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Vegetation structure and carbon sequestration potential in the tropical karst forest of Gunung Sewu, Indonesia

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Abstract. *Putri NRA, Setyawan AD, Kusumaningrum L. 2025. Vegetation structure and carbon sequestration potential in the tropical karst forest of Gunung Sewu, Indonesia. Intl J Trop Drylands 9: 50-63.* Karst ecosystems are ecologically fragile yet provide critical services, including biodiversity support, water regulation, and carbon sequestration. However, restoration in these environments remains complex due to thin soils, seasonal drought, and limited rooting volume. This study assesses vegetation structure, aboveground biomass (AGB), and carbon sequestration potential in the reforested karst landscape of the Paliyan Wildlife Reserve, Yogyakarta, Indonesia. A systematic inventory was conducted across 100 plots stratified by tree and pole size classes, encompassing 1,180 woody individuals from 19 species. Biomass was estimated using both species-specific and general allometric equations. Results reveal a total AGB of 136.77 Mg ha^{-1}, corresponding to 64.28 Mg C ha^{-1} or 235.88 Mg CO_2 ha^{-1}. Biomass was disproportionately stored in the tree stratum (78.23%) and overwhelmingly dominated by non-native species—particularly *Tectona grandis*, *Delonix regia*, and *Senna siamea*—which together accounted for over 70% of total carbon stock. Although restoration has successfully increased canopy cover and carbon storage, vertical stratification and native species richness remain low. Native taxa such as *Dalbergia latifolia* and *Casuarina equisetifolia* made minor but ecologically important contributions. These findings emphasize the ecological trade-offs of relying on fast-growing exotics, which, while effective for rapid biomass gain, may compromise long-term ecosystem resilience. The study advocates for a shift toward structurally diverse, native-enriched restoration strategies in tropical karst forests, aligned with biodiversity goals and climate mitigation targets under the UN Decade on Ecosystem Restoration, REDD+, and national policy frameworks. This research provides a critical empirical foundation for balancing carbon-oriented and biodiversity-conscious reforestation in vulnerable karst systems.

Keywords: Aboveground biomass, carbon sequestration, Gunung Sewu, karst forest, *Tectona grandis*

INTRODUCTION

Forests play a pivotal role in mitigating climate change by sequestering atmospheric carbon dioxide (CO_2) through photosynthesis and storing it in their biomass. This process reduces greenhouse gas concentrations and contributes to global climate regulation (Wilkes et al. 2018; Pratama et al. 2025). Globally, forests store approximately 289 gigatons of carbon, with tropical forests accounting for more than half of this total (FAO 2010; Rawal and Subedi 2022). However, the accelerating pace of deforestation, land-use change, and forest degradation threatens these natural carbon sinks, releasing stored carbon and amplifying climate instability (Wahyuni and Suranto 2021; Gunawan et al. 2024a, b).

In response to these challenges, forest restoration has emerged as a critical strategy to recover carbon stocks while simultaneously supporting biodiversity and ecosystem services. A key metric for evaluating restoration success is Aboveground Biomass (AGB), which directly correlates with carbon storage. Since destructive sampling is often impractical in protected or recovering areas, non-destructive methods such as allometric equations—based on tree Diameter at Breast Height (DBH), total height, and wood density—are widely applied and continually refined (Chave et al. 2014; Jara et al. 2015).

Karst ecosystems represent a unique subset of tropical landscapes, characterized by rugged limestone topography, thin soils, water scarcity, and limited rooting depth (Clements et al. 2006; Zerga 2024; Bai et al. 2025). These harsh conditions often limit conventional forestry practices but provide critical ecological services, including carbon sequestration, water regulation, and habitat support. Increasing interest has emerged regarding the role of reforested karst landscapes as carbon sinks, particularly in the face of ongoing land degradation (Aprilia et al. 2021; Song et al. 2022). However, restoring karst systems requires tailored strategies that consider their unique edaphic and hydrological constraints to ensure long-term ecological resilience.

Indonesia's karst regions, such as the Gunung Sewu Karst in southern Yogyakarta, have experienced severe degradation due to logging, shifting agriculture, and human settlement. The Paliyan Wildlife Reserve (PWR), located within this area, was historically managed as a production forest dominated by *Tectona grandis*. Since 2005, and especially after 2014, PWR has been the focus of ecological rehabilitation involving both exotic and native tree species (Wahyudi and Aminatun 2018). While there have been visible improvements in canopy cover, the impact of mixed-species planting on biomass accumulation and carbon retention remains poorly understood.

Previous studies in the Gunung Sewu region have addressed general aspects of biodiversity and forest structure (Septiasari et al. 2021; Yuslinawari et al. 2021; Hikari et al. 2023), but few have explicitly examined the relationship between vegetation structure and carbon storage in restored karst systems. Yet, it is well-established that forest structural parameters—such as stem diameter, basal area, and vertical stratification—are key drivers of biomass accumulation and carbon dynamics (Dovrat et al. 2019; Macias et al. 2017). Forests dominated by fewer, large individuals often store more carbon than diverse forests composed of smaller trees (Brown 1997). Consequently, comprehensive evaluations that integrate structural attributes with functional outcomes are essential for assessing reforestation success in karst environments.

The extensive use of fast-growing exotic species such as *Delonix regia*, *Senna siamea*, and *Gliricidia sepium* in restoration efforts introduces important ecological trade-offs. These species are valued for their rapid biomass accumulation and drought tolerance but can suppress native species regeneration, alter successional pathways, and reduce habitat heterogeneity (Ekayanti et al. 2015; Hendrati and Nurrohmah 2018). In contrast, native species like *Dalbergia latifolia* and *Casuarina equisetifolia* are better suited to local edaphic conditions and contribute to ecological stability through their high wood density and specialized adaptations.

This study aims to evaluate vegetation structure and carbon sequestration potential in the Paliyan Wildlife Reserve, a restored karst forest landscape within the Gunung Sewu UNESCO Global Geopark. Specifically, the objectives are to: (i) quantify stand structure across tree and pole strata; (ii) estimate aboveground biomass and carbon stocks using species-appropriate allometric equations; (iii) compare the relative contributions of native and non-native species; and (iv) assess the implications of species dominance and structural simplification for restoration effectiveness. The results are expected to inform both local and national forest restoration policies under REDD+, Indonesia's National Biodiversity Strategy and Action Plan (NBSAP), and global climate frameworks, including the UN Decade on Ecosystem Restoration.

MATERIALS AND METHODS

Study area

This study was conducted in the Paliyan Wildlife Reserve (PWR), located in Gunungkidul District, Yogyakarta, Indonesia (Figure 1). The reserve situated in the eastern part of the Gunung Sewu Karst, a geologically unique landscape, is characterized by conical limestone hills, shallow rocky soils, underground rivers, and seasonal water scarcity (Aprilia et al. 2021). Covering approximately 434.83 hectares, PWR is part of the broader Gunung Sewu UNESCO Global Geopark, recognized for its geomorphological diversity and, more importantly, its crucial ecological role.

The elevation in PWR ranges from 100 to 300 meters above sea level, with an average altitude of around 260 meters. The terrain is undulating to steep, with slope gradients often exceeding 40%, presenting considerable challenges for vegetation establishment. The climate is classified as tropical monsoon, with an average annual rainfall of 2,071 mm concentrated in the wet season, while the dry season may last up to six months. Air temperatures typically fluctuate between 24.7°C and 31.8°C, and relative humidity ranges from 26% to 58.3%, indicating a semi-arid microclimate typical of karst environments (Wahyudi and Aminatun 2018). This semi-arid microclimate significantly impacts the flora and fauna of the reserve, influencing their distribution, diversity, and survival strategies.

