear equation predicting soil C concentration (n = 91)

Estimated	C concentration (Response variable, mg g ⁻¹)	
	Full model*** (df = 73)	
	$g(C) = f(AGB, Fe_o, Al_o, interaction\ terms, depth)$	
AGB (Mg ha ⁻¹)		0.02 n.s.
Fe _o (mg g ⁻¹)		1.54 n.s.
Al _o (mg g ⁻¹)		-0.92 n.s.
depth ^(a)	depth1	-13.82 n.s.
	depth2	16.13 n.s.
Interaction terms	AGB:Fe _o	<-0.01 n.s.
	AGB:Al _o	<0.01 n.s.
	AGB:depth1	<0.01 n.s.
	AGB:depth2	<0.01 n.s.
	Fe _o :depth1	0.09 n.s.
	Fe _o :depth2	0.20 n.s.
	Al _o :depth1	0.24 n.s.
	Al _o :depth2	1.96 n.s.
	AGB:Fe _o :depth1	<-0.01 n.s.
	AGB:Fe _o :depth2	<0.01 n.s.
	AGB:Al _o :depth1	<-0.01 n.s.
	AGB:Al _o :depth2	-0.02 n.s.
Intercept		13.97 [*]
AIC		308.15
Adj. R ²		0.59

* Significance codes: *** p < 0.001; ** p < 0.01; * p < 0.05; • p < 0.05; n.s. p > 0.05.

(a) The ordinal variable depth was labelled as follow: depth0: 0–10cm, labeled as 0; depth1: 10–20cm, labeled as 1; depth2: 20–30cm, labeled as 2.

Table S2.3 Estimated means and confidential intervals in mediation analysis basing on 1,000 simulations for three soil depths.

Depth (cm)	Name	Estimation	Lower	Upper	Significance
10	ACME	0.00	-0.01	0.01	0.60
	ADE	0.01	0.00	0.02	0.18
	Total	0.01	0.00	0.02	0.10
	Prop.	0.24	-2.40	2.25	0.54
20	ACME	0.00	0.00	0.01	0.12
	ADE	0.02	0.00	0.03	0.03
	Total	0.02	0.01	0.03	0.00
	Prop.	0.18	-0.03	0.85	0.12
30	ACME	0.01	0.00	0.01	0.02
	ADE	0.01	0.00	0.02	0.06
	Total	0.01	0.00	0.02	0.00
	Prop.	0.43	0.10	1.03	0.02

* *ACME*: average causal mediation effects (effect of AGB on soil C via Fe_o), *ADE*: average direct effects (effect of AGB on soil C not via Fe_o), *Total*: sum of ACME and ADE (the effect of AGB on soil C via and not via Fe_o), *Prop.*: the proportion of ACME in Total.

Table S2.4 Full multivariate logistic equation predicting soil redox regime (n = 91)

Eh ⁷ (Response variable, binomial)		
Estimated	Full model***	
<i>g(redox regime) = logit(AGB, pH, TWI, depth, interaction terms)</i>		
AGB (Mg ha ⁻¹)	0.03 [*]	
pH	1.53 ^{n.s.}	
TWI	-0.66 ^{n.s.}	
depth ^(a)	depth1	-1.77 ^{n.s.}
	depth2	-3.69 ^{n.s.}
Interaction terms	AGB:depth1	-0.01 ^{n.s.}
	AGB:depth2	-0.01 ^{n.s.}
	pH:depth1	-1.48 ^{n.s.}
	pH:depth2	-1.14 ^{n.s.}
	TWI:depth1	0.83 ^{n.s.}
	TWI:depth2	0.81 ^{n.s.}
Intercept	-4.99 ^{n.s.}	
Residual standard error	0.84 (df = 85)	
AIC	79.26	

* Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ^{*} $p < 0.05$; n.s. $p > 0.05$. TWI: topographic water index.

^(a) The ordinal variable depths were labelled with numbers. *Depth0*: 0–10cm, labeled as 0; *depth1*: 10–20cm, labeled as 1; *depth2*: 20–30cm, labeled as 2.

Table S2.5 Summary statistics of topographic characteristics among vegetation category (n = 35)

Category	Mean (S.D.)				
	1	2	3	4	5
Elevation (m)	234.50 ^a (22.53)	186.57 ^b (12.69)	76.29 ^c (6.70)	78.83 ^c (22.35)	85.43 ^c (15.24)
Slope (°)	12.72 ^a (7.73)	6.65 ^a (2.20)	7.42 ^a (3.90)	7.70 ^a (4.16)	5.89 ^b (3.24)
TWI ^(a)	13.25 ^a (0.71)	13.98 ^{ab} (0.64)	15.50 ^{ab} (3.37)	14.24 ^b (0.85)	15.12 ^b (1.98)

* Variables showed significant differences (ANOVA $p < 0.05$) are marked in bold. All data acquired from the NASA SRTM Digital Elevation Model (DEM) at 30 m spatial resolution.

^(a) TWI (topographic water index) was firstly calculated for the whole scene (Entity ID: NASADEM_HGT_n05e117) at each cell in the DEM, and then extracted for each sampling plot basing on plot centers. We used a deterministic single-flow algorithm (i.e., for a single cell, flow will be routed to the steepest downslope neighbor) and a flow dispersion 1.0 (Kopecký et al., 2021).

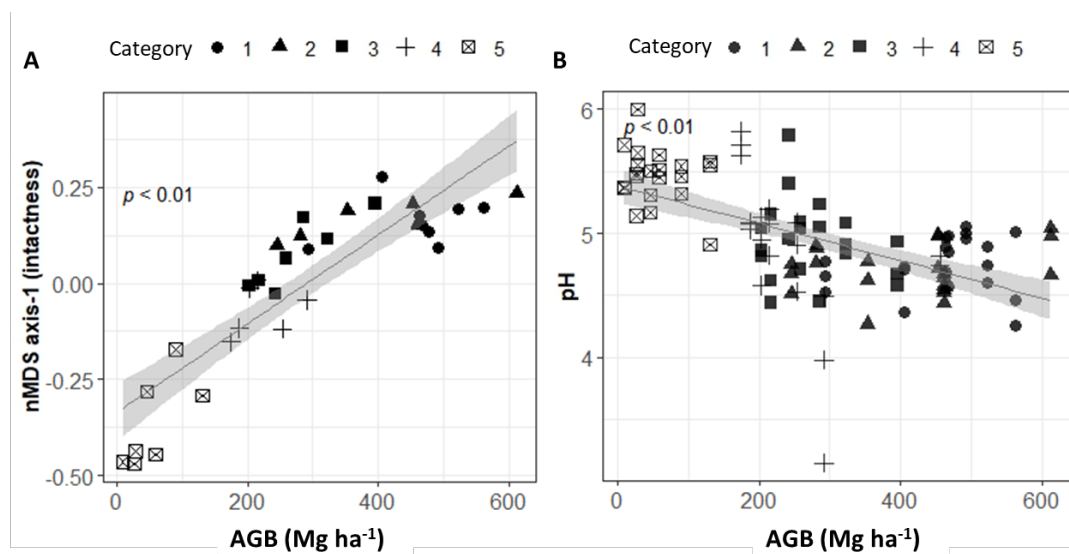


Fig. S2.1 (A) Simple linear regression between AGB and nMDS axis-1 value, which was referred to as intactness. (B) Simple linear regression between AGB and pH in top-30 cm soils. Different vegetation categories are indicated with different symbols. Regression significance is showed in the plot.

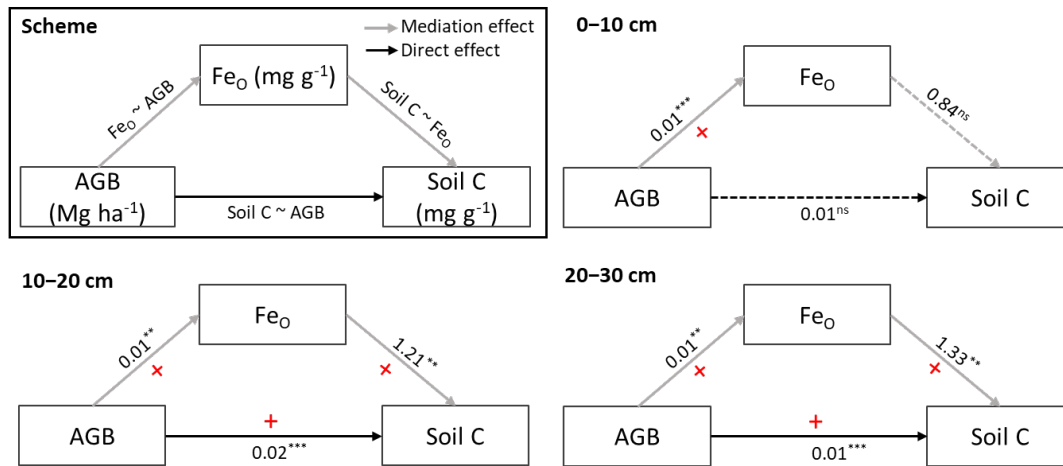


Fig. S2.2 Scheme plot of the mediation analysis. Numbers aligned with arrows represented the linear regression coefficients, presented with significance. It can be seen that at each depth, AGB and Fe_0 were always positively related. Soil C was significantly and positively related with AGB and Fe_0 in 10–20 and 20–30 cm soils.

* Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; · $p < 0.05$; n.s. $p > 0.05$

Chapter 3

Canopy structural degradation triggers soil water regime shift in logged Bornean lowland tropical forest

Based on publication

Qin, Q., Aoyagi, R., Takeshige, R. & Kitayama, K. Soil wetting triggered by selective logging in Bornean lowland tropical rainforests. *For. Ecol. Manag.* **569**, 122181 (2024) doi: 10.1016/j.foreco.2024.122181.

Abstract

Aboveground biomass removal and canopy opening by selective logging modifies soil moisture in the main root zone, impacting soil aeration and various biogeochemical processes in tropical production forests. This study investigated the relationship between canopy damage and topsoil (10 cm) moisture in two logged forests in Malaysian Borneo, while simultaneously controlling for logging intensity, time elapsed since historical logging, and topography. Volumetric soil water content (VSWC), canopy height model (CHM), leaf area index (LAI), and historical logging data were collected from 84 transects placed subjectively in 15 sites exhibiting varying canopies. We generated an index (PC1) quantifying the magnitude of canopy structural degradation from canopy structure metrics (CSM) combining CHM and LAI data within a 20-meter buffer for each transect. PC1 was analyzed for its impact on VSWC across logging periods, and contrasted with topography. VSWC was significantly higher in all logged forests (over $0.4 \text{ m}^3 \text{ m}^{-3}$) comparing to non-disturbed forests ($0.27 \text{ m}^3 \text{ m}^{-3}$). The immediate wetting could be a result of extracting mature individuals of late-successional species holding large biomass, while the persistent wet condition may be due to retarded canopy structure and biomass recovery. In the study area, canopy structure was a stronger predictor of soil moisture than topography. This study revealed soil wetting after selective logging in humid tropical forests, driven by reduced transpiration from biomass loss rather than increased evaporative demand on soil resulting from canopy opening. The elevation in soil moisture could have disrupted biogeochemical processes in the below-ground system, which in turn impede forest succession and put stress on the overall vulnerability of disturbed tropical rainforests.

