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Species Diversity and Ecological Characteristics of Secondary Forests in North Luwu, South Sulawesi, Indonesia

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Abstract

Sulawesi, as part of the Wallacea biogeographical region, has high biodiversity and endemism due to geological processes and unique local environmental conditions. Secondary forests in North Luwu Regency, South Sulawesi, developed after forest exploitation, especially since the 1970s, and are dominated by pioneer species such as Melastoma malabathricum *and* Colona scabra*. This study aims to identify species diversity and ecological characteristics of secondary forest vegetation in Tamboke Village, using a multi-level plot measurement method (seedlings, stakes, poles, trees) and analyzing diversity indices, evenness, species richness, species association, and ecological characteristics, including soil and the composition of climax and pioneer species. The results show a plant community structure that reflects the early succession phase, with a dominance of trees with a trunk diameter of < 30 cm and moderate species diversity (Shannon-Wiener index 1–3). The evenness and species richness indices reinforce the community profile with a dominant presence of pioneer species and indications of biodiversity degradation. Species association analysis revealed diverse interactions between species with varying association strengths. Vegetation patterns are associated with Ultisol soils, which are predominantly acidic in pH, sandy, and have moderate organic matter content, influencing species composition, regeneration processes, and successional dynamics. This study provides an important ecological basis for sustainable forest management and restoration strategies in secondary forest areas to support biodiversity conservation and climate change mitigation.*

Keywords: *secondary forest, succession, Wallacea, diversity, pioneer species*

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Introduction

Sulawesi, located in the Wallacea biogeographic region, is one of the tropical regions with high levels of biodiversity and endemicity. This uniqueness was formed due to geological processes for more than 200 million years, which led to the mixing of flora and fauna elements from the Asian and Australian continents (Mannan et al., 2024). In addition to geological history, local environmental conditions such as climate, topography, and ecological interactions also play a role in shaping the unique vegetation characteristics of the region. Information on vegetation composition is essential for understanding the role of forests in supporting ecosystem stability and biodiversity conservation efforts in Indonesia.

The most complex and productive form of tropical terrestrial ecosystems, secondary forests hold high ecological value and play a vital role in climate change mitigation, carbon storage, and species conservation (Xi & Brandt, 2024). Secondary forest vegetation often reflects past ecological conditions and the potential for natural succession after anthropogenic disturbance (Nytch et al., 2023). Research by Wirabuana et al. (2021) shows that the structure of secondary forest stands in this area is dominated by trees with a stem diameter of less than 30 cm (sapling and pole classes), which reflects the early growth phase and has a relatively low crown density. Analysis of vegetation structure and its ecological characteristics is important to assess the extent of damage and the potential for forest recovery. The presence of various plant strata, from seedlings to mature trees, reflects the dynamics and functions of an evolving ecosystem (Supriatna et al., 2020). Plant diversity in secondary forests has a relationship with soil physico-chemical properties such as available phosphorus and nitrogen, which had the strongest effect on trees (Zhao et al., 2022). Species diversity in secondary forests in Central Sulawesi had less species richness than primary forests. The number of species found in secondary forests is 421 species and 68 families, with the dominant taxonomic composition being Euphorbiaceae, Urticaceae, Annonaceae, Palmae, Ulmaceae, and Leguminaseae (Kessler et al., 2005). Marwa et al. (2024) reported that secondary forest in the lowland of the Doberai Peninsula still supports a high species richness of vegetation with a composition of 225 species and 83 families.

Secondary forests in Sulawesi also serve as habitats for various species. Habitat degradation, which tends to occur in secondary forests, results in a decline in bird and butterfly diversity (Kessler et al., 2005) as well as amphibian groups (Wanger et al., 2020), due to the reduction of canopy cover thickness. In terms of a conservation perspective, older secondary forests in Sulawesi, especially those located on small islands, have significant conservation value, particularly for endemic species (Veddeler et al., 2005; Lee et al., 2007). In addition to their biological, conservation, and ecological roles, secondary forests in Sulawesi also have the potential to contribute to carbon sequestration for climate change mitigation. However, anthropogenic activities such as mining can diminish the ecosystem function of secondary forests as carbon sinks (Nasution et al., 2024). Given the major role of secondary forests in biodiversity conservation and climate change mitigation, their management should be integrated into conservation strategies, along with the protection of primary forests for ecosystem restoration and the sustainability of ecological functions.

In North Luwu District, South Sulawesi, secondary forest areas developed as a result of past forest exploitation, particularly after the forest concession rights (HPH) activities that took place since the 1970s (Nurkin et al., 2002). The forest area in this region covers 474,760 ha (Hati et al., 2023). Most of the area is now dominated by pioneer vegetation, which is an indicator of land criticality (Zhao et al., 2021). Meanwhile, the reduced presence of endemic and commercial tree species indicates biodiversity degradation. Therefore, this study aims to identify species diversity and ecological characteristics of secondary forests in North Luwu as a basis for sustainable forest management and rehabilitation.

Plant community structure reflects the arrangement and relationships between species in an ecosystem (Deng et al., 2022). Changes in plant community structure can indicate changes in environmental conditions and the extent of disturbance (Götzenberger et al., 2012). Disturbances to natural forests cause changes in forest structure and composition, making it important to understand the ecological role of each plant species in the community. Collecting vegetation and edaphic data can reveal plant species that are dominant, rare, or have significant ecological roles. Therefore, research on the characteristics and diversity of vegetation in post-exploitation forests is needed to support conservation efforts and sustainable forest management, especially in Tamboke Village, North Luwu Regency, South Sulawesi, Indonesia.

Methods

Research time and location This research was conducted in August 2024 in the secondary forest of the Kalaena KPH Limited Production Forest block, Tamboke Village, Sukamaju District, North Luwu Regency, South Sulawesi. The area of the Tamboke Village secondary forest is 154 ha (Badan Pusat Statistik Kabupaten Luwu Utara, 2023). The research area is classified as a lowland tropical rainforest with an altitude of 391–950 m above sea level. The soil type in the secondary forest is red-yellow podzolic (RPK) soil derived from sedimentary rock parent material (Land System Indonesia, 2024). Based on data from the Makassar Class I Meteorological Station, the climate of the study area is included in type A based on the Schmidt and Ferguson classification. The average air temperature is 22.68 °C with a minimum air temperature of 14.60 °C and a maximum of 31.8 °C (Badan Pusat Statistik Kabupaten Luwu Utara, 2021). The research location is illustrated in Figure 1.