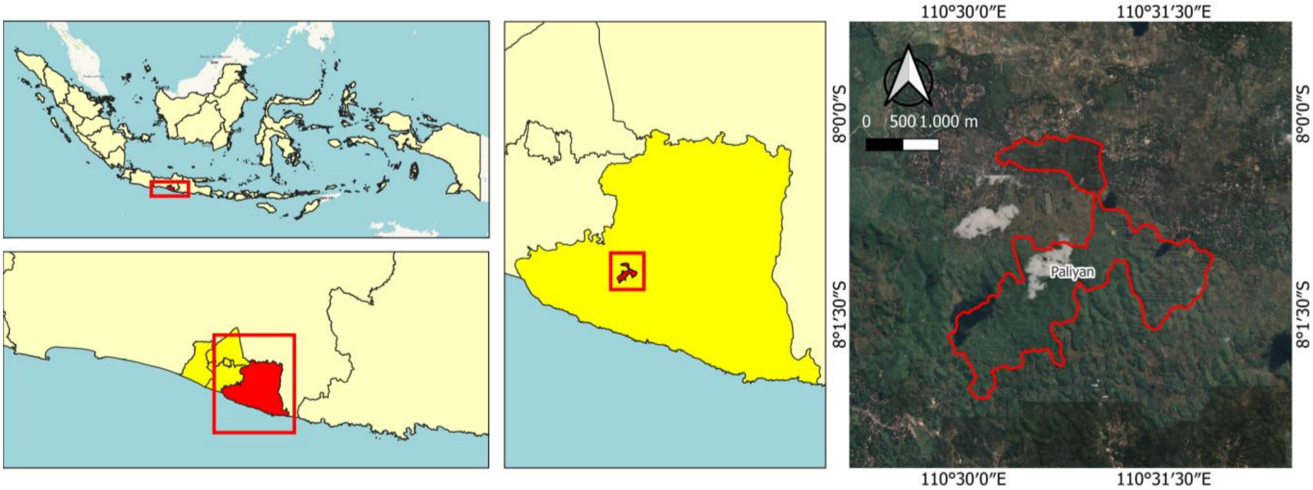

Figure 1. Map of the study area in Paliyan Wildlife Reserve, Gunung Sewu, Yogyakarta, Indonesia

Historically, the Paliyan site was exploited as a monocultural production forest dominated by *T. grandis*. Due to logging, land conversion, and soil degradation, the area experienced significant ecological decline. Since 2005, the site has undergone rehabilitation through reforestation and conservation programs, with intensified efforts starting in 2014 focusing on ecosystem restoration and native species reintroduction (Wahyudi and Aminatun 2018). These programs aimed to stabilize the fragile landscape, restore habitat functions, and enhance ecosystem services, including carbon sequestration and biodiversity conservation.

The PWR landscape now comprises a mosaic of vegetation patches, including reforested stands dominated by non-native species, regenerating native vegetation, and semi-natural karst scrubland. These different zones provided a representative sampling framework for examining stand structure and biomass accumulation across varying ecological conditions.

Sampling design and plot establishment

To evaluate vegetation structure and carbon sequestration potential, a systematic sampling design was meticulously applied across the Paliyan Wildlife Reserve (PWR). The sampling campaign was conducted in August 2024, encompassing both rehabilitated areas and semi-natural forest patches to capture variability in floristic composition and stand development stages. This approach ensures spatial representativeness and allows for meaningful comparisons between vegetation types within the restored karst landscape.

A total of 100 observation plots were established along pre-defined transects, with fixed intervals to minimize spatial bias. Each plot was classified into two strata based on vegetation size classes: tree plots for individuals with a Diameter at Breast Height (DBH)>20 cm, and pole plots for individuals with DBH between 10–20 cm. Tree plots were sized 20×20 meters (400 m^2), while pole plots measured 10×10 meters (100 m^2), following strict adherence to standard ecological protocols (Pearson et al. 2014; Preece et al. 2015).

Within each plot, all individuals meeting the respective DBH threshold were identified to species level, and their DBH and total height were measured using a diameter tape and digital hypsometer, respectively. Individuals with buttresses or irregular basal forms were measured slightly above the irregularity, as recommended in dendrometric standards (Chave et al. 2014). This stratified approach allowed for the separation of growth stages, which is important for understanding structural development and biomass accumulation across the landscape.

In total, data were collected from 1,180 individuals—659 at the pole level and 521 at the tree level. Regional floras, field guides, and consultation with herbarium references aided species identification. Basic environmental attributes such as GPS coordinates, elevation, slope gradient, and general soil condition were also recorded for each plot to support further ecological interpretation.

The selected plot number and distribution were calibrated to achieve a minimum 90% confidence level and a 10% margin of error, which is acceptable for biomass and carbon stock assessments in heterogeneous landscapes (IPCC 2003; Pearson et al. 2014). This robust sampling framework provides a reliable foundation for subsequent analysis of aboveground biomass, carbon storage, and species-level contributions in the PWR karst forest.

Vegetation data collection

Vegetation data were obtained through direct field observation using non-destructive measurement techniques. All trees and poles within the designated plots were identified to species level, relying on regional floras, local field guides, and consultation with botanical experts familiar with karst vegetation. In cases where field identification was uncertain, voucher specimens were photographed and cross-referenced with herbarium records and online taxonomic databases to ensure accuracy.

For each individual, two key biometric parameters were measured: Diameter at Breast Height (DBH) and total height. DBH was measured at 1.3 meters above ground level using a diameter tape. When buttresses or deformities were present, measurements were taken just above the irregularity to maintain consistency with allometric requirements (Chave et al. 2005, 2014). Tree height was recorded using a digital hypsometer, which provided reliable vertical estimates across variable canopy layers. These measurements are essential inputs for estimating aboveground biomass using allometric models.

Species were further categorized into two structural classes based on DBH thresholds: poles (10-20 cm) and trees (>20 cm). This classification reflects ontogenetic stages and allows the analysis of forest structural heterogeneity, particularly important in restored or secondary karst forests where stand maturity varies significantly. Structural stratification also enables comparative analysis of carbon accumulation across growth stages.

For each recorded species, wood density values (g cm^{-3}) were compiled from published sources, including the Global Wood Density Database (Zanne et al. 2009), national forestry reports, and species-specific studies relevant to tropical Southeast Asia (Rosmerita and Purwanto 2008; Siregar 2012). These values were later used in allometric calculations to estimate biomass and carbon stock.

In addition to biometric data, the Importance Value Index (IVI) was calculated for each species as a composite measure of its ecological role within the forest community. IVI incorporates three metrics—relative density, relative frequency, and relative dominance—providing a comprehensive picture of species significance in terms of abundance, distribution, and basal area (Odum 1971; Mueller-Dombois and Ellenberg 1974). Relative dominance was computed from basal area values derived from DBH, while frequency captured the proportion of plots in which a species was found.

All field data, including raw measurements and plot characteristics, were compiled into structured spreadsheets and cross-checked for consistency. This comprehensive dataset served as the analytical foundation for estimating biomass, calculating carbon storage, and interpreting the structural role of both native and non-native species in the Paliyan Wildlife Reserve.

Biomass estimation using allometric equations

To estimate Aboveground Biomass (AGB) without destructive harvesting, both species-specific and generalized allometric equations were applied. These models relate tree biometric parameters—particularly DBH, height, and wood density—to total biomass using empirically derived mathematical formulas (Chave et al. 2005, 2014). The use of allometric models is widely recommended for biomass estimation in tropical forests, particularly where field conditions or conservation status prohibit destructive methods.

For major species in the study area, species-specific equations were prioritized whenever available, as they offer greater accuracy for particular taxa and local growing conditions. Such models were sourced from peer-reviewed studies and forestry research relevant to Southeast Asia, particularly for species such as *T. grandis*, *S. siamea*, and *D. latifolia* (Rosmerita and Purwanto 2008; Siregar 2012; Ilyas 2013). When no specific model was available for a species, the general moist tropical forest equation developed by Chave et al. (2014) was used:

$$AGB = 0.0673\times(\rho\times D2\times H)0.976$$

$$\text{Carbon stock} = AGB\times0.47$$

Where AGB is the aboveground biomass (kg), ρ is wood density (g cm^{-3}), D is DBH (cm), and H is tree height (m). This three-variable equation has been validated across numerous tropical forest types and provides robust estimates for structurally diverse stands.

