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Research Article

Stand Structure Characteristics of Fragmented and Primary Forests and Their Correlation to Carbon Stocks

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ABSTRACT
Stand structure contributes to forest biodiversity and productivity. The disparity of stand structure between fragmented and primary forests and how they affect carbon storage are poorly understood. This study determined differences among some stand parameters in fragmented and primary forests and the correlation between forest stand structure and carbon stock. Twenty-five replicate quadrats were established in Bukit Durang and Division 5, representing the fragmented forests, and Lambir Hills National Park and Kubah National constitute the primary forests. All trees with diameter at breast height of 10 cm and above were measured, and the tree species were recorded. Aboveground biomass was calculated and converted to carbon stock. Statistical analyses showed that tree density is comparable among the forests. However, species abundance, species dominance, basal area aboveground biomass, and carbon stocks are different. Large-diameter trees significantly contribute to carbon storage. Principal component analyses revealed basal area, tree diameter and carbon stock were positively intercorrelated and associated. Species dominance and tree density are intercorrelated and strongly associated. Conversely, the number of species is negatively correlated to species dominance and tree density. This study showed the significance of tree diameter in impacting carbon stock.

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INTRODUCTION

Recognising the association between forest stand structure and productivity in natural communities is essential to sustaining ecosystem services for humanity (Guo et al. 2021; Wang et al. 2024). Ecosystems regulate the Earth's climate by taking out carbon dioxide (CO_2) from the environment, with photosynthesis sequestering carbon dioxide and depositing it in natural reservoirs like forests, oceans and soil (Friedlingstein et al. 2019; Anjum et al. 2022; McLaughlin et al. 2023). These reservoirs retain carbon for extended periods, preventing its contribution to global warming (Deemer et al. 2016; Li et al. 2018). Terrestrial forests are particularly effective in sequestering excessive CO_2, aiding its recovery into ecosystem pools (Jeyanny et al. 2014). According to Lal (2018), approximately 80 % of the Earth's terrestrial carbon accumulates within 1 m of the soil globally. Living tree biomass contributes to carbon sequestration until the tree's demise (Nave et al. 2019). Forests in different regions exhibit varying C stock rates, influenced by factors such as forest and tree structure attributes, plant diversity and tree aboveground biomass (AGB) (Dossa et al. 2013; Jeyanny et al. 2014). The distribution of C stocks across regions depends on vegetation type, climate and land-use history. Tropical rainforests, which cover 30 % of the Earth's tree-fill areas and 45 % of the total worldwide forest areas (Abbas et al. 2020), stock 50 % of the global carbon in trees (Global Resource Institute 2023). Intact tropical forests, characterised by massive old trees and diverse plant species, significantly contribute to carbon sequestration and storage (Watson et al. 2018).

However, deforestation, forest degradation and fragmentation threaten tropical forests' carbon stocks (C stocks) (Chaplin-Kramer et al. 2015; Maxwell et al. 2019). Selective logging activities are responsible for 50 % of emissions from forest degradation, deplete tree species with high carbon content, and increase the risk of biodiversity loss (Ellis et al. 2019). Although richness, diversity and biomass may recover to unlogged levels within 35 years after logging, community composition differs from nearby primary forests (Hayward et al. 2021). The disturbance of the mature forests can significantly impact aboveground biomass in forests where areas with high disturbance intensity typically have lower aboveground biomass (Temesgen et al. 2015; Wulder et al. 2020).

The status of the logged-over forest after some period in terms of carbon storage and forest structure is essential to know, especially the one surrounded by an oil palm plantation. Deforestation can decrease species diversity (Priatna et al. 2012). The forest structure in forest fragments differs from the primary forests due to the changes in microclimatic conditions, such as higher temperatures, light prevalence, and lack of moisture (Camargo & Kapos 1995; Oliveira et al. 2008). Forest fragmentation significantly affects diameter at breast height (DBH), crown diameter and tree density (Hending et al. 2023). Many forest fragments are degraded, with poor habitat quality and low ecological integrity (de Paula et al. 2011). However, degraded forests can still store and sequester carbon; consequently, protecting damaged habitats alleviates greenhouse effects by reducing carbon footprint and enhancing carbon sequestration (Gross 2020).

Estimating biomass and carbon is crucial for forest conservation (Matthew et al. 2018). Estimating C stocks in forests needs an accurate aboveground biomass estimation (Yeboah et al. 2014). The basal area of a tree is a valuable indicator of its biomass and carbon (Power et al. 2019). Thus, a relationship between these variables is anticipated since the basal area and biomass are correlated to the stem diameter (Torres & Lovett 2013). The correlation between carbon stock and DBH in tropical forests varies depending on the forest type (Banoho et al. 2020). Intact primary forest tends to have larger trees, which dominate the forest's carbon storage and are common across almost all types of forests, regardless of their niches or locations (Mildrexler et al. 2020; Bordin et al. 2021; Johnston et al. 2021). However, the relationship between C stock and the basal area varies depending on forest type and management practices (Dignac et al. 2017).

