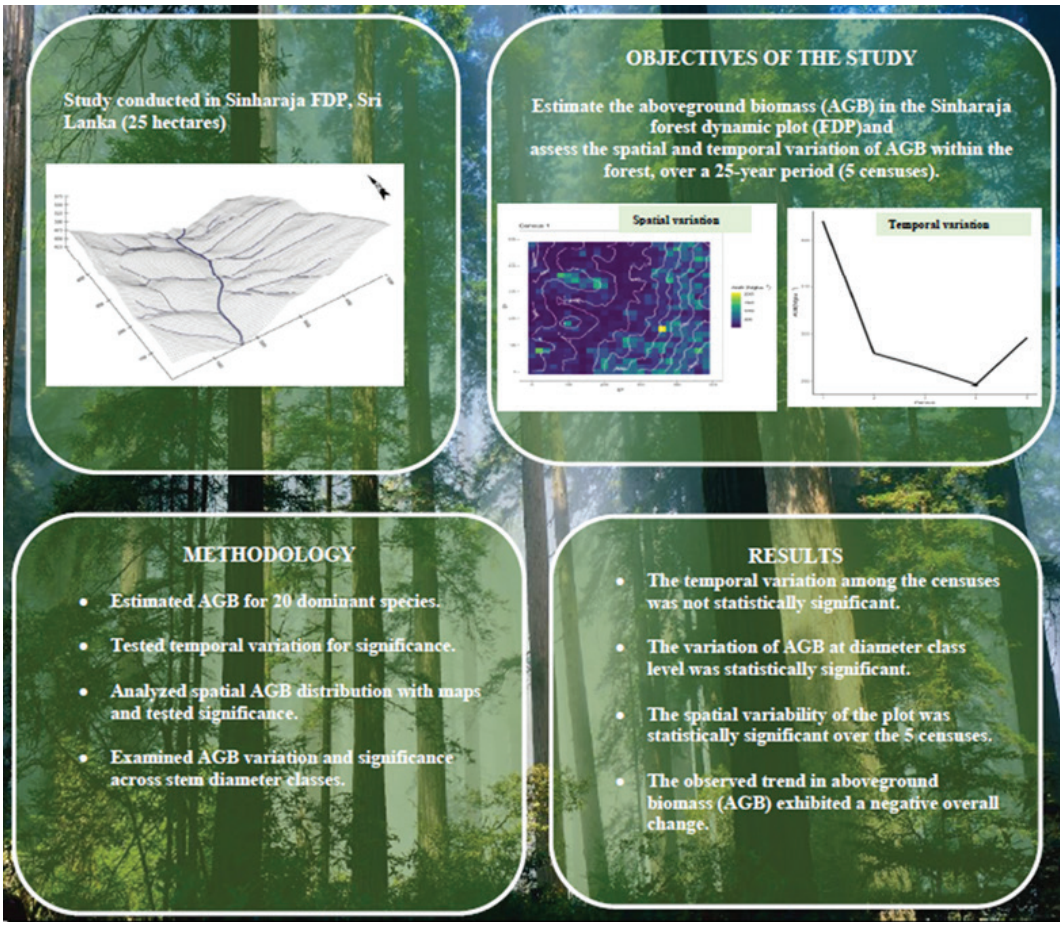
RESEARCH ARTICLE

Spatial and Temporal Variation of Tree Biomass in a Tropical Rainforest in Southwest Sri Lanka

H.M.S.I. Herath*, Pushpakanthie Wijekoon and Sisira Ediriweera



Highlights

- Although the temporal variation of Above Ground Biomass (AGB) over the 25 years was not significant, a few species exhibited significant temporal variation.
- The AGB variation at diameter class level was found to be highly significant.
- The spatial variability at 0.04ha level was also found to be significant across the five censuses
- The spatial variability of the plot at 0.04ha level was high and the spatial distribution of AGB in the Forest Dynamic Plot (FDP) was positively skewed.
- The FDP showed a declining trend of AGB over the 25 years, hence behaving more as a carbon source than a carbon sink

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Spatial and Temporal Variation of Tree Biomass in a Tropical Rainforest in Southwest Sri Lanka

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Abstract: The long-term patterns and spatial distribution of Above Ground Biomass (AGB) in Mixed Dipterocarp Forests (MDF) in tropical Asia remain understudied. This research investigates changes in AGB over a 25-year period within the Sinharaja Forest Dynamic Plot (FDP), a 25-hectare area in southwest Sri Lanka. The study uses 25 years of Diameter at Breast Height (DBH) measurements from the 20 most dominant species in the FDP, along with their wood-specific gravity data, to estimate AGB. The AGB estimates yielded an average of 300 Mg ha^{-1} (±17 $Mgha^{-1}$, 95% confidence interval). The total AGB exhibited wide spatial variation (3.4 to 1198 $Mgha^{-1}$ per 0.04 ha, n = 625), with significant spatial variation ($p < 0.05$) over 25 years. AGB showed a consistent decline from 1994 (324 $Mgha^{-1}$) to 2012 (289 $Mgha^{-1}$), with a slight increase in 2019 (299 $Mgha^{-1}$), showing a decreasing trend in AGB over the 25-years. Repeated ANOVA tests revealed that the temporal variation of AGB among the censuses was not statistically significant. However, at the diameter class level, statistical tests indicated significant ($p < 0.05$) AGB variation. The 1-3 cm diameter class had the highest stem percentage (66%) but <1% of the total AGB. The 30-50 cm diameter class contributes the most to total AGB (25%). Large trees (>70 cm diameter) have low stem percentage (0.14%), but carry 24% of the AGB. Findings of this study are important for estimating AGB and carbon sequestration in Mixed Dipterocarp Forests (MDF) in Asia, especially in Sri Lanka. The study area shows a noticeable decline in AGB, mainly due to the loss of large canopy tree species such as *Mesua ferrea*. This shift is transforming the area from a carbon sink into a carbon source.

***Keywords*:** Sinharaja; Above Ground Biomass; Mixed Dipterocarp Spatial variation; Temporal variation; Repeated ANOVA

INTRODUCTION

Tropical rainforests play a significant role in sequestering and storing carbon, accounting for approximately 25% of global terrestrial carbon (Bonan, 2008) They regulate atmospheric greenhouse gases (Lewis et al., 2009; Malhi & Grace, 2000) and help mitigate the effects of anthropogenic climate change (Bonan, 2008). Given the increasing CO_2 emissions from human activities, there has been a heightened focus on investigating the capacity of tropical rainforests to serve as carbon sinks. International climate change mitigation policies, such as REDD+ (Reducing Emissions from Deforestation and Forest Degradation), offer incentives and payments for enhanced terrestrial carbon storage, supporting biodiversity conservation and the maintenance of ecosystem services (Gilroy et al., 2014; Osuri et al., 2014).