Table 1 summarizes the allometric equations applied for major species found in the Paliyan Wildlife Reserve. These equations were used to calculate individual biomass, which was then scaled to a per-hectare basis based on plot size and sampling intensity.

The selection of models was based on equation availability, species relevance, and data completeness. When species-specific equations were not available, the general model (Equation 12, Table 1) was applied to ensure consistency in biomass estimation.

Carbon storage and sequestration calculation

Carbon storage was estimated by converting the Aboveground Biomass (AGB) values using a standard carbon fraction. According to the Indonesian National Standard (SNI 7724:2011), it is assumed that carbon constitutes approximately 47% of the dry biomass of woody plants. Thus, total carbon storage (Mg C ha^{-1}) was calculated by multiplying biomass by a factor of 0.47:

$$\text{Carbon stock}=AGB\times0.47$$

This coefficient is widely used in national and international forest carbon assessments and provides a reliable proxy for the amount of carbon retained in aboveground vegetation (SNI 2011; Duncanson et al. 2021). While actual carbon content may vary by species and site conditions, the use of a standardized fraction allows for comparability across studies and regions.

To express the climate mitigation potential of restored vegetation in terms of greenhouse gas offsets, carbon stock values were further converted into carbon dioxide equivalents (CO_2-eq). This was achieved using the molecular weight ratio of CO_2 to C, which is 44/12, or approximately 3.67 (IPCC 2003).

This transformation enables comparison of forest carbon sequestration capacity with anthropogenic CO_2 emissions and supports reporting in carbon markets and climate policy frameworks, including REDD+ and the Paris Agreement. Carbon calculations were conducted separately for each structural class—trees and poles—to evaluate growth stage contributions. Likewise, species-level carbon contributions were calculated to assess the relative importance of dominant taxa in overall carbon dynamics. These calculations were based on species-specific biomass estimates derived from the allometric equations presented in Table 1.

Table 1. Allometric equations used to estimate Aboveground Biomass (AGB) for major tree species in Paliyan Wildlife Reserve, Gunungkidul District, Yogyakarta Province, Indonesia

Species	Allometric equation	Reference
Tectona grandis L.f.	AGB = 0.0548 × DBH^2.5792	Siregar (2012)
Senna siamea (Lam.) H.S.Irwin & Barneby	AGB = 0.3699 × DBH^1.9374	Ilyas (2013)
Gliricidia sepium (Jacq.) Kunth	AGB = 0.019 × DBH^2.7192	Mulyana et al. (2020)
Acacia auriculiformis	AGB = 0.070 × DBH^2.58	Wicaksono (2004)
Dalbergia latifolia Roxb.	AGB = 0.7458 × (DBH^2 × H)^0.6394	Rosmerita and Purwanto (2008)
Anacardium occidentale	AGB = exp(−2.6516 + 1.9741 ln(DBH) + 0.7169 ln(H))	Biah et al. (2019)
Swietenia macrophylla G.King	AGB = 0.048 × DBH^2.68	Adinugroho and Sidiyasa (2006)
Artocarpus heterophyllus Lam.	AGB = 0.065 × DBH^2.28	Martin et al. (2010)
Calophyllum inophyllum	AGB = exp(−0.972 + 2.078 × ln(DBH))	Basuki et al. (2022)
Melia azedarach L.	AGB = 0.71 × DBH^2.451	Lukito and Rohmatiah (2022)
Gmelina arborea Roxb. ex Sm.	AGB = exp(−3.028 + 0.925 × ln(DBH^2 × H))	Khushi et al. (2019)
General (tropical forests)	AGB = 0.0673 × (ρ × D^2 × H)^0.976	Chave et al. (2014)

Note: AGB: Aboveground Biomass (kg), DBH: Diameter at Breast Height (cm), H: Total height (m), ρ: Wood density (g cm^{-3})

CO_2-eq=Carbon Stock×3.67

Finally, plot-level estimates were scaled up to a per-hectare basis and extrapolated to the entire area of the Paliyan Wildlife Reserve (434.83 ha), assuming that the sampled plots represent the average condition of the forest. This extrapolation provides landscape-level estimates of carbon storage and CO_2 sequestration, which are essential for evaluating the ecological and climate value of restoration interventions.

Data analysis and interpretation

All field data—including species identity, DBH, height, and wood density—were compiled into structured databases and cross-validated to ensure consistency prior to analysis. Biomass and carbon values were computed for each individual using the relevant allometric equations (Table 1), and then aggregated by plot, growth stratum (pole vs. tree), and species origin (native vs. non-native). These values were scaled to per-hectare estimates using plot area and sampling intensity as the basis for extrapolation.

Species dominance was assessed using the Importance Value Index (IVI), which integrates three components: relative density, relative frequency, and relative dominance. Relative density was calculated as the proportion of individuals of a species relative to the total number of individuals. Relative frequency was based on the number of plots in which a species occurred, while relative dominance was derived from the total basal area contributed by each species (Curtis and McIntosh 1950; Odum 1971). IVI scores were interpreted separately for poles and trees to account for structural differentiation.

To assess the role of species origin in biomass and carbon dynamics, each species was categorized as either native or non-native based on floristic records specific to Java and Southeast Asia. This classification enabled comparisons of structural and functional metrics—including individual abundance, basal area, IVI, biomass, and carbon storage—between origin groups. Such comparisons help evaluate the ecological trade-offs of using exotic species in forest restoration efforts, such as potential impacts on local biodiversity and ecosystem stability.

The relationship between structural parameters (e.g., DBH, height, basal area) and carbon accumulation was also examined descriptively to highlight which attributes most strongly influence carbon storage. Species-level contributions to total biomass and carbon stocks were ranked to identify key functional taxa driving sequestration patterns. These analyses were complemented by graphical visualizations presented in the Results section. These visualizations, designed for clarity and ease of understanding, clarify differences among species, strata, and origin types, making the results accessible to our audience.

All computations were performed using Microsoft Excel and supported by standard statistical functions for logarithmic, exponential, and ratio-based operations. The resulting dataset provides a comprehensive profile of vegetation structure and carbon dynamics in the Paliyan Wildlife Reserve, which is a testament to the thoroughness of our research process. It serves as the analytical foundation for interpretation in subsequent sections, ensuring the confidence of our audience in the validity of our results.

RESULTS AND DISCUSSION

Species richness and floristic composition

A total of 1,180 individual woody plants were recorded across all sampling plots in the Paliyan Wildlife Reserve, comprising 659 individuals in the pole stratum (DBH 10-20 cm) and 521 individuals in the tree stratum (DBH>20 cm). These individuals represented 19 unique species from 14 plant families, indicating moderate floristic diversity in this restored karst landscape. The two strata exhibited distinct patterns in terms of species richness, stem size, and vertical structure. Of the 19 total species, 4 occurred exclusively in the tree stratum, one species was unique to the pole stratum, and 14 species were shared between both layers (Tables 2 and 3). This pattern highlights a degree of vertical continuity in forest composition while also reflecting regeneration-stage specificity for certain taxa.

In the pole stratum, 16 species were identified, with an average DBH of 14.95 cm and a mean height of 10.57 m. The highest density was observed in Fabaceae (48% of pole individuals), followed by Lamiaceae (41%). Non-native species such as *T. grandis*, *G. sepium*, and *S. siamea* dominated the pole layer in terms of both abundance and basal area, reflecting either active replanting or successful vegetative regeneration following disturbance.