Key words: Forest degradation; Selective logging; Soil moisture; Leaf area index; Canopy height model

3.1 Introduction

Soil moisture plays a crucial role in various aspects of forest ecosystems, including plant transpiration and photosynthesis, soil biogeochemical processes via soil oxygen concentration, and mediates influences from precipitation and radiation anomalies (Seneviratne et al., 2010; Hall et al., 2013; Barcellos et al., 2018). The regulation of soil moisture in forests is primarily through evapotranspiration (ET), which consists of evaporation from canopy-intercepted water, soil, open water, and transpiration from plants (Wei et al., 2017). Previous studies across climate zones have consistently demonstrated that deforestation decreases mean annual ET and increases runoff at the catchment level (Wiekenkamp et al., 2016; Zhang et al., 2017). This change in the water balance could increase soil moisture, shifting the main root zone to wetter, oxygen-deficit conditions (Hall et al., 2015; Zhang et al., 2021). Such shift can generate important feedbacks in both above- and below-ground ecosystems, including redox-sensitive biogeochemical reactions (Hall et al., 2013), inhibited plant growth (Santiago et al., 2000; Mattos et al., 2023), and higher background tree mortality (Ferry et al., 2009).

In equatorial tropical rainforests, ET typically proceeds at its potential rate and is primarily regulated by plant physiology (Bonell and Hufschmidt, 2005; Kitayama et al., 2020), therefore governs water recycling in these ecosystems (Salati and Vose, 1984). However, timber extraction has led to an expansion of disturbed and degraded forests with altered canopy structure and biomass (Hosonuma et al., 2012), affecting ET and soil moisture through complex interactions (Senior et al., 2018). Selective logging is the primary form of timber production in Southeast Asia, which targets mature, commercially valuable individuals of dominant species, causes changes in canopy coverage, height, tree density, and leaf area index (LAI) (Slik et al., 2013; Bousfield et al., 2023; Santos et al., 2024). This disruption reduces thermal buffering, enhancing water evaporation from the soil surface while potentially suppressing canopy transpiration and intercepted evaporation (Senior et al., 2010; Jucker et al., 2018; Santos et al., 2024), which together brings uncertainties to total ET and soil moisture. Although impacts on the forest floor may diminish as logged forests recover (Asner et al., 2004; Senior et al., 2018), the role of large trees of dominant species in local hydrological regimes may not be fully compensated within decades (Lindenmayer et al., 2012). This is due to the fact that in well-developed forests ($LAI > 4$), canopy transpiration is mainly influenced by the maximum stomatal conductance determined by the water use strategy of dominant species.

For these reasons, canopy characteristics are commonly incorporated into observational and modeling studies on vegetation-soil moisture coupling (Hardwick et al., 2015; Banerjee and Linn, 2018; Milodowski et al., 2021), among which canopy structural variability and LAI have emerged as particularly robust and widely applicable. Canopy structural variability can be described using metrics related to canopy height, openness, and roughness (Jucker et al., 2018). High-resolution UAV (unmanned aerial vehicle) images and time series of medium-resolution Landsat images can help detect and quantify disturbances in dense, humid tropical canopies (Bourgoin et al., 2020). LAI serves as an index of transpiration (and photosynthetic) surfaces, and is directly and positively linked

to plant transpiration (Alam et al., 2021). When LAI is high (e.g., $\text{LAI} > 4$), plant transpiration becomes the dominant contributor to evapotranspiration (Kirkham, 2005; Wang et al., 2014). These variables effectively quantify forest structural degradation from human-induced disturbances.

Although forest research has primarily focused on drought stress in the context of global warming, it is also important to consider the potential soil wetting associated with deforestation and degradation. This study investigated topsoil moisture (top 10 cm) in relation to forest structural degradation following selective logging at different intensities over 30 years in two timber-producing forest reserves in northern Borneo. I combined data from Landsat time series-based disturbance history, current canopy height models (CHM) derived from high-resolution UAV images, and in-situ measurements of LAI and soil moisture at a fine scale (several meters). We tried to differentiate the effects of other factors from that of forest structural degradation, and specifically addressed the following two research questions and hypotheses:

1. How does soil moisture change with canopy structural degradation after selective logging of various intensities? The hypothesis is that structurally degraded canopies will have higher soil moisture than non-disturbed canopies, and this increase would not diminish within a decadal time scale.
2. What is the relative impact of canopy change on soil moisture compared to other factors, including time elapsed from disturbance and topography? The hypothesis is that canopy structure would be the primary factor influencing soil moisture change.

3.2 Materials and methods

3.2.1 Site overview

This research was conducted in two adjacent forest reserves in northern Borneo (Fig. 3.1A): Deramakot (5.23°–5.47°N, 117.30°–117.63°E; 55,083 ha) and Tangkulap (5.30°–5.52°N, 117.28°–117.37°E; 27,550 ha). The region has an elevation range of 20 to 300 m above sea level, an average daily temperature of 25.5°C, and an annual rainfall exceeding 3,000 mm with little seasonality (Ong et al., 2012). Ultisols is the predominant soil type, and the original vegetation consists of mixed dipterocarp lowland rainforests with dominant species in *Dipterocarpus* and *Shorea*. However, the current forest patches vary from near-pristine to highly degraded due to different logging histories. The first recorded timber production was in 1956 for Deramakot and 1970 for Tangkulap, both were conventional, high-impact selective logging (Ong et al., 2012). In 1995, reduced-impact logging was introduced to Deramakot as an improved method of selective logging, which required pre-harvest inventory, directional felling, liana cutting, and planning of skid trails, log decks and roads (Lagan et al. 2007). Reduced-impact logging contributed to maintaining forest intactness and now Deramakot holds higher biomass and a more pristine-like tree community composition (Kitayama et al., 2018). Contrarily, Tangkulap was under conventional logging until 2002, which formed extensive, severely degraded forest patches (Kitayama et al., 2018). All logging activities have been suspended in Tangkulap since 2003, yet highly degraded forests (fern thickets and liana-laden forests)

still cover 35.1% of entire Tangkulap after two decades of logging (Takeshige et al., 2022).

Based on this background, we sampled 15 sites exposed to varying intensities of selective logging at different periods: 2 non-disturbed forests; 8 logged before 2003, and 5 logged after 2017. Sites logged before 2003 were located in Tangkulap, and subjected to more intensive, conventional logging; while sites logged after 2017 were logged by reduced-impact logging, all located in Deramakot. Details on quantifying logging intensity and detecting disturbance years are in section 2.3. A total of 83 transect lines were established subjectively, averaging 40 m in length with a 20 m buffer belt. The transects had a total length of 3,000 m and covered 8.38 ha of diverse canopy types. Details on transect lines by site are summarized in Table S1.

Weather conditions during the study period were examined using ERA5T historical meteorological data, validated by observations from Sandakan International Airport (5.90°N, 118.06°E, 13 m above sea level; Meteoblue Inc., Switzerland). Field surveys were conducted from October 15th to 29th, 2023, during a relatively wet period. Total precipitation in October 2023 was 327.5 mm, and the mean diurnal air temperature was 27.92°C, comparable to the 30-year (1993 to 2022) average of precipitation (283.9 ± 76.6 mm) but higher than the average temperature ($27.03 \pm 0.32^\circ\text{C}$). The total diurnal precipitation and mean air temperature during the survey were consistent with historical meteorological data, with no extreme droughts or precipitation events occurring in the region (Fig. S3.1).

3.2.2 In-situ measurement of volumetric soil water content, microclimate, LAI, UAV surveys and image processing

Along transect lines, a total of 395 measurements on volumetric water content (VSWC, $\text{m}^3 \text{m}^{-3}$ or %) of top 10 cm soil and surface temperature were taken equidistantly (about 4 m apart) using a WET150 amplitude domain reflectometry sensor (Delta-T Devices, UK). Comparison between in-situ measurements from WET150 and direct determination of these soils by air-drying were showed in Fig. S3.2A as validation of the VSWC readings. Referential position and time of sampling points was collected with hand-held GPS (Garmin GPSmap 64csx, US).

Air temperature (T , °C) and relative humidity (RH , %) were monitored using Watch Logger KT 255F (Fujita, Japan. T accuracy $< \pm 0.5^\circ\text{C}$, RH accuracy $< \pm 5\%$) at 3 sites exhibiting distinguishing levels of canopy openness (for site details, see Fig. S3.3 table). Measurement was taken at 1.5 m height every 0.5 hour during field survey (see Fig. S3.3 table for details). Vapor pressure deficit (VPD, hPa) represents the difference between the saturation and actual vapor pressure. It was employed to represent the atmospheric evaporative demand and it is also significantly related to plant transpiration (Nemetschek et al., 2024). Previous studies have found that lower, thinner canopies are associated with higher average and variation in VPD (Hardwick et al., 2015; Jucker et al., 2020). VPD was calculated by the method described in Jucker et al., 2018 (for calculation, see Fig. S3.3). The pattern of our measurements and calculations aligns with records from the meteorological station located at 1560 m Mont. Kinabalu (6.08°N, 116.56°E; Kitayama unpublished data) during the same period (Fig. S3.1).

Within each transect, LAI was measured with LAI-2000 (LI-COR, US) following the manufacture's manual. This instrument estimate leaf area per ground area from canopy transmittance by calculating the angular distribution of brightness and comparing between above and below canopy under ideally homogenously overcast sky. We used the two-sensor mode because direct above-canopy measurement was difficult to obtain in humid tropical forests (for details for measurement, see Fig. S3.2B). All measurements were made during October, 2023, without taking into account seasonal variations, as their effects are expected to be small in this region (Hardwick et al., 2015; for validation of in-situ measurement, see Fig. S3.2B).

In-situ UAV images were collected using a DJI Mavic 2 Pro carrying its original RGB lens (DJI, China). Flight route was designed and controlled with UgCS ground control software (SPH Engineering, Latvia), setting front and side overlap at 90% and 80%, respectively, and a constant flight altitude of 100 m above the ground. In order to generate feasible CHMs, we ensured that (1) flat terrain was visible in each scene for land type classification, most of which was logging roads; (2) images were captured under high sun angles (11:00 to 14:00) to avoid shadows; (3) absence of wind and problematic clouds. Information of UAV surveys were summarized in Table S1. The raw images were then processed to generate digital surface model (DSM), orthomosaic, and digital terrain model (DTM) using a SfM (Structure for Motion) software Agisoft Metashape (Agisoft LLC, Russia; see Fig. S3.4 for the workflow). CHM was built by subtracting DTM from DSM, i.e., subtracting terrain elevation from forest surface elevation. The average spatial resolution of CHM was as high as 0.02 m for a total area of 136.85 ha, and the overall accuracy of DTM was validated for the area of interest (Fig. S3.2C).

3.2.3 Disturbance analysis with Landsat time series

To examine the timing and intensity of historical disturbances related to logging at site level, we generated a time series of normalized burn ratio (NBR) during the period of 1988 to 2023. This index is originally developed to identify burned areas and provide a measure of burn severity, but also has been proved sensitive to canopy changes caused by disturbances in this region (Ioke et al., 2022; Takeshige et al., 2022). Annual composition of surface reflectance was prepared on Google Earth Engine using the TimeSync Tool (Cohen et al., 2010). Then, NBR was calculated for each pixel as follows:

$$NBR = \frac{NIR - SWIR2}{NIR + SWIR2}$$

where NIR and SWIR2 are surface reflectance of near-infrared (Band 4 of Landsat 5 and 7; Band 5 of Landsat 8) and shortwave-infrared (Band 7), respectively. This index has been broadly used for capturing land use and land cover change, and was proved efficient for identifying vegetation type, specifically in the study area that fern thickets and liana-laden forests rather than bare soil marked the degraded forest patches undergone severe disturbances (Ioki et al., 2022; Takeshige et al., 2022).