This study investigated the variations in selected stand parameters between fragmented and primary forests. We also evaluated the intercorrelation among tree stand parameters. Studies (Ellis et al. 2019; Hayward et al. 2021) have shown differences in vegetation assemblage and forest structure between unlogged and logged forests throughout all groups of tree size. Moreover, fragmented forests are exposed to unfavourable environments such as temperature, humidity, wind and light intensity, which typically impact the ecosystem structure and function in tropical forests, causing habitat isolation, loss of biodiversity, and decreased soil fertility (Wade et al. 2003; Abdullah 2016). Thus, it highlights the importance of exploring the differences in stand characteristics between fragmented and primary forests. Many ecological studies have focused on undisturbed tropical forests; however, vast areas of tropical fragmented forests are still inadequately studied regarding their composition and structure (Feeley & Silman 2011; Baynes et al. 2016). The main objectives of the present study were to assess the differences in stand structure of fragmented and primary forests and the correlation between forest stand structure and C stock. The findings can provide valuable baseline data for forest managers, aiding in decision-making processes to achieve best management forest practices. Furthermore, the study contributes to understanding disturbed forests' health status and addresses the critical need for sustainable forest management procedures.

MATERIALS AND METHODS

Study Area

The locations of selected study areas are illustrated in Figure 1. The selected fragmented forests in this study were located at Bukit Durang (N3° 29’ 3.10”, E113° 49’ 15.60”) and Division 5 (Div 5) (N3°34’3.45”, E113°46’3.45”). The fragmented forests were located within an oil palm plantation owned by Saremas Sdn Bhd, a PPB Oil Palms Berhad subsidiary. Both forests are lowland mixed dipterocarp forests (MDF) with the historical selectively logged that ended in 1996. The fragmented forests in this study have been preserved as high conservation value (HCV) forests. The larger HCV area is Bukit Durang, approximately 989.9 ha, which is linear-shaped, while Div 5 forest is approximately 604 ha and is almost heart-shaped. Bukit Durang and Div 5 forest areas are approximately 10.06 km apart. The average terrain of the forests is within 45 to 75 m a.s.l and receives 1,700–5,800 mm of precipitation around the year (Malaysian Meteorological Department 2020).

This study examined the primary forests of Lambir Hills National Park (N4°12'9.44", E 114° 2'33.03") and Kubah National Park (N1°36'44.16", E 110°9'51.37"). Lambir Hills National Park (NP) is approximately 6,949 ha and consists of lowland MDF with an average annual rainfall of about 1700–5800 (Malaysian Meteorological Department 2020). Kubah NP is 2230 ha, mainly covered with mixed dipterocarp forest receives between 2000 and 3000 mm (Khan et al. 2017). Kubah NP had a historical selective logging activity decades ago and stopped in the 1960's when the forest area was left to regrow (Hazebroek & Abang Kashim 2001).

Field Sampling

Vegetation surveys in all study areas were conducted to understand forest stand characteristics. The quadrat plot sampling method was employed.