Data collection Data collection was carried out using a 150 m long transect method that followed the direction of the slope. Along the transect, several 20 m × 20 m observation plots were placed for tree-level observation. Within each main plot, nested subplots measuring 10 m × 10 m, 5 m × 5 m, and 2 m × 2 m were created for each of the pole, sapling, and seedling levels. The transect was repeated three times. Data collected at each growth level included species name, number of individuals, diameter at breast height (dbh), and total plant height. Growth stage criteria were determined based on morphological size, namely seedlings (height < 1.5 m, including herbaceous plants and shrubs), saplings (height ≥ 1.5 m and dbh < 10 cm), poles (dbh 10–20 cm), and trees (dbh ≥ 20 cm).

In addition to vegetation data, soil data was also collected by creating soil profiles at locations considered representative of each part of the slope (upper, middle, and lower). Soil samples were taken from each soil profile for chemical and physical analysis. Soil chemical analysis included soil pH, organic carbon, total nitrogen (N), available phosphorus (P), and available potassium (K), while soil physical analysis included soil texture and organic matter content, following standard soil analysis procedures in the laboratory. The observation plot is illustrated in Figure 2.

Data analysis The data and information obtained were tabulated and analyzed using the important value index (IVI) as shown in Equation [1] and Equation [2] (Mueller-Dombois & Ellenberg, 1974).

$$IVI\text{ (seedling and herbs)} = RD + RF \quad [1]$$
$$IVI\text{ (trees, pole, and sapling)} = RD + RF + Rdo \quad [2]$$

note: *IVI* = important value index (%); *RD* = relative density (%); *RF* = relative frequency (%); and *RDo* = relative dominance (%).

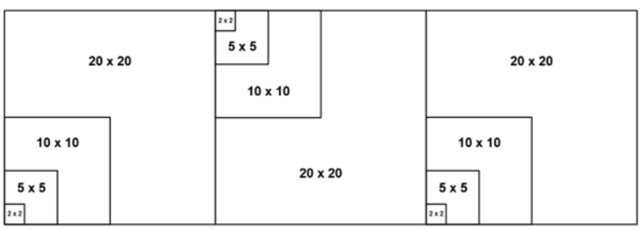

Figure 1 Plot sketch.

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Species diversity index (Shannon-Wiener) The species diversity index (Shannon-Wiener) is a parameter used to determine the level of species diversity. The formula for the species diversity index was shown in Equation *[3]* (Magurran, 2004; Ulfah et al., 2019).

$$H' = -\sum (P_i \times \ln P_i);\ P_i = n_i/N \qquad [3]$$

note: H' = Shannon-Wiener diversity index; P_i = proportion of number of individuals of species-i per total number of individuals of all species or abundance value of species-i; N = total number of individuals of all species; n_i = number of individuals of type-i; ln = natural logarithm. Criteria: $H' < 1$ (indicates a low level of species diversity); $1 \le H' \le 3$ (indicates a medium level of species diversity); and $H' > 3$ (indicates a high level of species diversity).

Evenness index (Krebs) Community balance is used to determine the uniformity index, which is a measure of the similarity of the number of individuals between species in a community. The more similar the number of individuals between species (the more evenly distributed), the greater the degree of balance. The uniformity index formula (e) is obtained from Pielou (1975) and Liu et al. (2025) as shown in Equation *[4]*.

$$e = \frac{H'}{\ln S} \qquad [4]$$

note: H' = Shannon-Wiener diversity index; S = number of species; e = evenness index. Criteria: $e < 0.4$ (small evenness of population); $0.4 \le e \le 0.6$ (moderate evenness of population); and $e > 0.6$ (high population evenness).

Species richness index (Margalef) The Margalef species richness index (*RMg*) is calculated using Equation *[5]* (Magurran, 1988; Nanlohy et al., 2024).

$$RMg = \frac{S-1}{\ln N} \qquad [5]$$

note: RMg = species richness index; S = number of species; N = total number of individuals observed. Criteria: $RMg < 3.5$ (low species richness); $3.5 \le RMg \le 5$ (middle species richness); and $RMg > 5$ (high species richness).

Type association (Mueller-Dombois and Ellenberg) Association estimation was measured to determine a relationship between two different types. The analysis is done using the two-type contingency table method (2 × 2) (*Greig-Smith, 1983; Karim et al., 2021*). The determination correlation between species can be seen in Table 1.

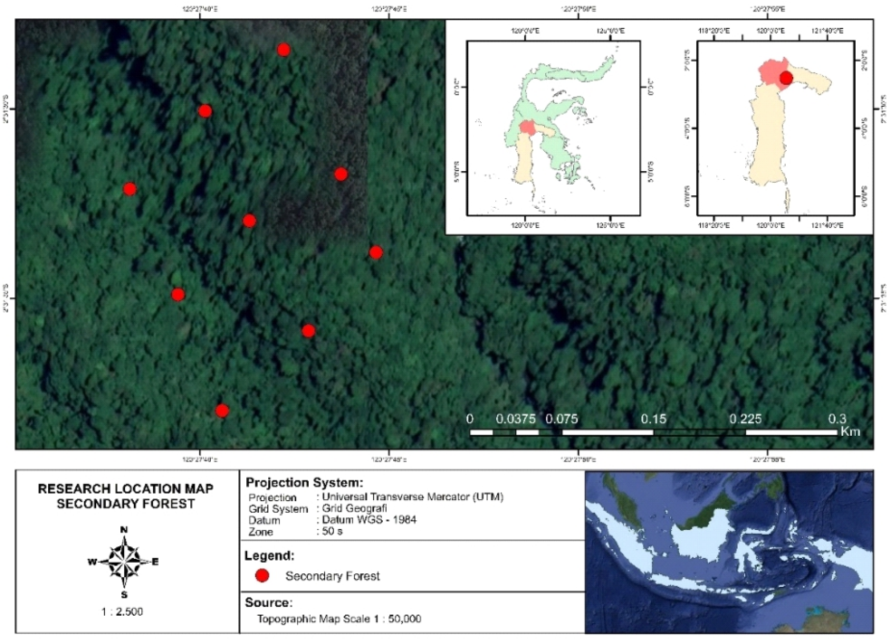

Figure 2 Research map location.

