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Recovery of Carbon and Vegetation Diversity 23 Years after Fire in a Tropical Dryland Forest of Indonesia

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Abstract: Understanding the recovery rate of forest carbon stocks and biodiversity after disturbance, including fire, is vital for developing effective climate-change-mitigation policies and actions. In this study, live and dead carbon stocks aboveground, belowground, and in the soil to a 30 cm depth, as well as tree and shrub species diversity, were measured in a tropical lowland dry forest, 23 years after a fire in 1998, for comparison with adjacent unburned reference forests. The results showed that 23 years since the fire was insufficient, in this case, to recover live forest carbon and plant species diversity, to the level of the reference forests. The total carbon stock, in the recovering 23-year-old forest, was 199 Mg C ha^{-1} or about 90% of the unburned forest (220 Mg C ha^{-1}), mainly due to the contribution of coarse woody debris and an increase in the 5–10 cm soil horizon's organic carbon, in the burned forest. The carbon held in the live biomass of the recovering forest (79 Mg C ha^{-1}) was just over half the 146 Mg C ha^{-1} of the reference forest. Based on a biomass mean annual increment of 6.24 ± 1.59 Mg ha^{-1} yr^{-1}, about 46 ± 17 years would be required for the aboveground live biomass to recover to equivalence with the reference forest. In total, 176 plant species were recorded in the 23-year post-fire forest, compared with 216 in the unburned reference forest. The pioneer species *Macaranga gigantea* dominated in the 23-year post-fire forest, which was yet to regain the similar stand structural and compositional elements as those found in the adjacent unburned reference forest.

Keywords: secondary forest; forest fire; Indonesia; Kalimantan; recovery; carbon pool

1. Introduction

Forests dominate carbon fixation by terrestrial ecosystems [1–3], and forest regrowth is essential for mitigating emissions from land-use change [4,5]. However, forest carbon stocks are at risk from human activities that degrade forests and from changing climate [6,7] that increases fire activity and associated emissions [8,9]. The 1997–1998 *El Nino* drought cycle in Indonesia triggered fires over millions of hectares of forest, causing smoke and pollution throughout southeast Asia [10]. The 1998 fires in East Kalimantan, Indonesia, were reported as one of Indonesia's largest forest-fire disasters [11].

Forest-disturbance regimes have intensified in many parts of the world over the last several decades, driven largely by more frequent occurrences of the extreme fire weather associated with rapid climate change and increased human ignitions. These changes are making it more difficult to achieve the basic goals of forest-ecosystem management, which

are to deliver ecological services to society, while conserving forest biological diversity and ecosystem function. Understanding the nature and rate of biodiversity recovery in disturbed regions is required, to identify management interventions for fostering restoration of both plant diversity and forest-ecosystem function.

The recovery of secondary forest carbon stocks, after fire disturbance, is a key contributor to climate-change mitigation. Not only in Indonesia, but globally, the extent of secondary forests has risen over time [12,13], while the area of primary forests has decreased [14]. In the long term, secondary forests will replace primary forests [15] and play an important role in global biomass turnover and carbon sequestration [16].

Although the immediate impact of fire on forest ecosystems has been widely studied, including in the tropical dryland forests of Indonesia [17–19], studies over decades of recovery are more limited, especially in tropical forests, where most disturbances are occurring. Multiple decades of forest regrowth are, likely, required for biomass to recover equivalent carbon to that emitted in a forest fire. Currently there are very few published studies from tropical forests that include all forest carbon pools [20,21]. Detailed measurements can help to reduce uncertainty, in estimates of the time required for forest regrowth to balance carbon losses [22]. Moreover, the recovery of forest carbon and plant biodiversity occurs at different rates after disturbance [23], with each varying according to forest type, climate and site factors, and degree of disturbance. This study aimed to analyze the recovery of plant biodiversity and of carbon stocks, in a secondary tropical forest of Indonesia, 23 years after fire. The broader aim is to enhance our understanding of carbon sequestration and the role of secondary forests in climate-change mitigation and biodiversity conservation.

2. Materials and Methods

2.1. Study Sites and Plot Design

The study area is a lowland dryland forest that is dominated by mixed dipterocarp species in the Bangkirai hills forest, at an elevation of 49–135 m (Figure S1), 58 km northwest of Balikpapan city, East Kalimantan, Indonesia (1°1′29″–1°1′47.1″ South, 116°0′52.3″–116°0′52.5″ East; Figure 1).

Much of the forest in the area was burned through by large forest fires, following the long and extremely dry seasons of 1997–1998, as described by [11,24,25]. NOAA-AVHRR hotspots, acquired in March 1998, at East Kalimantan, Indonesia, are presented in Figure S2. Some forest areas in the Bangkirai hills, are dominated by *Shorea laevis* (bangkirai; Dipterocarpaceae) and managed as nature leisure parks. The study sites were established in these forests in an area with naturally regenerated forests, since 1998, and in adjacent unburned forests. At the time of field measurements, the regenerated stands were 23 years old. Previous studies have reported the impacts of the dry season and the ensuing forest fire on mixed dipterocarp forest in the Bangkirai hills, East Kalimantan (e.g., [26]). The 1998 fires in the Bangkirai hills resulted in forest areas with around 500–583 standing dead trees per ha, and the number of live trees decreased to between 488 and 1000 per ha. Forest fire reduced live basal areas by 45–85%, leaving between 5.92–20.87 m^2 ha^{-1} basal areas of living trees in the burned area. Forest fires, also, have an impact on decreasing biodiversity, as the Shannon Diversity Index in burned areas is lower (<2) than in unburned areas.

