

Differences in the vegetation dynamic patterns of three tropical secondary forests in South Sulawesi, Indonesia

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Abstract. Putra PS, Yamada T, Achmad A, Nasri N, Hamzah AS, Ngakan PO. 2023. Differences in the vegetation dynamic patterns of three tropical secondary forests in South Sulawesi, Indonesia. *Biodiversitas* 24: 5065-5073. Degraded forests experience dynamics that drive them towards stable ecological conditions as a result of the succession process. Understanding the dynamics of forests through succession is a requirement for secondary forest management activities. The purpose of this research was to uncover the dynamics of population, species composition, and dominance in three secondary tropical forest communities: (i) Karst forest, (ii) Lowland forest, and (iii) *Pinus merkusii* plantation forest. Permanent plots with areas tailored to the richness of each forest community were constructed, and vegetation studies were conducted annually from 2019 to 2022. The results revealed that the ten most dominant species in each plot shared only one species. The rest were exclusive to a single community. During the four years of research, 25 out of a total of 90 species (Karst), 27 out of a total of 68 species (Lowland), and 12 out of a total of 43 species (Pine) experienced dynamics in the form of an increase or decrease in population. Tree density decreased in the Karst plot and fluctuated slightly in the Lowland and Pine forest plots. Meanwhile, the basal area cover continued to increase during the 4 years of observation. Comparing age and pre-succession land use history, soil type and restoration history appear dominant in determining the forest dynamics.

Keywords: Basal area, population, species composition, succession, tree density

INTRODUCTION

Most of the world's forest ecosystems have suffered anthropogenic disturbance (Barlow et al. 2016; De Lima et al. 2020) that causes changes in species composition and structure. The impact can last long, depending on the disturbance's severity and the forest ecosystem type (Verburg et al. 2001). For example, logging on a small scale may cause only localized damage and result in a small gap in the forest stand (Asner et al. 2004). If the gaps are not too large, forest patches can quickly regenerate through secondary succession, and the original vegetation can recover. Reforestation frequently takes a long period in more extreme cases of deforestation, such as deforestation caused by fire, clear-cutting, or clear-cutting followed by burning, as is common in shifting farming (Thong et al. 2020; Kusuma et al. 2023).

Tropical rainforests, home to world diversity, have been threatened for the last several decades by the significant growth in population (Oko and Odey 2022). In the Far East tropics, tropical rainforests cover most of the Indonesian archipelago. As in other parts of the tropics, tropical rainforests in Indonesia also experience anthropogenic disturbances in many ways, which cause forest degradation and even deforestation due to the conversion of forest land to agricultural land (Rahajoe et al. 2014; Gunawan et al. 2022). The conversion of forest area to agricultural land

may have altered the forest's role. Nonetheless, degraded forest function can be recovered naturally or artificially. As a result, understanding the potential succession rates of degraded and deforested forest areas is becoming increasingly relevant.

The process of natural succession in different forests may not work all the same. In the process, each degraded forest type undergoes a series of complex mechanisms, such as the presence of dormant seeds in the soil, seed dispersal, environmental conditions suitable for seed germination, and seed growth (Finch-Savage and Footitt 2017; Anju et al. 2022). Throughout this process, the seral community is replaced by other seral communities until a stable community is reached (Connell and Slatyer 1977). However, forests that require a long recovery process due to severe damage possibly develop into forests with different species composition and vegetation structure than the previous (Sutomo et al. 2011). The forest biotic component changes can also cause changes in soil properties, groundwater, carbon sequestration rate, and interactions between these components, affecting forest function (Stanturf et al. 2014; Pérez-Hernández and Gavilán 2021).

Many impacts of anthropogenic disturbance on tropical forest ecosystems have been studied; for example, Bhatt (2022), the impact on forest vegetation; Cardelús et al. (2020), the impact on forest soil; Chen et al. (2020), the impact on soil faunas, and Pyles et al. (2022), the impact on

carbon stock and sequencing. However, studies on the ability of tropical forests to recover following disturbances are lacking and have not been thoroughly studied. In recent decades, various secondary forest landscapes caused by anthropogenic disturbances have formed in the South Sulawesi region. The estimated secondary forest area in South Sulawesi is 840.3 thousand ha (Ministry of Environment and Forestry of the Republic of Indonesia 2019). Tropical forests have several uses and functions, including producing timber and non-timber products, environmental services (hydrology, climate, and ecotourism), as well as biodiversity and germplasm conservation areas (Sasaki et al. 2016; Shimamoto et al. 2018; Nations 2019). Therefore, a better understanding of the recovery processes of various tropical secondary forests after anthropogenic disturbance is needed.

