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Twenty-nine years of forest recovery following selective logging as evidenced by a two-census resurvey in lowland Leuser Sumatra Indonesia

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[2]Department of Biology, Faculty of Mathematics and Natural Science, Universitas Syiah Kuala. Jl. Syech Abdurrauf No.3, Kopelma Darussalam, Banda Aceh 23111, Indonesia. Tel.: +62-651-8012505, ♥email: syaukani@usk.ac.id
[3]Department of Biology Education, Faculty of Teacher Training and Education, Universitas Syiah Kuala. Jl. Tgk. Hasan Krueng Kalee, Banda Aceh 23111, Aceh, Indonesia
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Abstract. *Iqbar I, Djufri D, Darusman D, Syaukani S. 2026. Twenty-nine years of forest recovery following selective logging as evidenced by a two-census resurvey in lowland Leuser Sumatra Indonesia. Asian J For 10 (1): r100124. https://doi.org/10.13057/asianjfor/r100124.* Secondary forests are increasingly common across tropical regions following selective logging, yet long-term evidence of their successional dynamics remains limited, particularly in lowland dipterocarp forests of Sumatra. This study examines changes in tree species composition and stand structure based on a two-census resurvey conducted six years (2000) and twenty-nine years (2022) after logging in two permanent sample plots (0.5 ha total) at the Soraya Research Station, Leuser Ecosystem, Indonesia. Floristic composition, species dominance, diversity, and structural attributes were analysed using the Importance Value Index (IVI), Shannon diversity, and diameter and height distributions. Tree density increased from 602 to 704 individuals ha^{-1} over the 23-year interval, while species richness declined slightly from 95 to 88 species. A total of 142 species were recorded across both censuses, with only 14 species shared, indicating high species turnover within a limited sampling area. Shannon diversity decreased marginally (3.9 to 3.7), while evenness remained consistently high (0.84-0.83). Floristic similarity between censuses was low (Sørensen = 15.2%). Diameter distribution in the 29-year forest displayed an inverted J-shape, reflecting ongoing recruitment, although large-diameter trees remained scarce. These results indicate that structural recovery is progressing, whereas species composition continues to shift. The increasing importance of dipterocarp species suggests progression towards later successional stages, although compositional stabilization has not yet been achieved. This study underscores the importance of long-term resurvey data for understanding recovery processes in selectively logged tropical forests.

Keywords: DBH structure, floristic composition, forest succession, Importance Value Index, Leuser Ecosystem

INTRODUCTION

Unsustainable forest exploitation (particularly selective logging and the conversion of forests to agriculture or other land uses) has driven a profound transformation of tropical forest landscapes over the past several decades. Primary forests, once dominant across much of the tropics, have been extensively degraded or replaced, leaving a mosaic of secondary forests at various stages of recovery that underscores the scale and persistence of anthropogenic disturbance (Chazdon 2014; Aryapratama and Pauliuk 2022; Qin et al. 2024). Consequently, secondary forests now constitute a substantial proportion of tropical forest cover and are increasingly recognised as critical components of global conservation strategies.

Despite their historical classification as degraded ecosystems, secondary forests possess considerable ecological value. They contribute significantly to biodiversity conservation by providing habitat for a wide range of species, including those that persist in altered environments. Moreover, they play a vital role in carbon sequestration, often exhibiting rapid biomass accumulation during early stages of regrowth (Barlow et al. 2007; Poorter et al. 2016). In addition, secondary forests serve as natural laboratories for understanding ecological resilience and the processes underpinning ecosystem recovery (Indrajaya et al. 2022; Marwa et al. 2024; Souza Oliveira et al. 2025). When protected from further disturbance, these forests can progressively regain structural complexity and, in some cases, approach the composition and function of old-growth systems, although this recovery is often incomplete and context-dependent (Chazdon 2014; Pain et al. 2021; Reygadas et al. 2023; Bourgoin et al. 2024).

Forest recovery following disturbance is governed by ecological succession, a dynamic process characterised by temporal shifts in species composition, dominance patterns, and vertical stratification. Succession is a response to interacting drivers, including site availability, species availability, and species performance (Pickett et al. 1987).