The year of disturbance was firstly detected using the LandTrendr tool basing on the annual change tendency of NBR (Kennedy et al., 2010), and here we adopted an empirically

defined 0.03 threshold from a previous study in the same area (Takeshige, unpublished data). Due to the undetectable canopy fragmentation caused by reduced-impact logging in moderate-resolution satellite images (e.g., 30×30 m resolution of Landsat OLI; see Fig. S3.5 for an example), supplementary methods were employed to address this detection accuracy limitation. In instances where transects exhibited evidence of logging but no detected disturbances at pixel level, the logging year was determined by forest reserve manager and/or through photointerpretation (Bourgoin et al., 2020). For identified disturbances, the intensity was represented by the difference of pre- and post-disturbance NBR, which would be referred to as ΔNBR hereafter. To avoid potential biases due to annual composition images, we used the average value of the two years before disturbance as the pre-disturbance NBR, and the minimum value of the two years after disturbance to represent the post-disturbance NBR (Frazier et al., 2018). For plots experienced multiple disturbances, we only took the latest into consideration. For plots that have been under a disturbed status at the start of time series (1988), we assumptively set the pre-disturbance NBR as 0.76, referring to the average NBR from plots of pristine forests. Information from the time series analysis were summarized in Table S3.1.

3.2.4 Computation of forest canopy structure metrics and landscape-scale topography indices

Forest canopy structure metrics (CSM) was calculated for each transect belt, including: (1) mean, median, range, SD, coefficient of variance (CV), first and third quartile (1Q and 3Q), and gap ratio computed from the CHM. The gap ratio was artificially defined as the ratio of CHM < 5 m within each transect belt. Isolated fractions < 5 m² were removed to avoid noises generated from image processing; (2) mean and SD of LAI, calculated by the C2000 software installed in the LAI-2000 data logger.

To account for the confounding effects of topography on soil moisture, we employed the topographic water index (TWI) as an indicator of steady-state soil moisture. This index has been known to reflect the difference between catchment water supply and local drainage (Kopecký et al., 2021), and a higher TWI indicates a higher equilibrium level of soil moisture because of larger catchment area. TWI was calculated at landscape scale (the two forest reserves) using the NASA SRTM DEM at a 30 m spatial resolution with the most often used single-flow, eight-direction algorithm (Kopecký et al., 2021). The calculation was conducted under QGIS 3.28.

3.2.5 Statistical analyses

Fig. 3.2 illustrates the design of analyzing approaches in this research. Data from NBR time series (ΔNBR and year of disturbance) and TWI were subtracted at transect level. VSWC metrics including mean and SD were calculated for each transect. A principal component analysis (PCA) was performed on the transect CSM matrix, and the most explanatory principal component (PC) was used to quantify current canopy structural degradation.

The influence of historical disturbance on current canopy characteristics and therefore soil moisture was studied by considering the intensity of and the time elapsed from the

latest disturbance. To examine the influence of time, transects were grouped into three categories: non-disturbed forests, logged before 2003 (conventional logging cessation), and logged after 2017 (latest logging event of our study sites); to examine the influence of intensity, we compared ΔNBR between groups of logged forests using t-test. Simple linear regression was used to explore the basic trend of soil moisture change in relation to canopy structural change, while also checking for potential nonlinearities.

The compound effect of canopy structure and topography on soil moisture was investigated by the generalized additive model (GAM) approach. It allows for nonlinear smooth patterns between individual predictors and the dependent variable. The full model was listed as follows:

$$g(\widehat{\text{VSMC}}) = s(\text{PC1}) + s(\text{PC2}) + s(\text{TWI}_{\text{mean}}) + s(\text{TWI}_{\text{SD}})$$

where PC1 and PC2 were the first two PCs of CSMs. Function g denotes an identity link function that directly used soil volumetric moisture. Function s performs a thin-plate spline regression to individual predictors. We used the restricted maximum likelihood method for smoothness selection to avoid over-fitting (Wood, 2011). Prior to model fitting, we consulted a scatterplot matrix to identify possible linear smooth patterns between individual predictors and the dependent variable. The additive effect of each predictor was assessed through analysis of deviance, specifically ANOVA with Chi-square. This analysis was conducted using the gam package in R (Wood, 2011).

Finally, the temporal change of VSWC during field measurements was compared against VPD. All data analyses were under R version 4.3.3 (R Development Core Team 2024).

3.3 Results

3.3.1 Comparing topsoil moisture in forests with different canopy structure and disturbance history

Results of PCA on transect CSMs are presented in Fig. 3.3A, and loading of original variables are shown in Fig. 3.3B. The first two PCs accounted for 86.8% of the total variation in canopy traits. PC1 mainly captured canopy height and openness characteristics, showing an increase with higher mean, median, and 3Q of canopy height, LAI, but a decrease with higher gap rate and CHM heterogeneity represented by CHM CV. PC2 mainly captured the heterogeneity of LAI. It only explained 12.7% of the total variation, showing significant correlation with the absolute and relative dispersion of LAI. The three groups of disturbance periods aligned along PC1 axis (Fig. 3.3A). The non-disturbed group marked the highest average PC1. Forests disturbed after 2017 showed lower average PC1. Forests logged before 2003 exhibited the lowest average as well as the greatest variation of PC1. Given that larger PC1 corresponded to larger ΔNBR , i.e., more intensive historical logging (Fig. 3.3 table), PC1 would be used as the indicator of canopy structural degradation results from historical logging in the following analyses.

An overall trend of greater VSWC underneath more degraded canopies was observed in the two disturbed groups (Fig. 3.3A). Mean VSWC in the non-disturbed group was $0.27 \text{ m}^3 \text{ m}^{-3}$, significantly lower than the two disturbed groups, both exceeded $0.4 \text{ m}^3 \text{ m}^{-3}$ (Fig. 3.3 table). The insignificant linear relationship between soil moisture and PC1 in non-

disturbed forests may be a result of equilibrium in the local hydrological regime, but the high unexplained variability in disturbed forests revealed potential compound effects from other factors like topography, as well as nonlinearity between canopy structural change and soil moisture response (Fig. 3.3 table).

Notably, although canopy structure showed significant difference between the two disturbed vegetation groups, the same result was not observed in VSWC (see Fig. 3.3C density traces, and t-test in the table).

3.3.2 Nonlinear relationship between canopy structural degradation and topsoil moisture

The scatterplot matrix showed that PC2 and TWI SD were not significantly correlated with VSWC and these two variables were therefore assigned linear fittings (Fig. S3.6). The full model accounted for 40.7% of deviance (Table S3.2), but only PC1 had a significant smooth term, which explained 39.2% of deviance on its own (Table S3.2). The model:

$$g(VSWC) = s(PC1)^{***} + PC2 + s(TWI_{mean})$$

showing the largest adj. R^2 (0.38) and explained deviance (42.8%) was selected in the following analysis.

Fitted values were compared with observed values in Fig. 3.4A; fitted curves of individual predictors showing their additive effects were presented in Fig. 3.4B, 3.4C. Despite for the overall random distribution of model deviation, there were underestimations for low VSWC and overestimations for high VSWC (Fig. 3.4A). The effect of PC1 on soil moisture was initially negative when starting from the maximum (Fig. 3.4B). As PC1 decreased, its effect on VSWC steadily increased towards the positive side and then decreased again as PC1 dropped below -2, subsequently approaching 0 (Fig. 3.4B). Given that samples with $PC1 < -2$ were characterized by a high gap rate (mean gap rate = 71%), low canopy height (mean CHM 3Q = 5.71 m), and low LAI (mean LAI = 1.84), we inferred that these transects exhibited absence rather than degradation of canopy.

The additive effect of TWI was nearly linear (Table 3.1, Fig. 3.4C), likely due to its calculation at a coarser spatial scale (30×30 m), and the one-time measurement of VSWC did not capture variations at a larger time scale. However, the range of TWI was relatively small in my area of interest. It contributes to a topographically even distribution of steady-state soil moisture, which in turn highlighted the significant influence from forest canopy and ET on soil moisture.

3.3.3 Temporal change of VPD and soil moisture during measurements

The overall microclimate data during field survey under different canopy types was illustrated in Fig. S3.3. Air temperature in the disturbed group and open canopy reached its maximum at noon, earlier than the non-disturbed forest which reached its maximum at 3 pm. Relative humidity in non-disturbed forest remained above 99% throughout the day, while in the other two groups it decreased as air temperature increased, reached the minimum value between 2 pm and 3 pm in disturbed forests and at 1 pm in open canopies. The results were consistent with annual averages reported by previous studies on lowland

dipterocarp forests in Borneo and Peninsular Malaysia (Hardwick et al., 2015; Lion et al., 2016; Senior et al., 2018), suggesting that my microclimate data, although collected at a limited spatial scale and time span, is still moderately representative.

Both hourly and 24-h aggregated precipitation highly varied during the period of VSWC measurement (9 am to 12 pm, Fig. 3.6 table), yet there was a general pattern of increasing VPD and decreasing VSWC (Fig. 3.6). However, VPD and VSWC were significantly higher underneath disturbed canopies than non-disturbed canopies at all times, and the difference increased as noon approached (Fig. 3.6 table). These results suggest that comparing with non-disturbed forests, disturbed forests and open canopies exhibited a coupling of warmer, drier microclimate in the understory but wetter soil environment in the main root zone.

3.4. Discussion

This study combined in-situ measurements of canopy characteristics and soil moisture with Landsat time series data, revealing new insights into soil moisture change in selectively logged humid tropical rainforests of Malaysian Borneo. The findings present evidence of soil wetting in logged-over forests, where canopy exhibits structural degradation, and support our hypotheses that without extreme precipitation or drought events, (1) soil moisture is significantly higher underneath structurally degraded canopies than non-disturbed canopies. Additionally, such soil wetting phenomenon was observed irrespective of canopy degradation level (which correlates with logging intensity) or time elapsed from logging (Fig. 3.3). (2) Canopy status primarily influences soil moisture (Fig. 3.4B). There is also a decoupling between evaporative demand of soil and soil moisture, that although VPD was higher in the understory of more degraded canopies, soil moisture was still higher than that of non-disturbed forests (Fig. 3.5).

Based on these results, I suggest that decreased LAI, which represents reduced plant transpiration and interception evaporation, explained the spatial variation of soil moisture in the landscape of logged-over lowland tropical rainforests at the landscape level in this study. Furthermore, the elevated soil moisture in the main root zone underneath open canopies can create an anaerobic environment that affects cycling of crucial nutrients, such as carbon (C) and nitrogen (N). This in turn impedes vegetation recovery and biomass restoration in the disturbed forests. However, it should be noted that our measurement was conducted in a single season with ample rainfall as representative per-humid Bornean climate, and soil moisture patterns may be different from our account here during extreme weather events.