Table 1 Contingency table (2 × 2)

		Species B		
		Present	Absent	Total
Species A	Present	a	b	a + b
	Absent	c	d	c + d
	Total	a + c	b + d	N = a + b + c + d

Note: a = number of sampling units where both species A and species B are present; b = number of sampling units where only species A is present and species B is absent; c = number of sampling units where only species B is present and species A is absent; d = number of sampling units where both species A and species B are absent; and N = total number of sampling units observed. Source: (Greig-Smith, 1983; Karim et al., 2021).

Furthermore, the test was carried out using the chi-square calculation formula (^{2} count) as shown in Equation [6], and the test of the level of association strength was tested by the Ochiai index (Ludwig & Reynold, 1998; Karim et al., 2021).

$$\chi^2\text{count} = \frac{(ad-bc-N/2)^2N}{(a+b)(c+d)(a+c)(b+d)} \qquad [6]$$

The chi-square value obtained is then tested by comparing the chi-square count (^{2} count) with the chi-square table (^{2} table) at a free degree (df) equal to 1 (one) at the 5% level (3.481) to determine the relationship between types. Where if the ^{2} count tested is greater than or equal to the ^{2} table, then there is a very real association, and if the ^{2} count tested is smaller than the ^{2} table then there is no association, or the association is not real.

Furthermore, it was tested with the Ochiai index (OI) to determine the level of association strength using Equation *[7]*(Ludwig & Reynold, 1998; Karim et al., 2021).

$$OI = \frac{a}{\sqrt{a+b}\sqrt{a+c}} \qquad [7]$$

If the *OI* value is closer to 1, the association will be maximum, on the contrary, if the *OI* value is closer to 0, the association will be minimum or even no relationship with the following criteria: 1.00 ≤ *OI* ≤ 0.75 (very high); 0.74 ≤ *OI* ≤ 0.49 (high); 0.48 ≤ *OI* ≤ 0.23 (low); and *OI* < 0.22 (very low). The calculation of the association index value is carried out to determine how much the degree of association between the two species tested and whether it is maximum or minimum.

Principal component analysis Principal component analysis (PCA) was conducted using Minitab 22 to identify dominant variables influencing vegetation structure and species distribution across different land uses. PCA helps visualize patterns of similarity and variation among plots or species based on ecological parameters (density, dominance, frequency, diversity indices, and environmental factors). The results of PCA were presented in a biplot to show the relationships among variables and sample sites.

Results

Biodiversity and structure population Species composition is the species of plants that grow naturally as a constituent of a forest community unit. Based on observations in the secondary natural forest area of Tamboke village, there were 31 species consisting of 20 families found. The species composition in the secondary natural forest of Tamboke village, North Luwu Regency, South Sulawesi, can be seen in Figure 3. The figure indicated that the species composition is dominated by tree life forms, which are 20 families. More species are found in the Myristaceae and Syzygium families; 3 species belong to shrubs and 1 to vines. The population structure of the secondary natural forest of Tamboke village, North Luwu Regency, South Sulawesi can be seen in Figure 4. The results shows that a typical pattern of natural regeneration in forest ecosystems, where the number of individuals is very high in the early stages of growth (seedlings and herbs), but declines dramatically as it progresses towards the tree phase.

Distribution of types for each growth level *Important value index* The IVI is a quantitative parameter that can be used to express the level of mastery of species in a plant community. The IVI in each growth phase is obtained by calculating the value of relative density, relative dominance, and relative frequency, with the results of the IVI calculation showing the important role of a particular plant in maintaining the stability of the ecosystem it occupies. The importance value index of the entire number of individuals can be seen in Figure 5. Based on the calculation results, *C. scabra* has the

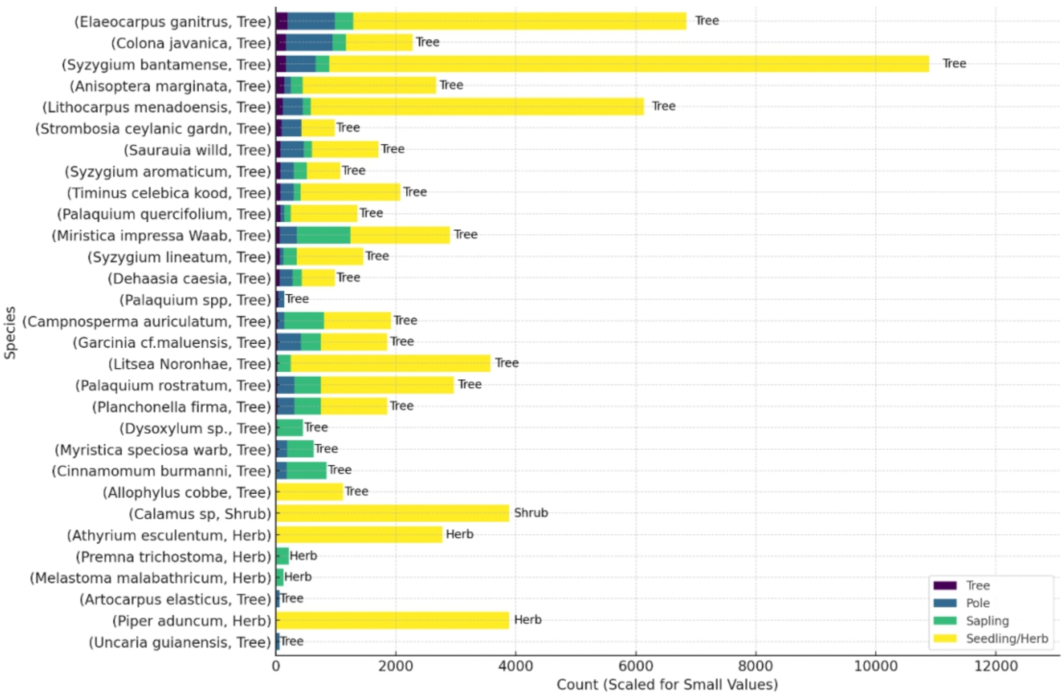

Figure 3 Species composition in secondary natural forests at Tamboke Village, North Luwu Regency, South Sulawesi.