These processes shape the trajectory and rate of recovery, yielding diverse outcomes across landscapes. Successional pathways are rarely linear and are shaped by disturbance intensity, soil properties (edaphic factors), microclimatic conditions, and landscape connectivity (Hermosilla et al. 2026; Mondragón-Valencia et al. 2026). Consequently, secondary forests often show pronounced spatial and temporal variability in their structural and compositional development (Guariguata and Ostertag 2001; Maya-Martínez et al. 2026).

In Southeast Asia, particularly in lowland dipterocarp forests, forest recovery can be especially protracted. These ecosystems are dominated by tree species in the family Dipterocarpaceae, many of which are characterised by slow growth rates, irregular mast fruiting, and limited seed dispersal. Classical ecological studies have shown that these traits constrain the re-establishment of late-successional species after disturbance (Whitmore 1998), while more recent research reinforces the view that recovery of species composition in these forests may take several decades to centuries (Cheng et al. 2024; Marod et al. 2024). Furthermore, repeated disturbances (such as logging cycles, fire, or land encroachment) can disrupt seed dispersal networks and reduce the availability of propagules, thereby altering successional trajectories and potentially leading to arrested succession or shifts towards alternative stable states (Curran et al. 1999; Zhu et al. 2023; Alias et al. 2024).

The Soraya Research Station, located within the globally significant Leuser Ecosystem in Subulussalam, Aceh Province, Indonesia, offers an exceptional opportunity to study long-term forest recovery in a lowland dipterocarp context. This area forms part of one of the largest remaining tracts of intact tropical rainforest in Southeast Asia, recognised for its high levels of biodiversity and endemism. The forest at Soraya was selectively logged in 1993 and then left to regenerate naturally without formal restoration interventions. Initial post-logging studies reported rapid increases in stem density and species richness in the years immediately after disturbance (Sist et al. 2003), suggesting strong early recovery dynamics.

However, the longer-term trajectory of this regenerating forest remains poorly understood. While parts of the Leuser landscape experienced varying degrees of anthropogenic pressure, including illegal logging and socio-political conflict, between approximately 2000 and 2016 (WWF 2017), there is no direct evidence that the permanent sample plots used in this study were subjected to additional disturbance during that period. Therefore, these plots can reasonably be interpreted as representing relatively undisturbed secondary forest recovery, providing a rare and valuable baseline for examining successional processes over multiple decades.

Long-term ecological datasets are essential for capturing the full dynamics of forest recovery, yet such datasets remain scarce in Southeast Asia. Most existing studies have focused on short-term responses within the first decade after disturbance (Berry et al. 2008), leaving significant gaps in our understanding of later successional stages. This study addresses this limitation by presenting a two-census, multi-decadal resurvey dataset spanning approximately 23 years, from 6 to 29 years after logging. By integrating analyses of floristic composition, species dominance, and forest structure, this research provides a comprehensive assessment of recovery processes in a lowland Sumatran forest.

The primary objective of this study is to assess changes in species composition, dominance patterns, and structural attributes over time. It is hypothesised that structural recovery (such as increases in basal area, canopy height, and stand complexity) occurs more rapidly than compositional recovery, which depends on slower processes such as the dispersal and establishment of late-successional species. Consequently, the forest is expected to show increasing structural maturity alongside ongoing compositional turnover. Understanding these dynamics is crucial for informing conservation strategies, restoration planning, and sustainable forest management in tropical regions where secondary forests are becoming the dominant forest type.

MATERIALS AND METHODS

Study area and period

This study was conducted at the Soraya Research Station in Aceh Province, Indonesia, located within the Leuser Ecosystem, one of Southeast Asia's most biologically important tropical rainforest landscapes (Figure 1). The Leuser Ecosystem spans approximately 2.6 million hectares across the provinces of Aceh and North Sumatra and is internationally recognised for its exceptional biodiversity and conservation significance. It forms part of the Tropical Rainforest Heritage of Sumatra, a UNESCO World Heritage Site known for its globally important ecosystems and endemic species.