Historical climate data at the site, based on WorldClim climate data version 2.1, for 1970–2000 [27], are shown in Figure S3. The average annual precipitation ranges from 2307 mm to 2313 mm in the Bangkirai hills, with the highest precipitation in March–April and the lowest in September–October. The average temperature is 26.3 °C, with a minimum of 23 °C and a maximum of 29.6 °C. An overview of forest-stand conditions in both the unburned and the 23-year post-fire areas, is presented in Figure 2.
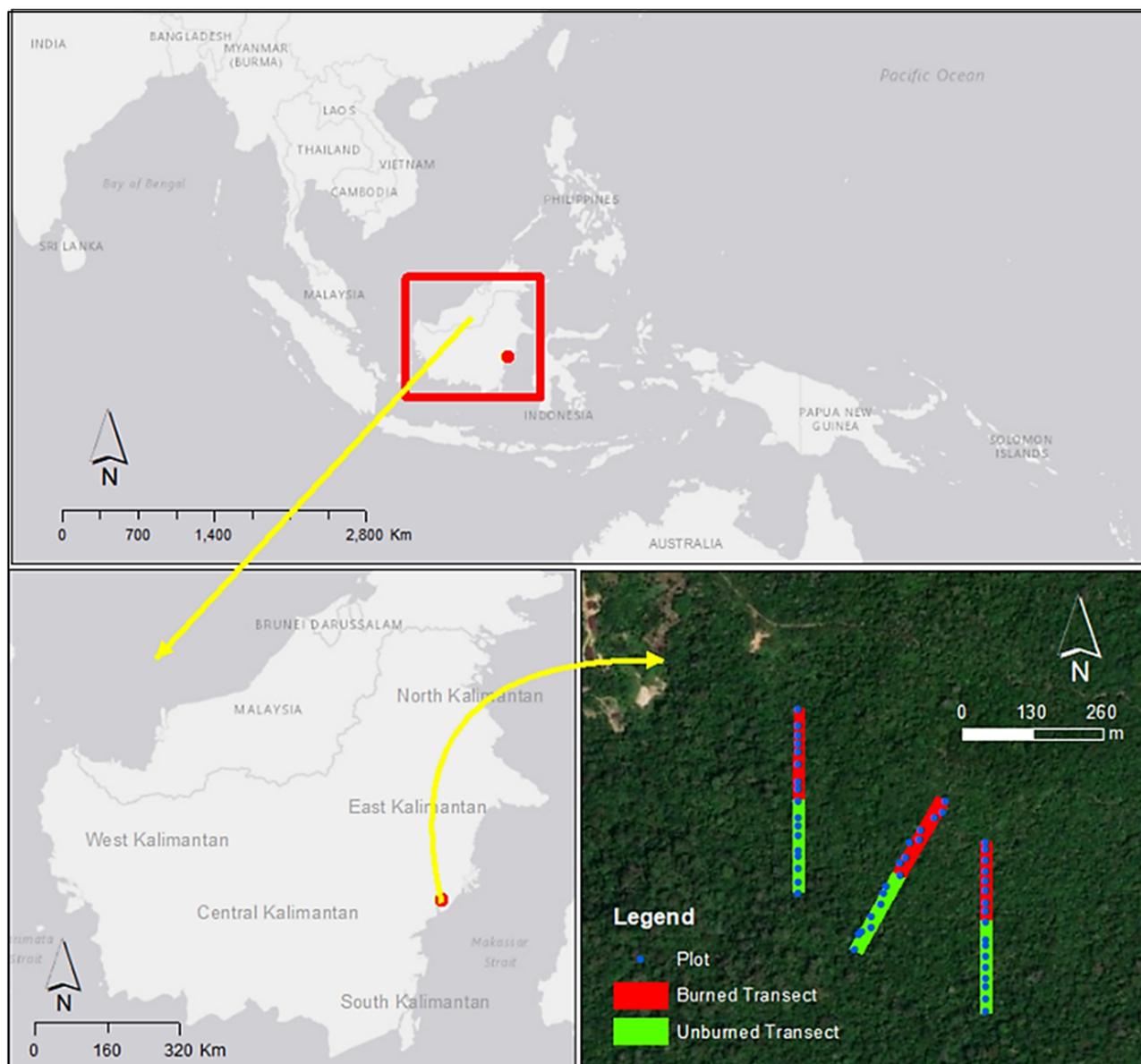
Figure 1. The geographic location of the study sites in East Kalimantan, Indonesia.

Three 20 m wide × 320 m long transects were laid, to cross from the unburned forest into the burned forest, with 160 m of transect in each forest condition. On each transect, 8 plots per forest condition were established, spaced ±3 m apart, resulting in 3 sites and 48 plots total (24 plots in burned areas and 24 plots in unburned areas, Figure 2).

2.2. Stand Structure and Carbon Stock Assesment

All woody plants in the study plots were identified, to species level, and recorded. Plants were categorized into four size classes, according to developmental stage, height, and diameter, at a height of 1.3 m (diameter at breast height; *DBH*), i.e., (1) understory: height < 1.5 m, (2) sapling: *DBH* < 10 cm and height ≥ 1.5 m, (3) pole: 10 cm ≤ *DBH* < 20 cm, and (4) tree: *DBH* ≥ 20 cm. Trees with *DBH* ≥ 10 cm were measured in 20 m × 20 m plots. Smaller trees with *DBH* < 10 cm were measured in subplots of 5 m × 5 m. Understory trees (seedlings and shrubs) were counted in 2 m × 2 m plots [28].

Density and basal area (*BA*), to represent stand structure, were calculated as:

$$Density = \frac{\sum Trees}{A} \tag{1}$$

$$BA = \frac{\sum \frac{1}{4}\Pi\left(\frac{DBH}{100}\right)^2}{A} \tag{2}$$

where *Density* = number of trees per ha (trees ha^{-1}), *A* = plot area (ha), *BA* = basal area (m^2 ha^{-1}), and *DBH* = diameter at breast height (cm).
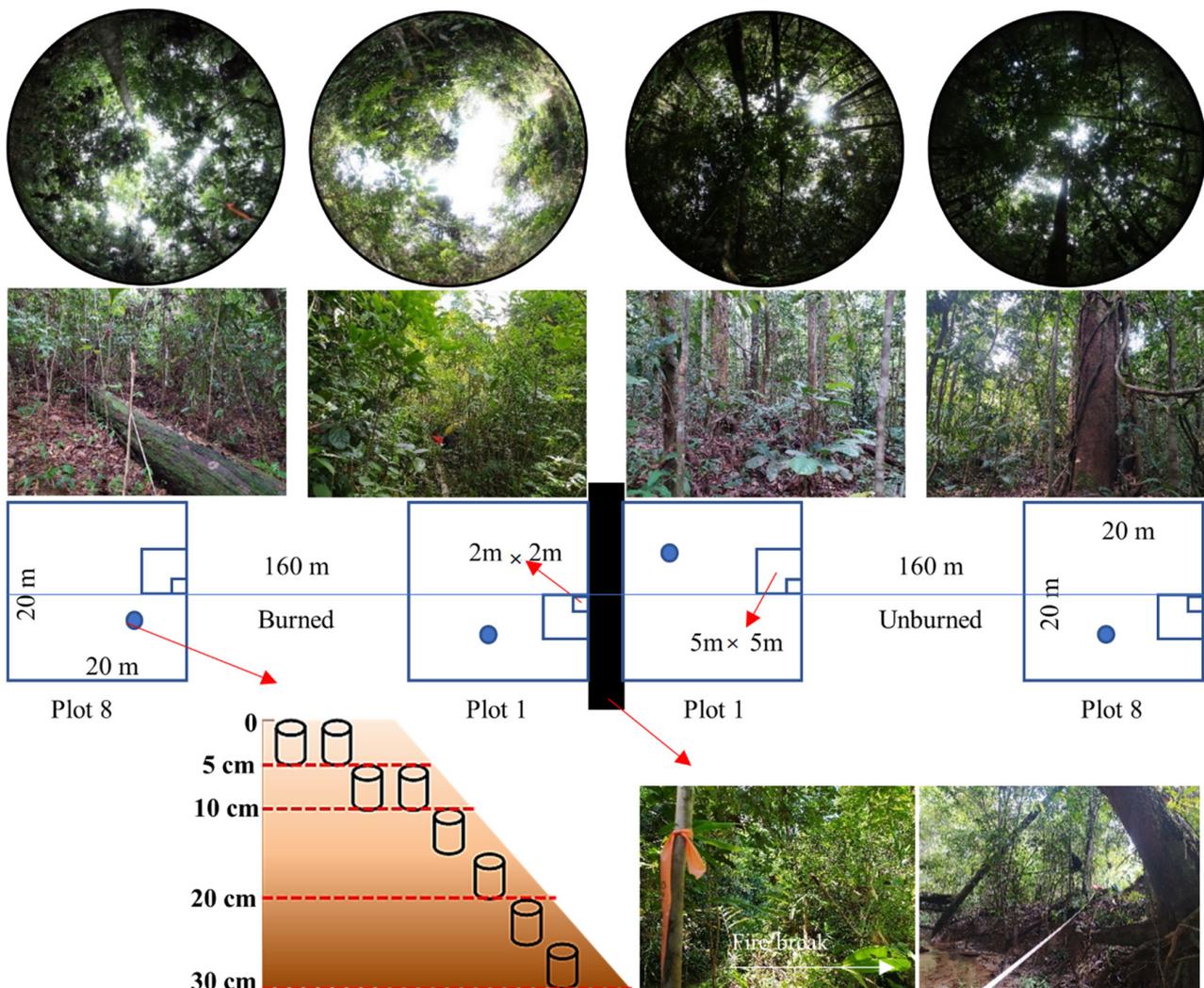
Figure 2. Study-plot design.