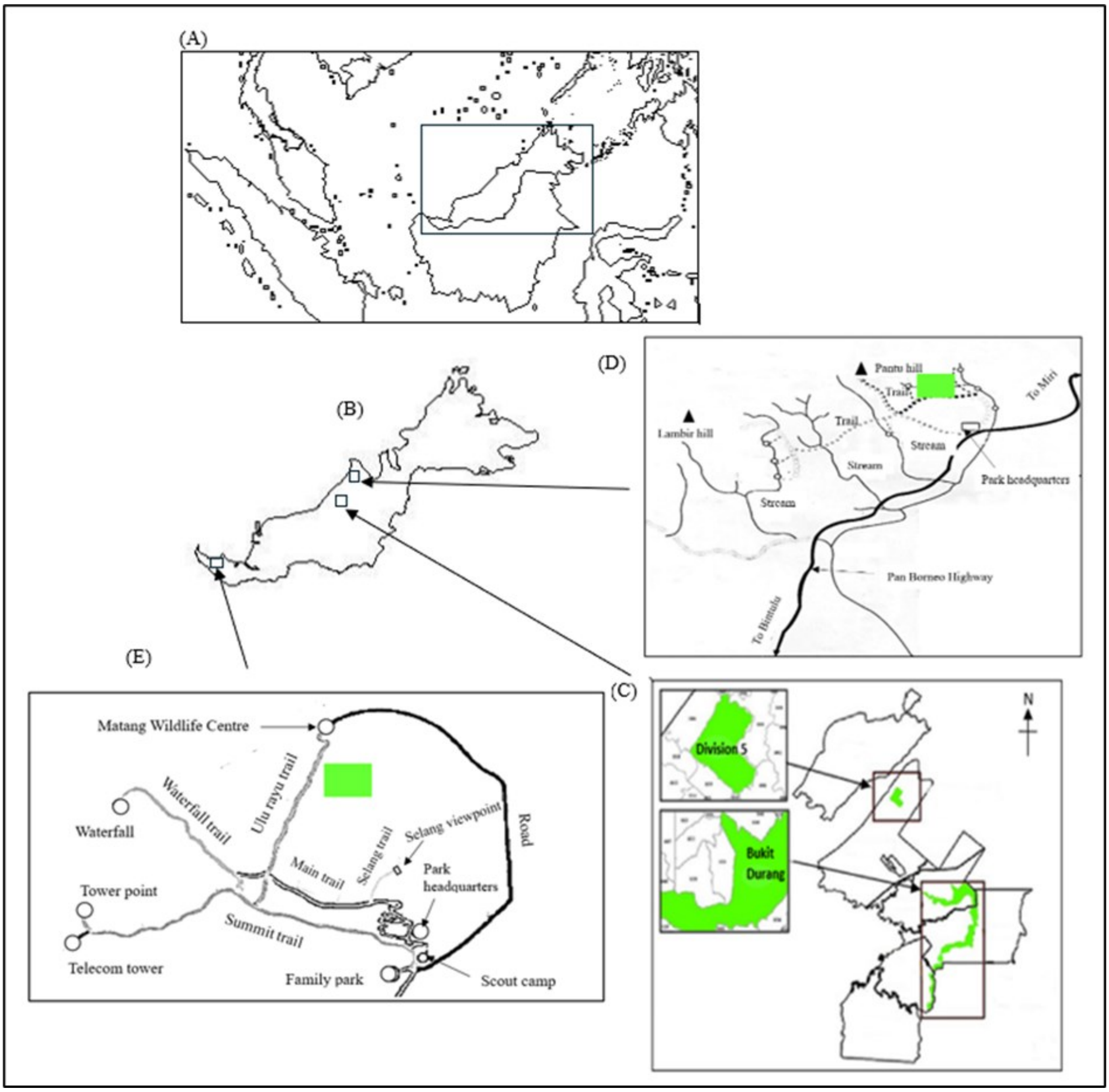

Figure 1. (A) Outline map parts of Malaysia and Indonesia. (B) Outline map of the Malaysian states of Sarawak and Sabah showing the study area. (C), (D) and (E) Location of the sampling area (shaded) of fragmented forests within the oil palm plantation, Lambir Hills National Park and Kubah National Park, respectively.

Quadrats were established and spaced at 100 m intervals on five parallel transect lines which were 100 m apart. This method provides a convenient method of enumerating the tree population as more ground can be covered with modest resources (Buckland et al. 2015). Twenty-five 20 m x 20 m replicate quadrats were created on the transect line in all study sites. Trees with DBH ≥10 cm were enumerated, and preliminary identifications of the tree species were performed according to their bark, slash, and leaf characteristics. Unidentified tree species were recorded at the genus level. Leave samples and fruits (if any) were collected for detailed species identification, which was conducted at the Universiti Malaysia Sarawak (UNIMAS) and Forest Department Sarawak herbarium.

Determination of forest stand parameters

The forest stand parameters refer to tree DBH, basal area, tree density, and number of species. Each tree DBH was measured at the breast height level (1.30 m above ground) using a tape diameter of the nearest cm. The total basal area of a species was calculated by multiplying the species tree density to obtain the species combined basal area in terms of m^2 ha^{-1}.

The calculation of a tree basal area is as follows:

$$\text{Basal area (BA)} = \frac{\pi D^2}{4}$$

Where π = Constant pi (approximately 3.14), D = tree diameter measured at breast height (DBH). The tree density (d) was computed by dividing the total number of trees (n) by the area of study site (m^2);

$$d = \frac{\text{Total number of trees (n)}}{\text{Area of study site } (m^2)}$$

Tree frequency (f) was determined by dividing the number of subplots the species present by the total number of subplots and multiple with 100;

$$f = \frac{\text{Number of subplot the species present}}{\text{total number of subplot}} \times 100$$

The importance value index (IVI) index describes and compares species dominance within each study area. It was determined by summing the total relative density, relative frequency and relative coverage (Gebeyehu et al. 2019). The IVI values vary from 0 to 300 and reflect each species dominance and abundance. A larger value indicates the more dominant a species is.

$$\text{Relative density (RD)} = \frac{\text{Number of individual species}}{\text{Total number of individual}} \times 100$$

$$\text{Relative frequency (RF)} = \frac{\text{Frequency of a species}}{\text{Sum of frequency of all species}} \times 100$$

$$\text{Relative dominance } (RD_o) = \frac{\text{Total basal area of a species}}{\text{Total basal area of all species}} \times 100$$

Estimation of Carbon Stock

Tree biomass and C stock were estimated using nondestructive methods. The AGB of all enumerated trees with a DBH of 10 cm and greater was computed by applying an allometric equation provided by Chave et al. (2005). The equation for the estimation of AGB is as follows:

$$AGB = p \times \exp(-1.499 + 2.148 \ln(D) + 0.207 (\ln(D))^2 - 0.0281 (\ln(D))^3$$

Where AGB is the dry weight of AGB (kg $tree^{-1}$), D is the diameter at breast height in centimetres (cm), and p is the basic density (g cm^{-3}) of the tree. Wood density values were acquired from the wood density database on the International Council for Research in Agroforestry (ICRAF 2007) website and PROSEA (1994, 1995, 1998). Air-dry wood density (10–18 % moisture content) was transformed to basic wood density by multiplying it by 0.861 (Vieilledent et al. 2018). Chave et al. (2005) equation is frequently used in forest inventory studies to approximate the aboveground biomass of trees in tropical forests. This equation is based on a large dataset of trees from different tropical forest sites worldwide. It incorporates the region's forest data, including Pasoh (Malaysia), Sumatra and Kalimantan (Indonesia), and provides a relatively simple and accurate way to estimate AGB. It uses a logarithmic transformation of D to consider the non-linear function between tree size and biomass. The equation was developed using a rigorous statistical approach and has been demonstrated to provide accurate aboveground biomass values throughout a broad range of tropical forest types and sizes. The equation is appropriate for determining the AGB of the different classes of forest locations included in this study. The C stock of all enumerated trees was estimated. A conversion coefficient of 0.5 was used to transform AGB (dry weight) to carbon equivalents (C) (ton) (Petersson et al. 2012). The AGB values were converted to C stock using the equation below.