In this study, we monitored vegetation dynamics over four years in three secondary forest community types. We evaluated natality newcomer hereafter: the individual that newly recorded as tree reach diameter ≥ 5 cm, mortality and diameter growth for every individual of each species composing each forest type that causes changes in the community structure and species composition of the forests. Because the secondary forests studied have different habitat characteristics, species composition, age, and restoration history, we predict that the succession rate in each forest community will be different, as indicated by differences in species composition and forest structure. The study is expected to provide a better understanding of how the dynamic of the succession process occurs in the three forest communities and this is a basic consideration of whether artificial restoration is efficiently and effectively

needed for forest recovery in these three types of forest communities.

MATERIALS AND METHODS

Study site

We conducted this research in three different secondary forest communities in the southern part of Sulawesi Island, Indonesia, as follows: (i) Karst forest (a 48-year-old secondary forest growing on shallow soil in a limestone habitat), (ii) Lowland forest (57-year-old ex-sifting cultivation area), and (iii) Pine forest (61-year-old *Pinus merkusii* Jungh. et de Vriese plantation forest) (Figure 1, Putra et al. 2023). We chose the three forest communities as study sites to evaluate as much variety as possible in successional determinants such as age, pre-succession history, restoration/reforestation history, soil type, and altitude (Table 1). The age of each forest and its land use history was determined based on information from the local people as the time since the last disturbance. The three forest communities had the same climate type (C-type) (Schmidt and Ferguson 1951). The mean annual rainfall in the three forest communities was 273.25 mm, and this climate type was characterized by a distinct dry season (monthly rainfall < 60 mm) and wet season (monthly rainfall > 100 mm) yearly. Initially, Karst forests were primary karst forest ecosystems that grew on shallow soil above limestone ramparts, while Lowland forests and Pine forests were primary lowland monsoon forest ecosystems.