3.4.1 Wetter topsoil water created by weakened transpiration in forests undergone selective logging

In the case of silty clay or clay loam soils in this study area, the permanent wilting point for VSWC is typically $0.28 \text{ m}^3 \text{ m}^{-3}$ (Campbell, 1985). Another study conducted in peninsula Malaysia reported an average permanent wilting point of $0.22 \text{ m}^3 \text{ m}^{-3}$ (Lion et al., 2017); and Hiiragi et al. (2022) reported that in a humid, well-developed tropical rainforest developed on Ultisols in the neighbor state of Sarawak, VSWC of the top-10 cm soil ranges between 0.15 and $0.35 \text{ m}^3 \text{ m}^{-3}$. These data are compatible with the overall average of VSWC

measured in our non-disturbed forest (Fig. 3.3 table). This indicates that there is a large amount of plant water uptake from soil, which allows ET to proceed at its potential rate in pristine humid tropical rainforest. In contrast, the overall average of VSWC measured during the same period ranged from 0.42 to 0.44 m³ m⁻³ in disturbed forest, corresponding to a typical field capacity in soils with the same texture, and soils measured in peninsula Malaysia (Campbell, 1985; Lion et al., 2017). This result probably indicates that destructive selective logging disrupts the water balance in humid tropical rainforests, resulting in significant soil wetting in the main root zone.

Notably, degraded canopies were characterized by two variables with opposing effects on ET and hence soil moisture: decreased LAI, which reduces plant transpiration and interception evaporation; increased canopy openness, which increases VPD at forest floor and thus promotes evaporation from the soil surface (Fig. 3.3). Corresponding to the latter, multiple studies have reported that VPD was significantly greater under more degraded canopies due to reduced thermal buffering provided to the substory (Jucker et al., 2018; Santos et al., 2024. Also see Fig. S3.3). However, during our field survey period, soil moisture was consistently higher under degraded canopies, even with enhancing plant transpiration and soil evaporation as noon approaches (Fig. 3.6). This result suggests a profound effect of reduced transpiration associated with foliage loss, which offsets the enhanced soil evaporation under open canopies.

Another possible mechanism involves limitation or even suppression of transpiration by increased stomatal resistance under hot and dry conditions. VPD at 12 hPa was statistically defined as a threshold to transpiration limitation in Bornean lowland rainforests via model simulation (Jucker et al., 2018). Maximum VPD under open canopies exceed this threshold even in a relatively wet period (Fig. S3.6), suggesting a potential heat stress on the substory vegetation, including tree seedlings, ferns, and lianas. Transpiration limitation is expected to hinder growth as it positively relates to photosynthesis (Grossiord et al., 2020), and growth failure elevates the risk of mortality for tree seedlings – notably, Bornean lowland rainforests are found specifically sensitive to drought-induced mortality comparing to other tropical rainforests (Phillips et al., 2010). The negative effect on growth and survival of remaining small, low trees in highly degraded forests potentially encourages the expansion of ferns and lianas.

Above all, elevated soil moisture, as a result of retarded transpiration, was observed in logged forests irrespective of logging intensity and time elapsed from logging (Fig. 3.4). This highlights the important role that selectively extracting mature individuals of late-successional species affects water cycling in logged forests (Bousfield et al., 2023), and successional failure after intensive logging has significant hydrological impacts. Previous studies in the same area have reported that as the coverage of fern/liana (e.g., *Dicranopteris linearis*, *Uncaria* spp., *Dinocloa* spp.) thickets increases, the recruitment of late-successional species significantly decreases while the mortality of seedlings and saplings increases, which together retards the rate of absolute net above-ground biomass accumulation (Sawada et al., 2022; Takeshige et al., 2023) and hence plant transpiration. Basing on these findings, I further suspect that the impeded forest recovery is both the cause and effect of

this hydrological change. Lianas are known to have a competitive advantage over trees in tropical seasonal forests in accessing water and nutrients in the upper soil layers (Deurwaerder et al., 2018), and exhibit strong stomatal control to maximize carbon fixation while minimizing water loss under high evaporative demand (Chen et al., 2014). Despite having an unconstrained below-ground water supply, the absence of canopy significantly altered microclimate near the ground to a drier and warmer condition, and the increased evaporative demand may put tree seedlings at a disadvantage when competing against ferns and lianas.

3.4.2 Elevated soil moisture disrupts C and N cycling in logged humid tropical rainforests

The forest canopy protects the forest floor from the direct impact of rain, and the surface debris and organic matter reduce runoff and ensure water absorption, both contribute to maintaining a good soil structure that mediates the recharge and release of water (Salati and Vose, 1984). However, after selective logging, changes in surface soil properties and nutrient levels have been widely observed, including compacted soils, increased pH, and a decline in total C, N, and phosphorus (P) pools (Guariguata and Ostertag, 2001; Olander et al., 2005). Recent studies suggest that some of these changes may lead to, or even represent, permanent shifts in the below-ground biogeochemistry (Mills et al., 2023; Qin et al., 2024), yet the mechanisms by which the immediate changes become permanent are poorly understood. This chapter offers a potential perspective from wetter soil regime, which directly affects soil aeration and may persist until a total recovery of biomass.

Soil wetting can limit O₂ concentration and influences redox reactions and biogeochemical processes in the below-ground system. Hot spots of soil moisture promote the reductive dissolution of soil iron (Fe) minerals (Barcellos et al., 2018), which destructs organo-mineral associations that sequester soil organic matter, increasing the consumption or even reducing the size of stabilized soil C pool as has been suggested in previous studies and Chapter 2 (Mills et al., 2023; Qin et al., 2024). Decreased O₂ concentration also inhibits microbial aerobic respiration and stimulates denitrification (Strawn et al., 2020). The former could shift the functional and/or community structure of soil microbes, promoting strategies of anaerobic growth with metabolically versatile (Hartmann et al., 2013). The latter can produce considerable emission of nitrous oxide (N₂O) and nitrogen gases (Keller et al., 2005), which has been observed in a study conducted in the same region comparing N₂O emission in pristine forest patches those that have undergone destructive selective logging (Mori et al., 2018). Thus, soil wetting can retard nitrification rate and enhance N loss, altering nitrogen regime of young secondary forests to a conservative pattern where N is otherwise considered relatively excessive (Davidson et al., 2007).

Above all, the disrupted C and N cycling in remnant forests potentially retard regeneration and reduce ecosystem resilience to future climate change.

3.5 Conclusion

This chapter examined the effects of selective logging-induced canopy structural

degradation on topsoil moisture in Bornean tropical rainforests. Soil volumetric water content was significantly elevated as canopy was structurally more degraded. Consistently higher moisture levels (~60%) under degraded canopies during the field survey suggest soils would be wetter in excess of field capacity without extreme precipitation or drought events. Degraded canopies exhibited decreased LAI, which reduces plant transpiration; and increased canopy openness, which promoted evaporative demand. Consistently wetter soils under degraded canopies indicate that reduced transpiration due to lower LAI outweighs the effect of increased evaporative demand from canopy openness. The increase in soil moisture content can immediately alter carbon and nitrogen cycles in logged-over forests, and the persistence of wetter soil water regime over a two-decade period may create positive feedbacks between soils and vegetation and retards forest recovery. Longer-term observation to monitor temporal changes of soil moisture and associated biogeochemistry is needed to substantiate these suggestions.

Tables

Table 3.1 Summarized information of GAM selection (n = 83)

Model		Deviance	Pr
Estimated Df of smooth terms	adj. R ²	explained	(>Chi)
$g(VSWC) = s(PC1)^{***}$			
PC1: 3.66	0.36	38.5%	—
$g(VSWC) = s(PC1)^{***} + PC2$			
PC1: 3.66	0.35	38.7%	0.66
$g(VSWC) = s(PC1)^{***} + PC2 + s(TWI_{mean})$			
PC1: 3.64; TWI mean: 2.02	0.37	41.8%	0.32
$g(VSWC) = s(PC1)^{***} + PC2 + s(TWI_{mean}) + TWI_{SD}$			
PC1: 2.89; TWI mean: 0.83	0.35	39.8%	0.16

* Variables with approximate significance of smooth terms were marked in bold ($p < 0.001$).

Figures

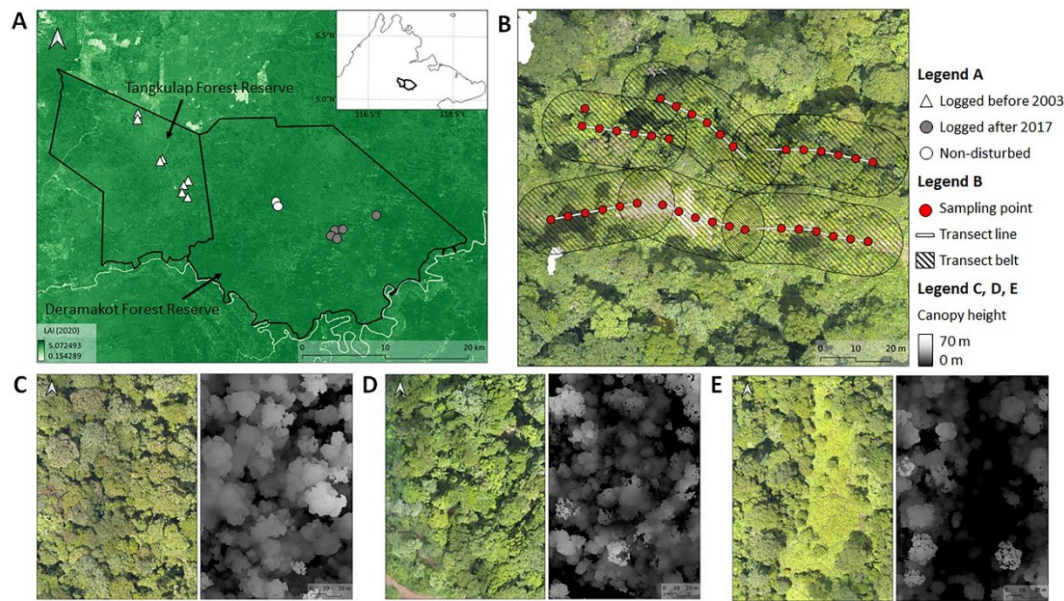


Fig. 3.1 (A) Location of Deramakot Forest Reserve and Tangkulap Forest Reserve, Sabah, Malaysia. Leaf Area Index (LAI) was calculated from an annual mosaic Landsat image of the year 2020 following the equation: $LAI = 0.57 \times e^{2.33 \times NDVI}$, where NDVI (Normalized Difference Vegetation Index) was calculated as the normalized difference between red band and near-infrared band; (B) Sampling scheme within a site. Transect lines about 40 m in length were subjectively established, each buffered by a 20-m-wide belt. Paired transects were set in parallel underneath contrasting canopies (e.g., closed and open canopies). Volumetric soil water content (VSWC) was measured at equidistant points along transect lines, every 2 points were spaced about 4 m apart. LAI and canopy metrics were calculated for each belt; (C) to (E) showed paired orthomosaic (left) and CHM images (right) illustrating the typical forest canopy that are non-disturbed, currently (2023) under logging, and degraded after logging in 1996, respectively.