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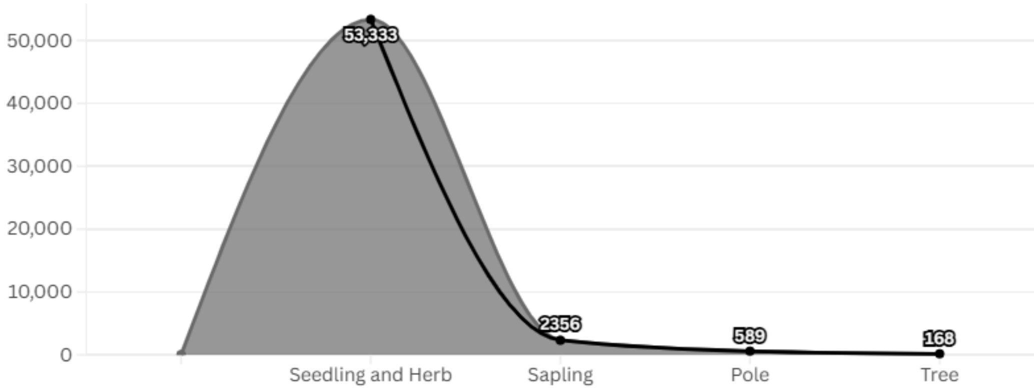

Figure 4 Structure population in the natural secondary forest at Tamboke Village, North Luwu Regency, South Sulawesi.

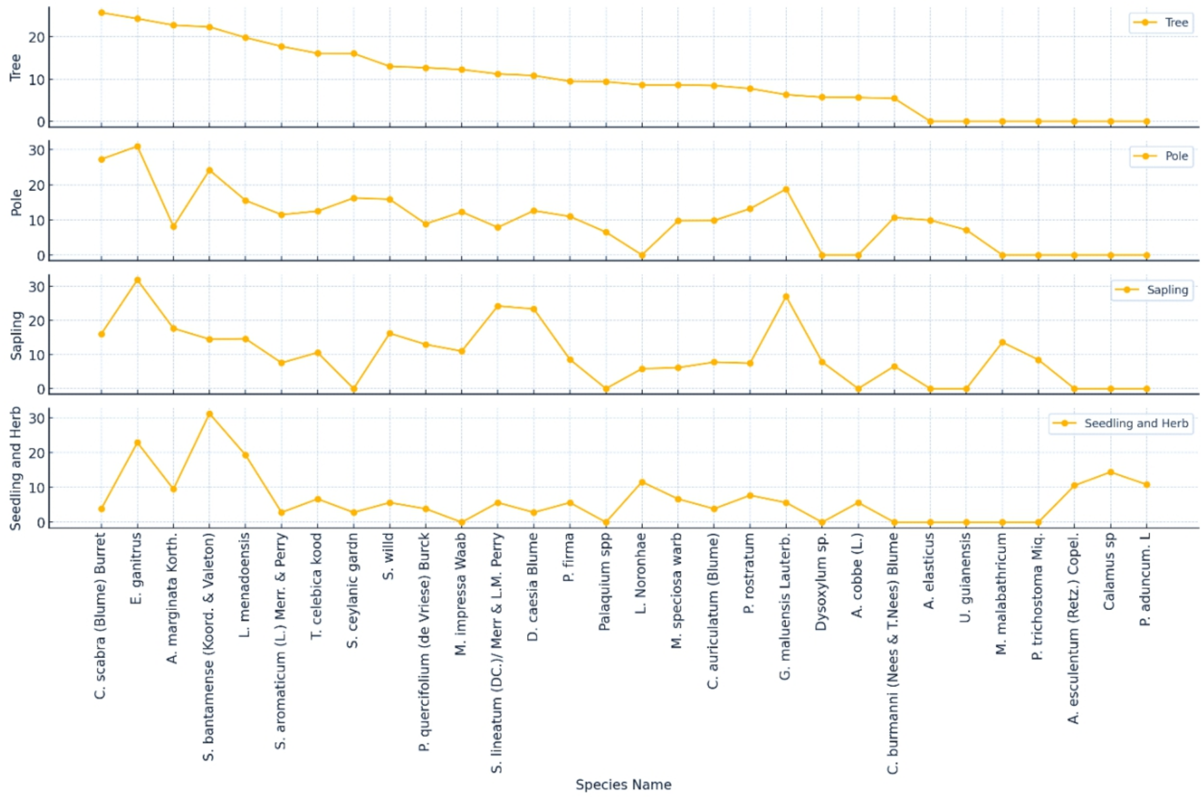

Figure 5 Important index value natural secondary forest at Tamboke Village, North Luwu Regency, South Sulawesi.

highest IVI value at the tree growth level (25.70%), indicating that this species plays a dominant role in the secondary forest of Tamboke Village.

Ecology index The ecological indices comprised the Shannon–Wiener diversity index (*H*′), Margalef's species richness index (*RMg*), and Pielou's evenness index (*J*′), as shown in Table 2. The results indicate moderate to moderately high species diversity across all growth stages. The highest diversity was observed at the pole stage ($H' = 2.83$), while the lowest occurred at the tree stage ($H' = 2.12$). Species richness was generally high, with the highest Margalef index recorded at the seedling stage ($RMg = 4.60$). Evenness was moderate at the tree level ($J' = 0.68$) and high at the pole-to-seedling stages ($J' = 0.89$–0.90), indicating a more uniform distribution of individuals in the lower growth strata.