The Soraya Research Station is situated in Aceh Singkil District in the southern portion of the Leuser landscape. Managed by the Forum Konservasi Leuser in collaboration with local conservation authorities, the station functions as a field base for ecological research, biodiversity monitoring, and conservation initiatives. The surrounding forest was formerly part of a logging concession and now represents a naturally regenerating lowland dipterocarp forest following historical selective logging.

The study site lies at approximately 02°55′30″ N and 97°55′43″ E, at elevations ranging from 120 to 160 m above sea level. The climate is humid tropical with mean annual rainfall ranging from 1,969 to 2,450 mm and no distinct dry season. Mean annual temperatures range from 25.3 to 26.6°C, and average relative humidity is approximately 87%. Soils are primarily Ultisols and Inceptisols derived from sedimentary and alluvial parent materials, with slightly acidic pH (5.1-5.8) and moderate fertility. The terrain is gently undulating with slopes generally between 5% and 15%, typical of lowland dipterocarp forest landscapes.

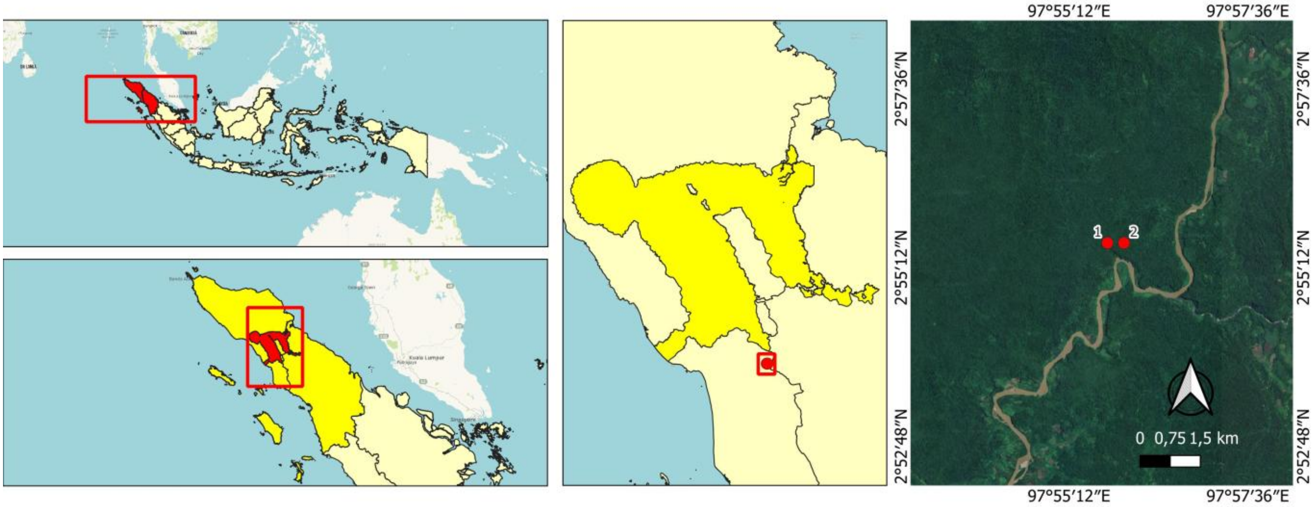

Figure 1. Map showing the location of the Soraya Research Station within the Leuser Ecosystem, Aceh Province, Indonesia, and the position of the permanent sample plots (1 and 2) used in this study

Vegetation in the area is characterised by emergent dipterocarp species such as *Shorea*, *Hopea*, *Dipterocarpus*, and *Vatica*, together with associated taxa from families including Euphorbiaceae, Moraceae, Lauraceae, and Annonaceae. The forest was selectively logged in 1993 and then allowed to regenerate naturally without silvicultural intervention. Vegetation censuses were conducted in 2000 (six years after logging) and again in 2022 (twenty-nine years after logging), providing a 23-year resurvey interval for assessing long-term successional changes.