In the tree stratum, 18 species were recorded. These individuals exhibited a higher average DBH of 26.09 cm and a taller mean height of 13.86 m, with stem density reaching 130.25 individuals ha^{-1}. As in the pole layer, the tree stratum was also dominated by introduced species, most notably *T. grandis*, *D. regia*, and *S. siamea*, which together contributed substantially to total basal area and canopy formation.

The Importance Value Index (IVI) further confirmed the dominance of a few fast-growing, structurally important taxa across both strata. Tables 2 and 3 present the IVI components—relative density, frequency, and dominance—highlighting the pivotal ecological roles of both native and non-native species. Although several native species were present, structural composition was largely shaped by exotic trees introduced during the forest rehabilitation phase, pointing to a restoration trajectory that favors biomass recovery but may constrain long-term species heterogeneity.

These IVI values confirm the structural dominance of a few exotic species in both strata. *Tectona grandis* and *G. sepium* ranked highest in the tree and pole strata, respectively. At the same time, native species such as *D. latifolia* and *Ficus benjamina* were less structurally prominent despite their ecological value.

Dominance and ecological role of major species

The vegetation structure of the Paliyan Wildlife Reserve is characterized by the predominance of a limited number of fast-growing species, most of which are non-native. *Tectona grandis* emerged as the most dominant taxon in the tree stratum, exhibiting the highest Importance Value Index (IVI) at 129.1%. However, it was not prominent in the pole layer, where *G. sepium* and *Tamarindus indica* held the highest IVI scores (Tables 2 and 3). These patterns reflect differences in recruitment dynamics, growth strategies, and the legacy of past forest management interventions. The historical use of *T. grandis* as a timber species in production systems explains its persistence and structural dominance in the upper stratum. In contrast, the frequent occurrence of *G. sepium* and *T. indica* in the pole layer likely results from recent replanting or natural regeneration, supported by their rapid juvenile development and high ecological plasticity.

Delonix regia, another introduced species, ranked second in the tree stratum with an IVI of 74.4%. Despite having fewer individuals than *T. grandis*, its high basal area and widespread presence across regenerating plots indicate strong competitive ability. Its broad canopy and notable drought tolerance confer advantages in karst environments where soil depth and water availability are limiting.

Senna siamea was also among the dominant taxa in both strata, with IVI values of 43.5% in the tree layer and 39.4% in the pole layer. As a nitrogen-fixing legume and early successional species, it contributes not only to rapid biomass accumulation but also to soil improvement and microclimatic buffering. Its adaptability to degraded soils and ecological functions may enhance early-stage forest development, despite its non-native status.

In the pole stratum, *G. sepium* exhibited the highest IVI (82.5%), highlighting its role as a colonizer in rehabilitated areas. Commonly used in agroforestry and restoration programs, this species is favored for its rapid growth, ease of propagation, and compatibility with other crops. Its dominance in the lower canopy likely reflects high vegetative propagation success and tolerance of disturbance.

Other prominent species in the pole layer include *T. indica* and *Melia azedarach*. Although native, *T. indica* showed strong performance with an IVI of 60.4%, suggesting a capacity to ascend into the tree layer in later successional stages. In contrast, *M. azedarach*, though introduced, was relatively abundant and broadly distributed, indicating a degree of ecological compatibility with restored karst landscapes.

Among native taxa, *D. latifolia* and *C. equisetifolia* contributed moderate but ecologically meaningful values. *D. latifolia* was primarily present in the tree stratum with an IVI of 15.9%, appreciated for its dense wood and role in structural reinforcement. *C. equisetifolia*, with an IVI of 23.9%, is well-adapted to rocky soils and plays an important role in erosion control and soil stabilization.

Table 2. Importance Value Index (IVI) of tree species in Paliyan Wildlife Reserve, Yogyakarta. Indonesia

Species name	**RD (%)**	**RF (%)**	**RDo (%)**	**IVI (%)**
Tectona grandis L.f.	38.5	32.0	58.6	129.1
Delonix regia (Bojer ex Hook.) Raf.	24.0	28.0	22.4	74.4
Senna siamea (Lam.) H.S.Irwin & Barneby	14.7	16.0	12.8	43.5
Casuarina equisetifolia L.	7.3	12.0	4.6	23.9
Dalbergia latifolia Roxb.	6.7	8.0	1.2	15.9
Hibiscus tiliaceus L.	2.1	3.0	0.4	5.5
Ficus benjamina L.	1.5	3.0	0.3	4.8
Tamarindus indica L.	1.0	2.0	0.2	3.2
Melia azedarach L.	1.0	2.0	0.2	3.2
Swietenia macrophylla G.King	0.9	2.0	0.2	3.1
Pterocarpus indicus Willd.	0.8	1.0	0.2	2.0
Artocarpus heterophyllus Lam.	0.7	1.0	0.1	1.8
Ficus racemosa L.	0.5	1.0	0.1	1.6
Mangifera indica L.	0.5	1.0	0.1	1.6
Gmelina arborea Roxb. ex Sm.	0.4	1.0	0.1	1.5
Alstonia scholaris (L.) R.Br.	0.3	1.0	0.1	1.4
Schleichera oleosa (Lour.) Oken	0.2	0.5	0.05	0.75
Pterospermum javanicum Jungh.	0.2	0.5	0.05	0.75

Note: RD: Relative Density, RF: Relative Frequency, RDo: Relative Dominance, IVI: Importance Value Index

Table 3. Importance Value Index (IVI) of pole species in Paliyan Wildlife Reserve, Yogyakarta, Indonesia

Species name	**RD (%)**	**RF (%)**	**RDo (%)**	**IVI (%)**
Gliricidia sepium (Jacq.) Kunth	31.4	24.0	27.1	82.5
Tamarindus indica L.	21.8	20.0	18.6	60.4
Melia azedarach L.	16.0	18.0	14.0	48.0
Senna siamea (Lam.) H.S.Irwin & Barneby	12.3	16.0	11.1	39.4
Delonix regia (Bojer ex Hook.) Raf.	8.5	14.0	9.2	31.7
Ficus benjamina L	3.5	4.0	2.8	10.3
Ficus racemosa L.	2.5	3.0	2.0	7.5
Gmelina arborea Roxb. ex Sm.	1.8	2.5	1.5	5.8
Swietenia macrophylla G.King	1.6	2.0	1.2	4.8
Alstonia scholaris (L.) R.Br.	0.9	1.5	1.0	3.4
Schleichera oleosa (Lour.) Oken	0.8	1.0	0.8	2.6
Pterocarpus indicus Willd.	0.7	1.0	0.7	2.4
Mangifera indica L.	0.6	0.8	0.5	1.9
Artocarpus heterophyllus Lam.	0.5	0.7	0.4	1.6
Pterospermum javanicum Jungh.	0.4	0.5	0.3	1.2

Note: RD: Relative Density, RF: Relative Frequency, RDo: Relative Dominance, IVI: Importance Value Index

Conversely, many native species such as *Ficus* spp., *Alstonia scholaris*, and *Pterospermum javanicum* exhibited low structural representation. These taxa were recorded sporadically and in low numbers, suggesting suppressed regeneration or competition with more aggressive exotics. Nevertheless, their ecological functions—including providing habitat, enhancing nutrient cycling, and tolerating seasonal drought—may become increasingly important as forest succession proceeds.

Collectively, the results reveal a structurally simplified forest dominated by a narrow suite of exotic species that were either intentionally planted or facilitated through assisted regeneration. While these species contribute substantially to aboveground biomass and canopy formation, their dominance may constrain ecosystem heterogeneity and resilience in the long term. The observed pattern emphasizes the need for restoration strategies that encourage native species recruitment and promote structural complexity to ensure ecological sustainability.

Comparison between native and non-native species

The species composition in the Paliyan Wildlife Reserve is overwhelmingly dominated by non-native species, which contributed disproportionately to stand structure, individual abundance, and overall biomass. Of the 1,180 recorded individuals, 1,083 (91.78%) were non-native, while only 97 (8.22%) belonged to native species. This asymmetry reflects the historical reliance on exotic species in the restoration process, particularly during the initial reforestation phase.