Despite the growing recognition of the importance of forest conservation, there is still limited understanding of the strengths and underlying mechanisms of carbon sequestration in tropical forests, highlighting the need for further research (Sullivan et al., 2017). Tropical rainforests exhibit biogeophysical effects that cool global climates. However, they are also vulnerable to warmer and drier conditions, and their interactions with fire, atmospheric gases, aerosols, and deforestation can potentially exacerbate climate change and global warming, leading to forest die-back and carbon release (Bonan, 2008). The scientific community is divided on whether carbon sequestration in tropical forests is increasing through biomass growth or if there is a net loss of stored carbon due to tree mortality and high respiration rates (Coomes et al., 2011). This uncertainty extends to the relationship between tree diversity and carbon stocks in tropical forests, which shows correlation at small spatial scales, particularly in young forests, but lacks correlation at the stand level (Brown et al., 1991). While plant diversity generally promotes aboveground biomass production, there may be a saturation point where increases in species richness no longer result in proportional gains in biomass (Cardinale et al., 2012).

Studies have been conducted to estimate aboveground biomass in various tropical forest regions. Research in South and Southeast Asia, the Amazon Basin, and the Congo Basin has provided regional estimates of aboveground biomass (Baker et al., 2004; Brown et al., 1991; Malhi et al., 2006). Aging tropical forest fragments in Central and South America have shown a decline in aboveground biomass due to an increase in pioneer species (Laurance et al., 2006). Similar trends have been observed in the old-growth forests of the Amazon, where the current rate of biomass sequestration is declining due to slower growth, increased tree mortality, and shorter lifespans of older trees (Brienen et al., 2015). African forests have also exhibited declining biomass over longer periods (Lewis et al., 2009). The estimation of aboveground biomass in tropical forest systems has demonstrated considerable

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variation influenced by factors such as site productivity, soil type, successional development, disturbance, regional climate change, and elevation (Alves et al., 2010; Ferry et al., 2010; Malhi et al., 2006; Nascimento & Laurance, 2002).

Mixed Dipterocarp Forests (MDF) in a seasonal wet equatorial South and Southeast Asia are particularly significant in terms of aboveground biomass and serve as the largest commercial timber resource per hectare among tropical forest types (Sullivan et al., 2017). However, research on aboveground biomass in these forests is limited, likely due to the challenges posed by multiple geopolitical boundaries and a low number of forest monitoring plots. Long-term studies on tree structure, growth, and composition in tropical wet Asia primarily rely on a small number of long-term monitoring forest plots, such as those in Lambir (Sarawak), Bukit Timah (Singapore), Pasoh Peninsular (Malaysia), Palanan (Philippines), and Sinharaja (Sri Lanka) (Davies et al., 2021). Existing studies on standing biomass in MDF suggest substantial variation in aboveground biomass accumulation due to differences in soil, topography, and specific regions like the Western Ghats in India, East Kalimantan, and Sumatra-Borneo (Rai, 1984; Yamakura et al., 1986). However, there is a lack of long-term research tracking biomass variation and accumulation in Asian MDF. Furthermore, to date, no studies documenting the trends in standing biomass and stored carbon have been conducted in the MDF of southwest Sri Lanka.

Therefore, the aim of this study was to investigate the variability of above-ground biomass (AGB) within the study sites and track its changes over a 25-year period. Specifically, we examined the proportion of AGB attributed to the 20 most dominant species and explored how these proportions are influenced by topography and time. We determined overall trends in standing biomass and carbon over a twenty-five-year period; and examined differences and variability of standing biomass and carbon among and within sites representing different elevations.

MATERIALS AND METHODS

Study site and Data

This study was conducted in the Sinharaja Forest Dynamic Plot (FDP) which is situated in the lowland wet zone of southwest Sri Lanka. In 1993, the Sinharaja FDP was established in the Sinharaja forest reserve which belongs to the global network named the Forest Global Earth Observatory (ForestGEO) as a forest research site. The whole region receives more than 5000 mm of rainfall every year. The plot is an undisturbed part of the forest at 6°24′N, 80°24′E which is a 25-ha area with dimensions 500m x 500m. This area is further divided into 625 quadrats of 20m x 20m (0.04ha)(Gunatilleke et al., 2006). This plot consists of a central valley bounded by two slopes, one steeper and higher facing southwest and reaching up to 575m, and the other less steep facing northeast and extending up to about 505m (Figure 1).

In 1994, all individual trees with dbh > 1cm in the 25ha plot were enumerated. All these trees were tagged, and stems' diameter and species composition were recorded.

Census was taken at regular intervals and the dataset used for the analysis was derived by combining five censuses over the periods 1994–1996, 2001-2003, 2007-2008, 2012-2013 and 2018-2019. It was noted that the trees censured represent 239 species and 70% of its species are endemic to the country. All trees with a diameter at breast height (dbh) ≥ 1cm were selected for the analysis. In the data cleaning process, the outliers identified as the trees showing large positive (> 99_{th} percentile) dbh values from the dataset were excluded as these unusual observations may be due to errors in data entry/fieldwork.

Selecting the most abundant species

The Importance Value Index (IVI) was used to select the most abundant species in a given forest area. According to Curtis & McIntosh (1950), the importance value index (IVI) of tree species is calculated as the sum of relative density, relative frequency, and relative area, i.e. IVI = Relative density + Relative frequency + Relative area. Each

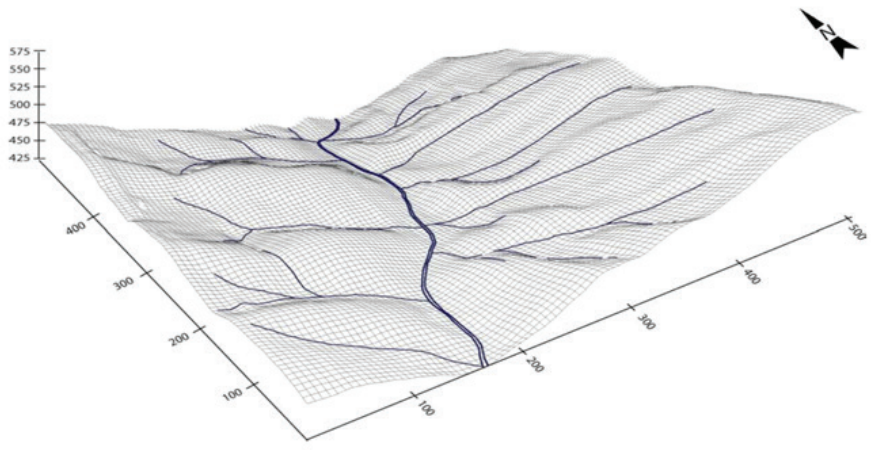


Figure 1: Topography of the 25ha forest dynamics plot (all scales in meters) in Sinharaja, Sri Lanka (Source: Chandrasekara & Pathiratne, 2005)

of these numbers falls between 0 and 100 and is expressed as a percentage.

Relative Density (RD) is defined as the number of a given species expressed as a percentage of all the given species. i.e.

$$RD = \frac{Number\ of\ individual\ species}{Total\ number\ of\ individuals} \times 100$$

Relative Frequency (RF) explains how often a particular species can be seen in the forest area

relative to other species. i.e.

$$RF = \frac{Frequency\ of\ an\ individual\ species}{Sum\ of\ frequency\ of\ all\ species\ studied} \times 100$$

Relative area is defined as the total basal area $\left(\frac{\pi \times DBH^2}{4}\right)$ of each stem of a given species relative to other species. i.e.

$$RA = \frac{Total\ basal\ area\ of\ an\ individual\ species}{Sum\ of\ total\ basal\ areas\ of\ all\ species\ studied} \times 100$$

The 20 species with the highest Importance Value Index (IVI) are considered the most abundant in the plot, accounting for approximately 65% of the total stems recorded in the Sinharaja FDP.