Data collection

To evaluate long-term forest recovery, two Permanent Sample Plots (PSPs) (Figure 1), each measuring 50 × 50 m (0.25 ha), were established at the Soraya Research Station, covering a total sampled area of 0.5 ha. The plots were situated in similar lowland dipterocarp forest conditions with comparable topography and minimal recent disturbance. Each PSP was divided into twenty-five 10 × 10 m subplots to support spatially explicit sampling.

All trees with a Diameter at Breast Height (DBH) $\geq$10 cm were tagged at 1.3 m above ground, mapped, and identified to species. During the 2022 resurvey, previously tagged individuals were relocated and remeasured. Newly qualifying trees were recorded as recruits, and missing individuals were classified as dead after verification against the original census records. Plot boundaries and permanent reference points were rechecked to ensure spatial consistency between the two censuses.

Stand variables were standardised to a per-hectare basis. Tree density (individuals ha^{-1}), species richness (species ha^{-1}), and basal area ($m^2\ ha^{-1}$) were calculated from the total sampled area. Basal area (BA) for each tree was calculated as:

$$BA = \pi(DBH/2)^2$$

Where, DBH is the diameter at breast height measured in centimetres and converted to metres for the calculation, producing basal area in m² per tree. Total basal area per hectare was obtained by summing individual basal areas and scaling to one hectare.

Data analysis

Analyses focused on temporal changes in floristic composition, species dominance, diversity, stand structure, and community similarity between the 2000 and 2022 censuses. Statistical analyses were performed using PAST version 3.20 (Hammer 2018) and R version 4.3.1 (R Core Team 2023).

Species dominance was evaluated using the Importance Value Index (IVI) following Mueller-Dombois and Ellenberg (1974):

$$IVI = RD + RF + RDo$$

Where, RD is relative density, RF is relative frequency, and RDo is relative dominance based on basal area.

Tree density (D) was calculated as:

$$D = n/A \times 10{,}000$$

Where, n is the number of individuals recorded in the plot, and A is the plot area in m².

Species diversity was quantified using the Shannon-Wiener Index (H′):

$$H' = -\sum p_i \ln p_i$$

Where p_i is the proportional abundance of species i.

Species evenness (E) was calculated as:

$$E = H' / \ln S$$

Bootstrap resampling with 1,000 iterations was used to estimate 95% confidence intervals for diversity metrics.

Floristic similarity between the two censuses was measured using the Sørensen similarity coefficient:

$$S_s = (2C / (A + B)) \times 100$$

Where, A is the number of species recorded in the first census, B is the number in the second census, and C is the number of species shared between censuses.

Vertical forest structure was examined by classifying trees into three height strata: understory (<10 m), canopy (10-25 m), and emergent (>25 m). Differences in the distribution of individuals among height strata between censuses were tested using chi-square tests.

RESULTS AND DISCUSSION

Floristic composition and species dominance

Comparison of the 2000 and 2022 censuses revealed substantial changes in species dominance. Based on Importance Value Index (IVI) rankings, seven dominant species differed between the two censuses, indicating marked turnover in the dominance structure (Table 1).

In the sixth year after logging, species with the highest IVI included *Streblus elongatus*, *Phoebe grandis*, *Shorea multiflora*, and *Castanopsis javanica*, together with several light-demanding Euphorbiaceae species (Figure 2). This composition reflects early-successional forest conditions characterised by rapid recruitment and growth of pioneer and mid-successional taxa.

By the twenty-ninth year after logging, the dominance structure had shifted towards canopy and late-successional species. *Shorea multiflora* showed the highest IVI in the 2022 census, followed by *S. elongatus*. Several species absent from the early top-ten rankings emerged as important components of the community, including *Artocarpus elasticus*, *Chrysophyllum prieurii*, *Barringtonia racemosa*, and *Syzygium zeylanicum*. Although pioneer Euphorbiaceae species such as *Croton argyratus*, *Endospermum diadenum*, and *Macaranga pruinosa* remained among the dominant taxa, their relative importance declined compared with the early successional stage.