Species association The species associated with the secondary natural forest area in Tamboke Village, North Luwu Regency, South Sulawesi, is the present data on Table 3, which shows the associations between species at the tree and seedling levels in the secondary natural forest, showing that the pattern of associations changes as individuals grow from the seedling phase to mature trees.

Ecological and edaphic characteristics Information related to the ecological characteristics in the research area is

Table 2 Species association in secondary natural forest

Name of species	Tree			Pole			Sapling			Seedling		
	Assoc type	IO	Assoc strength	Assoc type	IO	Assoc strength	Assoc type	IO	Assoc strength	Assoc type	IO	Assoc strength
Allophylus cobbe (L.)	-	0.33	L							+	0.00	VL
Anisoptera marginata Korth.	-	0.78	VH	+	0.00	VL	-	0.22	VL	-	0.00	VL
Artocarpus elasticus				+	0.00	VL						
Athyrium esculentum (Retz.) Copel.										-	0.00	VL
Calamus sp.										-	0.00	VL
Campnosperma auriculatum (Blume) Hook. f	-	0.38	L	-	0.38	L	-	0.00	VL	+	0.00	VL
Cinnamomum burmanni (Nees & T.Nees) Blume	+	0.00	VL	-	0.27	L	-	0.32	L			
Colona scabra (Blume) Burret												
Dehaasia caesia Blume	-	0.38	L	-	0.44	L	-	0.00	VL	+	0.00	VL
Dysoxylum sp.	+	0.00	VL				-	0.00	VL			
Elaeocarpus ganitrus	-	0.44	L	-	0.36	L	-	0.47	L	+	0.00	VL
Garcinia cf. maluensis Lauterb.	-	0.24	L	+	0.00	VL	+	0.00	VL	-	0.00	VL
Lithocarpus menadoensis	-	0.67	H	-	0.38	L	-	0.60	H	-	0.00	VL
Litsea noronhae	-	0.38	L				-	0.00	VL	+	0.00	VL
Melastoma malabathricum							+	0.00	VL			
Myristica impressa Waab	-	0.30	L	-	0.22	VL	-	0.00	VL	+	0.00	VL
Myristica speciosa warb	-	0.24	L	-	0.27	L	-	0.45	L			
Palaquium quercifolium (de Vriese) Burck	-	0.33	L	+	0.00	VL	+	0.00	VL	+	0.00	VL
Palaquium rostratum	-	0.19	VL	-	0.22	VL	-	0.00	VL	+	0.00	VL
Palaquium spp.	-	0.58	H	+	0.00	VL						
Piper aduncum L										+	0.00	VL
Planchonella firma	-	0.38	L	+	0.00	VL	-	0.00	VL	+	0.00	VL
Premna trichostoma Miq.							-	0.45	L			
Saurauia willd	-	0.45	L	+	0.00	VL	+	0.00	VL	+	0.00	VL
Strombosia ceylanic Gardn	-	0.45	L	+	0.00	VL				+	0.00	VL
Syzygium aromaticum (L.) Merr. & Perry	-	0.60	H	-	0.22	VL	-	0.45	L	-	0.38	L
Syzygium bantamense (Koord. & Valeton)	-	0.42	L	-	0.27	L	-	0.45	L	+	0.00	VL
Syzygium lineatum (DC.)/Merr & L.M. Perry	-	0.58	H	+	0.00	VL	-	0.45	L	+	0.00	VL
Timinus celebica Kood	-	0.45	L	-	0.22	VL	-	0.32	L	+	0.00	VL
Uncaria guianensis				+	0.00	VL						

Note: OI = Ochiai index; VH = very high); H = high; L = low); VL = very low)

Table 3 The ecological index diagram of natural secondary forest at Tamboke Village, North Luwu Regency, South Sulawesi

Growth stage	Shannon–Wiener (H′)	H′ category	Margalef (RMg)	RMg category	Pielou (J′)	J′ category
Tree	2.12	Moderate	4.38	High	0.68	Moderate
Pole	2.83	Moderate–High	3.97	Moderate–High	0.90	High
Sapling	2.78	Moderate–High	4.51	High	0.90	High
Seedling	2.76	Moderate–High	4.60	High	0.89	High

important to know, as it influences the composition of species and the status of each level. The results of edaphic characteristics based on the analysis of the physical and chemical soil properties, and the results of that analysis, are presented in Table 4 and Figure 6. The data on soil characteristics in the secondary natural forest, focusing on depth, color, texture, and soil class. Based on the data of soil chemistry at various depths in natural forest land, there is a change in soil chemistry with depth, so this affects the structure population. The PCA was carried out to determine the relationship between soil conditions and abundance of species and families; the results of the PCA are presented at Figure 7.

Ecological succession The composition of pioneer and climax species in the research plot is presented in Table 5. Based on the ecological index analysis, the comparison between pioneer species and climax species in the secondary natural forest ecosystem shows a regeneration pattern that reflects the dynamics of succession. Of the total of 30 species identified in Table 5, 16 are classified as climax species, while the other 14 are pioneer species.

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Table 4 Soil physical properties of secondary forest

Deepth (cm)	Soil color		Texture			Class
	Hue, value, chroma	Color name	Fraction (%)			
			Sand	Silt	Clay	
0–30	5 Yr 4/4	Dark reddish brown	59.8	4.6	35.6	Loamy sand
30–60	5 Yr 4/6	Dull reddish brown	46.0	27.4	26.6	Clays
60–90	5 Yr 4/8	Dull reddish brown	31.6	33.4	35.0	Loamy clay

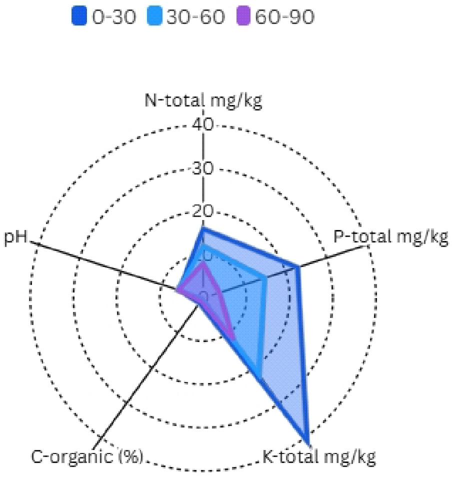

Figure 6 Chemical properties of soil at research area.