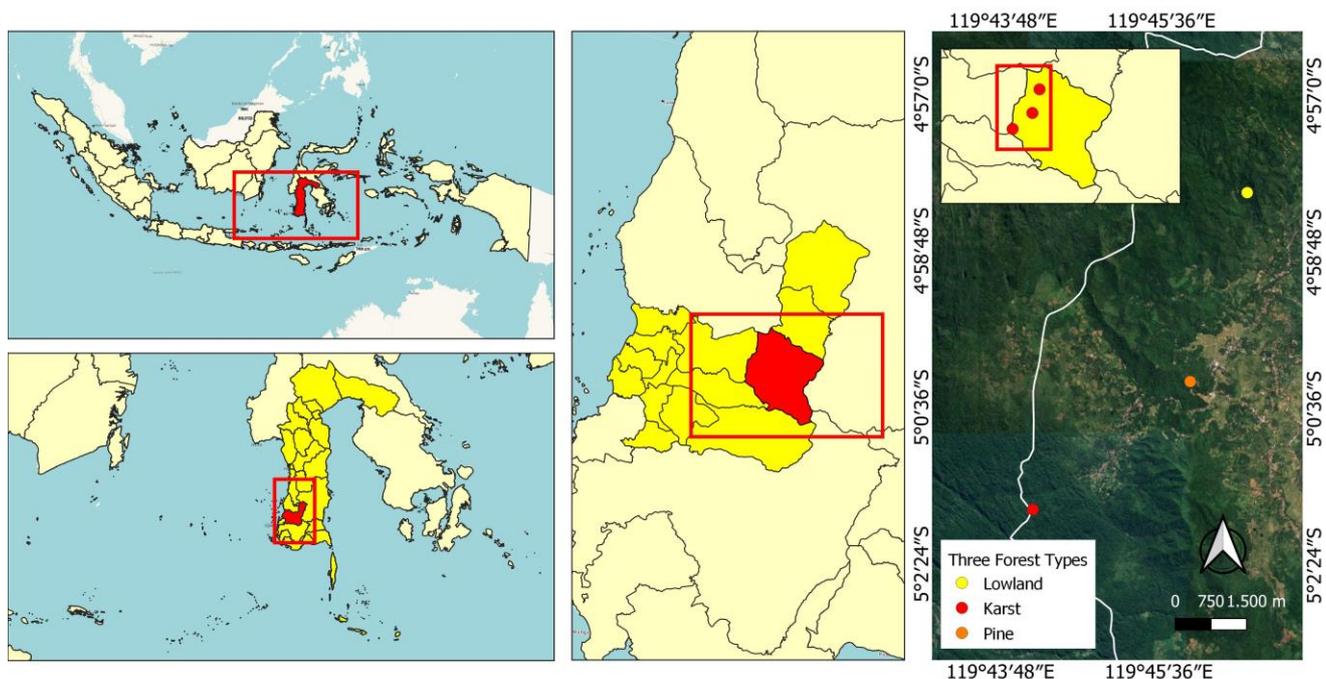


Figure 1. Map showing the locations of the three forest types studied

Vegetation analyses

Since 2019, we have set up a permanent plot in each studied forest community to measure the annual dynamics of forest structure and species composition. Plot sizes varied by forest community: 0.75 ha (50 m × 150 m) in the Karst forest, 1.00 ha (100 m × 100 m) in the Lowland forest, and 0.4 ha (50 m × 80 m) in the Pine forest. Determination of plot area is based on the nested plot technique method (Mueller-Dombois and Ellenberg 1974), where an increase in plot area no longer means an increase in the number of species included in the plot. Each permanent plot was made in a flat distance (flat projection) using a theodolite. To create a flat projection permanent plot, we first determined the point X_0Y_0 at the top-left of a slope (Figure 2). Next, an upper side plot line (Y_0 line, green line) was drawn from point X_0Y_0 to the right, following the contour line to the top right endpoint of the plot (point X_5Y_0 in the Karst forest plot, point $X_{10}Y_0$ in the Lowland forest plot, and point X_5Y_0 in the Pine forest plot). For every 10 m distance measurement, the difference in height level between the start point and the endpoint was measured (for example from point X_0Y_0 to point X_1Y_0). The difference height measurement results were coded "+" (plus) if there was an ascent from the starting point to the ending point or vice versa with a "-" (minus) sign if there was a descent from the starting point to the ending point. In the same way, the left side outline of the plot (X_0 line, red line) was made perpendicular to Y_0 line. After the outer lines X_0 and Y_0 were formed, in the same way, lines Y_2 , Y_3 , Y_4 , Y_5 , and so on were created starting from the left side of the plot to the right. Then, lines X_2 , X_3 , X_4 , X_5 , and so on were created starting from the top side of the plot towards the bottom. In this way, a flat projection plot was formed, which was divided into sub-plots measuring 10 m × 10 m. Therefore, there were 75 sub-plots in the Karst forest, 100 in the Lowland forest, and 40 in the Pine forest.

In the first stage observation, each tree with a diameter of ≥ 5 cm found in each sub-plot was first numbered consecutively using a number tag made of aluminum plates measuring 5 cm × 8 cm with an embossed number. The name of the species was recorded, then the girth of the stem was measured at a height of 130 cm above ground level. The number tag was installed 150 cm above the ground or 20 cm above the stem where the diameter is measured.

For trees with buttresses of height more than 130 cm above the ground, diameter measurements were taken at the height of 30 cm above the top end of the buttress. The

part of the stem measured for the diameter is marked with white paint surrounding the stem, approximately 3.5 cm wide. Specimens of all tree species were taken for the herbarium. After recording the species name and measuring the diameter, the coordinates of each tree in the plots were recorded by measuring the distance from the X- and Y-axes. This coordinate data was needed to make it easier to find them in the next measurement period.

The dynamics of forest structure and species composition

Re-measurements of tree girth in each plot were recorded yearly from 2020 to 2022 to determine the dynamics of the basal area (BA) and species composition of the forest stand in the plots. The girth of dead trees was not re-measured but was recorded as dead. Trees that had just reached a diameter of ≥ 5 cm in the following year's measurement period were recorded as follows: the species' name, diameter, and their X and Y coordinates in the same manner as the first measurements. The dynamics of the BA were determined by comparing the results of measurements of the BA of living trees from year to year.

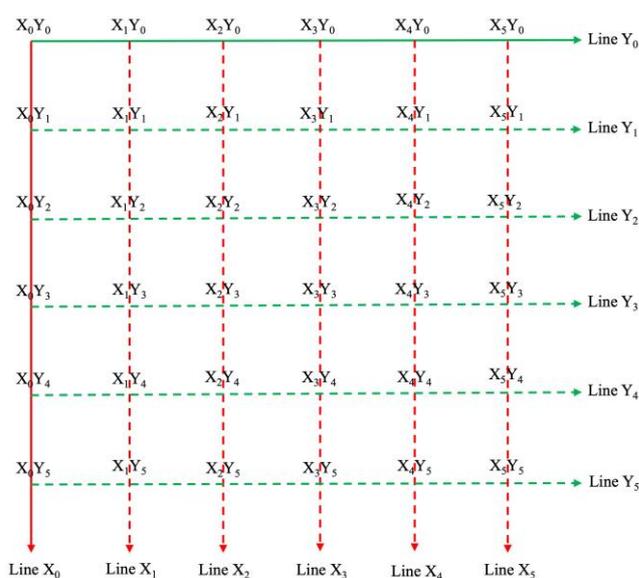


Figure 2. Sketch of the steps for setting a permanent plot

Table 1. Differences in the determinants of succession that potentially determine forest structure and species composition

Successional determinant	Forest community		
	Karst	Lowland	Pine
Age	48	57	61
Pre-succession history	Shifting cultivation	Shifting cultivation	Shifting cultivation
Restoration/reforestation history	Natural	Natural	<i>P. merkusii</i> plantation
Soil type	Rendzina with clay texture and exposed limestone rocks	Cambisol with silty clay mixed with small, medium, and large stones	Luvisol with a loamy texture
Altitude (m asl)	271	563	501

Data analysis

The data collected in this study included the density and girth of tree trunks at 130 cm above the ground. Tree trunk girth data was used to calculate the BA of individual trees in each plot (Karst, Lowland, Pine forests) using the following formula (Mueller-Dombois and Ellenberg 1974).

$$r = \frac{\sqrt{\text{Girth}}}{2\pi}$$

$$\text{BA} = \pi r^2$$

Where:

BA: basal area,

π : constant 3.14,

r: trunk finger at 130 cm above the ground.