Estimation of Above Ground Biomass (AGB)

To understand the long-term trends over the 25 years, the AGB of the 20 most dominant species in the 25ha Sinharaja FDP plot were estimated using the following allometric equation (Chave et al., 2014).

$$AGB = \exp(-1.803 + 0.976 \times E + 0.976 \times \ln(WSG) + 2.736 \times \ln(dbh) - 0.0299 \times \ln(dbh^2)) \quad (1)$$

In order to calculate the AGB, site specific Wood Specific Gravity WSG (g cm^{-3}) is important. All WSG values of local tree species that had been collected from previous research were employed (Ediriweera et al., 2024). The measure of environment stress variable E, which is a constant value of -0.1114033 for the Sinharaja FDP was also used for this estimation. The total AGB (dry weight basis) of each stem is estimated using the above equation in kg. The AGB values for each stem of the selected 20 species for the 25 ha FDP were repeatedly calculated for the five censuses from 1994 - 2019.

Categorization of stems into diameter classes

The stems of the 20 most dominant were studied under eight different diameter classes, so that each class has a considerable number of stems. Then the aggregate AGB values for each of the 20 dominant species across the eight diameter classes and the five censuses were separately calculated. The evaluation of AGB was carried out at the diameter class level so that fine variations of AGB can be analysed in the Sinharaja FDP. These diameter classes allow us to understand how stems at different size classes behave and contribute separately to the variations of total AGB. The 8 diameter class levels and the number of stems for each class over the 5 censuses for the 20 most dominant species are shown in Table 1.

Statistical analysis

Testing the temporal variation of AGB across censuses and diameter classes

First, the aggregate AGB values across the diameter classes and 5 censuses for the 20 most dominant species of the plot together were calculated, and the two-way repeated ANOVA test was applied to identify the significance of the temporal variation of AGB across the 5 censuses and the significance of the variation of AGB across diameter classes. Then, the aggregate AGB values for the five censuses of each 20 dominant species were obtained separately and one-way repeated ANOVA test was used to understand the significance of temporal variation of AGB for each species. The variation of AGB across diameter classes for each dominant species was tested using one-way ANOVA or Kruskal-Wallis test based on ANOVA model assumptions.

Testing the significance of the spatial variation of AGB over the five censuses in the FDP

To understand the spatial distribution and the variation of AGB in Sinharaja FDP over the five censuses, first the aggregate AGB values of each of the 625 quadrats (quadrat size 20m x 20m (0.04ha)) were estimated in $Mgha^{-1}$. The first five rows of this data table are shown in Table 2.

The estimated values were used to visualize the spatial distribution of AGB in the Sinharaja FDP across five censuses. To better observe spatial variation, maps were created separately for smaller stems (1cm ≤ dbh < 10cm) and larger stems (dbh ≥ 10cm). This separation was

Table 1: Number of stems in each stem diameter class over the five censuses in the Sinharaja Forest Dynamic Plot.

Diameter class (cm)	Census 1	Census 2	Census 3	Census 4	Census 5
1-3	100628	91267	82641	78555	103313
3-5	22458	23738	24420	25189	25650
5-7	6893	7278	7539	7628	7951
7-10	4577	4713	4726	4785	4866
10-30	7690	7832	8061	8156	8243
30-50	1511	1417	1403	1389	1433
50-70	534	506	488	449	408
>70	215	179	173	177	205

Table 2: Aggregate Above Ground Biomass values in Mgha-1 of the first five quadrats in the Sinharaja Forest Dynamic Plot across the five censuses.

Quadrat	Census 1	Census 2	Census 3	Census 4	Census 5
0	23.79	18.90	20.32	23.65	29.81
1	13.00	14.79	18.95	18.96	21.17
2	18.47	20.60	22.96	23.66	20.87
3	47.98	50.32	53.50	55.40	79.92
4	32.82	33.74	35.76	36.40	37.35

essential due to the large disparity in AGB values between the two stem size groups, making it difficult to analyze them together.

To gain deeper insights into the spatial dynamics of AGB distribution, spatial maps were generated for 11 specific AGB categories ranging from 200 Mg ha^{-1} to 2200 Mg ha^{-1}. These maps enabled us to assess the relative AGB content at the quadrat level, allowing for a detailed analysis of the distribution of quadrats across these categories. This approach helped identify patterns in the spatial distribution, revealing whether a greater number of quadrats contained higher AGB values or if the distribution was more balanced across different AGB categories.

The significance of the variation of AGB values of each quadrat (Table 2) over the 25 years (5 censuses) was tested, using the Friedman test based on the validity of the assumptions related to the ANOVA model. Then, all pairwise comparisons were conducted using the sign test with the Bonferroni method.

RESULTS AND DISCUSSION

Selecting the most dominant species and estimating the AGB

Among the 20 most dominant species, the five holding the largest proportion of mean AGB over the 5 censuses were *Mesua ferrea* (96.7 Mgha^{-1}), *Durio ceylanica* (45.1 Mgha^{-1}), *Shorea trapezifolia* (40.2 Mgha^{-1}), *Garcinia hermonii* (18.2 Mgha^{-1}) and *Shorea disticha* (17.9 Mgha^{-1}). See Table A1 in the appendix for the full list.

The total AGB (Table 3) for each of the 5 censuses were also calculated to understand the AGB change over the 5 censuses.

Table 3: Total Above Ground Biomass (AGB) in Mg and Mgha^{-1} for the five censuses in the Sinharaja Forest Dynamic Plot.

Census	Total AGB (Mg)	Total AGB (Mgha^{-1})
1	8101.94	324.08
2	7397.49	295.90
3	7321.27	292.85
4	7233.21	289.33
5	7479.86	299.19

The first census recorded the highest AGB value of 324.08 Mgha^{-1}. Subsequently, the average annual change in AGB for the trees in the plot was observed over four census intervals. The average change of AGB per year for the trees in the plot was as follows: a decrease of 5.63 Mgha^{-1} year^{-1} in the first interval, followed by decreases of 0.61 Mgha^{-1} year^{-1} and 0.7 Mgha^{-1} year^{-1} in the subsequent two intervals. However, in the final interval, there was an increase in AGB of 1.97 Mgha^{-1} year^{-1}. Referring to Figure 2, it can be observed that the largest decrease in AGB occurred during the first census interval, amounting to 28 Mgha^{-1}. This decline continued in the following two censuses. However, in the final census interval, there was a notable increase in AGB, reaching 9.86 Mgha^{-1}.