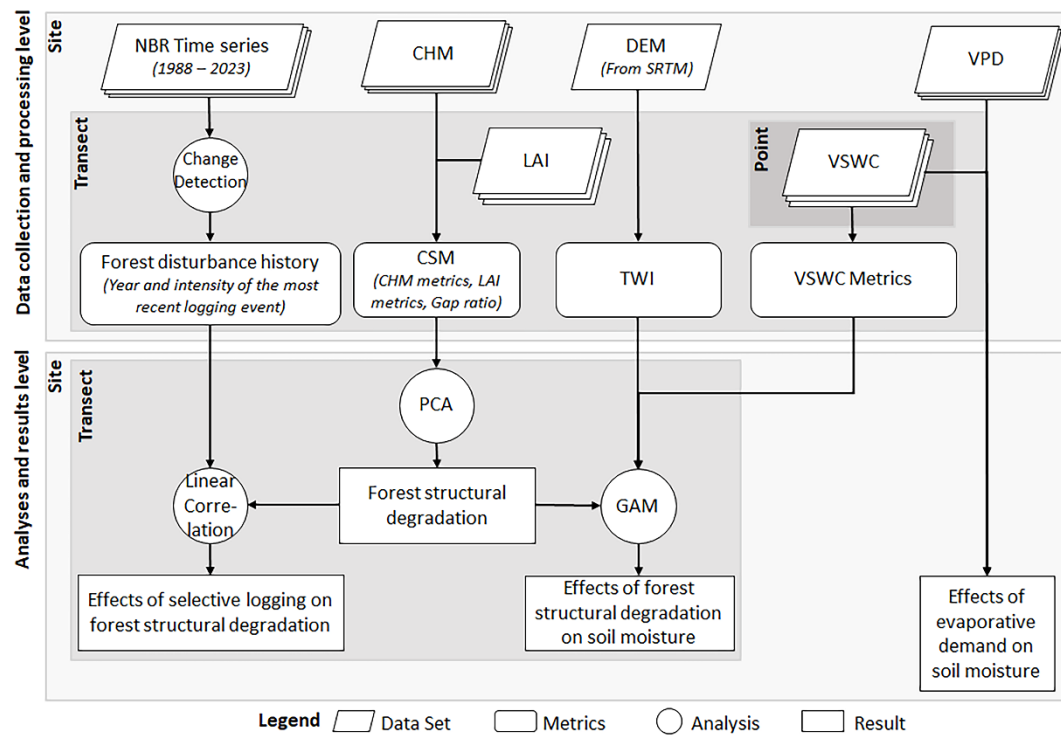
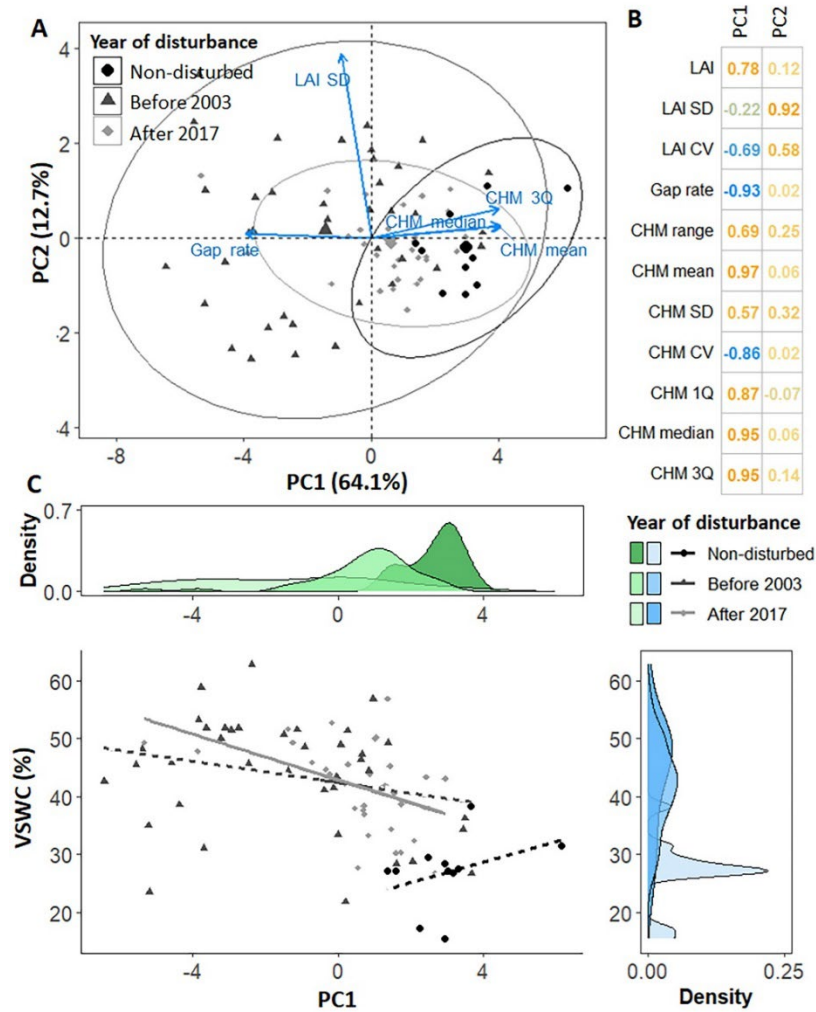


Fig. 3.2 The overall design of the research. Data and results were specified to different scales (site, transect and point). NBR: normalized burn ratio; CHM: canopy height model (m); DEM: digital elevation model (m); SRTM: surface radar topography mission; VPD: vapor pressure deficit (hPa); LAI: leaf area index; CSM: canopy structure metrics; VSWC: volumetric soil water content ($\text{m}^3 \text{m}^{-3}$); TWI: topographic wetness index; PCA: principal component analysis; GAM: generalized additive model.



Year of disturbance	ΔNBR	PC1	VSWC (m ³ m ⁻³)	Linear regression	
				Equation	adj. R ²
Non-disturbed	–	2.99 (a)	0.27 (a)	$g(VSWC)$ $= 21.34^{***} + 1.84PC1$	0.03 n.s.
After 2017	0.02 (a)	0.64 (b)	0.42 (b)	$g(VSWC)$ $= 43.06^{***} - 1.95PC1^{**}$	0.18 **
Before 2003	0.19 (b)	-1.44 (c)	0.44 (b)	$g(VSWC)$ $= 42.56^{***} - 0.80PC1$	0.03 n.s.

Fig. 3.3 (A) Result of PCA on CSM. (A) Biplot displaying the scores of each sample and coordinates of the top 5 contributors from the original variables. 95% confident ellipses were fitted for canopies grouped by year of disturbance. Centroids of each group were marked as larger points; (B) Correlation matrix of original variables with the first 2 PCs and ΔNBR . (C) Scatter plot with simple linear regression between VSWC (volumetric soil water content) and PC1 grouped by year of the most recent disturbance. On the top and right are the density trace of PC1 and VSWC, respectively. Group means of VSWC, PC1, and simple linear regression results were listed in the table below. Group means were compared with t-test ($p < 0.05$). Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot$ $p < 0.05$; n.s. $p > 0.05$.

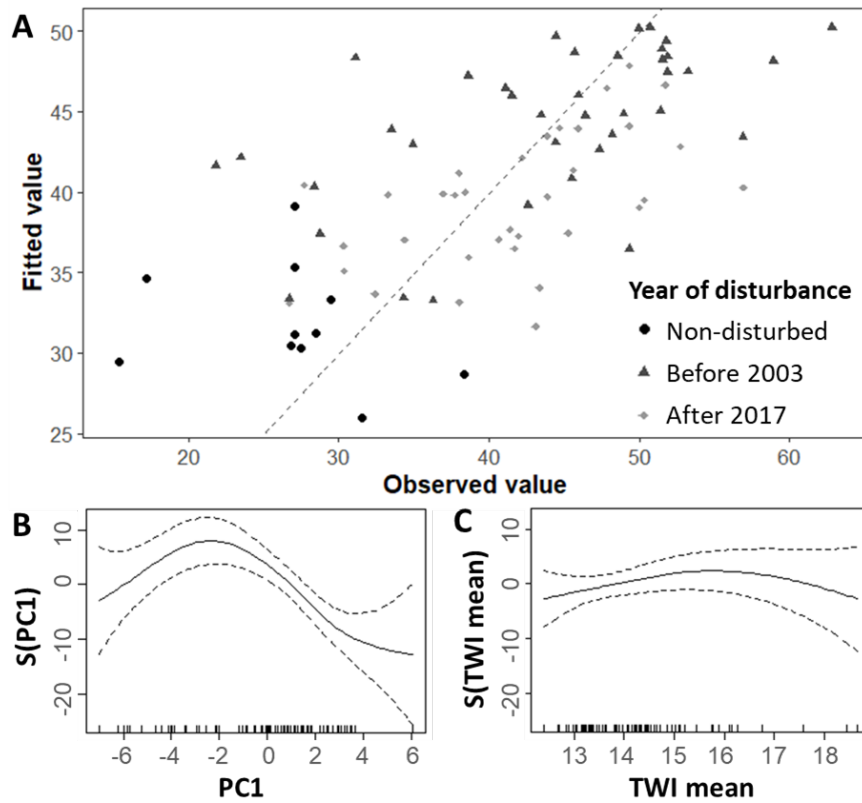
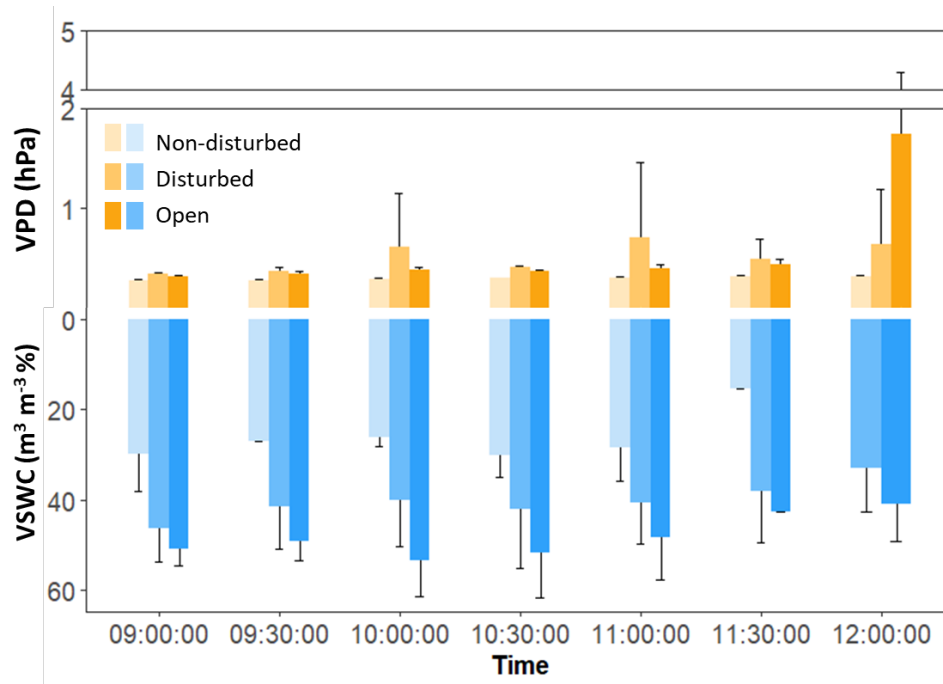


Fig. 3.4 (A) Observed and fitted value of VSWC (volumetric soil water content, $\text{m}^3 \text{m}^{-3} \%$). Dashed line represents a 1 to 1 line; (B) smoothed curve showing additive effect of PC1 and (C) TWI mean in GAM ($n = 83$, model Df = 76.14). Dotted lines represented 95% confidence intervals. Marks along the x-axis represent observations.