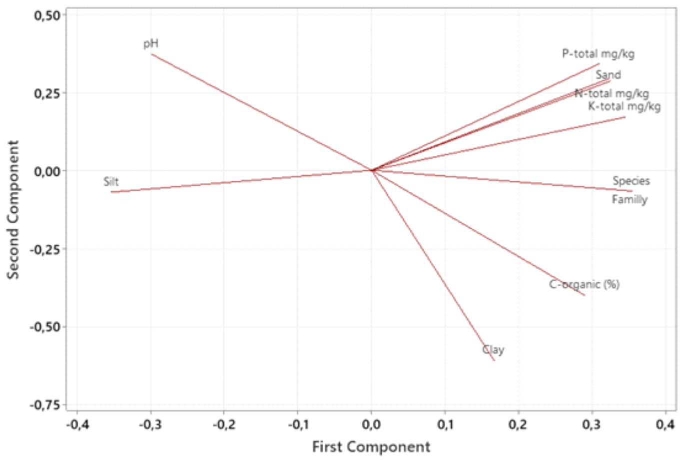

Figure 7 PCA analysis of the relationship between soil conditions and abundance of species and families.

Discussion

Species composition is the species of plants that grow naturally as a constituent of a forest community unit. Based on observations in the secondary natural forest area of Tamboke village, there were 31 species consisting of 20 families found. The species composition is dominated by tree life forms, which are 20 families. Most species are found in the Myristaceae and Syzygium families; then 3 species belong to shrubs and 1 to vines. Based on observations in the field, it shows that not all plant species are found completely in each phase of growth, such as the type of *U. guenensis,* which is only found in the pole phase. This is because this species is generally found in the area around the river.

Vegetation in a tropical forest ecosystem can be classified based on its level of growth, ranging from trees, poles, saplings, seedlings, and herbs. The data presented that tree species dominate the vegetation structure of this forest, which is dominated by families such as Malvaceae, Dipterocarpaceae, and Elaeocarpaceae. These three families showed a wide distribution across all growth stages, indicating that species within these families play an important role in the dynamic of forest succession. For example, *A. marginata* from Dipterocarpaceae had significant representation at the tree stage (14 individuals ha^{-1}) and sapling (200 individuals ha^{-1}) levels, and *C. scabra* from the family Malvaceae is a pioneer species indicating good regeneration and an important role in canopy structure. In addition, species from Elaeocarpaceae, such as *E. ganitrus*, had high numbers at all growth stages, especially at the seedling level (5,556 individuals ha^{-1}), reflecting their high potential for natural regeneration (Williams et al., 2024). This pattern suggests that certain species contribute greatly to forest biodiversity and sustainability. The presence of climber species, such as *Calamus* sp. from Arecaceae, which occurs only at the seedling stage (3,889 individuals ha^{-1}), indicates that this forest provides favorable conditions for a variety of life forms, including tree-dependent liana and epiphytic species, to grow towards the canopy (Umar et al., 2014).

Meanwhile, some tree species have a more restricted distribution, such as *A. elasticus* from Moraceae, which is only found at the pole stage (6 individuals ha^{-1}). This could indicate low regeneration rates or specific environmental requirements for germination and early growth (Li et al., 2022). In addition, some species from Lauraceae, such as *C. burmanni* and *D. caesia*, are distributed from tree to seedling stage, indicating significant regeneration potential in humid forest environments (Irawan et al., 2023). The presence of species with high numbers at the seedling level, such as *S. bantamense* (10,000 individuals ha^{-1}), indicates the potential for future dominance of this species. However, high seedling numbers may also indicate ecosystem disturbances that allow fast-growing species to dominate the forest floor (Wan et al., 2023). These dynamics underscore the importance of understanding patterns of natural regeneration and competition between species in tropical forest ecosystems.

Overall, the structure and composition of vegetation in this forest community shows a diverse regeneration pattern with different species dominating at different growth stages. The presence of high numbers of tree species at all growth stages suggests that the forest is still in a good state of

Table 5 Composition of pioneer and climax species

Name of species	Family	Climax species	Pioneer species	Reference
Calamus sp.	*Arecaceae*		√	Nurdin et al. (2021)
Saurauia willd	*Actinidiaceae*		√	Hamilton and Stevenson (2020)
Campnosperma auriculatum (Blume) Hook. f	*Anacardiaceae*		√	Marwa et al. (2024)
Athyrium esculentum (Retz.) Copel.	*Athyriaceae*		√	Dani et al. (2024)
Garcinia cf.maluensis Lauterb.	*Clusiaceae*	√		Putra et al. (2023)
Anisoptera marginata Korth.	*Dipterocarpaceae*	√		Cvetković et al. (2022)
Elaeocarpus ganitrus	*Elaeocarpaceae*	√		Marwa et al. (2024)
Lithocarpus menadoensis	*Fagaceae*	√		Culmsee et al. (2011)
Premna trichostoma Miq.	*Lamiaceae*		√	Amran et al. (2023)
Cinnamomum burmanni (Nees & T.Nees) Blume	*Lauraceae*	√		Putra et al. (2023)
Dehaasia caesia Blume		√		Karim and Akmal (2019)
Litsea noronhae		√		Putra et al. (2023)
Colona scabra (Blume) Burret	*Malvaceae*		√	Brink and Escobin (2003)
Melastoma malabathricum	*Melastomataceae*		√	Mas'ud et al. (2023)
Dysoxylum sp.	*Meliaceae*		√	Helmanto et al. (2021)
Artocarpus elasticus	*Moraceae*	√		Putra et al. (2023)
Myristica impressa Waab	*Myristicaceae*	√		Helmanto et al. (2021)
Myristica speciosa Warb		√		Helmanto et al (2021)
Syzygium aromaticum (L.) Merr. & Perry			√	Hartoyo et al. (2025)
Syzygium bantamense (Koord. & Valeton)		√		Putra et al. (2023)
Syzygium lineatum (DC.)/ Merr & L.M. Perry		√		Helmanto et al. (2021)
Strombosia ceylanic gardn	*Olacaceae*		√	Priatna et al. (2022)
Piper aduncum L.	*Piperaceae*		√	Mas'ud et al. (2023)
Timinus celebica Kood	*Rubiaceae*		√	Mas'ud et al. (2023)
Uncaria guianensis			√	Karim and Ahmad (2019)
Palaquium quercifolium (de Vriese) Burck	*Sapotaceae*	√		Putra et al. (2023)
Palaquium rostratum		√		Putra et al. (2023)
Palaquium spp.		√		Putra et al. (2023)
Planchonella firma		√		Marwa et al. (2024)
Allophylus cobbe (L.) Raeusch Syn.	*Sapindaceae*		√	Karim and Ahmad (2019)
Total		16	14	