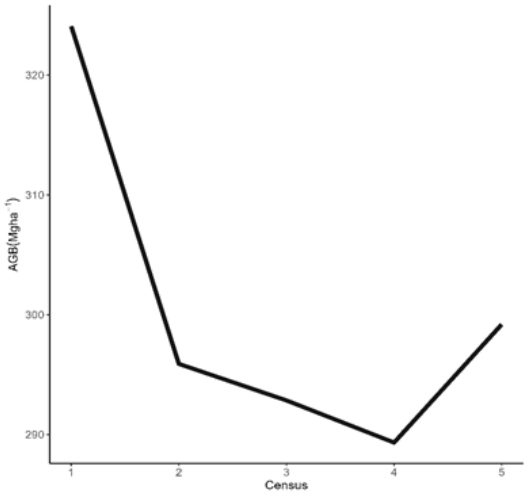


Figure 2: Total aboveground biomass (AGB) variation of the two most dominant species across the five censuses

Testing the temporal variation of AGB across censuses and diameter classes

The table 04 below shows the respective values of AGB for *Mesua ferrea* (Table 4) under the eight diameter classes. Similar results were obtained for each of the 20 species, and finally the full design consisted of aggregate AGB for all 20 dominant species, which allows us to analyse the temporal variation of AGB and variation of AGB across diameter classes for all the species in general as well as for each species separately.

The two-way repeated ANOVA conducted to determine the differences in AGB of different diameter classes showed that only the effect of diameter class on the total AGB of the 20 species is significant at 5% significance level. However, the effect of 5 censuses (temporal variation) on the total AGB of the 20 species is not significant at a 5% significance level. The reason for this non-significance across censuses may be that the FDP is an undisturbed

Table 4: Aggregate Aboveground Biomass (AGB) Across Five Censuses for Mesua ferrea by stem Diameter Class (cm)

Diameter class (cm)	Census 1	Census 2	Census 3	Census 4	Census 5
1-3	100628	91267	82641	78555	103313
3-5	22458	23738	24420	25189	25650
5-7	6893	7278	7539	7628	7951
7-10	4577	4713	4726	4785	4866
10-30	7690	7832	8061	8156	8243
30-50	1511	1417	1403	1389	1433
50-70	534	506	488	449	408
>70	215	179	173	177	205

forest area within the Sinharaja forest reserve, and there has been little change in the overall AGB values.

The table 05 below illustrates the use of either one-way ANOVA or the Kruskal-Wallis test, depending on the validity of ANOVA model assumptions, to assess the variation in AGB across diameter classes for each dominant species.

Table 6 presents the results of one-way repeated ANOVA showing the significance in temporal variation in AGB and the ANOVA or Kruskal-Wallis test results for the effect of diameter class on AGB, with the test choice detailed in Table 5.

Note that the temporal variation is non-significant ($p>0.05$) over the 5 censuses for the 20 species (Table 6) except for *Aporosa sp* (APOR**) and *Urophyllum ellipticum* (UROPEL). These two species have a significant variation of AGB across the 5 censuses at 10% significance level. The reason for these two species showing such a variation may be that they are identified as understory species and have a relatively shorter life span.

The aggregate AGB values of the 20 most dominant species within each diameter class for each census are shown in the following table 07.

Table 07 allows us to see the distribution of the total AGB of the Sinharaja FDP among the 8 dbh classes. Note that the smaller diameter classes (3-7cm) and 10-30cm diameter class generally show a continuous net increase in AGB throughout the 5 censuses and the diameter class 50-70cm shows a continuous net negative AGB change throughout the 5 censuses. The diameter class of 30 - 50 cm, which

Table 5: Choice of ANOVA or Kruskal-Wallis Test for testing Aboveground Biomass (AGB) Variation Across Diameter Classes for Each Species, Based on Shapiro-Wilk Normality Test.

Species code	Species name	Shapiro-Wilk test p value	ANOVA(A) or Kruskal(K)
MESUNA	*Mesua nagassarium*	<0.001	K
AGROIN	*Agrostistachys intramarginalis*	0.322	A
HUMBLA	*Humboldtia laurifolia*	0.1789	A
CULLCE	*Durio ceylanica*	0.14	A
GARCHE	*Garcinia hermonii*	<0.001	K
SHORTR	*Shorea trapezifolia*	<0.001	K
SHORDI	*Shorea disticha*	0.675	A
APOR**	*Aporosa sp*	0.811	A
MYRIDA	*Myristica dactyloides*	<0.001	K
PSYCNI	*Psychotria nigra*	0.017	K
SHORAF	*Shorea affinis*	0.0009661	K
MESUFE	*Mesua ferrea*	<0.001	K
UROPEL	*Urophyllum ellipticum*	0.8671	A
SHORWO	*Shorea worthingtonii*	0.4606	A
PALAPE	*Palaquium petiolare*	0.07432 (10%)	A
SCHUCA	*Schumacheria castaneifolia*	0.2582	A
SHORST	*Shorea stipularis*	0.2881	A
SHORME	*Shorea megistophylla*	<0.01	K
SHORCR	*Shorea cordifolia*	<0.01	K
XYLOCH	*Xylopia championii*	<0.01	K

Table 6: The significance effects of diameter class and census(time) variable on Above-ground Biomass (AGB) for the 20 most dominant species.

Species code	Species name	Significance of diameter class variable	Significance of the census variable
MESUNA	*Mesua nagassarium*	***	NS
AGROIN	*Agrostistachys intramarginalis*	***	NS
HUMBLA	*Humboldtia laurifolia*	***	NS
CULLCE	*Durio ceylanica*	***	NS
GARCHE	*Garcinia hermonii*	***	NS
SHORTR	*Shorea trapezifolia*	***	NS
SHORDI	*Shorea disticha*	***	NS
APOR**	*Aporosa sp*	***	*
MYRIDA	*Myristica dactyloides*	***	NS
PSYCNI	*Psychotria nigra*	***	NS
SHORAF	*Shorea affinis*	***	NS
MESUFE	*Mesua ferrea*	***	NS
UROPEL	*Urophyllum ellipticum*	***	*
SHORWO	*Shorea worthingtonii*	***	NS
PALAPE	*Palaquium petiolare*	***	NS
SCHUCA	*Schumacheria castaneifolia*	***	NS
SHORST	*Shorea stipularis*	***	NS
SHORME	*Shorea megistophylla*	***	NS
SHORCR	*Shorea cordifolia*	***	NS
XYLOCH	*Xylopia championii*	***	NS

Significant codes: *** = $p < 0.001$, * = $0.05 < p < 0.01$, NS - Non-significant

Table 7: The aggregate Aboveground Biomass (AGB) in Mg ha^{-1} Across Five Censuses for All Species, by Diameter Class (cm) and Percentage Contribution to Total AGB for each diameter class.

Diameter class(cm)	Census 1	Census 2	Census 3	Census 4	Census 5	AGB%
1-3	2.42	2.43	2.41	2.35	2.59	0.81
3-5	3.52	3.71	3.81	3.92	3.96	1.25
5-7	3.34	3.50	3.62	3.67	3.81	1.19
7-10	5.59	5.75	5.73	5.79	5.85	1.91
10-30	60.17	60.59	62.66	63.25	64.15	20.70
30-50	83.85	76.61	74.38	72.67	74.60	25.45
50-70	83.86	77.04	73.41	67.68	61.45	24.21
>70	81.28	66.23	66.79	69.95	82.74	24.44

contains the highest percentage of AGB, has shown a net loss in AGB from the first to the fourth census, followed by a net gain from the fourth to the fifth census. This fluctuation mirrors the overall AGB trend observed in the FDP. A similar trend was observed by Ediriweera et al. (2024), where the study examined the 40-year variation of AGB in MDF in southwestern Sri Lanka. Additionally, this study observed that approximately 2% of the total AGB was consistently in stems less than 5 cm in diameter, while stems under 10 cm accounted for less than 5% of the total AGB. The dbh class contributing most to the AGB was 30 - 50 cm diameter (around 25%). About 50% of AGB was in stems < 50cm dbh classes. The intermediate size class was where the distributions of AGB stocks and fluxes reached their peak (Piponiot et al., 2022). Interestingly, large trees (≥ 50 cm) constitute less than 1% of stems in the FDP carried almost 50% of the total AGB in the plot.