Species richness, density, and diversity

Tree density increased from 602 individuals ha^{-1} in 2000 to 704 individuals ha^{-1} in 2022, indicating ongoing recruitment and stand development during the 23-year resurvey interval (Figure 3). Species richness declined slightly from 95 species in 2000 to 88 species in 2022, while the numbers of genera (50-52) and families (28-30) remained relatively stable. Across both censuses combined, a total of 142 unique species were recorded. The Shannon-Wiener Diversity Index (H′) declined modestly from 3.9 to 3.7, and species evenness remained high (0.84 to 0.83), indicating that relative abundance among species remained broadly balanced despite compositional changes. The relative stability in the number of genera and families suggests that higher taxonomic and functional composition remained broadly consistent despite notable species turnover.

Floristic similarity and turnover

Floristic similarity between the two censuses was relatively low. The Sørensen Similarity Index was 15.2%, indicating limited overlap in species composition between early- and late-successional stages. Among the 142 species recorded in both censuses, only 14 (~10%) were present in both surveys, confirming high species turnover. The remaining species were unique to one census. Persistent taxa included *S. elongatus*, *S. multiflora*, *Artocarpus kemando*, and *M. pruinosa*. These species represent a mixture of pioneer, mid-successional, and late-successional functional groups, suggesting that some taxa persist throughout multiple stages of forest recovery.

Structural attributes of the forest

Diameter-class distributions showed clear structural development between the sixth and twenty-ninth years after selective logging. In the six-year-old forest, stem density was highest in the 10-20 cm DBH class, accounting for approximately 65% of all stems, with progressively fewer individuals in larger diameter classes.

By the twenty-ninth year, the forest displayed a typical inverted J-shaped diameter distribution, with 58.2% of stems in the 10-20 cm class, 28.8% in the 20-30 cm class, and 13.0% of individuals with DBH ≥30 cm (Figure 4). This increase in medium- and large-diameter trees indicates continued stand development and the gradual formation of larger cohorts.

Table 1. Dominant species ranked by IVI in 2000 and 2022

2000 (6th year)	**Family**	**IVI**	**2022 (29th year)**	**Family**	**IVI**
Streblus elongatus (Miq.) Corner	Moraceae	29.31	*Shorea multiflora* (Burck) Symington	Dipterocarpaceae	65.91
Phoebe grandis (Nees) Merr.	Lauraceae	16.62	*Streblus elongatus* (Miq.) Corner	Moraceae	54.82
Shorea multiflora (Burck) Symington	Dipterocarpaceae	16.53	*Croton argyratus* Blume	Euphorbiaceae	16.53
Artocarpus kemando Miq.	Moraceae	12.74	*Artocarpus kemando* Miq.	Moraceae	13.34
Castanopsis javanica (Blume) A.DC.	Fagaceae	11.85	*Chrysophyllum prieurii* A.DC.	Sapotaceae	8.95
Chisocheton sp.	Meliaceae	11.06	*Artocarpus elasticus* Reinw. ex Blume	Moraceae	8.56
Blumeodendron tokbraii (Blume) Kurz	Euphorbiaceae	8.97	*Barringtonia racemosa* (L.) Spreng.	Lecythidaceae	6.77
Macaranga diepenhorstii (Miq.) Müll.Arg.	Euphorbiaceae	8.39	*Macaranga pruinosa* (Miq.) Müll.Arg.	Euphorbiaceae	6.28
-	-	-	*Endospermum diadenum* (Miq.) Airy Shaw	Euphorbiaceae	5.29
-	-	-	*Syzygium zeylanicum* (L.) DC.	Myrtaceae	4.91

Note: IVI values are presented to two decimal places. Dashes (-) indicate that no additional species were ranked within the top ten for that census

Vertical stratification was evident in both censuses. In the early survey, most individuals were concentrated in the understory (<10 m). By 2022, although the majority of trees remained within the understory and canopy layers (10-25 m), the number of emergent trees (>25 m) had increased slightly, reflecting the gradual recruitment of canopy-forming species.

Overall, the comparison of the two censuses indicates progressive structural development, including increased representation of medium- and large-diameter trees and clearer vertical stratification. However, the relatively small proportion of very large trees (>50 cm DBH) suggests that the forest has not yet reached full structural maturity, consistent with its intermediate successional stage.