Vegetation dynamics in each forest community were calculated by comparing the density and BA data from the first (2019), second (2020), third (2021), and fourth (2022) stages of measurement. To compare vegetation dynamics between study sites, we standardized the vegetation structure data for each plot in ha (individuals/ha for density and m²/ha for the BA).

RESULTS AND DISCUSSION

Species composition of the top ten dominant tree species in each forest

Data from year 2019 sample plot analysis showed that the number of species in plots varied across the forest communities studied. The highest number of species was found in the Karst forest plot, with 90 species; then the Lowland forest, with 61 species; and lastly, the Pine forest, with 42 species. Of the top 10 dominant species in each plot, only *Dracontomelon dao* (Blanco) Merr. & Rolfe was found in all three plots. *Diospyros celebica* Bakh. was found in two plots: in the Karst forest and the Lowland forest plots (Table 2). The most dominant species in the Karst forest plot were long-lived secondary tree species such as *Kleinhovia hospita* L., *Cananga odorata* (Lamk.) Hook, and *Pterospermum celebicum* Miq. In the Lowland forest plot, apart from two palm species (*Areca catechu* L. and *Arenga pinnata* Merr.), the other dominant species were tree species typical of the primary forest, such as *D. celebica*, *Palaquium obovatum* (Griff.) Engl., and *Mangifera longipetiolata* King. In the Pine forest plot, apart from *P. merkusii*, which dominated 86.57% of the BA, *Arthropphyllum diversifolium* Blume, a short-lived secondary tree species, and *Cinnamomum iners* Reinw. ex Blume, which can grow in open areas or under shade from another tree, was also found with a considerable BA cover value.

Table 2. Basal area of each plot's top ten dominant tree species (≥ 5 cm in diameter)

Species	Family	Basal area (m ² /ha)		
		Karst	Lowland	Pine
<i>Kleinhovia hospita</i> L.	Sterculiaceae	5.84		
<i>Cananga odorata</i> (Lamk.) Hook	Annonaceae	3.41		
<i>Pterospermum celebicum</i> Miq.	Sterculiaceae	2.06		
<i>Garcinia balica</i> Miq.	Clusiaceae	1.27		
<i>Samanea saman</i> (Jacq.) Merr.	Fabaceae	1.23		
<i>Albizia splendens</i> Miq.	Fabaceae	1.21		
<i>Cordia myxa</i> L.	Boraginaceae	1.11		
<i>Ficus racemosa</i> L.	Moraceae	0.83		
<i>Diospyros celebica</i> Bakh.	Ebenaceae	1.99	5.04	
<i>Dracontomelon dao</i> (Blanco) Merr. & Rolfe	Anacardiaceae	1.57	0.40	0.26
<i>Areca catechu</i> L.	Arecaceae		10.67	
<i>Arenga pinnata</i> Merr.	Arecaceae		6.26	
<i>Palaquium obovatum</i> (Griff.) Engl.	Sapotaceae		4.88	
<i>Mangifera longipetiolata</i> King	Anacardiaceae		2.55	
<i>Artocarpus heterophyllus</i> Lam.	Moraceae		0.84	
<i>Lansium domesticum</i> Corrêa	Meliaceae		0.67	
<i>Aleurites moluccana</i> (L.) Wild.)	Euphorbiaceae		0.79	
<i>Gymnacranthera paniculata</i> (A.DC.) Warb.	Myristicaceae		0.38	
<i>Pinus merkusii</i> Jungh. et de Vriese	Pinaceae			52.77
<i>Arthropphyllum diversifolium</i> Blume	Araliaceae			2.01
<i>Cinnamomum iners</i> Reinw. ex Blume	Lauraceae			1.65
<i>Neolitsea cassiaefolia</i> (Bl.) Merr.	Lauraceae			0.64
<i>Alstonia scholaris</i> (L.) R.Br.	Apocynaceae			0.36
<i>Schima wallichii</i> (DC.) Korth.	Theaceae			0.29
<i>Flacourtia rukam</i> Zoll. & Moritzi	Flacourtiaceae			0.27
<i>Coffea canephora</i> Pierre ex A.Froehner	Rubiaceae			0.24
<i>Litsea ochracea</i> (Blume) Boerl.	Lauraceae			0.17
Other species		9.23	14.41	1.94
Total Basal Area (BA)		29.75	46.89	60.60
Total species		90	61	42

Dynamics of total BA and density of trees in Karst forest

The density of trees ≥ 5 cm in diameter was reduced year over year (Figure 3A) from 2019 to 2022. The total tree density in the first measurement (2019) was 1,123 trees/ha. A year later, in 2020, the density decreased to 1,107 trees/ha, of which 19 individuals had died, and three newcomer individuals were found. In the third year of observation (2021), the density of trees with a diameter of ≥ 5 cm dropped again to 1,106 trees/ha, of which nine individuals were found dead, and eight newcomer individuals were recorded. A drop in total density occurred again in the fourth stage (2022) to 1,091 trees/ha. At that time, 17 dead individuals were found, and two newcomers had reached a diameter of ≥ 5 cm.