$$\text{Total Carbon Stock (Mg C } ha^{-1}) = \text{Total AGB} \times 0.50$$

Data Analysis

Differences in stand parameters (DBH, basal area, species abundance), AGB and C stocks among the study areas, were made using Analysis of variance (ANOVA). The parameter means of the study areas were compared using Tukey's HSD tests. Principal component analysis (PCA) with varimax rotation was performed to determine the variables responsible for the most variations in the datasets. The association between C stock and tree structure parameters was established by performing the PCA. The PCA also identified the principal components (PCs) that are dominant factors in determining the correlative effect among tree structure parameters. Principal components with eigenvalues of 1.0 or more that explained 70 % of the variation were selected as the dominant factors. These datasets included stand structure parameters, IVI, and C stock across the combined datasets in the overall study areas. Statistical analyses were done using IBM Statistical Software Statistical Product and Service Solution (SPSS) 2.0 for Windows Version 9.1.

RESULTS AND DISCUSSION

Stand Structure

Generally, the trend of tree density with DBH≥10 cm recorded in fragmented forest areas is comparable to the primary forests (Table 1). The statistical analyses show that the tree density in the study areas is comparable.

Nevertheless, Bukit Durang (723 trees ha^{-1}) showed a relatively higher tree density than other study areas. The past recorded data reported that the number of trees per ha in other tropical primary forests found in southern regions of Sarawak was relatively comparable to this study, such as in Semenggoh Nature Reserve (710 trees ha^{-1}) (Diway et al. 2009), Bako National Park (792 trees ha^{-1}) and Batang Ai National Park (813 trees ha^{-1}) (Ling & Julia 2012). The tree density in other disturbed forests was reported to be comparable, as in the fragmented forest of Bukit Jugam, Bintulu logged-over forest (728 trees ha^{-1}) (Demies et al. 2019). The higher tree density in fragmented forests suggests that the study areas might be experiencing favourable conditions for regrowth or could have a different composition of tree species that are more resilient to the disturbance factors present. Species resilient to forest disturbance are important in understanding the potential for forest recovery in fragmented areas and can provide insight into strategies for promoting regrowth and restoration in deteriorated forests (Nunes et al. 2021; Mills et al. 2023).

The number of species differed between study areas. Div 5 and Kubah NP recorded more species than the other two study areas. According to MacKinnon et al. (1997), an intact rainforest typically can have up to 240 different plant species within one ha. Comparatively, the present study recorded a higher species number per hectare in the lowland mixed dipterocarp forests in Semenggoh Arboretum, Sarawak (61 species ha^{-1}) (Ling & Julia 2012), Batang Ai NP (45 species ha^{-1}) and Pasir Tengkorak Forest Reserve, Langkawi Island (120 species ha^{-1}) (Hayat & Abd Kudus 2010). However, the number of species observed within the study area was relatively low compared to Kuala Keniam, Pahang NP (371–450 species ha^{-1}) (Suratman 2012).

The comparatively lower species number in Lambir Hills NP than in other study areas could be attributed to the forest's high basal area, which implies that the forest is in an advanced stage of maturity with larger, older trees, promoting increased competition for resources among tree species. Competition among trees in closed-canopy forests like mature tropical ones usually reduces individual tree growth and mortality, primarily due to the limited light levels beneath the canopy (Lasky et al. 2014; Rozendaal et al. 2020). The intense competition also diminishes tree species' adaptive

Table 1. Structural characteristics of Bukit Durang, Division 5, Lambir Hills National Park and Kubah National Park of trees with DBH ≥ 10 cm.

	Study area			
	Fragmented forest		Primary forest	
Variable	Bukit Durang	Division 5	Lambir Hills National Park	Kubah National Park
Tree density (trees ha^{-1})	723 (± 39)[a*]	785 (± 47)[a]	747 (± 31)[a]	684 (± 37)[a]
Number of species (ha^{-1})	161 (± 22)[b]	218 (± 28)[c]	131 (± 27)[a]	213(± 18)[c]
Basal area (m^2 ha^{-1})	29 (± 3)[a]	30 (± 2)[a]	43 (± 3)[b]	29(± 2)[a]
Aboveground biomass (Mg ha^{-1})	355(± 36)[b]	299 (± 26)[a]	501 (± 46)[c]	290 (± 24)[ab]
Aboveground carbon stock (Mg C ha^{-1})	178(± 18)[b]	150 (± 13)[a]	251 (± 23)[c]	145 (± 12)[ab]

*Mean (±standard error) values within a row followed by different letters show significant differences at $P < 0.05$ using Tukey's test.

capability, elevating forest ecosystems' susceptibility to environmental stress (Magalhães et al. 2021). Intense competition might constrain the establishment and survival of certain species, ultimately leading to a decreased species count in the Lambir Hills NP study area.