In each of these 2 m × 2 m plots, destructive biomass samples were taken from the understory, fine woody debris (FWD, diameter < 2.5 cm), and litter (live and dead leaves, tree fruits, small twigs, and branches, diameter < 0.6 cm) [29]. Coarse woody debris (CWD; diameter ≥ 2.5 cm) were measured for diameter, at the point of intersection with the 160 m long line transect [30]. CWD were classified by decay classes (sound and rotten). Samples from the sound and rotten classes were collected, for wood density and carbon-content analysis. Standing dead trees were measured in 20 × 20 m plots and classified as (1) standing dead trees without leaves, (2) standing dead trees without leaves and twigs, and (3) standing dead trees (only the stems). Soil was sampled in 5 cm increments, from

the surface to a 30 cm depth, using a soil core (196.35 cm^3), with sample intensity shown in Figure 2.

Sub-samples (circa 200 g) of FWD, understory, and litter were dried at 60 °C in the FORDA laboratory in Bogor, until the samples reached a constant weight. The volumetric-water-displacement method was used to calculate the wood density of CWD. The carbon contents of the understory, litter, FWD, CWD, and soil samples were determined, using a loss-on-ignition (LoI) method. The samples were analyzed at the laboratories of the Center for Research and Development of Agricultural Land Resources, Indonesia. In total, 1 g to 2 g samples of understory, litter, FWD, CWD, and soil were burned, for at least 6 h at 550 °C in a quenching furnace, and the residues were weighed. Organic matter was divided by a conversion factor of 1.922, to calculate the carbon content [31]. The carbon content of live and standing dead trees was assumed to be 0.47%, on a dry-weight basis [32].

Using the biomass equation for lowland tropical forests, from [33], the aboveground tree biomass (AGB_T) was determined as:

$$AGB_T = 0.171 \times D^{2.56} \times G^{0.909} \left(Adj\ R_{sq} = 0.943,\ RMSE = 951 \right) \tag{3}$$

where AGB_T = aboveground tree biomass (kg), D = diameter at breast height (cm), and G = wood density (g cm^{-3}). The total amount of aboveground tree biomass in an area was referred to as aboveground biomass (AGB, Mg ha^{-1}).

A Monte Carlo simulation ($n = 5000$) was used to determine the recovery time, based on the value of the aboveground biomass Mean Annual Increment (MAI) and the aboveground biomass of the unburned forest as a reference. MAI (Mg ha^{-1} yr^{-1}) was calculated as:

$$MAI = \frac{AGB}{t} \tag{4}$$

where t = the total years after a fire.

Belowground biomass (BGB, Mg ha^{-1}) was calculated as a percentage of AGB, following the method of [34], using a root-to-shoot ratio of 0.207 for $AGB < 125$ Mg ha^{-1} and 0.212 for $AGB \geq 125$ Mg ha^{-1}. Deadwood was categorized into three categories, i.e., standing dead trees, CWD, and FWD. Standing-dead-tree biomass was reduced by 2.5 percent (for moderate defoliation) or 30 percent (in the absence of leaves, branches, or shoots), to account for the absence of leaves and branches [35].

Soil C-stock was determined using an equivalent mass method [36], as:

$$Msoil_h = BD_h \times h \times 100 \tag{5}$$

$$Cstock_h = Msoil_h \times Corg_h \tag{6}$$

where $Msoil_h$ is the mass of soil sample at depth h (Mg ha^{-1}), BD is the bulk density at depth h (g cm^{-3}), h is the depth of sample (cm), $Corg_h$ is the C fraction of the soil sample at depth h, and $Cstock_h$ is the soil C content at depth h (Mg C ha^{-1}).

Soil C stock was the sum of soil C stocks for each collected depth of 0–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm. The sum of carbon in biomass (AGB, BGB, understory), dead organic matter (DOM), i.e., standing dead trees, CWD, FWD, litter, and soil to a 30 cm depth, formed the estimate of total ecosystem carbon.

2.3. Biodiversity Assesment

Frequency, density, and dominance of the relative value of the vegetation were calculated, and then, summed to generate an important value index (IVI) [37], as:

$$IVI = FR + DR + DomR \tag{7}$$

where IVI is the Important Value Index (%); FR is the relative frequency (%), a ratio of a species' frequency to the total frequency; DR is relative density (%), a ratio of a species's

number of individuals to the total number of individuals for all species; and *DomR* was relative dominance (%), a ratio of a species's basal area to the basal area of all species.

Species diversity was estimated using the diversity index of Shannon and Simpson, the evenness index, and species richness. Each index denotes a unique aspect of community diversity [38]. The diversity values were estimated using the vegan package [39] of R [40]. The diversity parameters of the evenness index of Pielou (*J*), the diversity index of Shannon (*H'*) and Simpson (*D*), and the species richness of Margalef (*S*) were calculated as:

$$S = \sum species \tag{8}$$

$$H' = -\sum_i pi \; x \; log_b pi \tag{9}$$

$$D = \sum_i pi^2 \tag{10}$$

$$J = H'/\log S \tag{11}$$

where *i* and *b* are the logarithm bases, while *pi* is the relative abundance of the species.

The diversity index *H'* > 2 shows that the community is stable [41]. The Simpson index *D* ranges from 0 to 1, with zero representing no dominance, and 1 representing maximum dominance. Decreased species richness and evenness reduce ecosystem productivity and stability, resulting in reduced functional diversity within the same ecosystem [42].

2.4. Statistical Analysis

A Tukey-Kramer analysis of variance established any statistical differences between the 23-year post-fire and unburned plots, where the differences were considered significant at the 5% level. The Jaccard index statistic [43] was used to measure the similarity and diversity of communities in burned and unburned plots as:

$$Jaccard \; index = \frac{c}{a + b + c} \tag{12}$$

where the *Jaccard index* ranges from 0 to 1, *c* is the number of species shared between the two sites, and *a* and *b* are the numbers of species unique to either site. The greater the value of the Jaccard index, the closer the two communities are, in terms of species similarity.

Plant-species composition of both burned and unburned plots was analyzed using non-metric multidimensional scaling (MDS) ordination. The default monoMDS function, which contains a square root transformation Wisconsin and a different index, Bray–Curtis, was used to order a species matrix of the number of each plant species in each plot. The analysis was done with the vegan package, and ordination was visualized using the ggplot2 package [44].

Biophysical parameters, such as soil pH, temperature, humidity, and light intensity, were measured at the center of each plot. A digital soil analyzer tester meter was used to measure soil pH. Temperature, humidity, and light intensity were measured using a portable multi-functional anemometer.

3. Results

3.1. Site Biophysical Characteristics

Results of site biophysical characteristics are presented in Table 1. Burned sites were slightly hotter and drier than unburned sites. Light intensity in burned sites was almost seven times greater than in unburned sites (Table 1).