regeneration. Some species with limited distribution can be important indicators for understanding ongoing ecological dynamics. This regeneration pattern is strongly influenced by environmental factors, such as light availability, soil moisture, and competition between species. The presence of climber and shrub species also contributes to the structural diversity of the forest, which in turn affects ecological interactions within the plant community.

The population structure of the secondary forest in Tamboke Village, characterized by high densities at early growth stages and a sharp decline toward pole and tree stages, indicates substantial mortality during forest development. This pattern reflects strong competition for light, water, and nutrients, which is typical of regenerating tropical forests (J. Liu, 2025). While such mortality is part of natural self-thinning processes, excessive losses at later stages may limit the recruitment of late-successional species and slow the development of structurally complex forests. From a management perspective, high mortality in dense pioneer stands suggests the need for selective interventions, such as limited thinning, to reduce competition and improve the survival of shade-tolerant species (Li et al., 2022; Zhu et al., 2022). Despite ongoing regeneration, several risks may constrain long-term forest recovery. Prolonged dominance of aggressive pioneer species can suppress late-successional establishment and lead to arrested succession. In addition, declining soil nutrient availability with depth and the proximity of the forest to Tamboke Village increase vulnerability to human disturbances, such as fuelwood extraction and edge effects. These risks highlight the importance of adaptive management that combines ecological monitoring with targeted interventions and community involvement to ensure sustained recovery and ecosystem resilience (Poorter et al., 2021).

The distribution of species for each growth level can be seen from IVI; it is a quantitative parameter that can be used to express the level of mastery of species in a plant community. The dominant species in the plant community will have a high important value index, so the most dominant species certainly has the greatest important value index (Engel et al., 2023). Based on the analysis of *C. scabra,* it has the highest IVI value at the tree growth level (25.70%), and it occupies a significant number of open spaces in secondary forest succession in Tamboke. This indicates that the species can be used as a cover crop because it grows easily and quickly but also protects the soil surface in open areas. According to (Dharma & Zakaria, 2022) the high INP value indicates that the species has better adaptability to the surrounding environment compared to other species. As a pioneer species, *C. scabra* is able to grow quickly in open or disturbed areas (Souza, 2021; Yatar et al., 2024) and has good tolerance to direct sunlight and limited nutrients (Vitasse et al., 2021). This dominance indicates that the area may still be in the early or middle stages of ecological succession.

M. malabatrichum is found in association with *C. secabra*, and it is recommended as an enrichment plant. Besides being suitable for the biophysical conditions of the environment, it also has medicinal requirements and possesses medicinal properties. It can also serve as a source of income for the surrounding community if developed and managed.

C. scabra and *E. ganitrus* also showed high IVI values (24.28%) at the tree level, indicating that those species have an important role in the plant community. *E. ganitrus* is a species that can grow in many different types of forests, from lowlands to mountains, and on soils with different levels of fertility (Sharma et al., 2023). The significant presence of *E. ganitrus* is due to its seed dispersal mechanism, which involves fauna such as birds and mammals, thereby expanding its growing area. In contrast, *C. burmanni* has the lowest IVI value, which can be attributed to its slow growth rate and its preference for specific environmental conditions, such as soil moisture and partial shade. Competition with faster-growing species and limitations in seed dispersal may have contributed to the low dominance of this species in the study site.

At the pole growth stage, *E. ganitrus* showed the highest IVI value (30.92%), indicating that this species is highly competitive in the intermediate growth phase before reaching the mature tree stage. Characteristics such as rapid growth and tolerance to various soil types allow this species to thrive. *C. scabra* took second place with an IVI value of 27.24%, still showing its role as a pioneer species capable of growing in disturbed environments. In contrast, *Palaquium* spp. had the lowest IVI value (6.51%), indicating that the population of this species in the pole phase is still limited. This could be attributed to slower growth rates as well as competition with more dominant species in utilizing resources such as light, water, and nutrients. The preference of *Palaquium* spp. for a more stable environment with higher shade may also contribute to the low IVI value at this phase.

At the seedling level, *S. batanmese* showed the highest IVI value (31.25%), indicating the dominance of this species in the early phase of regeneration. It is likely that this species has a high seed germination rate and good adaptation to varied environmental conditions. In contrast, *C. scabra* and *Z. aromaticum* had the lowest IVI values (2.83%), indicating that these two species had low abundance and dominance in the seedling phase. *C. scabra*, as a pioneer species, faces regeneration challenges under environmental conditions that are less stable with respect to resources (light, water, nutrients). *S. ceylanicus*, as a more shade-tolerant species, may be more dependent on more closed forest conditions. Meanwhile, *S. aromaticum*, or clove, better known as a plantation crop, may not be fully suited to the study habitat, resulting in limited regeneration. These results provide insight into plant community dynamics and show how different species contribute to ecological succession in a forest ecosystem.