In the pole stratum, non-native species accounted for 589 of 659 individuals (89.38%), while natives contributed only 70 individuals (10.62%). This imbalance was mirrored in ecological metrics, with non-natives attaining a cumulative IVI of 259.89%, compared to 40.11% for native species. Structurally, non-native poles also exhibited greater average DBH and height, indicating more rapid growth and establishment advantages.

The tree stratum showed an even more skewed distribution. Non-native trees made up 494 of 521 individuals (94.82%), and attained a combined IVI of 280.98%, compared to just 27 individuals (5.18%) and 19.02% IVI for native species. *Tectona grandis*, *D. regia*, and *S. siamea* were the dominant non-native contributors. At the same time, native species such as *C. equisetifolia* and *D. latifolia* were present in low numbers and with limited spatial occurrence.

In terms of biomass, non-native species contributed the majority of aboveground carbon across both strata. To provide clearer insight into species-level contributions, Table 4 presents dominant taxa along with total biomass values summarized by structural class. As shown in Table 4, non-native trees stored 102.36 Mg ha^{-1} of biomass, compared to 4.59 Mg ha^{-1} in native trees. In the pole stratum, non-natives contributed 27.71 Mg ha^{-1}, while natives stored only 2.11 Mg ha^{-1}.

These patterns are visualized in Figure 2, which presents a comparative analysis of native and non-native species across tree and pole strata, using three structural indicators: average DBH, total number of individuals, and Importance Value Index (IVI). Non-native species consistently outperformed native taxa across all metrics, underscoring their overwhelming structural dominance within the restored forest.

The results shown in Figure 2 confirm that non-native species, particularly in the tree stratum, dominate not only in terms of abundance but also in stem size and ecological importance. This pattern underscores the role of fast-growing exotic taxa such as *T. grandis* and *D. regia* in shaping the current forest structure. In contrast, native species—although ecologically valuable—remain underrepresented in both size and spatial distribution, especially within the tree layer. These structural imbalances reflect the legacy of past planting strategies and highlight the need for enrichment interventions that prioritize native species recruitment and promote vertical stratification.

The reliance on non-native species during rehabilitation efforts has successfully accelerated canopy development and biomass recovery. However, it has also resulted in a structurally homogeneous forest with low native species representation. This composition may pose long-term ecological risks, such as reduced habitat heterogeneity, which can lead to decreased species diversity and ecosystem stability, limited food resources for native fauna, and decreased resilience to pests, diseases, or climate fluctuations, such as increased susceptibility to invasive species or extreme weather events (Ekayanti et al. 2015).

Nevertheless, the presence of native taxa—though limited—suggests a promising potential for future recovery if active enrichment or natural regeneration is supported. Species like *D. latifolia* and *C. equisetifolia* demonstrate traits suitable for karst environments, including high wood density and drought resistance, can significantly contribute to improving ecological stability and emphasizing their role in future restoration planning, can provide a sense of reassurance, particularly in promoting functional redundancy and biodiversity conservation.

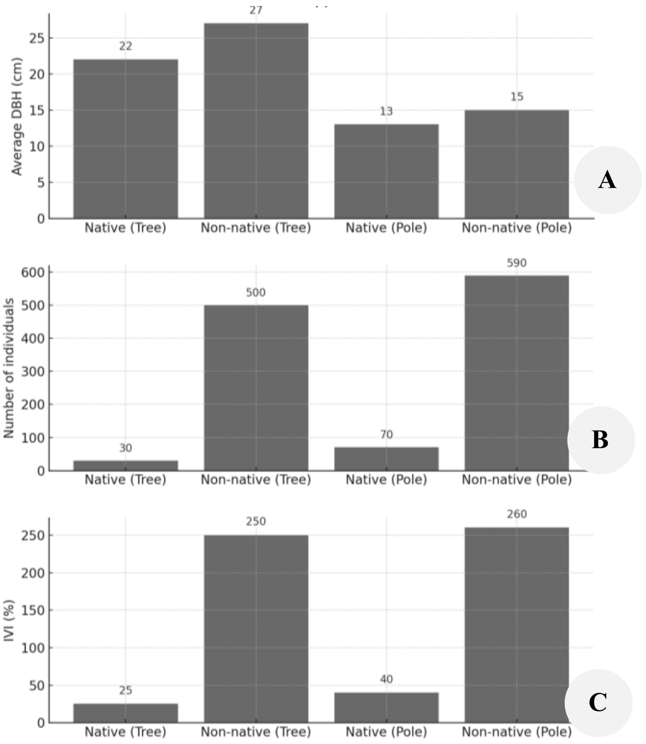

Figure 2. Comparison of native and non-native species across tree and pole strata in the Paliyan Wildlife Reserve, Yogyakarta, Indonesia, based on A. Average Diameter at Breast Height (DBH), B. Number of individuals, and C. Importance Value Index (IVI). Native species consistently exhibited lower structural dominance across all parameters compared to non-native species in both strata

Biomass estimation at tree and pole levels

The total Aboveground Biomass (AGB) in the Paliyan Wildlife Reserve was estimated at 136.77 Mg ha^{-1}, distributed across tree and pole strata. Biomass accumulation was highly skewed toward the tree stratum, which contributed 106.95 Mg ha^{-1} or 78.23% of total AGB, while the pole stratum contributed 29.82 Mg ha^{-1} or 21.77%. This pattern reflects the advanced development of tree-sized individuals in certain plots and their dominant structural role in the restored forest.

Non-native species accounted for the majority of biomass in both strata. In the tree layer, non-native species contributed 102.36 Mg ha^{-1}, while native species contributed only 4.59 Mg ha^{-1}. In the pole layer, non-natives contributed 27.71 Mg ha^{-1}, compared to 2.11 Mg ha^{-1} from native species. These differences reflect the disparity in species abundance, DBH distribution, and wood density between exotic and native taxa.

The total carbon stock, derived by applying a 0.47 conversion factor to AGB, amounted to 64.28 Mg C ha^{-1}. This translates to a total sequestration of 235.88 Mg CO_2 ha^{-1}, using the IPCC conversion ratio of 3.67. The contribution of each vegetation stratum and species origin to carbon storage and CO_2-equivalent sequestration is presented in Table 5.

These values are illustrated in Figure 3, which shows the distribution of aboveground biomass by vegetation stratum and species origin. Tree-level non-native species are the primary biomass contributors, followed by pole-level non-natives. Native species occupy a small proportion of the total biomass in both strata.

Figure 4 summarizes the conversion to CO_2-equivalent sequestration and visualizes the restored forest's total potential for mitigating atmospheric carbon. The tree stratum alone accounted for 183.39 Mg CO_2 ha^{-1}, while the pole stratum contributed 52.49 Mg CO_2 ha^{-1}. These values demonstrate the functional importance of structural development, particularly in the tree layer, for maximizing carbon sequestration services in karst ecosystems.

These results confirm that current restoration efforts—despite their strong reliance on non-native species—have successfully established a high-biomass forest with moderate-to-high carbon accumulation potential. However, long-term sustainability will depend on the forest's ability to maintain and diversify structural attributes, especially in response to environmental stressors typical of karst systems.