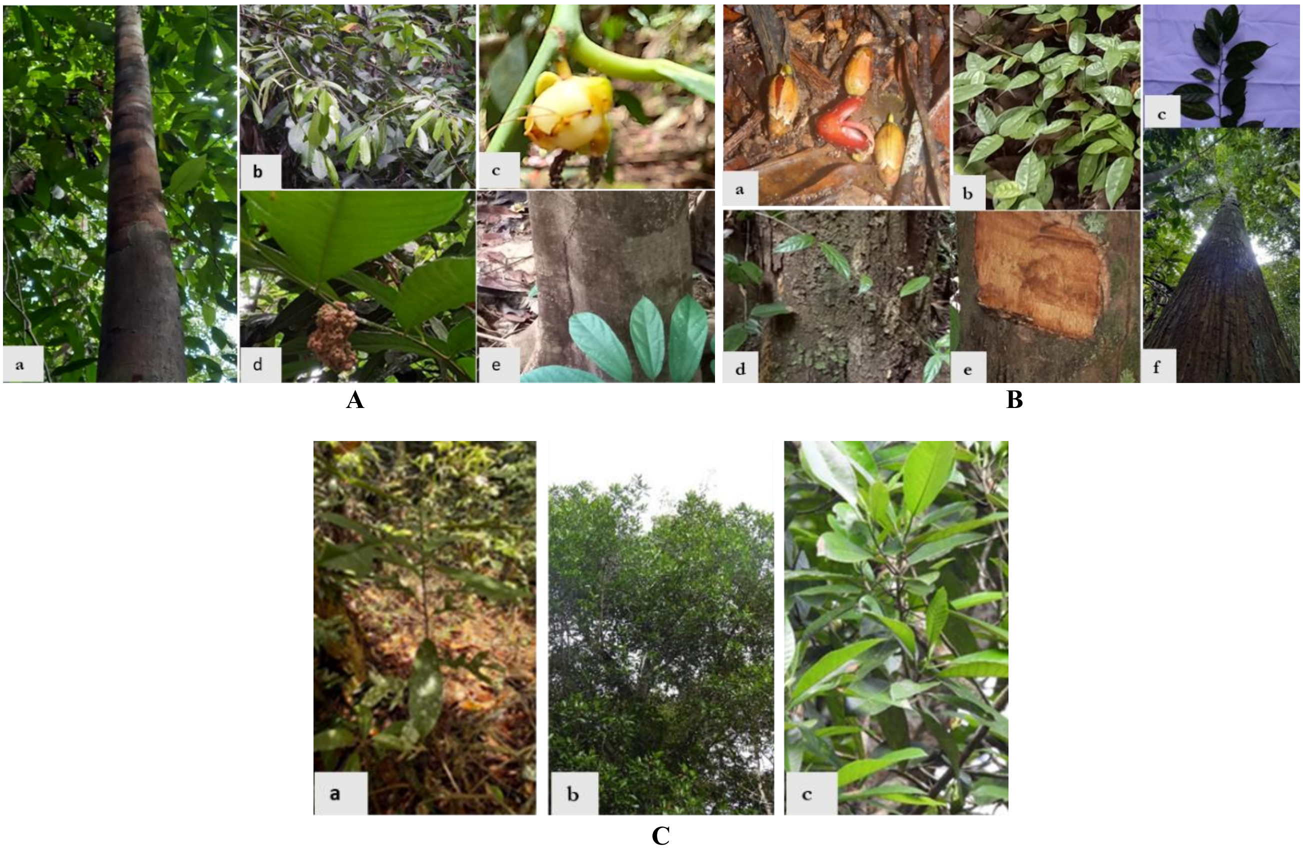

Figure 2. Tree species recorded in both the 6-year and 29-year censuses at Soraya Research Station. A. *Streblus elongatus*: a. Mature stem, b. Leaves, c. Flower, d. Inflorescence, e. Base of stem; B. *Shorea multiflora*: a. Fruits, b. Seedling, c. Mature leaves, d. Base of stem, e. Bark, f. Mature tree; C. *Artocarpus kemando*: a. Seedling, b. Mature canopy, c. Leaves