Evaluating the spatial variation of AGB within the plot

The below spatial maps (Figure 3) show the visual representation of the total AGB distribution in the 25 ha FDP for each census showing the spread of AGB as well as how it has changed over the course of 25 years.

The total AGB densities varied on average from 3.4 $Mgha^{-1}$ to 1198 $Mgha^{-1}$ at the 0.04 ha scale within the plot, which implies a very high spatial variability at the 0.04 ha scale within the FDP. A reduction of AGB when comparing the spatial map for census 1 (Figure. 3(a)) and census 2 (Figure.

3(b)) can be clearly observed. A decline in AGB can also be seen in most of the quadrats when comparing the spatial maps of censuses 2 and 3 (Figure. 3(b) and 3(c)). However, very few quadrats seem to have gained AGB. The total AGB distributions in census 3 and census 4 seem to be very similar, but there is a slight decrease in total AGB. Further, the spatial distribution for census 5 (Figure. 3(e)) shows an increase of AGB in most of the quadrats when compared with the spatial distribution of census 4 (Figure. 3(d)).

The results of the Friedman test indicate that the spatial distribution of AGB at 0.04 ha was found to be significantly different across the 5 censuses ($p<0.05$). The sign test with Bonferroni method indicates that all pairwise comparisons between the 5 censuses were also found to be significantly different.

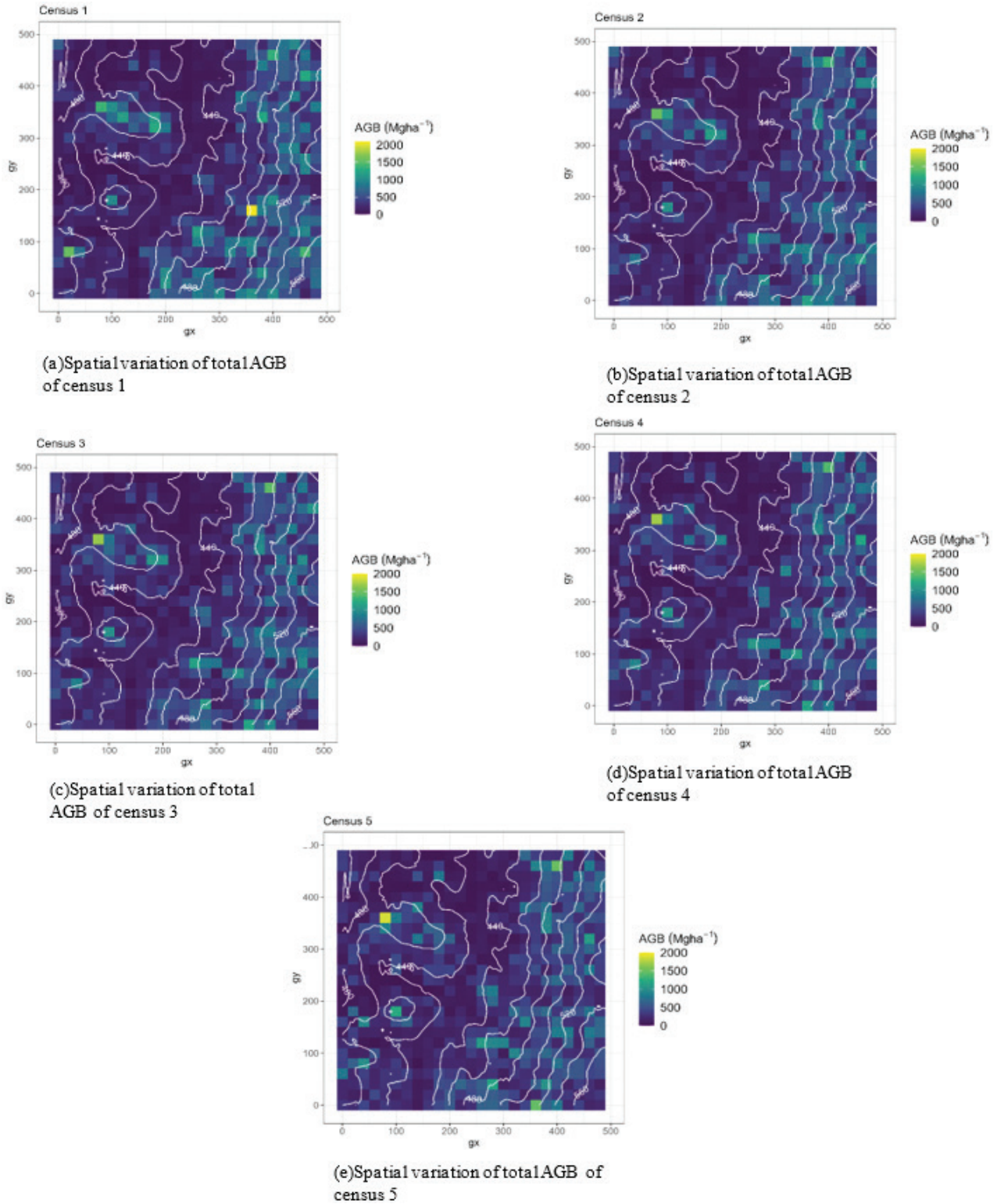


Figure 3: Spatial variation Total Above Ground Biomass of Sinharaja Forest Dynamic Plot over the 5 censuses. Spatial distribution is shown with resolution of 20m × 20m (0.04 ha)