Lambir Hills National Park has a significantly higher basal area than the other study areas because the forest area is intact without major disturbances, which suggests that Lambir Hills NP might have a more established and mature ecosystem than the other three study areas. An undisturbed forest with minimal disturbance can maintain its ecological balance (Shumba et al. 2020).

The variability in spatial and temporal disturbances in historically disturbed forests significantly impacts the regeneration, dominance and long-term survival of woody species within a forest ecosystem (Altman et al. 2016). The primary cause for the reduction in basal area, affecting tree growth and establishment, could be attributed to past anthropogenic disturbances in the fragmented forests (Bukit Durang and Div 5) and Kubah NP.

This study found varied C stocks in fragmented (Bukit Durang and Div 5) and primary forests (Lambir Hills National Park and Kubah National Park). Carbon stock values of fragmented forests and Kubah NP study areas were 145–149 Mg C ha^{-1}, which is lower than the typical C stock for tropical forests, estimated to be around 209 Mg C ha^{-1} (Slik et al. 2013). The primary forests of Lambir Hills NP have remarkably higher C stocks (251 Mg C ha^{-1}) in comparison to the other study areas, surpassing the typical C stock levels found in tropical forests. The results are expected as Shen et al. (2021) stated that fragmented forests had lower aboveground biomass than intact forests and suggested that this is due to the disturbance and reduced habitat quality. Previous studies reported that disturbed forests that have experienced selective logging have lower C stocks than natural forests (Berenguer et al. 2014; Rutishauser et al. 2015; Longo et al. 2016) since selective logging removes the large trees, leaving behind smaller and younger trees with lower carbon storage values.

The notably higher C stock in Bukit Durang than in Div 5 suggests that these forest areas have different carbon sequestration rates due to distinct contributing factors such as forest structure and species composition. Key elements contributing to the differences in diversity and vegetation carbon storage patterns in tropical forests include factors such as climatic variations and edaphic influences (Hofhansl et al. 2020). The post-logging impact on C stocks remains evident despite two decades since selective logging in both the fragmented forests and six decades in Kubah NP. This study indicates that forest recovery occurs relatively slowly after several decades of disturbance.

Lambir Hills National Park study area showed a remarkably high C stock value since the big and old trees dominated the forest. The intact primary forest tends to contain considerable amount of AGB since it retains trees with greater diameter (Ngo et al. 2013). The old-growth forests generally have more AGB than logged forests, even after 20 years of logging. Rozendaal et al. (2022) reported in their meta-analysis study that the AGB values of pristine forests were significantly greater than those of logged forests. This was because the old-growth forests have more time to accumulate C stocks by retaining large trees, resulting in greater AGB values.

Species Composition

Table 2 shows the top five dominant tree species in fragmented and primary forests. In this study, fragmented forests had high abundance of fast-growing species. The abundance of *Macaranga triloba* in Bukit Durang and Div 5 is evident. *Macaranga* spp. is a major feature of disturbed vegetation in Malaysian forests (Demies et al. 2019; Takeshige et al. 2023). Fast-growing tree species are commonly found to be dominant in disturbed forest (Demies et al. 2019). Their study in a logged-over area of Anap Muput FMU, Bintulu, Sarawak recorded that pioneer species such as *Macaranga* spp., *Nauclea* spp., *Porterandia* spp., *Glochidion* spp. and *Gironniera* spp. dominate the area.

Lambir Hills National Park had high IVI values of *Dryobalanops aromatica*, with 21.4. The other species, such as *Xanthophyllum velutinum*, *Vatica nitens*, *Shorea falcifera*, and *D. globosus* have IVI ranging from 11.1 to 18.6. Kubah National Park was observed to have a high value of IVI of *Syzygium havilandii*, at 6.9. Other species' IVI represented by *Santiria tomentosa*, *Santiria rubiginosa* and *Shorea macroptera* ranged from 2.1 to 2.7. Generally, the study areas are dominated by the genera *Shorea*. This observation is typical because *Shorea* is highly distributed in Bornean dipterocarp forests (Purwaningsih & Kintamani 2018). All study areas showed a prominent presence of tree family belonging to the Dipterocarpaceae family. The dominance of Dipterocarpaceae in the study areas is in the order of Lambir Hills NP (33 %), Bukit Durang (30 %), Div 5 (27 %) and Kubah NP (23 %). It is well-known that Dipterocarpaceae predominates the lowland tropical forest of Borneo. A comprehensive research by Slik et al. (2005) reported that 21.9 % of the trees recorded in the lowland dipterocarp forest of Borneo were prevalently Dipterocarpaceae. This family also had the highest basal area contribution in the tropical forest (Gobilik 2008). Some of the trees in this family grow large and tall and often reach emergent or upper canopy heights. Their ability to attain substantial sizes over long periods contributes to their higher representation in the basal area of the forest area.