Although the density lessened continuously during the four years of observation, the BA increased (Figure 3B). The total BA grew from 29.75 m²/ha in 2019 to 30.24 m²/ha in 2020. In 2021, the BA again increased to 31.05 m²/ha, and it rose to 31.63 m²/ha in 2022. The growth in BA is the difference between adding the BA of living trees minus the BA of dead trees plus the BA of newcomer trees that had just reached a diameter ≥ 5 cm.

Dynamics of total BA and density of trees in Lowland forest

In contrast to the Karst forest, the total density of trees with a diameter of ≥ 5 cm in the permanent plot in the Lowland forest grew from year to year (Figure 4A). In the second year of observation (2020), the density grew to 1,694 trees/ha, at which time 22 dead individuals and 44 newcomer individuals were found. A year later, in 2021, the density of trees with a diameter of ≥ 5 cm grew up to 1,696 trees/ha, with 32 newcomer individuals and 30 dead. A rise in total density occurred again in 2022 to 1,701 trees/ha. At this stage, 21 new individuals were found, and 16 had died.

Not only did total density rise, but the total BA also grew yearly (Figure 4B). In the first year of observation in 2019, the total BA was 46.89 m²/ha and grew to 47.23

m²/ha in 2020. The increase occurred again in 2021 and 2022 to 47.63 m²/ha and 48.06 m²/ha, respectively.

Dynamics of total BA and density of trees in Pine forest

In the Pine forest, the total density of trees with a diameter of ≥ 5 cm showed a different pattern each year (Figure 5A). The total density did not change between the first observation year in 2019 and the second year in 2020. This is because eight tree newcomers replaced eight individuals which died. In 2021, the total tree density rose to 1,280 trees/ha; at that time, 20 individuals were confirmed dead, and 27 newcomers were found. A year later, in 2022, the total density of trees decreased to 1,253 trees/ha, in which 27 individuals were found dead, and no newcomers were found.

Unlike the total density, the total BA of trees ≥ 5 cm in diameter in the Pine forest increased over the four years of observation (Figure 5B). The total BA rose from 60.60 m²/ha in 2019 to 60.83 m²/ha in 2020; in 2021 the BA grew to 60.95 m²/ha and 61.02 m²/ha in 2022.

Population dynamics at the species level

In the first year of observation (2019) in the Karst forest, 90 species were found in a plot of 0.75 ha. In four years of observations, it was recorded that two species disappeared (*Beilschmiedia* sp. and *Melicope* sp.), replaced by the emergence of two newcomers, *Santiria* sp. and *Euphorianthus* sp. As many as 16 species experienced a drop in the number of individuals, and conversely (*K. hospita*, *Morinda elliptica* (Hook.f.) Ridl., *Aphanamixis polystachya* (Wall.) R.Parker, *P. celebicum*, *G. paniculata*, *D. dao*, *Albizia splendens*, *Lagerstroemia speciosa* (L.) Pers., *Alstonia scholaris*, *Wrightia tinctoria* (Roxb.) R.Br., *Melicope triphylla* (Lam.) Merr., *Tabernaemontana pandacaqui* Poir., *Mallotus floribundus* (Blume) Müll.Arg., *A. pinnata*, *Litsea firma* (Blume) Hook. f., and *Litsea timoriana* Span.). Five species experienced growth in the number of individuals (*D. celebica*, *Garcinia balica*, *Sageraea lanceolata* Miq., *A. diversifolium*, and *Diospyros* sp.). Therefore, 25 species experienced the dynamics of the number of individuals during the four years of observation.