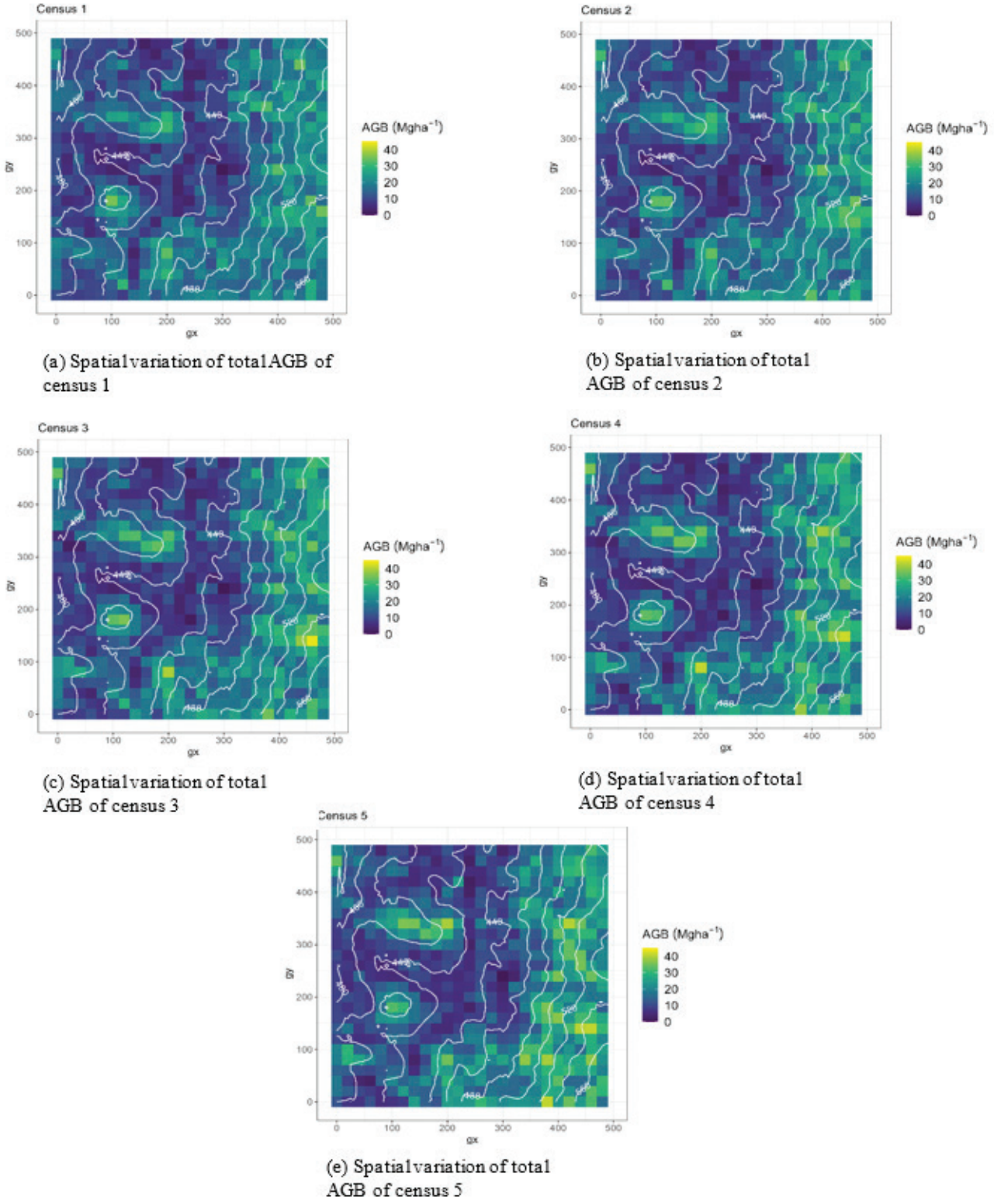


Figure 4: Spatial variation Total Above-ground Biomass (AGB) over the 5 censuses from stems ranging DBH between 1 cm - 10cm in the Sinharaja Forest Dynamic Plot. Spatial distribution is shown with resolution of 20m × 20m (0.04ha)

In figures 3 and 4, it can be noted that the AGB content in quadrats situated in elevated areas is higher compared to the quadrats situated along the valley.

When observing spatial maps for AGB, there is a gain in AGB in the 1cm -10cm dbh category of stems, consistently over the 25 years. Note that this variation of AGB for this category of stems is a contrast to the overall trend of the AGB in the FDP

To understand exactly the spatial distribution of AGB in each census, spatial maps (Figure 5) were drawn for specified AGB categories. These spatial maps visualise the composition of AGB content in each quadrat clearly in the specified category.

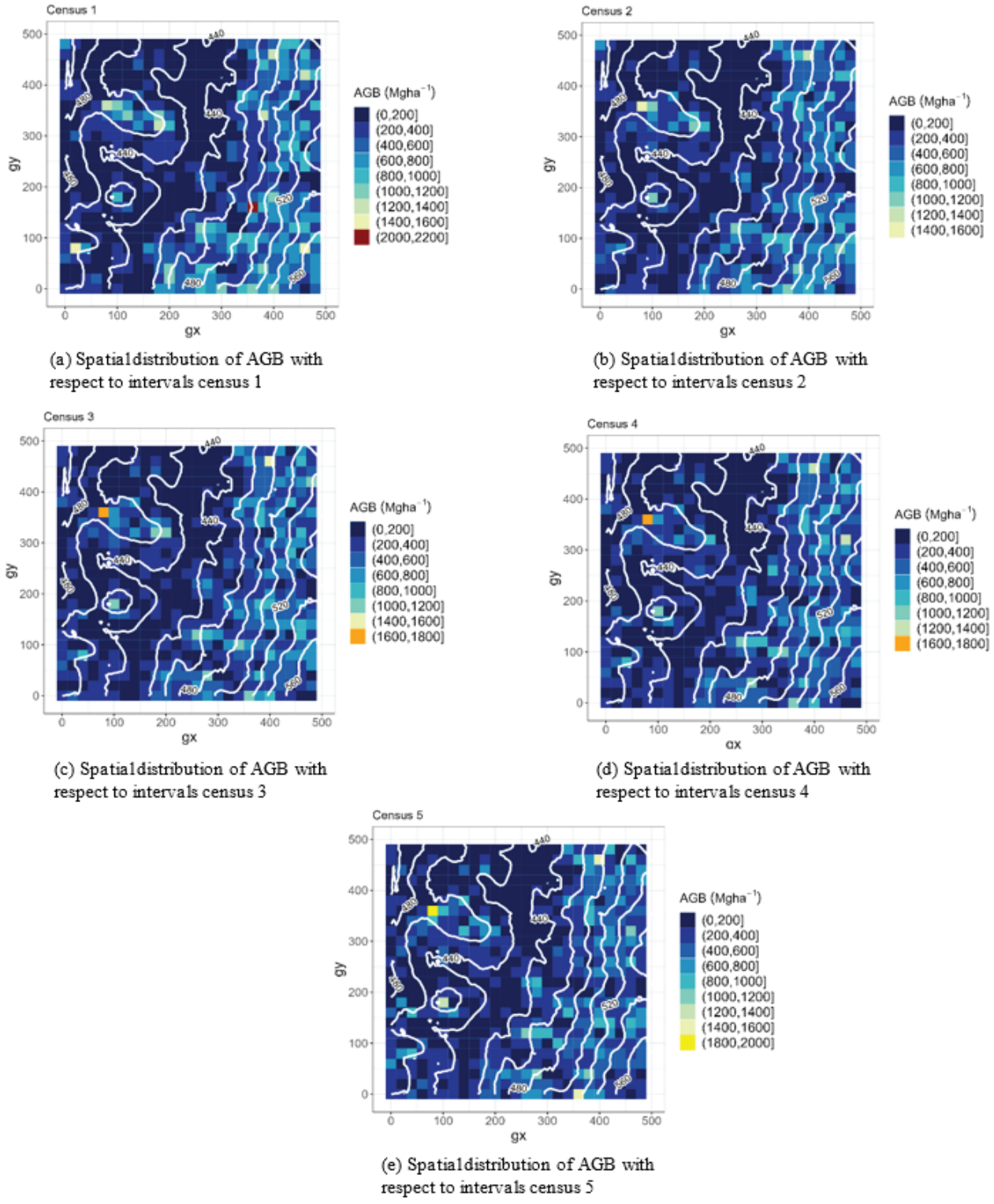


Figure 5: Spatial distribution of Above-ground Biomass (AGB) under different categories over the 5 censuses. Spatial distribution is shown with resolution of 20m × 20m (0.04ha)

According to Figure 5, it is clear that the quadrats that lie along the valley contain the AGB mostly in the range of 0-200 Mgha^{-1}. The AGB content in the quadrats gradually increases when moving up the slopes and quadrats with higher AGB around 600-1000 Mgha^{-1} values are found at elevated areas. Further, we can observe a few quadrats having relatively very high AGB values as well (>1000 Mgha^{-1}). Most quadrats (80%) had AGB values < 600 Mgha^{-1}and on average around 42% of quadrats contained AGB values < 200 Mgha^{-1}.