Carbon stock distribution among diameter classes

The distribution of C stocks by diameter class in fragmented and primary forests is shown in Table 3. Generally, the variation of C stock in the mid-diameter class (15–19.9 to 45–49.9 cm) is small. Although tree density decreased with diameter size, the C stock appears constant among these diameter classes. Lambir Hills National Park and Bukit Durang exhibited high C stock for DBH ≥ 60 cm. There were 20 and 15 trees with DBH ≥ 60 cm in Lambir Hills NP and Bukit Durang, respectively. In contrast, Div 5 and Kubah NP exhibit lower C stocks within the same diameter range, with only seven and three trees, respectively, indicating a substantial contribution to carbon storage in these forests comes from the presence of trees with larger diameters. Smaller trees in the diameter range of 10–14.9 cm DBH appear to have a relatively smaller contribution to C stocks despite their higher abundance. This finding concurs with early research by Chave et al. (2005) and Qie et al. (2017). The limited presence of large tree populations in forest

Table 2. Top five dominant species according to the Importance Value Index in fragmented and primary forests with DBH ≥ 10 cm.

	Bukit Durang				
No.	Species	RD (%)	RF (%)	RD_o (%)	IVI
1	*Macaranga triloba* Müll.Arg.	7.1	3.6	6.1	5.6
2	*Elateriospermum tapos* Blume	4.8	3.2	5.5	4.5
3	*Shorea parvifolia* Dyer	3.9	1.8	4.5	3.4
4	*Shorea pubistyla* P.S.Ashton	3.2	2.0	4.9	3.4
5	*Shorea subcylindrica* Slooten	4.2	2.0	2.6	2.9
	Division 5				
No.	Species	RD (%)	RF (%)	RD_o (%)	IVI
1	*Shorea macroptera* Dyer	5.6	2.7	5.4	4.5
2	*Elateriospermum tapos* Blume	1.5	1.7	1.8	1.7
3	*Shorea beccariana* Burck	1.7	1.7	1.8	1.6
4	*Shorea amplexicaulis* P.S.Ashton	1.7	0.8	2.0	1.5
5	*Palaquium pseudorostratum* H.J.Lam	1.6	1.8	1.0	1.5
	Lambir Hills National Park				
No.	Species	RD (%)	RF (%)	RD_o (%)	IVI
1	*Dryobalanops aromatica* C.F.Gaertn.	5.4	3.5	12.6	21.4
2	*Xanthophyllum velutinum* Chodat	8.6	4.7	5.3	18.6
3	*Vatica nitens* King	8.2	4.5	4.3	17.0
4	*Shorea falcifera* Dyer ex Brandis	3.6	3.1	4.8	11.5
5	*Dipterocarpus globosus* Vesque	3.6	3.5	4.0	11.1
	Kubah National Park				
No.	Species	RD (%)	RF (%)	RD_o (%)	IVI
1	*Syzygium havilandii* (Merr.) Merr. & L.M.Perry	8.0	3.6	8.9	6.9
2	*Santiria tomentosa* Blume	2.5	2.1	3.5	2.7
3	*Santiria rubiginosa* Blume	1.5	1.5	3.4	2.1
4	*Shorea macroptera* Dyer	2.9	1.7	1.8	2.1
5	*Castanopsis evansii* Elmer	2.1	1.7	2.0	1.9

Table 3. Tree density and carbon stock distribution by diameter class.

Diameter class (cm)	Fragmented forest				Primary forest			
	Bukit Durang		Division 5		Lambir Hills National Park		Kubah National Park	
	No. of tree	C stock (Mg C ha^{-1})	No. of tree	C stock (Mg C ha^{-1})	No. of tree	C stock (Mg C ha^{-1})	No. of tree	C stock (Mg C ha^{-1})
10–14.9	262	9	322	11	265	10	263	9
15–19.9	179	13	186	14	150	12	155	13
20–24.9	97	14	107	16	108	18	103	16
25–29.1	61	15	55	14	59	16	54	14
30 –34.9	37	15	36	14	48	20	33	13
35–39.9	27	16	31	18	27	16	25	16
40–44.9	17	14	19	16	26	22	20	17
45–49.9	10	10	13	14	25	30	13	13
50–54.9	8	12	7	9	11	15	5	7
55–59.9	10	18	2	4	8	15	10	17
≥ 60	15	42	7	20	20	77	3	10

areas reduces carbon sequestration potential in forest ecosystems (Lutz et al. 2018).

Carbon Stock Distribution Among Tree Species

The top five cumulative C stocks for tree species in fragmented and primary forests are shown in Table 4 and Table 5, respectively. Generally, shade-

Table 4. Top five cumulative carbon stocks for tree species in fragmented forests.

Bukit Durang			Division 5	
No.	Species	C stock (Mg C ha^{-1})	Species	Carbon (Mg C ha^{-1})
1	*Elasteriospermum tapos*	13	*Shorea macroptera*	8
2	*Shorea pubistyla*	8	*Ternstroemia citrina*	5
3	*Glochidion obscurum*	7	*Elateriospermum tapos*	4
4	*Shorea parvifolia*	7	*Lithocarpus bennettii*	4
5	*Macaranga triloba*	6	*Dipterocarpus sublamellatus*	4

Table 5. Top five cumulative carbon stocks for tree species in primary forests.