Time	VPD (hPa)			VSWC ($\text{m}^3 \text{m}^{-3} \%$)			Precipitation (mm, SD)	
	Non-disturbed	Disturbed	Open	Non-disturbed	Disturbed	Open	Hourly sum	24-h sum
09:00	0.28 (a)	0.34 (b)	0.31 (b)	29.76 (a)	46.43 (b)	50.96 (c)	0.67 (1.16)	10.61 (10.28)
09:30	0.28 (a)	0.37 (b)	0.34 (b)	27.10	41.56 (a)	49.25 (b)	–	–
10:00	0.30 (a)	0.61 (b)	0.38 (a)	26.10 (a)	39.95 (b)	53.47 (c)	0.08 (0.12)	10.22 (9.81)
10:30	0.31 (a)	0.41 (b)	0.38 (c)	30.29 (a)	42.12 (b)	51.60 (c)	–	–
11:00	0.32 (a)	0.91 (b)	0.41 (a)	28.55 (a)	40.71 (b)	48.26 (b)	0.12 (0.27)	10.20 (9.59)
11:30	0.33 (a)	0.49 (b)	0.45 (a)	15.40	38.04	42.60	–	–
12:00	0.32 (a)	0.65 (b)	1.75 (b)	–	32.98 (a)	40.90 (a)	0.18 (0.44)	10.14 (9.27)

Fig. 3.5 Half-hourly change of VPD (vapor pressure deficit) measured at 3 sites with different canopy conditions, and VSWC (volumetric soil water content) measurement from all sites during field survey. Group means of VPD and VSWC were compared with t-test (skipped increments with only one measurement). For VPD, there were 113 measurements in the non-disturbed group, 289 measurements in the disturbed group, 149 measurements in the open canopy group. For VSWC, there were 40 measurements in the non-disturbed group, 294 measurements in the disturbed group, 59 measurements in the open canopy group. Mean and SD of precipitation during field survey were showed in the table, aggregated at 1 or 24-hour sum. This data was based on ER5T simulation validated using meteorological data monitored at Sandakan International Airport.

Supplementary

Table S3.1 Information of UAV survey, Landsat time series and LAI measurement at each site.

Site ID	Number of transects	UAV survey			Landsat time series ^(a)		LAI measurement	
		Area (ha)	Date	Time	Disturbance year	Δ NBR	Total readings	Bad readings ^(c)
1	1	9.45	10/15	12:21	–	–	10	0
2	11	11.02	10/21	12:15	–	–	100	0
3	5	7.23	10/17	12:32	1995	0.40	40	15
4	6	6.84	10/19	12:06	1988	0.29	48	21
5	4	7.99	06/12	13:19	1996	0.17	32	2
6	5	7.74	06/13	13:59	1996	0.03	40	5
7	7	11.98	06/09	14:59	1996	0.05	56	1
8	4	10.44	06/07	12:56	1996	0.39	32	7
9	1	11.02	06/07	13:12	1996	0.38	8	7
10	6	8.24	06/13	13:30	1998	0.23	48	11
11	9	9.18	10/24	11:04	2018	0.12	72	0
12	6	3.82	10/22	11:27	2017	0.18	48	10
13	7	8.26	10/24	11:26	2018	0.02	56	0
14	5	12.89	10/28	11:56	2018	0.11	40	0
15	7	10.75	10/28	10:51	2022	– ^(b)	56	4

^(a) Data listed here represents the most recent and significant disturbance detected at one of the transects within a certain site. Not every transects of this site were disturbed or under the same disturbance intensity.

^(b) We ignored Δ NBR at this site as only 1 value of post-disturbance NBR (year 2023) could be used for calculation, which may give erroneous results.

^(c) In paired readings, those with below-canopy brightness greater than the above-canopy brightness are bad readings. These readings were removed when calculating LAI.

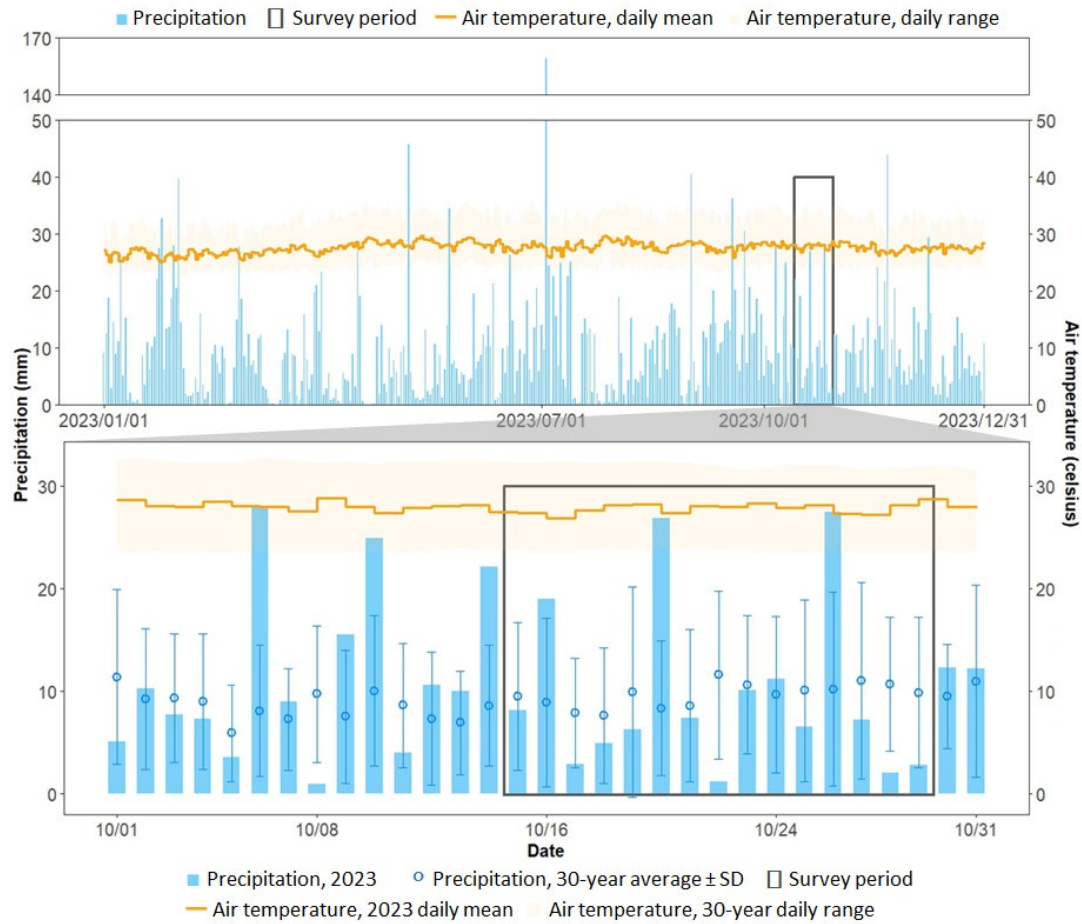


Fig. S3.1 ERA5T simulation of daily total precipitation (bars) and mean air temperature (solid line; 2 m above ground) basing on meteorological data monitored at Sandakan International Airport. The figure above shows annual precipitation and air temperature dynamics in year 2023; the figure below zooms to October 2023, and compared daily precipitation and mean air temperature with 30-year averages (1993 to 2022). The period of field survey is marked in the box.

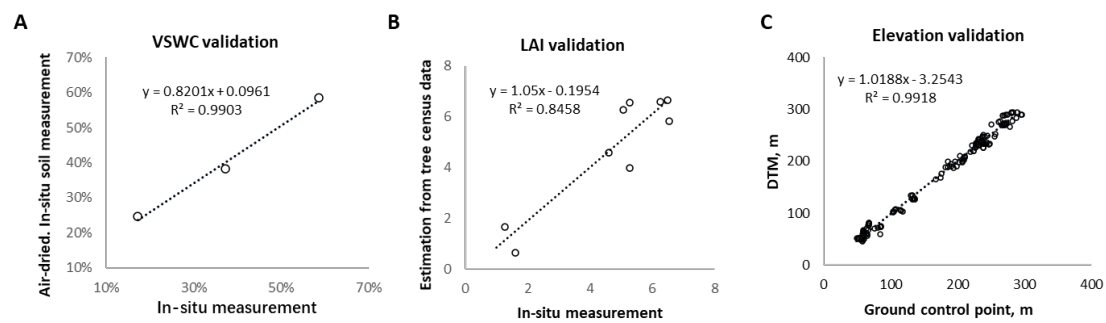
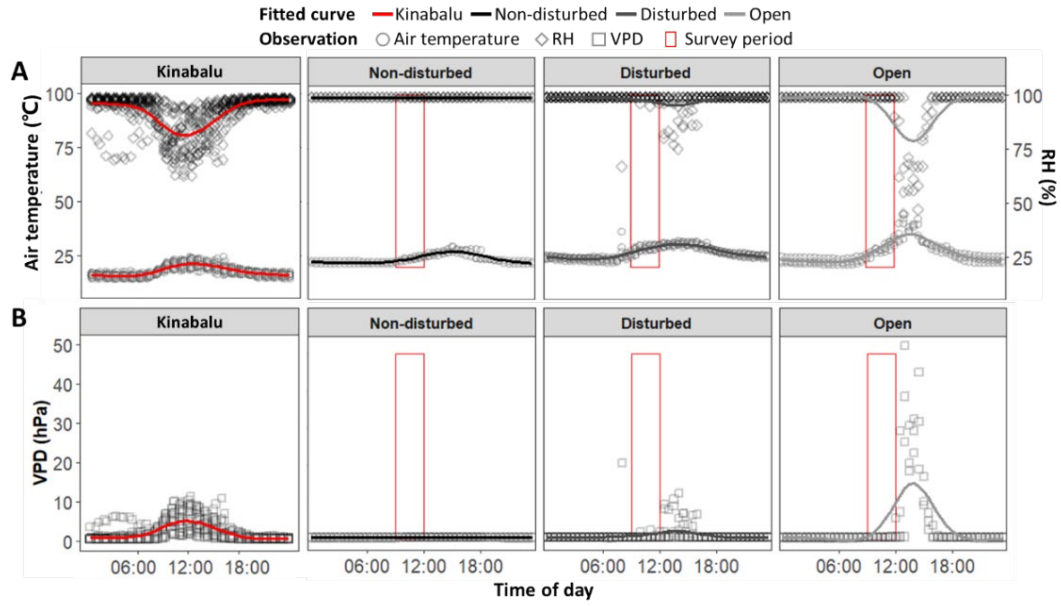


Fig. S3.2 (A) Comparisons of the in-situ measurements of soil volumetric moisture (VSWC) with a WET150 sensor with direct measurements of volumetric soil moisture of the same soil after air-drying ($n = 3$, %); (B) Validation of in-situ measurement with allometric-estimation of LAI ($n=9$). The in-situ measured LAI was measured following the equipment protocol: the reference (above-canopy) optical sensor was mounted on a tripod 2 m above the ground and separately placed no more than 150 m from the sampling site, where the sensor's field of view was free of obstacles at least 100 meters ahead and had no covering above. Measurements were taken every 30 seconds. The second optical sensor collected multiple measurements for below-canopy brightness within transect belts, positioned 1.5 m above the ground. The number of below-canopy measurements for each transect belt was determined based on canopy heterogeneity (Table S3.1). Both sensors were covered with a 5-degree opening view cap, pointing in the same direction, and maintained level during measurements. Readings from the two sensors were then compiled to generate the mean and standard deviation (SD) of LAI for each transect belt. The estimated LAI was basing on tree census data (e.g., diameter at breast height) collected in 2018 and 2019, following the allometries proposed by Yamakura et al. (1986) using tree census data from Sawada et al., 2022; (C) Accuracy assessment of DTM using elevation collected from a referential map provided by the Deramakot Forest Management Department at ground measurement points within the transect belts ($n=158$). A simple linear regression was fitted to each plot.