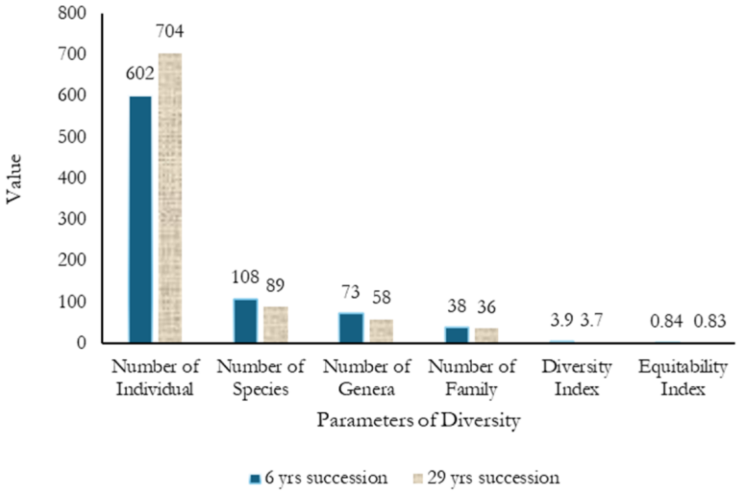

Figure 3. Changes in stand characteristics from the sixth to the twenty-ninth year after selective logging at Soraya Research Station, including tree density (individuals per hectare), species richness, number of genera, and number of families

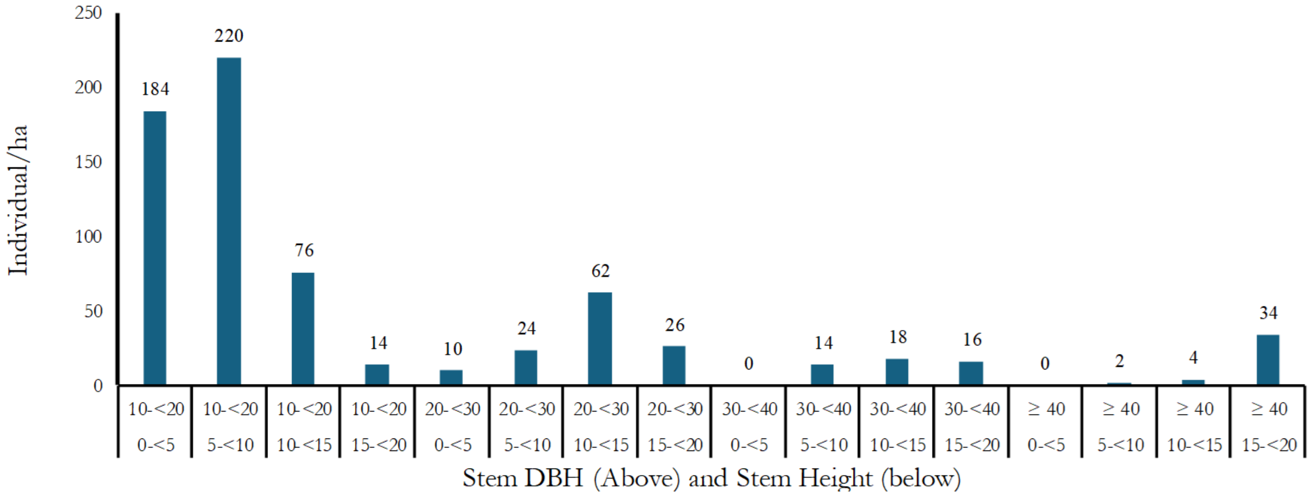

Figure 4. Distribution of tree stems by Diameter at Breast Height (DBH, cm) and height (m) classes in the 29-year-old secondary forest at Soraya Research Station

Discussion

Successional changes in species dominance

The marked replacement of dominant species between the 6th and 29th years after selective logging shows a clear reorganisation of the dominance hierarchy during secondary forest succession at Soraya Research Station. The Importance Value Index (IVI) results indicate a shift from early dominance of light-demanding and mid-successional taxa, particularly members of Euphorbiaceae and Moraceae, to increasing dominance of dipterocarps and other shade-tolerant canopy species. The significant rise in the IVI of *S. multiflora* reflects its growing contribution to stand structure and canopy formation during later successional stages.