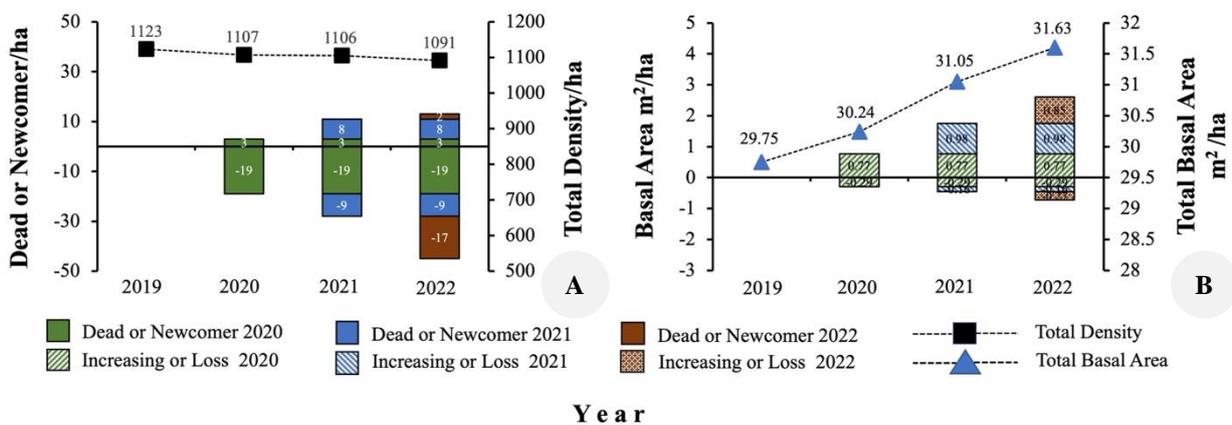


Figure 3. The dynamics of forest structure based on A. Total density; and B. Total basal area in the Karst forest over four years (2019 to 2022)

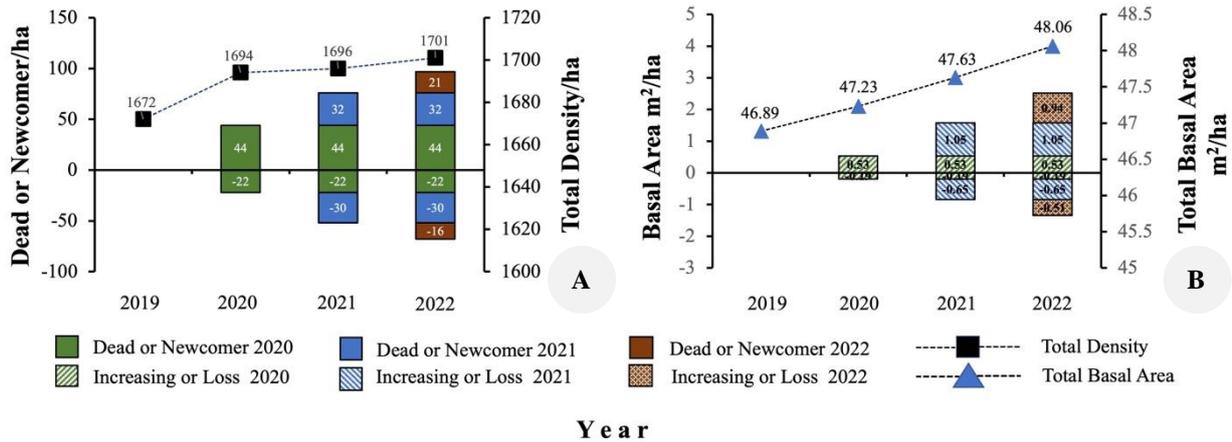


Figure 4. The dynamics of forest structure based on A. Total density and; B. Total basal area in the Lowland forest over four years (2019 to 2022)

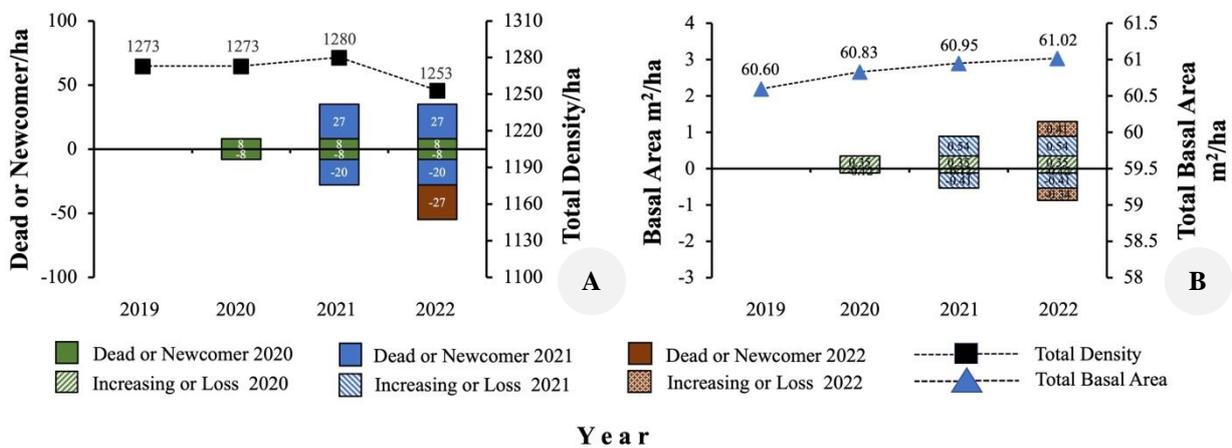


Figure 5. The dynamics of forest structure based on A. Total density and; B. Total basal area in the Pine forest over four years (2019 to 2022)