Table 1. Biophysical condition of the observation sites.

Plot	Top Soil pH	Temperature (°C)	Humidity (%)	Light Intensity (Lux)
Burned	5.9 ± 0.17 *	29.65 ± 0.48 *	87.9 ± 1.47 *	5770.06 ± 3330.64 *
Unburned	5.56 ± 0.2 *	28.31 ± 0.21 *	90.93 ± 0.61 *	876.43 ± 304.73 *

* mean ± standard error of mean.

3.2. Stand Carbon Stock Recovery

The total tree density (sapling, pole, and large tree) of the 23-year post-fire forest (5755 ± 226 trees ha^{-1}) was significantly lower than the total tree density of the unburned forest (9067 ± 371 trees ha^{-1}). In both forest conditions, saplings accounted for more than 90% of total tree density, followed by smaller trees (pole; 5%), while large trees contributed only 2% to the total tree density. Comparison for all pairs, using Tukey-Kramer, showed that seedling, pole, and large tree densities were not significantly different at the 0.05 level, while saplings showed a significant difference between the two forests (Figure 3a). The total basal area (sapling, pole, and large tree) of the 23-year post-fire forest (18.67 ± 1.97 m^2 ha^{-1}) was significantly less than the total tree density of the unburned forest (25.92 ± 1.01 m^2 ha^{-1}). Unburned forest had significantly higher basal area for all DBH categories, except for the 20–30 diameter class (Figure 3b).
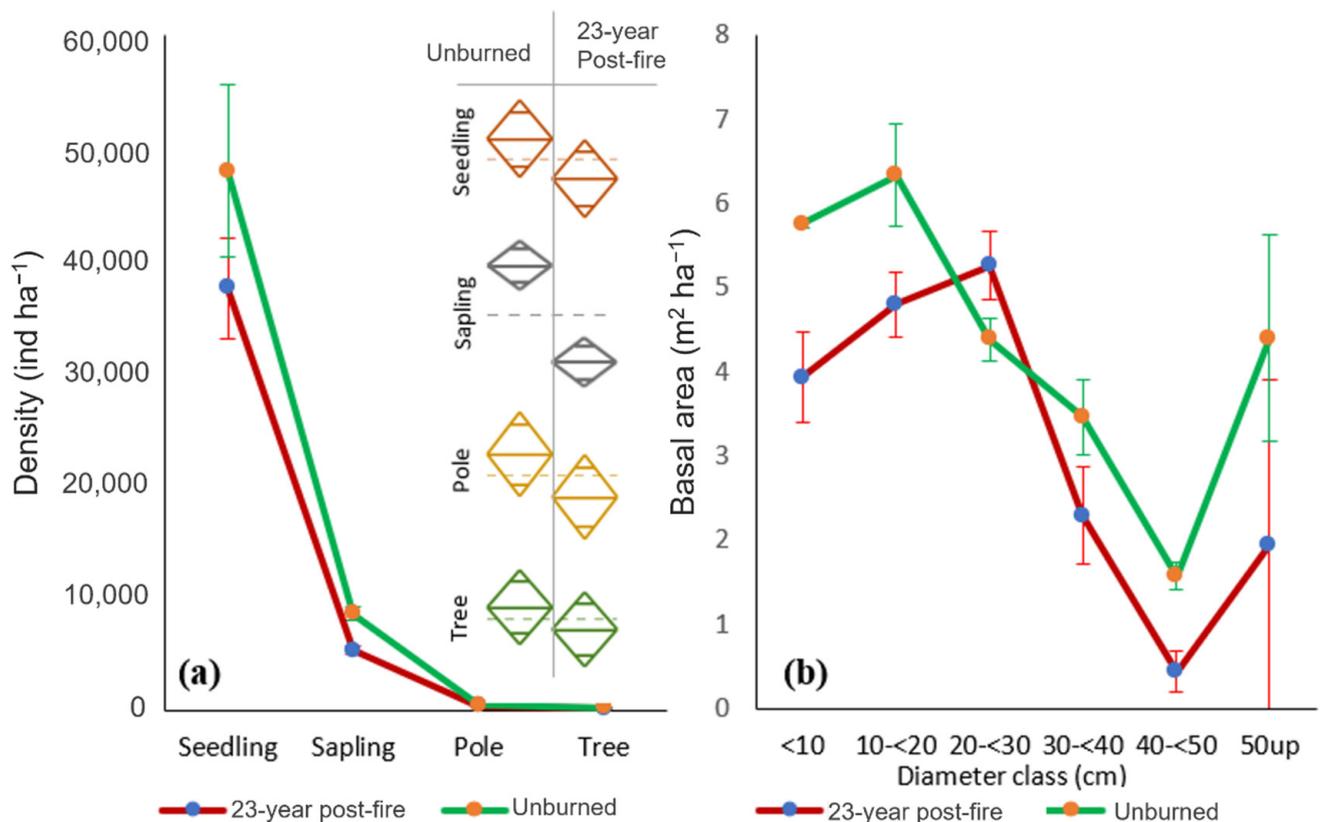
Figure 3. Horizontal stand structures: (**a**) density and (**b**) basal area in the 23-year post-fire forest and in the unburned forest.

The aboveground biomass (AGB) from the sapling to the tree level in the 23-year post-fire forest (142.87 ± 36.33 Mg ha^{-1}) was significantly less than the AGB of the unburned forest (264.60 ± 34.32 Mg ha^{-1}). The combined AGB of the seedling and understory classes were similar among the unburned and 23-year post-fire forests. The total AGB value (trees + understory) of the 23-year post-fire forest was 143.57 ± 36.48 Mg ha^{-1}, while the unburned forest was 265.30 ± 34.16 Mg ha^{-1}.

The mean annual increment (MAI) of AGB in the 23-year post-fire forest was 6.24 ± 1.59 Mg ha^{-1} year^{-1}. Based on Monte Carlo simulation, using MAI, it will require 46 ± 17 years to recover the live carbon pool to the unburned-forest level (Figure S4).

The Tukey-Kramer comparison showed no significant difference (0.05 level) between the belowground biomass of the 23-year post-fire forest and the unburned forest. BGB in the 23-year post-fire forest was 30.08 ± 7.91 Mg ha^{-1}, compared to 56.24 ± 7.24 Mg ha^{-1} in the unburned forest.

In contrast, the 23-year post-fire forest had significantly higher deadwood mass (124.36 ± 33.16 Mg ha^{-1}) than the unburned forest (64.24 ± 15.83 Mg ha^{-1}; Figure 4). The litter mass of the 23-year post-fire (4.73 ± 0.92 Mg ha^{-1}) and unburned forests (4.29 ± 0.29 Mg ha^{-1}) were similar.

Figure 4. Deadwood mass in the 23-year post-fire forest and in the unburned forest.

The soil bulk density and C-org values were not significantly different among the burned and unburned forests, for each of the sampled depths, except for the 5–10 cm soil horizon (Table 2). The soil carbon–organic content declined with soil depth (Figure 5b), while soil bulk density increased with soil depth (Figure 5a). Soil carbon stock to a 30 cm depth in the 23-year post-fire forest was 55.5 ± 5.13 Mg C ha^{-1}, while in the unburned forest, it was significantly lower at 41.6 ± 2.68 Mg C ha^{-1}.

Table 2. Bulk density and C-org at 0–5 cm, 5–10 cm, 10–20 cm and 20–30 cm depth in the 23-year post-fire forest and in the unburned forest.