Such shifts in dominance correspond with successional trajectories observed in lowland dipterocarp forests in Southeast Asia, where late-successional species gradually increase in importance following canopy closure after selective logging (Hu et al. 2022; Poorter et al. 2023). However, the continued presence of several pioneer and light-demanding species among the dominant taxa at year 29 indicates that competitive replacement remains incomplete. This persistence suggests spatial heterogeneity in recovery conditions within the plots and emphasises that dominance reorganisation in secondary forests can persist over several decades.

Floristic turnover and community reassembly

The low Sørensen similarity between the two censuses (15.2%) indicates considerable species turnover during the 23-year resurvey interval. Only a small proportion of species persisted across both surveys, demonstrating that community composition remains highly dynamic. High turnover during secondary succession is commonly observed in tropical forests and reflects the combined effects of species colonisation, local extinction, and differential recruitment.

In the Soraya forest, early-successional species were gradually replaced or supplemented by later-successional taxa, resulting in substantial compositional change. These dynamics suggest that community reassembly is still in progress. Similar patterns have been reported in other Southeast Asian secondary forests, where floristic convergence toward primary forest composition can require several decades or longer.

Although overall species turnover was high, several taxa persisted across both surveys and contributed significantly to stand structure. Species such as *S. elongatus*, *S. multiflora*, and *A. kemando* remained important components of the forest community. Persistent species may play key ecological roles during succession by contributing to canopy formation, stabilising stand structure, and facilitating recruitment of additional shade-tolerant species.

Structural development of the regenerating forest

Structural attributes of the Soraya forest demonstrate clear but incomplete recovery following selective logging. The inverted J-shaped diameter distribution observed in the twenty-ninth year is typical of regenerating tropical forests and reflects continuous recruitment of small-diameter individuals combined with the gradual growth of larger trees. The increasing proportion of trees in medium diameter classes indicates that individuals established during earlier successional stages are progressively maturing.

Vertical stratification also became more apparent between censuses. Although most individuals remain within the understory and canopy layers, the number of emergent trees increased slightly over time. These changes indicate the gradual development of vertical complexity, which is an important characteristic of mature tropical forest structure.

Despite this progress, the relatively low abundance of very large trees suggests that the forest has not yet reached structural maturity. The development of large emergent trees is one of the slowest components of tropical forest recovery, particularly in dipterocarp-dominated ecosystems where individual trees may require many decades to reach large diameters.

Implications for forest recovery in the Leuser ecosystem

The results of this study indicate that the Soraya secondary forest remains in an intermediate stage of succession nearly three decades after selective logging. Although stand structure has developed considerably and canopy-forming species are increasing in importance, species composition continues to change, and floristic stability has not yet been reached.

The gradual increase in dipterocarp dominance suggests that, under conditions of protection and minimal disturbance, selectively logged forests retain significant potential for long-term ecological recovery. This finding highlights the conservation value of secondary forests within the Leuser Ecosystem, particularly as large areas of primary forest across Southeast Asia continue to decline. Maintaining effective protection and long-term ecological monitoring will therefore be essential for supporting forest regeneration and understanding the long-term dynamics of secondary forests in the region.

In conclusion, nearly three decades after selective logging, the Soraya secondary forest exhibits clear structural development but remains compositionally dynamic. Changes in dominant species and low floristic similarity between censuses indicate that community reassembly is ongoing rather than stable. While the increasing importance of dipterocarps suggests progression towards later successional stages, the limited presence of large trees shows that full structural maturity has not yet been achieved. These findings highlight the long timescales required for recovery in lowland dipterocarp forests and emphasise the importance of ongoing protection and long-term monitoring within the Leuser Ecosystem, without implying convergence towards primary forest conditions.

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