In the Lowland forest, 61 species were found in the first year of observation. Of the total number of species, 27 species experienced dynamics in the number of individuals during the four years of research. Twelve species grew in the number of individuals in four years of observations (*A. catechu*, *D. celebica*, *Garcinia celebica* L., *C. iners*, *D. dao*, *Lansium domesticum*, *G. paniculata*, *Horsfieldia bivalfis* Merr., *Anacolosia frutescens* Blume, *Melicope lunu-ankenda* (Gaertn.) T.G. Hartley, *Diospyros* cf. *sundaica* Bakh., and *Syzygium* sp.). Seven newcomer species were added (*Hypobathrum microcarpum* (Blume) Bakh.f., *Baccaurea* sp., *Ganophyllum falcatum* Blume, *Syzygium* sp2., *Canthium glabrum* Blume, *Saurauia* sp., and *Pandanus tectorius* Parkinson). A total of eight species experienced a decrease in the number of individuals (*A. pinnata*, *Flacourtia rukam*, *M. longipetiolata*, *Leea aculeata* Blume ex Spreng., *Saurauia oligolepis* Miq., *A. diversifolium*, *L. speciosa*, and *Vitex cofassus* Reinw. ex Blume). No species were lost from the Lowland forest plot during the four years of observation.

Of 42 species in the 0.40 ha Pine forest plot, 12 species experienced dynamics in the number of individuals. Seven of the 12 species that experienced this dynamic were included in the ten most dominant species, *P. merkusii*, *C. iners*, *N. cassiaefolia*, *S. wallichii*, *D. dao*, *F. rukam*, and *C. canephora* (see also Table 2). No species were lost from within the plots in this forest community. However, seven species experienced a loss in the number of individuals (*P. merkusii*, *C. iners*, *C. canephora*, *F. rukam*, *C. glabrum*, *Ficus* sp., and *Leea indica* (Burm.f.) Merr.). On the other hand, four species experienced an increase in individuals (*N. cassiaefolia*, *S. wallichii*, *D. dao*, and *Bischofia javanica* Blume), and one newcomer species, *G. falcatum*, was recorded. It was confirmed that seven *P. merkusii* trees had died, and no newcomer trees were recorded of this species. The four species that experienced population increases were all broadleaf tree species; the newcomer species was *G. falcatum*, a broadleaf species with a small tree habitus.

Discussion

This study found that the population and species composition of trees with a diameter of ≥ 5 cm in three permanent plots spread across three types of forest communities showed different dynamic patterns. During four years of research, tree density decreased in the Karst forest, increased in the Lowland forest, and fluctuated in the Pine forest. However, the BA in the three plots has risen yearly. There were quite a large number of species experiencing population dynamics in each plot during the four years of investigation: 25 of the 90 species in the Karst forest plot, 27 of the 68 species in the Lowland forest plot, and 12 of the 43 species in the Pine forest plot. When viewed from the perspective of species richness, the number of species in the Karst and Pine forest plots does not seem to have experienced marked dynamics over the four years, but this is not the case for the Lowland forest. However, all forest communities experienced species composition dynamics. In the Karst forest, two species disappeared and were replaced by two newcomer species. No species were lost in the Lowland forest, and seven newcomer species were recorded. There were also no missing species in the Pine forest, and one new species was recorded. Dead trees are usually (but not always) old trees with large diameters, while newcomers are small trees grown from saplings and have just reached ≥ 5 cm in diameter.

The dynamics of population and species composition indicated that while old trees with large diameters died, a canopy gap was formed, which was then used by the saplings to develop into new trees (Yamamoto 2000; Feldmann et al. 2018). Consequently, the continuous growth in BA cover may be due to gaps formed by dead trees, causing the remaining trees to undergo growth spurts, as the contribution from newcomer trees may not be significant. Depending on the size of the canopy gap, the ratio between the number of newcomers replacing the dead trees and the rate of increase in the dominance of the remaining trees determines the level of population dynamics, species composition, and dominance (Zhu et al. 2019). The rise in the number of individual species remaining will decide the level of population dynamics, while the number of newcomer species will determine the species composition dynamic. However, increasing the growth rate of the remaining trees will mandate consistent growth in the BA until the available space does not allow for any increase in BA reached. If these conditions are met, moderate population dynamics and species composition may occur with dead trees, but the BA cover will no longer experience growth.

The three forest communities analyzed were secondary forests of different ages. Age is one of the environmental factors that determine the level of dynamics of a secondary forest community in the succession process (Zhang et al. 2021). Older secondary forest communities will generally be more stable with slower growth than younger ones (Rugani et al. 2013; Tian et al. 2022). However, age is not the only factor determining the dynamic level of a secondary forest community (Muscolo et al. 2014; Duarte et al. 2021); this study indicates that Lowland forests

experience more significant dynamics than younger Karst forest due to the death of 5 large pioneer trees.