	Non-disturbed	Disturbed	Open	Kinabalu
Measuring period	10/26 – 10/29	10/17 – 10/23	10/26 – 10/29	10/17 – 10/29
Air temperature _{mean} (°C)	24.31	26.97	26.98	17.79
RH _{mean} (%)	99.00	98.11	94.75	91.21
VPD _{max} (hPa)	0.42	20.41	52.09	11.31
CHM _{mean} (m)	39.10	13.90	3.85	–
Gap rate (%)	0	4.42	68.56	–
Year of disturbance	–	1991	1996	–
ΔNBR	–	0.28	0.46	–

Fig. S3.3 (A) Air temperature (T , °C) and relative humidity (RH , %) measured at Mont. Kinabalu meteorological station (1560 m), non-disturbed site, disturbed canopy site, and open canopy site at Deramakot and Tangkulap Forest Reserves. Air temperature was measured every 0.5 h. Survey period was marked with a box (9 am to 12 pm). Air temperature in the disturbed group and open canopy reached its maximum at noon, earlier than the non-disturbed forest which reached its maximum at 3 pm. Relative humidity in non-disturbed forest remained above 99% throughout the day, while in the other two groups it decreased as air temperature increased, reached the minimum value between 2 pm and 3 pm in disturbed forests and at 1 pm in open canopies; (B) VPD (vapor pressure deficit, hPa) measured at Mont. Kinabalu meteorological station (1560 m) and calculated for non-disturbed site, disturbed canopy site, and open canopy site at Deramakot and Tangkulap Forest Reserves. The calculation followed by the method described in Jucker et al. (2018), being expressed as $[(100 - RH)/100] \times e_s$, where e_s denotes saturation water vapor pressure that can be

derived from T using Bolton's equation $e_s = 6.112 \times e^{\frac{17.67 \times T}{T + 243.5}}$ (Bolton, 1980). Canopy structural traits within a 20-m buffer and historical disturbances were summarized in the table below. VPD_{max} denotes the highest value over the entire measurement for each site.

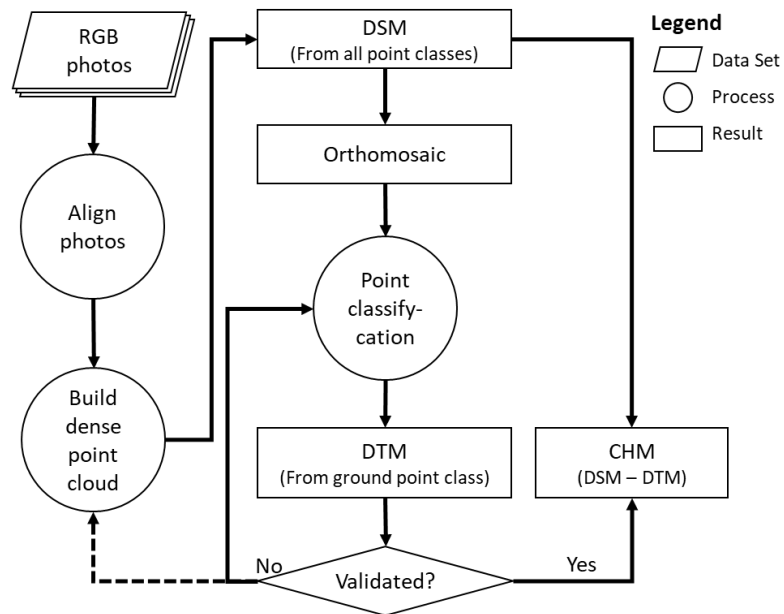


Fig. S3.4 Workflow for generating CHM from UAV imagery using Agisoft Metashape. During the validation process, elevation extracted from the DTM was compared to the referential elevation at ground control points. The predefined threshold of difference between the two was 10%.

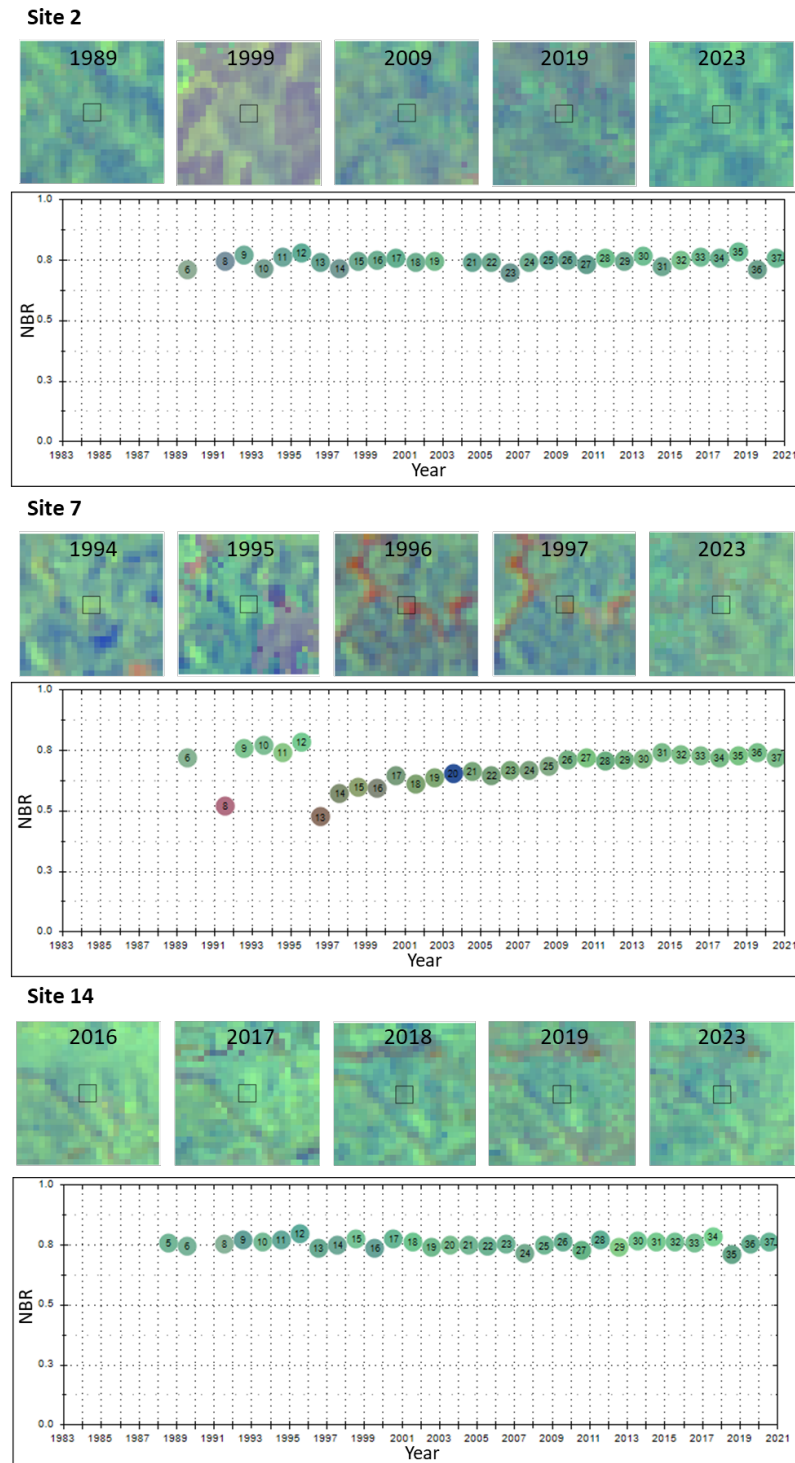


Fig. S3.5 Example of photointerpretation of logging events basing on NBR (normalized burn ratio) time series generated from Landsat annual mosaic imageries (1988 – 2023): (A) Site 2, non-disturbed forest, (B) Site 7, selective logging (conventional) detected in 1996, (C) Site 14, selective logging (reduced-impact logging) in 2018 confirmed by the forest manager and observation. Satellite imageries showed annual NBR of the years pre and- post-disturbance as well as 2023. The centered square in each scene were 90×90 m², within which target transects located.

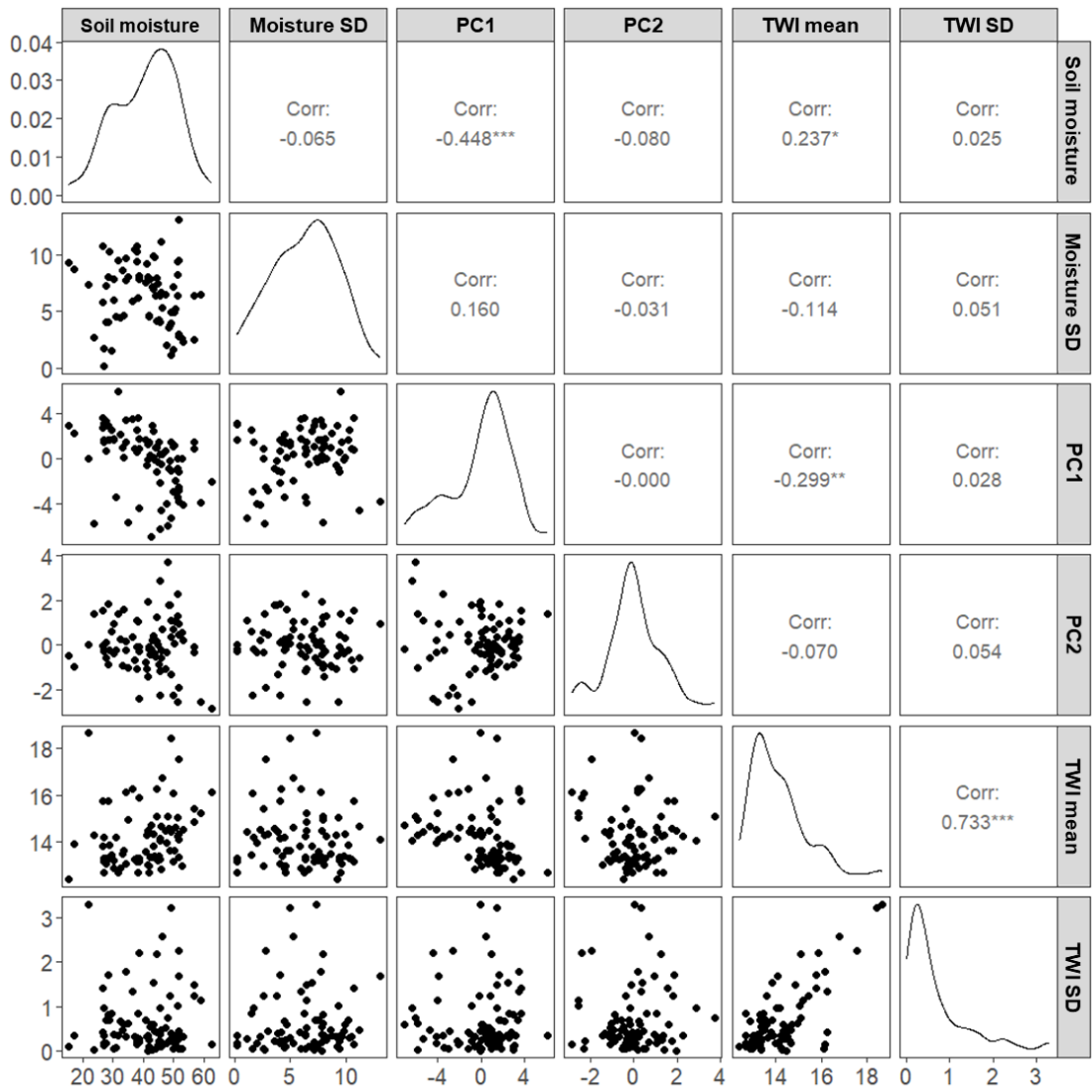


Fig. S3.6 Scatter plot matrix for the GAM dataset. The diagnose showed distribution density.