Since it is difficult to quantify the number of quadrats using spatial maps, we obtained the frequency distribution (Figure 6) of the quadrats in each of the AGB intervals related to figure 5 to understand the variation of the number of quadrats for each AGB interval across the 5 censuses.

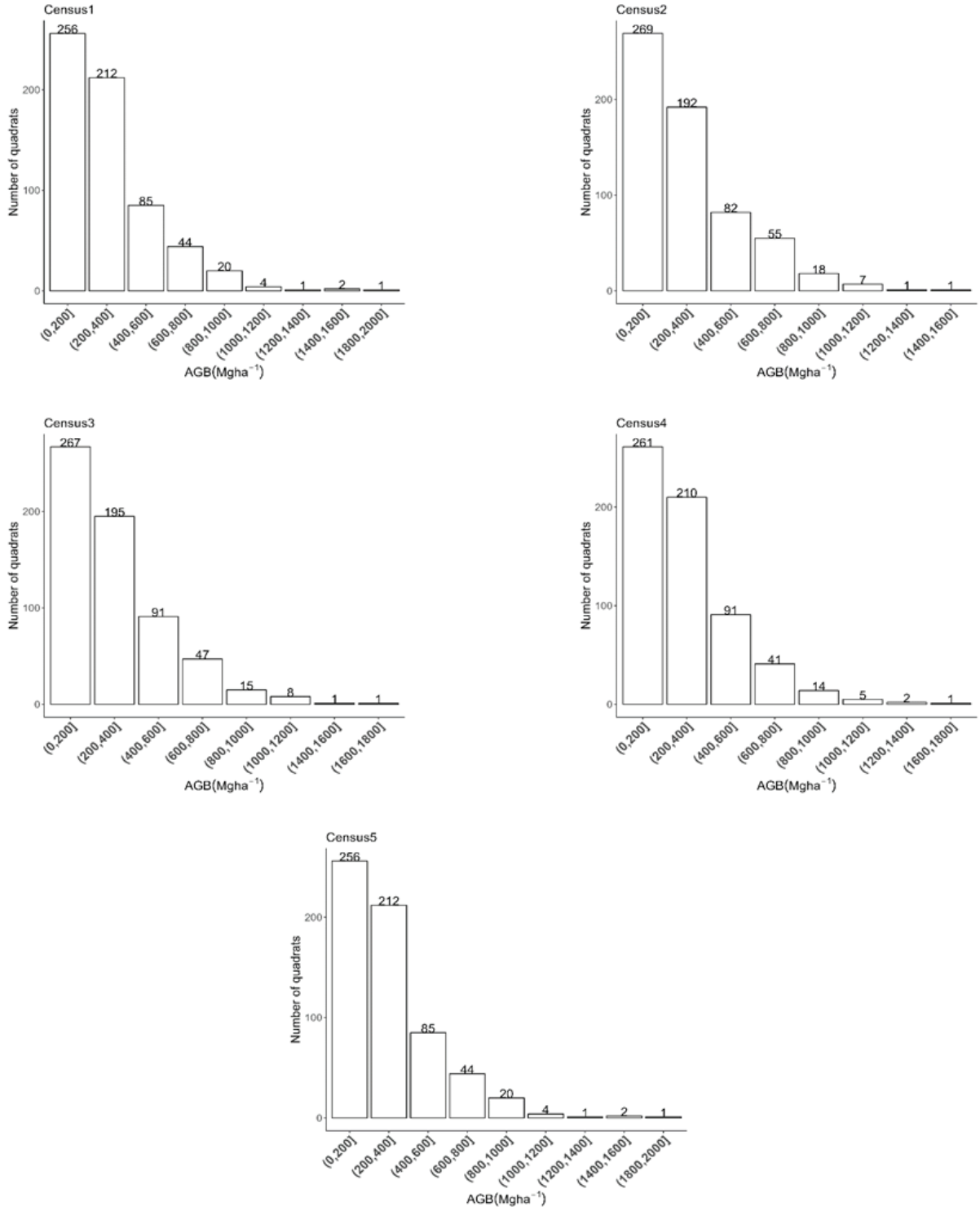


Figure 6: Frequency distribution of quadrats within each Above-ground Biomass (AGB) interval in for the five censuses

Figure 6 illustrates that across all five censuses, the majority of quadrats in the FDP exhibit relatively low AGB values. The frequency distribution of AGB is positively skewed, with a long tail extending towards higher AGB intervals, forming a reverse J-shaped distribution. Such distribution patterns are commonly observed in forest inventories, where the number of small trees per unit area typically exceeds the number of larger trees. This is consistent with general forest dynamics, as smaller trees are more numerous in most forest ecosystems compared to larger, mature trees

CONCLUSIONS

The findings of this study suggest that the temporal variation of AGB in the FDP over 25 years was not significant. When the analysis was conducted at species level only a couple of species showed a slight significance in temporal variation. It was apparent that the AGB at diameter class levels were significantly different. Overall, the spatial variability of AGB FDP was very high. Further, the spatial distribution of AGB at 0.04 ha level for the five censuses was significantly different. The spatial analysis also suggested that the

majority of quadrats had relatively lower AGB values, and therefore the distribution of AGB in the FDP was skewed to the right. In the 25-ha permanent plot, the AGB estimates dropped from 324 $Mgha^{-1}$ to 299 $Mgha^{-1}$ over the 25 years which corresponds to an average decrease of 1 $Mgha^{-1}$. Our study area is witnessing a notable reduction in AGB, primarily due to the loss of large canopy tree species like *Mesua ferrea*. This shift is altering the ecosystem's role from acting as a carbon sink to becoming a carbon source.

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AUTHOR CONTRIBUTION

Conceptualization, Designing the methodology, Supervision, Editing the manuscript: P.W., S.E; Managing literature survey, Statistical analysis and writing the first draft: H.M.S.I. All authors contributed to the discussion, reviewed the final manuscript, and approved it for submission.

DECLARATION OF CONFLICT OF INTEREST

The authors declare that there are no conflicts of interests.