Table 4. Biomass contribution of dominant species by stratum and species origin

Species name	Stratum	Species origin	AGB (Mg ha^{-1})
Tectona grandis L.f.	Tree	Non-native	65.31
Delonix regia (Bojer ex Hook.) Raf.	Tree	Non-native	16.27
Senna siamea (Lam.) H.S.Irwin & Barneby	Tree	Non-native	12.85
Gliricidia sepium (Jacq.) Kunth	Pole	Non-native	9.18
Melia azedarach L.	Pole	Non-native	6.47
Tamarindus indica L.	Pole	Native	5.22
Casuarina equisetifolia L.	Tree	Native	3.62
Dalbergia latifolia Roxb.	Tree	Native	2.97
Ficus benjamina L.	Tree	Native	2.12
Others (combined)	Tree & pole	Mixed	12.76
Subtotal	Tree	Non-native	102.36
	Tree	Native	4.59
	Pole	Non-native	27.71
	Pole	Native	2.11
Total	—	—	136.77

Table 5. Carbon stock and CO_2-equivalent by vegetation stratum and species origin

Stratum	Species origin	AGB (Mg ha^{-1})	Carbon stock (Mg C ha^{-1})	CO_2-eq (Mg CO_2 ha^{-1})
Tree	Non-native	102.36	48.11	176.56
Tree	Native	4.59	2.16	7.93
Pole	Non-native	27.71	13.02	47.77
Pole	Native	2.11	0.99	3.63
Total	All	136.77	64.28	235.88

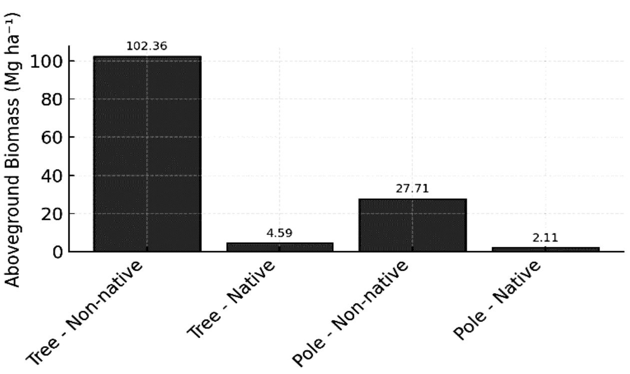

Figure 3. Distribution of aboveground biomass by stratum and species origin in Paliyan Wildlife Reserve. Yogyakarta, Indonesia

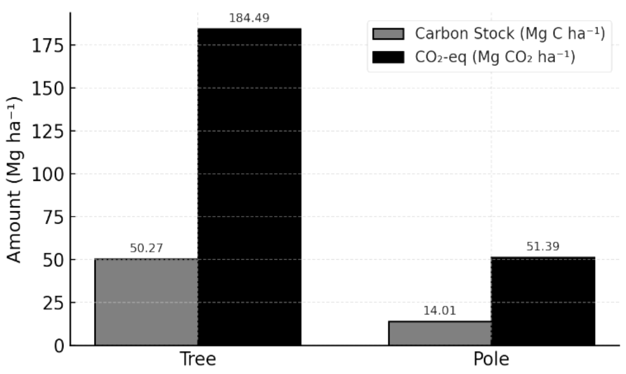

Figure 4. Total carbon stock and CO_2-equivalent by vegetation stratum in Paliyan Wildlife Reserve, Yogyakarta, Indonesia

Carbon storage and sequestration potential

The restored vegetation in the Paliyan Wildlife Reserve demonstrates moderate to high carbon storage capacity for a secondary forest in a karst ecosystem. Based on aboveground biomass estimates, the total carbon stock is 64.28 Mg C ha^{-1}, which translates to 235.88 Mg CO_2 ha^{-1}. These values are broadly comparable to other restored forests in tropical Southeast Asia and underscore the climate mitigation potential of karst reforestation efforts when supported by sustained silvicultural intervention (Indrajaya et al. 2022; Kiswanto et al. 2023).

The tree stratum accounts for the majority of this carbon reserve, with 50.27 Mg C ha^{-1}, equivalent to 183.39 Mg CO_2 ha^{-1}. The pole stratum contributes 14.01 Mg C ha^{-1}, or 52.49 Mg CO_2 ha^{-1}, highlighting the lesser but still notable role of younger or smaller trees in carbon accumulation. This stratified contribution reflects differences in DBH, height, and wood density between the two structural classes, as well as the dominance of fast-growing exotics in both strata.

Carbon storage is also highly skewed by species origin. As presented in Table 5, non-native species collectively store 61.13 Mg C ha^{-1} (223.33 Mg CO_2 ha^{-1})—constituting 95.1% of total carbon—whereas native species contribute only 3.15 Mg C ha^{-1} (11.55 Mg CO_2 ha^{-1}). This disparity mirrors the structural and numerical dominance of introduced species in the reserve. It indicates that the current sequestration potential is largely driven by a few highly productive exotic taxa, notably *T. grandis* and *D. regia*.

The stratified sequestration pattern is further illustrated in Figure 4, which visualizes the total CO_2-equivalent captured per vegetation stratum. The disproportionate contribution of the tree layer reinforces the importance of promoting vertical growth and stand maturity in restoration programs, especially in challenging karst terrain.

While the current restoration design has effectively enhanced biomass and carbon retention, it remains ecologically unbalanced due to limited native species participation. The urgency and significance of enhancing the role of native trees with high wood density—such as *D. latifolia*, *C. equisetifolia*, and *Schleichera oleosa*—cannot be overstated. This action may improve both biodiversity value and long-term carbon persistence. Native species are also more resilient to regional climatic cycles and may provide critical habitat functions not fulfilled by exotics.

The current carbon storage profile suggests strong climate mitigation potential, especially if restoration efforts are reoriented to incorporate native functional traits and improve structural heterogeneity. Such a shift would not only enhance resilience and ecosystem service delivery but also align with national and global forest restoration frameworks under the Paris Agreement and the UN Decade on Ecosystem Restoration, making our collective efforts part of a larger, impactful movement.

Species-level contributions to biomass and carbon stocks

A limited number of species, particularly fast-growing, non-native taxa, disproportionately contribute to the overall aboveground biomass and carbon storage in the Paliyan Wildlife Reserve. Species-level analysis reveals that only a few dominant species account for the majority of stored biomass and sequestered carbon, reflecting their structural prominence and functional roles within the restored karst forest.

Tectona grandis emerged as the single most important species, contributing 65.31 Mg ha^{-1} of AGB, which translates to 30.70 Mg C ha^{-1} and 112.66 Mg CO_2 ha^{-1}. This contribution alone represents nearly 47.7% of the total AGB across the landscape. Its dominance is attributed to large individual size, high wood density, and wide spatial distribution across plots.

Delonix regia and *S. siamea*, both non-native species, followed as major contributors. *D. regia* stored 16.27 Mg ha^{-1} of AGB (7.64 Mg C ha^{-1}; 28.06 Mg CO_2 ha^{-1}), while *S. siamea* accounted for 12.85 Mg ha^{-1} (6.04 Mg C ha^{-1}; 22.16 Mg CO_2 ha^{-1}). Together with *T. grandis*, these species accounted for more than 70% of the reserve's total carbon stock. While Table 4 emphasizes species dominance by stratum and origin, Table 6 further elaborates on the functional carbon contributions of each species, including their role in CO_2 sequestration.

Only *C. equisetifolia* and *D. latifolia* made appreciable contributions among native species. Although their shares were modest compared to exotics, they represent important ecological functions—such as drought resilience, soil stabilization, and habitat support—and are critical to long-term forest health.

These species-level contributions are also illustrated in Figure 5, which presents a comparative visualization of AGB, carbon stock, and CO_2 sequestration by dominant species. The figure highlights the steep drop-off in contribution beyond the top five species, emphasizing the monodominant nature of the current forest composition.

This finding reinforces the restored forest's structural dependency on a narrow set of non-native species. While effective in rapid biomass accumulation, such dependency could pose ecological risks related to resilience, biodiversity support, and susceptibility to pests or climate shifts. Increasing the presence of functional native species through targeted enrichment or protection of natural regeneration would be a necessary step toward ecological balance and long-term carbon stability.