Chapter 4

General discussion

The aim of this thesis was to elucidate the mechanistic understanding of the below-ground responses to logging-induced forest degradation in humid tropical timber-producing rainforests, with a particular emphasis on soil carbon (C) loss resulting from increased microbial decomposition of soil organic matter (SOM). The destabilization of SOM is characterized by the destruction of soil aggregates formed by physiochemically associated organic and mineral compounds. In soils of humid tropical regions, aluminum (Al) and iron (Fe) (hydr)oxides accumulated during weathering significantly favor soil aggregation, while mineral solubility is influenced by soil redox states. Soil oxygen (O₂) concentration, under the influence of soil moisture, defines soil redox states.

Against this background, a hypothetical two-fold hypothesis of soil C loss in degraded humid tropical rainforests was proposed and examined: (1) decreased OM input from reduced litter production, and (2) increased consumption of mineral-associated OM. The wetter soil regime after logging, resulting from weakened evapotranspiration due to canopy damage and biomass loss, initiates the second process by promoting Fe (hydr)oxides as electron acceptors in soil redox reactions and anaerobic respiration. These biogeochemical processes destruct the association between soil minerals and OM, which subsequently releases the protected soil C due to increased microbial availability.

In Chapter 2, the relationship between soil C, Al and Fe (hydro)oxides, and soil redox potential (Eh) was examined along a gradient of forest degradation caused by selective logging at different intensities and periods. A mediation analysis revealed that the decrease of short-range-ordered (SRO) Fe minerals was a significant mediator of soil C loss in deeper soils (Fig. 2.2C). Such decrease of SRO Fe mineral content was observed in reductive soils, which were defined as soils with Eh below an empirical threshold of Fe reductive dissolution at 0.05 V (Fig. 2.3C). The reductive shift in the soil was initiated when forest degradation exceeded a certain threshold, which can be represented by AGB dropping below half of the pristine level (Fig. 2.3A, 2.3B). These results indicate that the hypothetical two-fold mechanism is primarily supported, yet how forest degradation links to soil moisture change – the main reason of soil Eh change – remains unclear.

As such, Chapter 3 examined the relationship between soil moisture and canopy degradation, which governs evapotranspiration (ET) and hence soil moisture in humid tropical rainforests. Soil moisture was measured along transects traversing diverse canopies in 15 sites, being grouped according to the time elapsed from the latest logging event. A composite indicator of canopy degradation significantly correlated to historical logging intensity was generated from PCA (Fig. 3.3A). Soil moisture was significantly higher under disturbed canopies, regardless of the intensity and period of disturbance (logging), and time of the day (Fig. 3.3C, Fig. 3.6). An autocorrelation analysis demonstrated that effects of forest degradation to increased soil moisture were observed at both small and large spatial scales (Fig. 3.5D). A composite canopy indicator consisted of two variables, gap rate and leaf area index (LAI). A smaller canopy indicator was associated with a higher gap rate and a lower LAI. These two variables exerted opposing influences on ET: higher gap rate increased VPD and evaporative demand from the soil surface, whereas lower LAI decreases transpiration. The negative relationship between this indicator of canopy

structural degradation and soil moisture suggests that in this study area, influence of reduced transpiration is greater than that of increased evaporative demand on soil moisture (Fig. 3.4B).

Above all, the results substantiated the hypothesis and further suggested that (1) losing half of the pristine-level biomass could trigger a soil reductive shift, and (2) soil wetting occurs as long as LAI decreases, and thus could persist before a complete recovery of canopy which may take decades. Probably, SRO Fe minerals are preferentially reduced, leached, or transformed into more stable phases in wetted, reductive soils in my sites. It is inferred that soils shift to a wetter, reductive condition, resulting in irreversible decline in soil C sequestration capacity due to Fe mineral leaching and/or morphological change in degraded forests if the recovery of AGB with closed upper canopies is long suppressed.

4.1 Implications of soil regime shift for sustainable forest management in timber-producing humid tropical rainforests

Soils in humid tropical forest are generally considered unlimited in water supply throughout a year, i.e., monthly precipitation exceeds monthly potential ET (Kramer and Chadwick, 2018). However, soil water content measured in non-disturbed forests can be relatively low (being close to the permanent wilting point, Fig. 3.3C) as substantial plant transpiration occurs during the day. In this regard, one of the potential benefits of reduced-impact logging (RIL), as compared to conventional selective logging, could be the maintenance of hydrological conditions in humid tropical rainforests, not only because it preserves the role of mature individuals of dominant species in transpiration, but also because of the dynamic gap-filling process during secondary succession (Asner et al., 2004) and therefore a shorter period of soil wetting after logging. Consequently, the restoration of C stock in both above- and below-ground is possible in these timber-producing forests harvested with RIL.

On the other hand, degraded forests failed to restore the ecological services (e.g., AGB, species composition) in this study area, typically showing an arrested succession due to fern and/or liana invasion (Takeshige et al., 2022). To date, such arrested successional has been explained from the perspective of (1) the lack of seed dispersal due to less mature, reproductive individuals (Imai et al., 2014; Sawada et al., 2022; Takeshige et al., 2023); (2) darker forest floor created by dense fern/liana thickets, which increases seedling mortality (Miyazaki, unpublished data). My study provides a third possible mechanism involving soil saturation with water, oxygen deficiency, and drier microclimate (VPD near the ground). Fine roots are known to be sensitive to soil aeration status, as roots are susceptible to O₂ deficiency (Qi et al., 1994). The compacted and stagnant soil created by machinery use as well as canopy loss can significantly inhibit root development and, in turn, the recovery of soil physical structure (Wilpert and Schäffer, 2005). Meanwhile, lianas exhibit strong stomatal control to maximize C fixation while minimizing water loss under high evaporative demand (Chen et al., 2014). This adaptation confers a competitive advantage on lianas over tree species in drier microclimates underneath degraded canopies. Such environmental stressors create positive feedbacks between plant and soil, indicating a degradation of both

above- and below-ground systems.

4.2 From stand level to landscape level: the effects of soil wetting in the study area

Takeshige et al. (2022) have estimated that the forests that are highly degraded and thus highly unlikely to recover (being threatened by fern and liana invasion) showed different spatial distribution patterns by comparing Deramakot versus Tangkulap. Such degraded area covered 28.5% of Deramakot, while the ratio is higher at 35.1% in Tangkulap (Takeshige et al., 2022). In Deramakot, these areas clustered to the southeast of the reserve, a consequence of the region's history of intensive logging prior to the implementation of RIL and/or forest fires during the 1982–1983 dry period; while in central Tangkulap, highly degraded forest patches distributed along logging roads and exhibited intensive convergence at the center of the reserve (Takeshige et al., 2022).

On the other hand, as being observed in sites showing significant canopy openness, the lacking of canopy buffering of precipitation and radiation leads to a homogenized effect of topography on soil moisture – which is potentially higher (Chapter 3). As suggested by Salati and Vose (1984), major deforestation can have a considerable scaling effect on the surrounding remnant forests via the reduction of water recycled to the atmosphere. Consequently, local cloud cover and precipitation will decline, leading to a net decrease in the total amount of water within the system. Based on these findings, it can be reasonably inferred that the large area of highly degraded canopy and wetting soil in Tangkulap may disrupt the water and heat balance, thereby affecting the remnant forests at a larger scale, namely the landscape level.

4.3 Limitations and future research

This thesis examines whether/how the coupling of altered moisture condition and C cycles in humid tropical rainforest ecosystems could lead to a regime shift in the below-ground. While the hypothesis may be feasible overall, the field measurements of soil moisture and Eh were collected as snapshots of the system that do not provide firm information for oscillation as well as long-term patterns.

One seemingly contradictory fact is that the reductive/anaerobic soil environment is believed to suppress respiration and contribute to C accumulation. However, previous study (Mills et al., 2023) and the results presented in Chapter 2 collectively suggest that soil respiration consuming SOM is probably elevated in degraded post-logging forests, where soil reductive shift occurred. Also, the decreasing C/N ratio in degraded, reducing soils indicates the consumption of more labile SOM (Fig. 2.3D). One possible explanation for this phenomenon involves the biotic part of Fe cycle, specifically Fe(III)-reducing bacteria that catalyze Fe(III) in anaerobic respiration (Hall and Silber, 2015; Kappler et al., 2021). Specifically, the availability of reducible, SRO Fe oxides to catalyze anaerobic microbial respiration in humid tropical ecosystems may partially offset soil C accumulation under reducing conditions (Hall and Silber, 2015). This capability has been demonstrated for different microorganisms in almost every anoxic environment, while the inland tropical

soils in high-rainfall areas may be ideal habitats for Fe-reducing bacteria (Dubinsky et al., 2010). An incubation experiment using soil collected from humid tropical forests in Puerto Rico suggested that spatially and temporally dynamic redox conditions led to an exceedingly high abundance of Fe-reducing bacteria; and in soils from high-rainfall sites, Fe(III) reduction rate could account for up to 44% of organic C oxidation (Dubinsky et al., 2010).

Although it has been acknowledged that shifts in vegetation can significantly impact soil pH, water content, and nutrient availability, there is currently a lack of field data on how microbial community and/or functional composition change under shifts in soil moisture and redox regime. Another study conducted in the same study area by Jiang et al. identified Acidobacteria as a major phylum of soil bacteria, in which *Geothrix fermentans* has been known as a Fe(III) reducer (Kappler et al., 2021); meanwhile, changes in the functional structure of bacteria have been observed in relation to the degradation gradient of forest ecosystems (Jiang et al., unpublished data). It is possible that changes in soil moisture and redox potential may have contributed to the observed shifts in bacterial community and functional composition, among which Fe-reducing species or functions could be promoted to oxidizing SOC.

4.4 Conclusion

In conclusion, this thesis suggests that the sharp decline of above-ground biomass combined with reduced LAI by destructive selective logging causes a reduction of soil organic carbon in degraded logged-over tropical rainforests in north Borneo. A two-fold mechanism explains the soil C loss: one is the limited C input due to decreased above-ground biomass and the other is the destabilization of soil C protected by organic-mineral associations, specifically by SRO Fe minerals. The latter mechanism relates to the reductive shift in soil Eh due to soil wetting caused by suppressed transpiration. A threshold of soil reductive shift was identified as the point at which half of the AGB had been lost from the pristine level. Soil wetting, as the main driver of soil redox change, occurs immediately after selective logging and could persist before a complete forest restoration. My results imply that a regime shift in soil ecosystem occurs in degraded forests where secondary succession is arrested in the contemporary landscapes of the tropics. These results emphasize the importance of sustainable forest management not only for the above-ground but also for the below-ground system, as the reductive shift can permanently reduce soil C sequestration capacity.

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