	Lambil Hill National Park		Kubah National Park	
No	Species	Carbon (Mg C ha^{-1})	Species	Carbon (Mg C ha^{-1})
1	*Dryobalanops aromatica*	41	*Syzygium havilandii*	13
2	*Shorea falcifera*	17	*Santiria rubiginosa*	6
3	*Shorea parvifolia*	16	*Santiria tomentosa*	5
4	*Xanthophyllum velutinum*	12	*Shorea havilandii*	5
5	*Elateriospermum tapos*	12	*Koompassia malaccensis*	5

tolerant species are slow-growing and comprise dipterocarp and non-dipterocarp tree species that dominate the carbon values in these study areas. Slow-grower trees with greater DBH, height, wood density and basal area typically showed higher AGB and C stock (Yeboah et al. 2014). Slow-growing tree species were consistently found to contribute significantly to high C stocks in all study areas. Tree species *Elasteriospermum tapos* (13 Mg C ha^{-1}) in Bukit Durang, *Shorea macroptera* (8 Mg C ha^{-1}) in Div 5, *Dryobalanops aromatica* (41 Mg C ha^{-1}) in Lambir Hills NP, and *Syzygium havilandii* (13 Mg C ha^{-1}) in Kubah NP were the primary contributors to the high levels of C stock in their respective study areas.

The high population of tree species of *D. aromatica* accounted for the high contribution of C stocks (41 Mg C ha^{-1}) in Lambir Hills NP. In this study, *D. aromatica* was also recorded to possess a high IVI (21.4). In contrast, the species IVI in other investigation regions fell within the range of 4.5–6.9. For instance, in the mixed dipterocarp forest of Endau Rompin National Park, Johor, the non-dipterocarp trees such as *Litsea costata*, *Dillenia reticulata* and *Syzygium* sp. were recorded as major contributors to the total forest carbon with the values of more than 12 Mg C ha^{-1} (Matthew et al. 2018). These non-dipterocarp tree species were recorded to have high numbers, large DBH, tall tree height and high wood density, contributing to the considerably high cumulative carbon content.

Correlation of Carbon Stock with Stand Parameters

The principal component analysis showed the association of C stock with some stand structure characteristics (Table 6 and Figure 2). It shows two principal components described 49 % of the variation. The first component explains 31.1 % of the total variation, and the second explains 17.8 %. Basal area, DBH and C stock were positively intercorrelated and associated with PC1 (Table 6). Species IVI and tree density are intercorrelated and strongly associated with PC2. In contrast, species number is negatively correlated to species IVI and tree density with PC2.

Kauppi et al. (2014) recorded that trees with large diameters significantly impact the carbon density in forests, suggesting that tree populations with large diameters are responsible for storing high amounts of carbon within the forests. These groups of trees also provide significant weight as the foundation structures in forest ecosystems. They are also crucial in forest ecosystems as a food provider, shelter, microclimate modulation and hydrological system (Lindenmayer et al. 2014; Bradford & Murphy 2019). A study in Gunung Leuser National Park, Indonesia, recorded that carbon storage highly depends on the variation of tree diameters (Onrizal & Auliah 2020). Van Do et al. (2020) stated that basal area and AGB are correlated to trees of more than 30 DBH in old-growth forests of Vietnam, suggesting that forest areas with a higher concentration of huge trees will have a higher C stock.

Table 6. Variations from principal component analysis of stand structure across all the study areas explained by principal component axes.

Parameters	Component*	
	1	2
Basal area	**0.94**	0.02
Diameter at breast height	**0.91**	0.03
Carbon stock	**0.65**	0.09
Importance value index	0.11	**0.92**
Number of trees	-0.01	**0.73**
Number of species	-0.14	**-0.65**
Wood density	-0.02	0.41
Eigenvalues	2.18	1.25
% Variance	31.09	17.84
Cumulative explanation %	31.09	48.93

*Loading scores of stand characteristics in the first two principal component axes. Loading scores in bold are considered significant.

The PCA showed the correlation of C stocks with DBH, and the basal area is the strongest among the variables considered, suggesting that the higher C stock will be found in the forested region having the larger basal area. The result indicated that the basal area is possibly one of the significant elements that characterise the carbon content of living trees in a forest. The finding parallels the studies done by Dossa et al. (2013), Stephenson et al. (2014), Jeyanny et al. (2014) and Lutz et al. (2018). The basal area affects primary forests' C stock (Mensah et al. 2016). Wassihun et al. (2019) pointed out that increased basal area increases AGB and C stock. Joshi and Dhyani (2021) recorded a strong positive correlation between carbon stock and basal area in the forest that is dominated by *Shorea robusta* in Dhangadhi, Nepal. Over time, old trees with larger trunks and more extensive root systems contribute to higher biomass stocking (Köhl et al. 2017).