	Soil Depth (cm)			
	0–5	**5–10**	**10–20**	**20–30**
Bulk Density (g cm^{-3})				
23-year post-fire	0.93 (a) $\pm$ 0.050 *	1.11 (a) $\pm$ 0.050 *	1.20 (a) $\pm$ 0.053 *	1.27 (a) $\pm$ 0.037 *
Unburned	0.85 (a) $\pm$ 0.075 *	0.92 (b) $\pm$ 0.067 *	1.11 (a) $\pm$ 0.072 *	1.19 (a) $\pm$ 0.046 *
C-org (%)				
23-year post-fire	2.19 (a) $\pm$ 0.517 *	2.05 (a) $\pm$ 0.520 *	1.55 (a) $\pm$ 0.377 *	1.12 (a) $\pm$ 0.179 *
Unburned	1.90 (a) $\pm$ 0.255 *	1.64 (a) $\pm$ 0.243 *	1.22 (a) $\pm$ 0.055 *	1.06 (a) $\pm$ 0.018 *

* mean $\pm$ standard error of mean, levels not connected by same letter are significantly different at the 0.05 level

As in soil C-org, in other carbon pools (understory, litter, woody debris, sound deadwood, and rotten deadwood), the carbon fraction values in the 23-year post-fire forest and the unburned forest were not significantly different (Table 3).
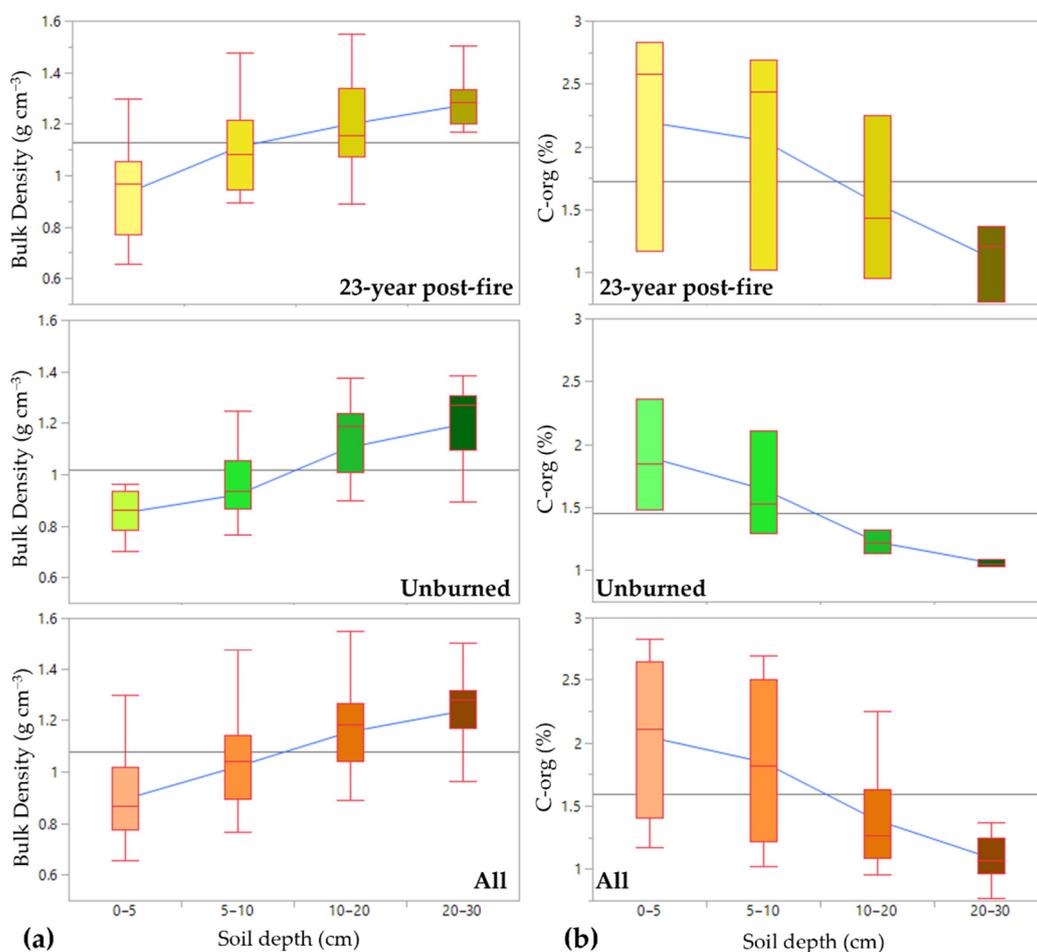
Figure 5. The trend of bulk density (**a**) and C-org (**b**) values with increasing soil depth in the 23-year post-fire forest (top panels), in the unburned forest (middle panels) and the average of all burned and unburned forests samples together (bottom panels).

Table 3. Mean carbon fraction (%) in the understory, litter, woody debris, sound deadwood, and rotten deadwood.

Carbon Pool	Carbon Fraction (%)		
	Burned	Unburned	All
Litter	50.09 ± 0.51 *	48.91 ± 0.47 *	49.50 (a) ± 0.36 *
Understory	40.51 ± 0.57 *	40.71 ± 0.88 *	40.62 (a) ± 0.52 *
Fine Woody Debris	41.25 ± 1.03 *	43.82 ± 1.02 *	42.73 (a) ± 0.77 *
Coarse Woody Debris Sound	49.54 ± 0.66 *	49.99 ± 1.21 *	49.76 (a) ± 0.63 *
Coarse Woody Debris Rotten	48.19 ± 0.65 *	48.61 ± 2.00 *	48.40 (a) ± 0.95 *

* mean ± standard error of mean, levels not connected by same letter are significantly different at the 0.05 level

The total carbon stock in unburned forests (219.78 ± 24.69 Mg C ha^{-1}) was not significantly different from the burned, secondary forests (198.96 ± 33.14 Mg C ha^{-1}). However, the distribution of carbon among pools was different between the two forests. In unburned forests, live tree biomass was the dominant carbon pool (146.58 ± 18.89 Mg C ha^{-1}), followed by soil organic carbon (SOC) (41.62 ± 2.54 Mg C ha^{-1}), and dead organic matter (DOM) (31.58 ± 9.53 Mg C ha^{-1}). In contrast, in burned secondary forests, live tree biomass (79.17 ± 20.22 Mg C ha^{-1}) and DOM (65.53 ± 19.02 Mg C ha^{-1}) were similar, while SOC was 54.26 ± 11.32 Mg C ha^{-1} (Figure 6).
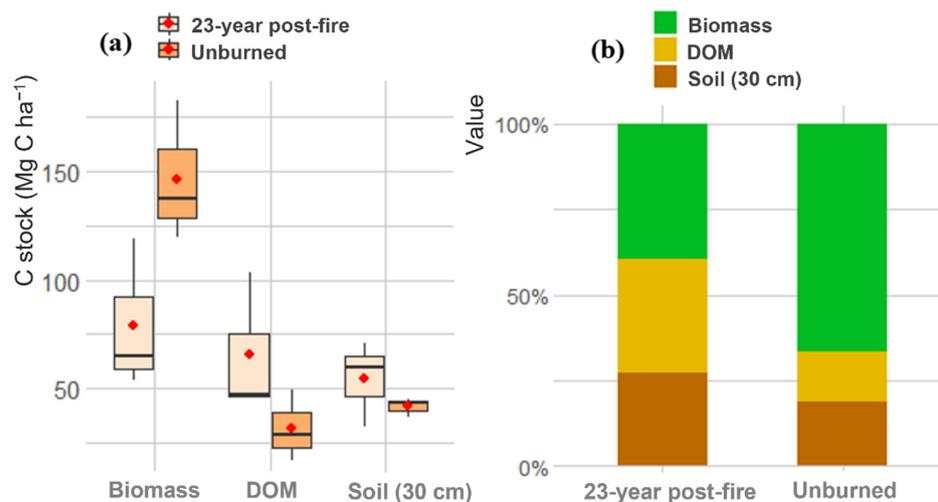
Figure 6. C stocks (**a**) and percentage of carbon of each pool (**b**) in the 23-year post-fire forest and in the unburned forest.