Discussion

Structural dynamics of reforested karst vegetation

The structural profile of the Paliyan Wildlife Reserve, as revealed by the dominance of small- to medium-diameter stems and limited vertical stratification, reflects a forest in the early-to-intermediate stages of recovery following anthropogenic disturbance and reforestation intervention. Despite two decades of rehabilitation efforts, most individuals remain concentrated in the pole and lower tree strata, with a mean DBH of 14.95 cm for poles and 26.09 cm for trees. This structure is typical of secondary tropical forests in karst areas where soil depth, moisture availability, and rooting space are severely constrained (Eamus and Froend 2006; Kühnhammer et al. 2023).

The dominance of a few exotic species—particularly *T. grandis*, *D. regia*, and *S. siamea*—has resulted in a simplified canopy architecture. These species exhibit rapid vertical growth and competitive crown expansion, but their spatial dominance may inhibit the establishment of native species and limit vertical layering. The forest lacks the emergent stratum and complex understory layers typically found in mature tropical karst forests, such as those in southern China (Guo et al. 2017; Zeng et al. 2024) or northern Vietnam (Ngo and Hölscher 2014), where native hardwoods such as *Pistacia weinmannifolia* or *Parashorea chinensis* form intricate vertical profiles supporting diverse faunal assemblages.

Vertical structure in karst ecosystems is often shaped not only by tree age but also by microhabitat heterogeneity, soil pocket distribution, and karstic rock porosity (Clements et al. 2006). In Paliyan, limited stratification may also result from uniform planting patterns and insufficient recruitment of shade-tolerant or understory species. The observed vertical profile shows a dominance of mid-canopy trees with a sparse representation of higher and lower strata. This reduces niche availability for epiphytes, shrubs, and forest-dependent vertebrates, which are known to rely on vertical complexity for habitat and resource partitioning (Slik et al. 2013).

In terms of basal area and stem density, the values in Paliyan (ranging between 130-230 individuals ha^{-1} per stratum) are comparable to other reforested sites in tropical Southeast Asia (Chua et al. 2013; Chanlabut and Nahok 2022), but still fall short of natural old-growth karst forests, which typically exhibit stem densities >350 individuals ha^{-1} and a basal area exceeding 30 m^2 ha^{-1} (Chave et al. 2008). The relatively small mean DBH and height in both strata indicate that forest biomass accumulation is still in progress and that structural maturity has not yet been achieved.

Although pole-level contributions to stand structure remain high, these individuals represent a valuable recruitment layer for future canopy development. However, without effective thinning, enrichment, or natural mortality cycles, the current density of small stems may lead to stagnation or self-thinning without significant gains in vertical complexity or biomass.

These findings underscore the importance of monitoring forest structural attributes—not just species composition—as indicators of restoration success in karst regions. While the existing plantation has achieved moderate canopy closure and biomass recovery, it remains structurally simplified and compositionally imbalanced. Further interventions should prioritize structural enhancement through vertical stratification, recruitment of native mid-story species, and management of competitive dynamics among dominant exotic taxa.

Dominance of non-native species: Ecological trade-offs

The reliance on non-native species in the reforestation of the Paliyan Wildlife Reserve has produced rapid early-stage biomass accumulation and partial canopy closure, as evidenced by the dominance of *T. grandis*, *D. regia*, *S. siamea*, and *G. sepium*. These species contributed more than 90% of total stem count and accounted for over 95% of estimated carbon stock, underscoring their functional significance in shaping the current forest structure (Tables 4 and 6). Their use reflects a pragmatic restoration approach widely practiced in tropical regions: selecting fast-growing, drought-tolerant exotics to stabilize degraded lands and rapidly re-establish vegetation cover (Parrotta et al. 1997; Erskine et al. 2006; Cunningham et al. 2015; Pancel 2016).

However, this strategy comes with important ecological trade-offs. The overwhelming dominance of a few exotic taxa has resulted in a floristically impoverished and structurally homogeneous forest, potentially reducing habitat heterogeneity and narrowing the spectrum of ecological niches available to native flora and fauna. Such simplification may impair key ecosystem functions—including pollination, seed dispersal, and recruitment—that depend on complex native plant–animal networks (Holl and Aide 2011; Brancalion et al. 2017).

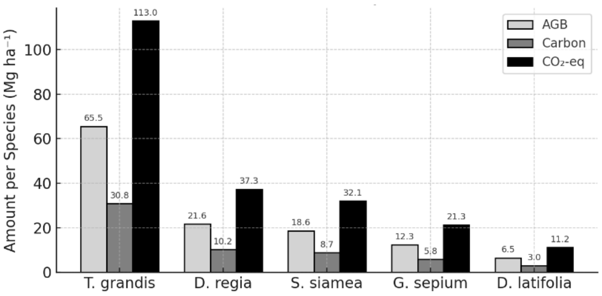

Figure 5. Species-level contribution to aboveground biomass, carbon stock, and CO$_2$ sequestration in Paliyan Wildlife Reserve, Yogyakarta, Indonesia

Table 6. Species-level contributions to aboveground biomass, carbon stock, and CO$_2$-equivalent

Species name	**Origin**	**AGB (Mg ha^{-1})**	**Carbon Stock (Mg C ha^{-1})**	**CO$_2$-eq (Mg CO$_2$ ha^{-1})**
Tectona grandis L.f.	Non-native	65.31	30.70	112.66
Delonix regia (Bojer ex Hook.) Raf.	Non-native	16.27	7.64	28.06
Senna siamea (Lam.) H.S.Irwin & Barneby	Non-native	12.85	6.04	22.16
Gliricidia sepium (Jacq.) Kunth	Non-native	9.18	4.31	15.82
Melia azedarach L.	Non-native	6.47	3.04	11.17
Tamarindus indica L.	Native	5.22	2.45	8.99
Casuarina equisetifolia L.	Native	3.62	1.70	6.24
Dalbergia latifolia Roxb.	Native	2.97	1.40	5.14
Ficus benjamina L	Native	2.12	1.00	3.67
Others (combined)	Mixed	12.76	6.00	22.97
Total	—	136.77	64.28	235.88

Several of the dominant exotic species in Paliyan, particularly *S. siamea* and *G. sepium*, are reported to exert allelopathic effects and possess aggressive root systems, which can suppress native species regeneration. Their vigorous vegetative propagation and prolific seeding capacity further contribute to the development of dense, monospecific stands that limit biodiversity recovery (Lugo 1997). These attributes, while useful for short-term soil protection, may hinder long-term ecosystem diversification and resilience.

From a carbon perspective, exotic species such as *T. grandis* function as efficient carbon sinks due to their favorable wood density and fast growth, especially under managed conditions. Yet, their long-term contribution to sequestration is contingent upon climatic stability, pest resistance, and continued stand vitality. Exotic-dominated stands—particularly in fragile substrates like karst—may be more vulnerable to abiotic stressors, including drought, fire, and pathogen outbreaks (Richardson et al. 2007; Castro et al. 2020).

Moreover, the broader goal of ecosystem multifunctionality—encompassing carbon storage, soil stabilization, hydrological regulation, and cultural services—is unlikely to be fully achieved through exotic-dominated plantings alone. Native species tend to support richer trophic webs and more complex ecological interactions, thereby enhancing the system's adaptive capacity and long-term sustainability (Benayas et al. 2009; Sayer et al. 2013).

Thus, while non-native species have functioned effectively as pioneer colonizers, their continued dominance may jeopardize the ecological integrity and multifunctional potential of the restored forest. Future restoration strategies should prioritize gradual transition toward diverse, native-enriched assemblages, integrating assisted enrichment, selective thinning, and facilitation of natural regeneration to steer ecosystem development toward structurally complex and ecologically resilient forest systems.

Vegetation structure as a driver of carbon sequestration

The distribution and magnitude of aboveground carbon stocks in the Paliyan Wildlife Reserve are closely linked to structural parameters of vegetation, DBH, total height, and basal area. These attributes not only reflect individual tree biomass but also determine stand-level carbon accumulation across successional stages. The analysis confirms that individuals with larger DBH and greater height disproportionately contribute to aboveground biomass and carbon reserves, a trend consistent with findings in other tropical forest systems (Slik et al. 2013; Chave et al. 2014).