REFERENCES

Alves, L. F., Vieira, S. A., Scaranello, M. A., Camargo, P. B., Santos, F. A. M., Joly, C. A., & Martinelli, L. A. (2010). Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management*, **260**(5), 679–691. https://doi.org/10.1016/j.foreco.2010.05.023

Baker, T. R., Phillips, O. L., Malhi, Y., ... Vásquez Martínez, R. (2004). Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**(1443), 353–365. https://doi.org/10.1098/rstb.2003.1422

Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, **320**(5882), 1444–1449. https://doi.org/10.1126/science.1155121

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., ... Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, **519**(7543), 344–348. https://doi.org/10.1038/nature14283

Brown, S., Gillespie, A. J. R., & Lugo, A. E. (1991). Biomass of tropical forests of south and southeast Asia. *Canadian Journal of Forest Research*, **21**(1), 111–117. https://doi.org/10.1139/x91-015

Cardinale, B. J., Duffy, J. E., Gonzalez, A., ... Naeem, S. (2012). Biodiversity loss and its impact on humanity. Nature, **486**(7401), 59–67. https://doi.org/10.1038/nature11148

Chandrasekara, H. U., & Pathiratne, A. (2005). Influence of low concentrations of Trichlorfon on haematological parameters and brain acetylcholinesterase activity in common carp, *Cyprinus carpio L*. *Aquaculture Research*, **36**(2), 144–149. https://doi.org/10.1111/j.1365-2109.2004.01197.x

Chave, J., Réjou-Méchain, M., Búrquez, A., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology, ***20***(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Coomes, O. T., Takasaki, Y., & Rhemtulla, J. M. (2011). Land-use poverty traps identified in shifting cultivation systems shape long-term tropical forest cover. *Proceedings of the National Academy of Sciences of the United States of America*, **108**(34), 13925–13930. https://doi.org/10.1073/pnas.1012973108

Curtis, J. T., & McIntosh, R. P. (1950). The interrelations of certain analytic and synthetic phytosociological characters. Ecology, ***31***(3), 434–455. https://doi.org/10.2307/1931497

Davies, S. J., Abiem, I., Abu Salim, K., ... Zuleta, D. (2021). ForestGEO: Understanding forest diversity and dynamics through a global observatory network. Biological Conservation, ***253***, 108907. https://doi.org/10.1016/j.biocon.2020.108907

Ediriweera, S., Bandara, C., Lakkana, T., ... Ashton, M. S. (2024). Old-growth mixed dipterocarp forests show variable losses and gains in aboveground biomass and standing carbon over forty years. Forest Ecosystems, ***11***, 100163. https://doi.org/10.1016/j.fecs.2023.100163

Ferry, B., Morneau, F., Bontemps, J. D., Blanc, L., & Freycon, V. (2010). Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**(1), 106–116. https://doi.org/10.1111/j.1365-2745.2009.01604.x

Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Baptiste, B. L. G., Medina Uribe, C. A., Haugaasen, T., & Edwards, D. P. (2014). Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. *Nature Climate Change*, **4**(6), 503–507. https://doi.org/10.1038/nclimate2200

Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Esufali, S., Harms, K. E., Ashton, P. M. S., Burslem, D. F. R. P., & Ashton, P. S. (2006). Species-habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology*, **22**(4), 371–384. https://doi.org/10.1017/S0266467406003282

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., ... D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences of the United States of America, ***103***(50), 19010–19014. https://doi.org/10.1073/pnas.0609048103

Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., ... Wöll,

H. (2009). Increasing carbon storage in intact African tropical forests. Nature, ***457***(7232), 1003–1006. https://doi.org/10.1038/nature07771

Malhi, Y., & Grace, J. (2000). Tropical forests and atmospheric carbon dioxide. *Trends in Ecology \& Evolution*, **15**(8), 332–337. https://doi.org/10.1016/S0169-5347(00)01906-6

Malhi, Y., Wood, D., Baker, T. R., ... Vinceti, B. (2006). The regional variation of aboveground live biomass in old-growth Amazonian forests. Global Change Biology, ***12***(7), 1107–1138. https://doi.org/10.1111/j.1365-2486.2006.01120.x

Nascimento, H. E. M., & Laurance, W. F. (2002). Total aboveground biomass in central Amazonian rainforests: A landscape-scale study. *Forest Ecology and Management*, **168**(1–3), 311–321. https://doi.org/10.1016/S0378-1127(01)00749-6

Osuri, A. M., Madhusudan, M. D., Kumar, V. S., Chengappa, S. K., Kushalappa, C. G., & Sankaran, M. (2014). Spatio-temporal variation in forest cover and biomass across sacred groves in a human-modified landscape of India's Western Ghats. *Biological Conservation*, **178**, 193–199. https://doi.org/10.1016/j.biocon.2014.08.008

Piponiot, C., Anderson-Teixeira, K. J., Davies, S. J., ... Muller-Landau, H. C. (2022). Distribution of biomass dynamics in relation to tree size in forests across the world. New Phytologist, ***234***(5), 1664–1677. https://doi.org/10.1111/nph.17995

Rai, S. N. (1984). Aboveground biomass in tropical rain forests of western Ghats, India. *Indian Forester (India)*, **110**(8), 754-764

Sullivan, M. J. P., Talbot, J., Lewis, S. L., ... Zemagho, L. (2017). Diversity and carbon storage across the tropical forest biome. Scientific Reports, *7*, 39102. https://doi.org/10.1038/srep39102

Yamakura, T., Hagihara, A., Sukardjo, S., & Ogawa, H. (1986). Aboveground biomass of tropical rain forest stands in Indonesian Borneo. *Vegetatio*, **68**(2), 71–82. https://doi.org/10.1007/BF00045057

APPENDIX

Table A1: Total AGB values of each species over the 5 census intervals in $Mgha^{-1}$

Species code	Species name	Census 1	Census 2	Census 3	Census 4	Census 5	Mean AGB
MESUNA	*Mesua nagassarium*	137.21	104.37	80.57	80.57	80.57	96.66
CULLCE	*Durio ceylanica*	35.56	38.52	50.48	50.48	50.48	45.10
SHORTR	*Shorea trapezifolia*	32.12	34.93	44.70	44.70	44.70	40.23
SHORDI	*Shorea disticha*	17.92	17.21	18.35	18.35	18.35	18.04
GARCHE	*Garcinia hermonii*	17.67	18.36	18.44	18.44	18.44	18.27
SHORST	*Shorea stipularis*	17.20	17.67	18.30	18.30	18.30	17.95
MYRIDA	*Myristica dactyloides*	10.79	10.81	11.40	11.40	11.40	11.16
PALAPE	*Palaquium petiolare*	10.48	10.27	10.44	10.44	10.44	10.41
SHORME	*Shorea megistophylla*	8.57	8.28	7.91	7.91	7.91	8.12
MESUFE	*Mesua ferrea*	7.54	5.80	5.50	5.50	5.50	5.97
SHORAF	*Shorea affinis*	7.30	7.67	9.32	9.32	9.32	8.58
SHORWO	*Shorea worthingtonii*	5.88	5.92	6.31	6.31	6.31	6.14
SHORCR	*Shorea cordifolia*	4.90	4.91	5.80	5.80	5.80	5.45
XYLOCH	*Xylopia championii*	4.89	4.88	4.76	4.76	4.76	4.81
AGROIN	*Agrostistachys intramarginalis*	2.08	2.20	2.51	2.51	2.51	2.36
SCHUCA	*Schumacheria castaneifolia*	1.38	1.34	1.28	1.28	1.28	1.31
HUMBLA	*Humboldtia laurifolia*	1.06	1.23	1.64	1.64	1.64	1.44
PSYCNI	*Psychotria nigra*	0.58	0.62	0.56	0.56	0.56	0.58
APOR**	*Aporosa sp*	0.53	0.55	0.61	0.61	0.61	0.58
UROPEL	*Urophyllum ellipticum*	0.40	0.36	0.32	0.32	0.32	0.34