3.3. Biodiversity Recovery

The unburned forests had higher numbers of plant species present than the burned forests (219 vs. 179). Unburned forests had higher numbers of taxa present than the burned forests, in all vegetation size categories, with 68 families and 146 genera recorded in unburned plots vs. 58 families and 126 genera in the 23-year post-fire forest. The five most abundant species were, likely, more dominant in the 23-year post-fire forest (IVI value of 83.9–135.8%) than in the unburned forest (IVI value of 59.1–77.5%; Table 4).

Table 4. List of five species with the highest important value index (IVI), by growth level, in the 23-year post-fire forest and in the unburned forest.

Unburned Forest		23-Year Post-Fire Forest	
Species	**IVI (%)**	**Species**	**IVI (%)**
Seedling/Understory			
Stachyphrynium cylindricum	26.0	*Clidemia hirta*	30.1
Guioa sp.	10.4	*Guioa* sp.	19.3
Korthalsia sp.	10.4	*Stachyphrynium cylindricum*	17.2
Ficus sp.	6.9	*Fordia splendidissima*	8.6
Agelaea borneensis	5.2	*Scleria* sp.	8.6
Sapling			
Syzygium sp.	15.1	*Fordia splendidissima*	53.6
Fordia splendidissima	14.8	*Pternandra rostrata*	22.6
Macaranga lowii	13.1	*Syzygium* sp.	10.8
Pternandra rostrata	9.7	*Litsea firma*	10.6
Urophyllum arboreum	9.2	*Macaranga gigantea*	7.5
Pole			
Macaranga gigantea	16.0	*Macaranga gigantea*	27.7
Syzygium sp.	14.4	*Dillenia reticulata*	22.7
Macaranga hypoleuca	14.2	*Macaranga conifera*	21.4
Madhuca kingiana	13.7	*Vernonia arborea*	17.1
Macaranga conifera	9.7	*Litsea firma*	13.2
Large tree			
Horsfieldia sp.	19.6	*Macaranga gigantea*	63.6
Shorea laevis	17.4	*Schima wallichii*	22.9
Koompassia malaccensis	15.1	*Dipterocarpus confertus*	19.3
Eusideroxylon zwageri	12.7	*Vernonia arborea*	15.0
Syzygium sp.	12.4	*Macaranga conifera*	14.8

The community similarity index (Jaccard index) of the unburned forest and the 23-year post-fire forest yields a ratio of 0.4, indicating that the post-fire forest has not yet reached a similar species composition, 23 years after the fire. The response of plant species composition to site circumstances was determined using non-metric multidimensional scaling (MDS; Figure 7). It can be seen that the 23-year post-fire forest was, still, compositionally different from the unburned forest. Several plots in the burned forest show the same composition as the unburned forest, possibly due to a neighboring effect.
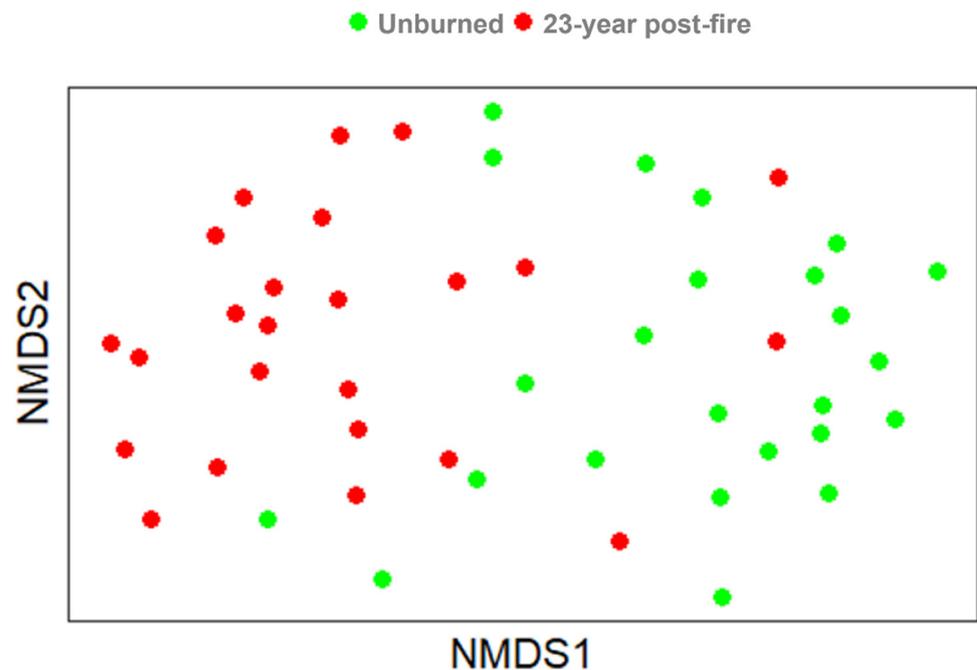
Figure 7. Non-metric multidimensional scaling (NMDS) plot of species composition for the 23-year post-fire forest (red dots) and for the unburned forest (green dots).

The distribution of species diversity indicator values in the unburned and 23-year post-fire forests is given in the violin diagram, in Figure 8. Among the taxa levels, the unburned forest has a richness of 50 (family), 94.67 (genera), and 126 (species). In comparison, the 23-year post-fire forest had a reduced richness, of 41.67 (family), 71.33 (genus), and 91.67 (species). The level of diversity in a community, from the various taxonomic groups based on the Shannon and Simpson index, shows the same pattern with the value of H′ species > 3 in the unburned forest and the 23-year post-fire forest. Pielou's evenness index (J) in the 23-year post-fire forest was as high as in the unburned forest, with a J value > 0.8.

A similar trend was observed at tree category levels (seedlings, saplings, poles, and large trees). The 23-year post-fire forest had lower diversity indices than the unburned forest (Figure 8). At the sapling and pole levels, the 23-year post-fire forest and the unburned forest had higher species richness and diversity indices than on other growth levels. Sapling and pole levels in the unburned forest had an H′ > 3, which showed that the community was very stable. Meanwhile, at the large tree and seedling levels of the unburned forests and all growth levels, the 23-year post-fire forest had a stable community, with an H′ value between 2 to <3.