Structurally dominant species—particularly *T. grandis*, *D. regia*, and *S. siamea*—play an outsized role in carbon storage despite limited species diversity. For instance, *T. grandis* alone contributed nearly 48% of total aboveground biomass, owing to its superior DBH range and high wood density. This pattern reflects a functional concentration of carbon storage capacity in a small subset of fast-growing, high-biomass species. Similar phenomena have been documented in reforested sites where a few high-performing taxa act as biomass anchors, driving carbon accumulation far beyond what would be predicted by species richness alone (Jensen et al. 2021).

This structural bias has important implications for carbon-oriented forest restoration. Forests with a higher proportion of large-diameter individuals store substantially more carbon, making the protection and promotion of such individuals essential for maximizing sequestration. Yet in karst environments, where soil depth, water availability, and rooting space are limited, the development of large trees is inherently restricted. Thus, species selection and spatial planning become critical determinants of biomass potential (Pérez-Cordero and Kanninen 2003).

The strong correlation between DBH and carbon stock underscores the importance of managing for stem growth and longevity. Strategies should emphasize long-lived species with favorable allometric traits, while minimizing disturbance and avoiding premature harvesting. In contrast, species with low wood density, short life cycles, or small maximum diameters—even if present in high densities—may contribute little to long-term carbon reserves.

Moreover, spatial heterogeneity in karst systems further complicates carbon accounting. Vegetation growth is often patchy due to shallow soil pockets and uneven microtopography, which constrain root development and tree stature. Accurate stand-level carbon estimates therefore require plot-based assessments that account for structural variability and species-specific biomass equations, reinforcing the need for spatially explicit, species-sensitive restoration design.

Ultimately, the vegetation structure observed in Paliyan offers a dual message: first, targeted planting of structurally dominant species can accelerate early-stage carbon accumulation in degraded karst forests; second, such accumulation may be ecologically precarious unless accompanied by species diversity and adaptive structural complexity. Forest managers must balance short-term carbon objectives with long-term goals of ecological functionality, biodiversity conservation, and resilience to environmental change.

Contribution of native species to ecosystem stability

Although native species contributed less than 10% of the total individual count and stored only 3.15 Mg C ha^{-1} (or 11.55 Mg CO_2 ha^{-1}) across strata (Table 5), their ecological role in supporting long-term ecosystem stability far exceeds their numerical and biomass representation. Native taxa such as *D. latifolia*, *C. equisetifolia*, *T. indica*, and *Ficus* spp. provide essential structural, hydrological, and trophic functions that are poorly replicated by exotic species.

Unlike many introduced trees, native species possess morphological and physiological adaptations finely tuned to the harsh edaphic conditions of karst ecosystems—including shallow, discontinuous soils, fractured limestone bedrock, and high evapotranspiration rates. *Casuarina equisetifolia*, for instance, thrives in nutrient-poor substrates and plays a significant role in stabilizing slopes and preventing erosion, while *D. latifolia*, with its dense and durable wood, contributes to long-term carbon retention and structural resilience (Eamus and Froend 2006).

These native species also enhance biodiversity conservation by providing critical resources such as fruit, nectar, and nesting substrates. For example, fruit-bearing *Ficus* trees act as keystone species that sustain frugivorous birds and mammals during periods of seasonal scarcity (Shanahan et al. 2001; Mulyani et al. 2021; Hendrayana et al. 2022). In contrast, exotic species such as *D. regia* and *S. siamea* often lack co-evolved relationships with native fauna, limiting their contribution to ecosystem complexity and trophic connectivity (Holl and Aide 2011).

Strategically incorporating native species into restoration trajectories is thus imperative for restoring functional integrity. This includes enrichment planting in canopy openings, protecting naturally regenerating seedlings, and prioritizing propagation of locally adapted genotypes. While native species may not match exotics in short-term biomass gain, their contribution to ecosystem resilience, nutrient cycling, and successional dynamics becomes increasingly valuable over time (Benayas et al. 2009; Brancalion et al. 2017).

Moreover, native species offer important safeguards against climate uncertainty. Their long evolutionary history in the region equips them with tolerance to local stressors such as periodic drought, fluctuating light regimes, and endemic pests and diseases. As climate variability intensifies, these inherent adaptive traits become central to ensuring restoration outcomes are robust and enduring (Suding et al. 2004; Thinkampheang et al. 2024).

Therefore, while exotic species may serve as initial facilitators of canopy closure and carbon input, native species must form the foundation of long-term ecosystem persistence. Achieving this requires a shift from purely biomass-centric metrics toward function-oriented indicators that reflect ecological stability, biotic interactions, and regenerative capacity. In karst ecosystems, where environmental constraints are acute, this balance is especially crucial to restoring not only carbon stocks but also the ecological identity embedded in native plant assemblages.

Implications for biodiversity and restoration policy in karst regions

The results of this study have direct relevance for restoration policy in karst landscapes, which are ecologically sensitive yet often marginalized in national land-use planning. Although reforestation in the Paliyan Wildlife Reserve has achieved considerable biomass recovery and carbon sequestration, the observed low structural complexity and dominance of non-native species suggest limited support for ecological processes and native biodiversity. These findings underscore the need for restoration strategies that prioritize not only biomass accumulation but also long-term ecological integrity, particularly in environmentally constrained karst systems where recovery trajectories are inherently variable and site-specific (Clements et al. 2006; Eamus and Froend 2006).

Restoration in karst regions should move beyond standardized plantation paradigms and adopt biodiversity-centered frameworks that emphasize native species inclusion, structural layering, and microhabitat diversification. Integrating functionally diverse native trees into enrichment schemes and maintaining heterogeneous landscape mosaics can enhance system resilience, ecological connectivity, and adaptive capacity. Such approaches are demonstrably more effective than exotic monocultures in sustaining ecosystem services like pollination, hydrological buffering, nutrient cycling, and resistance to biotic or climatic stressors (Holl and Aide 2011; Sayer et al. 2013; Brancalion et al. 2017).

These recommendations are in alignment with both global and national restoration mandates, including the UN Decade on Ecosystem Restoration (2021-2030), Indonesia's National Biodiversity Strategy and Action Plan (NBSAP), and REDD+ frameworks that promote synergies between carbon sequestration and biodiversity conservation. To meet these objectives, restoration policies must explicitly recognize karst landscapes as priority zones—not only for their carbon potential but also for their role as refugia of endemic biodiversity and ecosystem services.

By highlighting the functional outcomes and trade-offs of current reforestation practices, this study contributes empirical insights that can inform more adaptive, inclusive, and ecologically grounded restoration planning. Karst ecosystems demand context-sensitive management—balancing early carbon gains with the restoration of long-term ecosystem functionality, structural complexity, and biological heritage.

In conclusion, this study assessed the structure, biomass, and carbon stock of reforested vegetation in the Paliyan Wildlife Reserve, a karst landscape in southern Yogyakarta. The results show that while aboveground biomass and carbon sequestration have reached moderate levels—136.77 Mg ha^{-1} AGB and 235.88 Mg CO$_2$ ha^{-1}—the vegetation structure remains simplified and heavily dominated by non-native species. The tree stratum contributed nearly 80% of total carbon stock, with a few fast-growing exotics accounting for over 90% of ecosystem-level storage. Although these species accelerated early restoration success, their dominance has limited native species regeneration, reduced vertical complexity, and constrained long-term ecological resilience. The low representation of native trees—despite their vital ecological functions—underscores the need to shift restoration strategies toward structurally diverse, native-enriched, and functionally adaptive systems. These findings support restoration policies aligned with the UN Decade on Ecosystem Restoration, Indonesia's NBSAP, and REDD+ co-benefit frameworks, which recognize karst forests not only for climate mitigation but also for sustaining ecological and cultural resilience.

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