Ma et al. (2023) stated that basal area becomes more influential in determining AGB when forests are developed. The basal area is commonly associated with the diameter increment of stands in the forest (Chave et al. 2005). This study's results suggest that the size of trees and the total cross-sectional area of trees have a more substantial impact on C stocks. Trees with higher wood densities generally contain more carbon per unit volume, contributing to the forest carbon stocks. However, this study observed no significant correlation between wood density and C stock across the study areas based on the PCA analysis, which agrees with Francis et al. (2017), who reported that biomass is not related to wood density. However, the results contradicted the results of Dossa et al. (2013) and Jeyanny et al. (2014). They stated that the wood density significantly influences C stocks in forests. The ecological complexity within the study areas might be attributed to uncorrelated wood density with C stock. The wood density of trees within the study areas could be influenced by geographical area and species-specific

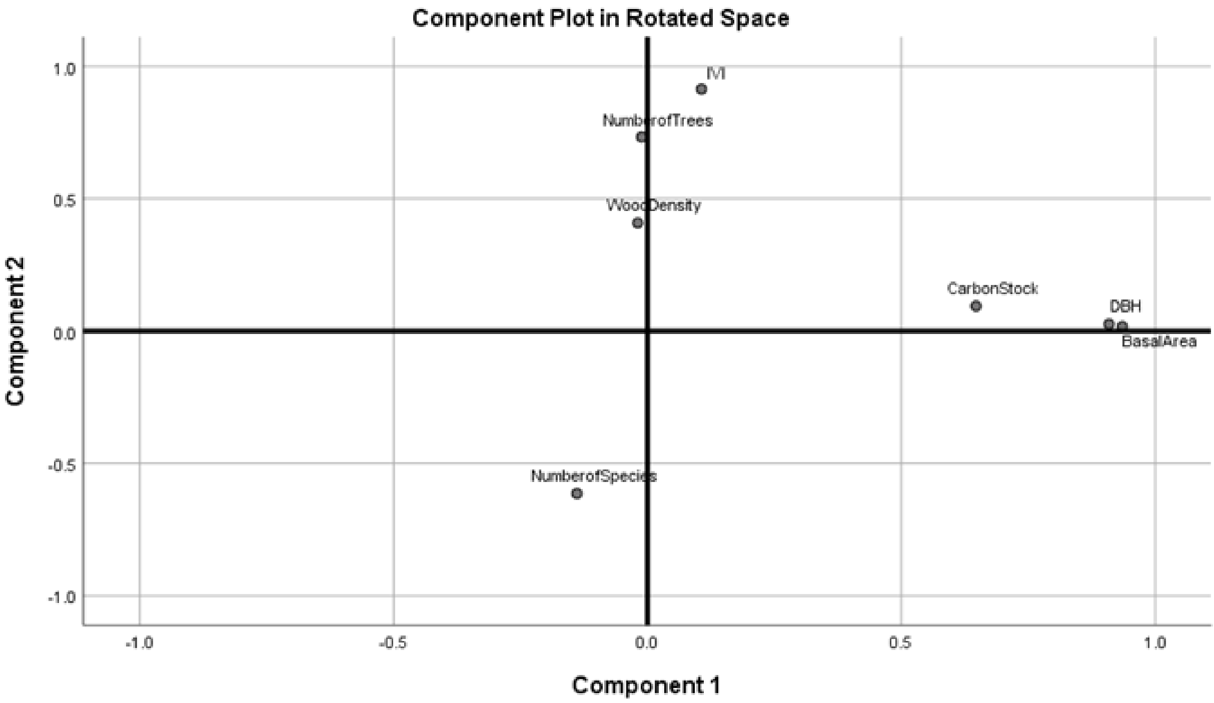

Figure 2. Distribution of stand structure attributes, importance value index and carbon stock in relation to axes of combined data of all the study areas.

factors because different tree species had varying carbon sequestration rates and tree sizes (Pérez-Cruzado et al. 2012). Wood density varies greatly across the tree species in tropical forests (Djomo et al. 2017), and tree diameter does not influence the variation of wood density (Ramananantoandro et al. 2016), implying that large trees do not necessarily have high wood density, which explains why wood density is not correlated with C stocks in this study. Species composition, soil properties and climatic influences have higher dynamic influence on carbon (Saimun et al. 2021). Thus, the forests dominated by low carbon sequestration and smaller trees have low C stock. Regarding species abundance, a negative association with species dominance (IVI) is shown, concurring with results from Shirima et al. (2015). It has been reported that greater stem density and basal area can reduce the species richness of an area (Djuikouo et al. 2014).

CONCLUSIONS

This study has demonstrated that tree density with DBH ≥ 10 cm between fragmented and primary forests is comparable. Fragmented forests were shown to have higher number of species. Generally, tree basal area and AGB are greater in the primary forest. The DBH and basal area significantly correlated with forest carbon stock. The findings highlight the vital role of large trees in storing carbon in forest ecosystems. Preserving large trees will keep carbon stored in the forest for a long time. Thus, removing large-diameter trees will result in major carbon emissions to the environment. Disturbed forests, such as fragmented forests and Kubah NP, have declined certain characteristics typical of undisturbed virgin forests. This includes alterations in the entire composition of forest species and a reduction in large tree diameters, thus decreasing C stocks. Generally, historically disturbed forests possess the potential for recovery, exhibiting the capability to develop stand structures comparable to primary forests, provided no human-caused disturbances occur. The present study has provided valuable insights into the correlation between tree DBH and C stock. The findings emphasise the necessity of conservation initiatives to deal with the issues related to forest degradation and fragmentation. The potential future forest fragmentation and disturbances could negatively impact the presence of large trees and species diversity, which is particularly crucial for preserving C stocks and biodiversity in tropical forests.

AUTHOR CONTRIBUTION

A.N. conducted data collection, performed data analyses and wrote manuscript drafts. I.J. and M.H.B. were involved in the design and implementation of the research, results analyses and manuscript review.

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CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

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