The species richness, Shannon index, Simpson index, and evenness at the taxon levels, were similar among the unburned forest and the 23-year post-fire forest (Table 5). Yet, the species richness index was significantly lower in the 23-year regrowth than in the unburned forests, in both saplings and large trees.
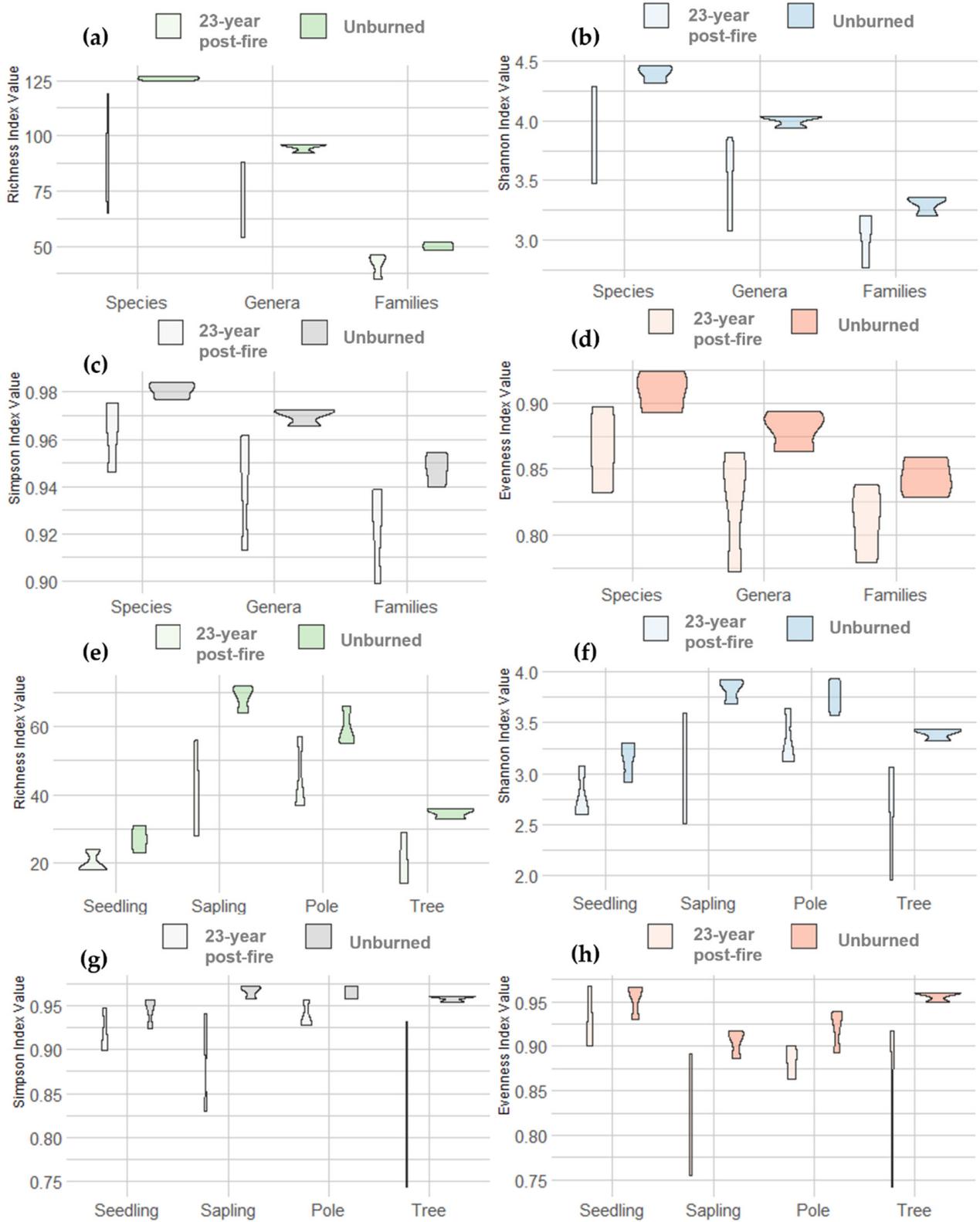
Figure 8. Biodiversity on taxon levels: (**a**) species richness, (**b**) Shannon index, (**c**) Simpson index, and (**d**) J evenness index; biodiversity on growth levels: (**e**) species richness, (**f**) Shannon index, (**g**) Simpson index, and (**h**) J evenness index in the 23-year post-fire forest and in the unburned forest.

Table 5. Diversity value in the 23-year post-fire forest and in the unburned forest, by taxon and growth level.

Forest		Diversity Index							
		Richness Index *		Shannon Index *		Simpson Index *		Evenness Index *	
Growth Level									
Seedling	23-Year Post-Fire	20	(a)	2.78	(a)	0.92	(a)	0.93	(a)
	Unburned	27	(a)	3.13	(a)	0.94	(a)	0.95	(a)
Sapling	23-Year Post-Fire	41.33	(a)	3.09	(a)	0.90	(a)	0.83	(a)
	Unburned	68.67	(b)	3.83	(a)	0.97	(a)	0.91	(a)
Pole	23-Year Post-Fire	43.67	(a)	3.32	(a)	0.94	(a)	0.88	(a)
	Unburned	59.33	(a)	3.76	(a)	0.97	(a)	0.92	(a)
Large tree	23-Year Post-Fire	21	(a)	2.59	(a)	0.87	(a)	0.86	(a)
	Unburned	34.67	(b)	3.39	(a)	0.96	(a)	0.96	(a)
Taxonomy Level									
Families	23-Year Post-Fire	41.67	(a)	3.02	(a)	0.92	(a)	0.81	(a)
	Unburned	50	(a)	3.3	(a)	0.95	(a)	0.84	(a)
Genera	23-Year Post-Fire	71.33	(a)	3.51	(a)	0.94	(a)	0.82	(a)
	Unburned	94.67	(a)	4	(a)	0.97	(a)	0.88	(a)
Species	23-Year Post-Fire	91.67	(a)	3.89	(a)	0.96	(a)	0.87	(a)
	Unburned	126	(a)	4.4	(a)	0.98	(a)	0.91	(a)

* Levels not connected by same letter are significantly different at the 0.05 level.

4. Discussion

4.1. Carbon Recovery 23 Years after Fire

Twenty-three years post-fire, the density of seedlings, poles, and large trees, but not of saplings, in the Bangkirai hills's burned forest approached the condition of the nearby unburned forest. Previous studies in the rainforests of East Kalimantan, Indonesia, reported that fire events had significantly increased the mortality rate of small-diameter trees, resulting in the loss of seedlings, saplings, and poles after fire [24]. In general, the basal area of the 23-year post-fire forest, for each diameter class, was lower than that in the unburned forest. However, the dominance of the pioneer species *Macaranga gigantea*, at the tree level in the burned forest, is seen in the higher occurrence of trees in diameter class 20–30 cm, relative to the unburned forest. The species composition and structure of the burned forest indicates that it has not yet recovered fully, following the fire in 1998. This conclusion is supported by the observed lower-canopy cover density, higher forest-floor temperature, and lower humidity in the burned plots than in the unburned plots. The impacts of fire on soil pH in the burned plots, also, remain evident after 23 years, with more alkaline soil pH, due to alkaline ash deposits, than in the unburned plots [45].

Carbon storage in the burned tropical secondary forest is lower than in the unburned forest [19]. Aboveground biomass (AGB) from the sapling to the tree level of the 23-year post-fire forest, in our sites, was lower than in the unburned forest. However, it was higher than in forests < 12 years post fire [18,46], indicating carbon recovery. Meanwhile, the biomass of the understory and seedlings in the burned sites was similar to the unburned forest. In general, trees with DBH > 10 cm contribute most to the AGB biomass, with 89.4% in the 23-year post-fire forest and 92% in the unburned forest, while the understory and seedlings contributed less than 1% of AGB.