The consistent decrease in density and increase in the BA cover without significant changes in species composition in the Karst forest plot was caused by several early-stage secondary tree species, mainly *K. hospita* and *P. celebicum*, dying without being replaced by a newcomer of late-secondary or primary tree species. This indicates that the primary tree species in this young secondary forest community, such as *Diospyros* spp. and *G. balica*, had not yet been old enough to produce seeds/seedlings to replace individuals of the dead secondary species. The largest *D. celebica* tree in the Karst forest had only reached a diameter of 26.56 cm and was starting to bear fruit. The slight uptick in the population of several primary tree species in the Karst forest, including *D. celebica*, *Diospyros* spp., *S. lanceolata*, and *G. balica*, came from the germination of seeds brought by dispersal agents to this area (Corlett and Hau 2000; Adyn et al. 2022).

In the Lowland forest plot, there was a significant rise in density and number of species between 2019 and 2020, as six large trees died during the three years before this research started. The six dead trees consisted of 5 pioneer trees, *Erythrina subumbrans* (2 dead in 2016 with diameters of 40.83 cm and 63.15 cm, and 3 dead in 2018 with 58.63 cm, 72.96 cm, and 64.71 cm), which died due to age. The other was a primary tree species (*P. obovatum*) with a diameter of 74.81 cm, which was uprooted by strong winds. The death of these six trees created a canopy gap large enough to encourage seedlings of a climax species to grow to ≥ 5 cm in diameter (see Hoi and Dung 2021), giving rise to marked population dynamics and species composition. Accordingly, it takes about seven years for the Lowland forest to stabilize its population dynamics and species composition after experiencing the death of these six large canopy trees.

As a plantation forest with a spacing of 3 m x 3 m, not all of the planted *P. merkusii* trees can grow optimally to reach the canopy layer. The death of seven *P. merkusii* trees with diameters ranging from 23.03 cm - 26.11 cm, among *P. merkusii* trees which reached a diameter of 95.54 cm, was most likely caused not by old age but stunted growth due to competition for space (see Xue et al. 2016; Chen et al. 2022); a study by Earle (2023) in Thailand showed that *P. merkusii* could reach an age of more than 378 years, while the Pine forest community in this study was only 61.

The dominance of broadleaf tree species in the sub-canopy layer and the absence of newcomer *P. merkusii* capable of reaching ≥ 5 cm in diameter indicate that in time, this introduced species from the island of Sumatra will not survive as the dominant tree in this forest community. Without human intervention, through a long succession process, *P. merkusii* plantation forests can develop into broadleaf lowland tropical forests. *N. cassiaefolia*, *S. wallichii*, *D. dao*, and *B. javanica* have the potential to become the dominating species in the next seral community, given the increasing number of individuals of the three species.

The succession process in the three forest communities studied is ongoing. Several key species such as species that produce leaves or fruit that are food for wildlife (such as *D. dao*, *Ficus* spp., *Listea firma*, *Garcinia* spp., *Artocarpus* spp., *Parartocarpus* sp., *Syzygium* spp., *Cordia myxa*) and timber producing tree species (such as *Palaquium* spp., *Diospyros celebica*, *Vitex cofassus*, *Schima wallichii*) are starting to be discovered in the current seral stage. However, because the area of secondary forest studied reached thousands of hectares, and there was no remaining primary forest as a source of seed dispersal; it is not easy to predict what species of seed dispersal agents will bring to forest communities hereafter (Turner et al. 1998). Even if the dispersal agent carries seeds from the same tree species, there is no guarantee that they can germinate and develop in all three forest communities, given that each forest community grows on a different soil type. In addition, the different soil types usually develop forest communities with varying species compositions (Sellan et al. 2019). Of the ten most dominant species in each forest community, only one was found in all forest communities, that is *D. dao*; the rest were specific to only one or two forest communities. However, the age and history of pre-succession land use for the three forest communities were almost identical. In addition, *P. merkusii* does not appear to have good regeneration ability under its mother tree stand. Therefore, predicting whether the succession processes in these three adjacent forest communities will reach the same climax is difficult, even though there was a model have been developed to predict succession direction (Poorter et al. 2023).

In conclusion, the comparisons of the age of the stands, the background of deforestation that initiated the formation of secondary forest, the history of restoration, the structure of the stand, and the composition of the tree species that make up each stand, it can be concluded that the succession process in the three forest communities is quite complex. The succession process, in particular in the Karst forests and Lowland forests, is ongoing toward climax condition so that no restoration action is needed. The existence of understorey stands of broadleaf trees without pine saplings in the *Pinus merkusii* plantation forest shows that this needle-leaf plantation forest can change into a natural broadleaf forest if the natural succession process is allowed. However, direction of development of each forest type is not easy to predict. The comparison of age and pre-succession land use history, soil type, and restoration history appear dominant in determining the dynamics and direction of succession.

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