Twenty-three years post fire, a lot of deadwood remained in the forests, mainly as fallen CWD, making it the largest contributor to the DOM carbon pool (91% deadwood mass), compared to fine woody debris, which accounted only for 1–2% of deadwood mass, in both forest conditions. Carbon built into litter is a minor pool of carbon aboveground [47]. The impact of fire on the litter was not noticeable 23 years after the fire.

The soil bulk density and C-org in the 23-year post-fire forest and the unburned forest were not, statistically, significantly different within most depths sampled, except for the 5–10 cm depth. Soil depth is critical in determining the distribution of soil-carbon storage.

Although soil carbon–organic content declined with depth, the total carbon storage capacity of the deeper soil layers was larger than that of the surface soil layers, due to increased soil bulk density with depth. Carbon stocks in the top 30 cm of soil at our sites were in the range of the soil-carbon stock of mineral soils in Indonesia, ranging from 42.21 Mg C ha^{-1} to 167.64 Mg C ha^{-1} [48]. The soil organic C in the uppermost layer (0–10 cm) is, mostly, determined by the intensity and duration of the fire [49]. Increases in soil C, following fires, can be detected in both the surface and deeper soil layers, due to inputs from partially burned plant components and carbonized particles [49,50]. In our sites, an increase in soil C at the 5–10 cm depth indicated carbon transportation to a deeper layer, 23 years after the fire.

About 23 years after the fire, carbon stocks in living vegetation are around 54% of the level of the unburned forest. However, the surviving vegetation plays a crucial role in forest recovery, enabling an increase in tree density and biomass [51]. An aboveground biomass MAI of ± 6 Mg ha^{-1} yr^{-1} is obtained after 23 years of regenerated growth following a fire. After a fire, the increment rate decreases with recovery time [18,46]. In contrast, dead organic matter was higher in post-fire secondary forests, due to the carbon redistribution from live to dead pools.

Total carbon sequestered in the unburned forests is equivalent to 806 ± 88 MgCO$_2$-e ha^{-1} of atmospheric carbon dioxide (uncertainty level of 22.6%). The regenerated 23-year post-fire forest resulted in carbon storage in live biomass of 291 ± 43 MgCO$_2$-e ha^{-1}, accounting for all carbon pools, 730 ± 68 MgCO$_2$-e ha^{-1}, or 90% of the unburned forest, illustrating the importance of accounting for all carbon pools in greenhouse gas inventories, especially in relation to forest fires.

4.2. Vegetation Recovery

The forest, 23 years after fire, was still dominated by the pioneer species *Macaranga gigantea*, at the tree level. Inequalities in species-dispersal capacity, between burned and unburned forests, may exacerbate differences in species composition [19]. The number of tree species in our unburned forests were similar to the number of species found in the unburned forests in East Kalimantan, which ranged between 160 species ha^{-1} and 276 species ha^{-1} [52]. The 23-year post-fire plots had a lower number of families, genera, and species than the unburned plots. Species that play a dominant role in the community will have a high IVI value [37]. The occurrence of a specific species within a community with a high IVI, also, shows the ability of the species to adapt to their habitat and high tolerance for the environment. *Macaranga gigantea* was the species that had the highest IVI value at the large tree and pole levels, in the 23-years post-fire forest. At our study sites, pioneer species were no longer dominant at the seedling level, compared to the first few years after the fire [53,54]. At the sapling level, *Fordia splendidissima* became the main species that dominated the 23-years post-fire forest (53.6%). *Fordia splendidissima* was, also, commonly found in the unburned forest, second after *Syzygium* sp. *Fordia splendidissima* became the dominant species in both unburned forests and burned forests shortly after the fire, as reported by [55]. The unburned and 23-year post-fire forests had similar species composition, at the seedling and understory levels. Although the unburned forest and the 23-year post-fire forest had different species with the highest IVI values (*Stachyphrynium cylindricum* in the unburned plot and *Clidemia hirta* in the 23-year post-fire plots), the same species were found in both forest conditions, such as *Stachyphrynium cylindricum* and *Guioa* sp., dominating > 30%, indicating species-richness recovery in the burned plots. However, species richness of the saplings and large trees had not yet recovered to the levels found in the unburned forests.

The species diversity, richness, and evenness, at all taxon levels, had recovered to the levels found in the unburned forest, except for richness in the saplings and large trees. Tukey-Kramer tests on the biodiversity metrics (diversity indices of Shannon and Simpson, the evenness index, and species richness), of the 23-year post-fire forest vs. the unburned forest, revealed statistically insignificant differences. Yet, the species richness index was

significantly different in the 23-year post-fire than in the unburned forests, for both saplings and large trees. However, the value of biodiversity parameters, at all taxon levels, in the unburned forest was higher than in the 23-year post-fire forest. Basal area in the forest 23 years post-fire increased by 26-74%, compared to the basal area in the forest 5 years post-fire [17]. However, basal area in the forest 23 years post-fire was 73% in the unburned forest. This difference in the species composition and stand structure has implications for carbon storage [19,46,56], due to the regeneration and regrowth of fire-resistant stands.

Fires have altered existing environmental variables [57] that influence the density, and, thus, species diversity and richness [58]. Tree mortality by fire was inversely related to both tree diameter and bark thickness [24], suggesting that the diameter structure of a population may be as good a predictor of a species's fire susceptibility as the bark features. Resprouting is an important functional plant feature that allows plants to survive after disturbance [59]. When meristematic tissues, specifically buds, are shielded from fire after a fire, resprouting occurs [60]. Following a fire, seed germination is a frequent post-fire recruitment method for recovery. Seed release, seed germination, and flowering were all enhanced by fire [61]. However, recovery of species composition to the pre-fire level is slow [19,62].

5. Conclusions

Twenty-three years after the 1998 fire, the recovering secondary forest is dominated by the pioneer species *Macaranga gigantea* and is, yet, to recover overstory canopy similar to the unburned reference forest. The live aboveground biomass in the burned forest remains at 50–60% of the unburned forest, attesting to a relatively slow recovery rate for a tropical environment. The main tree component in the fire-recovering forest is seen in the relatively high frequency of trees with DBH 20–30 cm. However, when considering the total ecosystem carbon that includes biomass (aboveground and root), dead organic matter, and soil organic carbon to a 30 cm soil depth, there was not much difference between the unburned reference forest (220 Mg C ha^{-1}) and the adjacent burned forest (199 Mg C ha^{-1}). Twenty-three years after the fire, total carbon stocks from all carbon pools had reached 90% of the unburned forest. This study identified the importance of accounting for the carbon redistributed from live to dead organic matter and, also, from aboveground to soil horizons in the burned forest. For the purpose of greenhouse gas (GHG) inventory, this study demonstrates the importance of including all carbon pools in carbon stock estimates of secondary forests, following disturbance events. Although parameters, such as light intensity at the forest floor and related temperature increases, indicate that, structurally, the burned forest is yet to fully recover after 23 years, the rate of live aboveground-biomass recovery, after the 1998 fire, is about 6 Mg ha^{-1} year^{-1}, indicating that the live aboveground-biomass carbon will be recovered after about 46 ± 17 years. We acknowledge that our study represents one forest-area case study, on the effects of fire on the recovery of vegetation and carbon stocks in dryland forests of Indonesia, and that more observations across a broader range of disturbed forests are required, to describe the dynamics of forest-carbon recovery at a landscape level.

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