The dynamics and diversity of species also influence ecological succession in forest ecosystems, as indicated by the values of the ecological index. The ecological index consists of the *H′*, *RMg*, and *J′*. The secondary natural forest area of Tamboke Village shows the interesting dynamics of tree species diversity along with the development of growth rates. At the tree level, the *H′* of 2.12 indicates moderate species diversity, according to Williams et al. (2024), which suggests that secondary forests older than 20 years usually have an *H′* value of more than 3.0, while the results of this study obtained an *H′* value lower than 3.0, indicating that the recovery process has not yet reached an optimal level. The *J′* value of 0.68 indicates that the tree phase has a moderately even distribution of individuals among species, and the *RMg* of 4.38 confirms high species richness. Along with growth to the pole level, *H′* increased to 2.83, followed by an increase in *J′* to 0.90, while *RMg* slightly decreased to 3.97. This change indicates that competition and natural selection began to structure species dominance more evenly at the pole level. At the sapling level, *H′* slightly decreased to 2.78, *J′* remained high at 0.90, and *RMg* increased to 4.51. This pattern indicates that regeneration processes are still stable, although competition among species is becoming more pronounced. At the seedling level, *H′* reached 2.76, the *J′* slightly decreased to 0.89, and the *RMg* increased to 4.60. The relatively stable values of the *H′*, *J′*, and *RMg* from the pole to the seedling level indicate ongoing natural selection, where species with higher adaptability and competitive ability are able to survive and regenerate effectively.

Research conducted in a protected forest in China (Yao et al., 2020) showed a similar pattern, where *H*' and evenness decreased from trees to seedlings due to competition for light and space. Overall, this secondary natural forest showed a pattern of decreasing species diversity as growth rates increased, indicating a strong natural selection process in shaping the tree community structure.

This condition also affects the associations between existing species and the associations between species at the tree and seedling levels in the secondary natural forest, showing that the pattern of associations changes as individuals grow from the seedling phase to mature trees. At the tree level, some species showed positive (+) associations, indicating a tendency for these species to grow together in the same habitat. For example, *A. cobbe* and *C. burmanni* showed positive associations with OI values of 0.33 and 0.00, respectively, indicating that these two species may have similar habitat requirements or mutually supportive ecological interactions.

However, at the seedling level, almost all species showed a very low level of association (VL) with OI values close to zero. This indicates that in the early stages of growth, competition between species is not too strong, and growing success is mostly determined by environmental factors such as the availability of light, water, and nutrients around the

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growing area(Paembonan et al., 2021). Some species, such as *A. marginata*, *C. auriculatum*, and *E. ganitrus*, showed negative associations at the tree level with high (H) or low (L) categories, indicating a tendency not to grow together in one habitat space. This may be attributable to variations in resource needs, microhabitat disparities, or potential allelopathic interactions among species. However, the association between these species also changed to very low (VL) at the seedling level, reflecting that the dynamics of interactions and competition between species can change significantly with forest development and succession. This change in association pattern confirms that interactions between species in secondary forest communities are dynamic and strongly influenced by growth stages and surrounding environmental conditions (Mukharomah, 2021).

Information related to the ecological characteristics in the research area is important to know, as it influences the composition of species and the status of each level. Ecological characteristics are also determined by edaphic characteristics, which include the physical and chemical properties of the soil. The physical soil characteristics in the secondary natural forest, focusing on depth, color, texture, and soil class. In the top layer (0–30 cm), the soil is dominated by loamy sand with a dark reddish brown color (5 Yr 4/4). This texture shows a high proportion of sand (59.8%), but still contains significant fractions of dust (4.6%) and clay (35.6%). In the next layer (30–60 cm), the texture changes to clay with a dull reddish brown color (5 Yr 4/6). The proportion of sand decreased (46.0%), while dust increased (27.4%) and clay decreased slightly (26.6%). In the deepest layer (6090 cm), the texture becomes clayey loam with a dull reddish brown color (5 Yr 4/8). The proportion of sand continues to decrease (31.6%), dust increases (33.4%), and clay increases (35.0%). This change in texture with depth indicates weathering and sedimentation processes affecting the soil profile. The reddish-brown color of all layers indicates the presence of iron oxide, which is common in tropical soils. In general, the soil texture in this secondary natural forest varies from loamy sand to loamy clay, indicating that the soil has a good ability to retain water and nutrients. This condition strongly supports the growth of various plant species, including pioneer species. Pioneer species, such as *Macaranga* spp. and *Trema* spp., generally have the ability to grow fast and adapt well to various soil types, including soils with varied textures such as those found in this secondary natural forest. In addition, adequate nutrient availability and the ability of the soil to retain water are also important factors for pioneer growth.

This condition is also supported by the characteristics of its chemical soil properties. Figure 6 shows that at a depth of 0–30 cm, concentrations of N-total 16 mg kg^{-1}, P-total 23 mg kg^{-1}, K-total 41 mg kg^{-1}, C-organic 1.46%, and pH 5.83 were found. As depth increased (30–60 cm), there was a significant decrease in N-total (12 mg kg^{-1}), P-total (15 mg kg^{-1}), K-total (22 mg kg^{-1}), and C-organic (0.42%), while pH slightly increased to 6.18. At 60–90 cm depth, N-total, P-total, and K-total continued to decrease (8 mg kg^{-1}, 4 mg kg^{-1}, and 12 mg kg^{-1}, respectively), but C-organic slightly increased to 0.94% with pH 6.02. This data indicates a change in soil chemistry with depth. The highest concen-trations of macronutrients (N, P, K) are found in the topsoil (0–30 cm), which is important for plant growth (Lutter et al., 2023), including pioneer species. Pioneer species, such as *C. scabra*, which dominated in the previous results, generally have the ability to grow quickly and adapt to a variety of soil conditions. Adequate nutrient availability in the topsoil supports the initial growth and development of pioneer species. In addition, soil pH that tends to be neutral to slightly acidic (5.83–6.18) also supports the availability of nutrients for plants. Good physical and chemical soil conditions in the topsoil are very important for successful forest growth and regeneration, especially in the early succession stage, where pioneer species play an important role in the formation of new forest stands.

Environmental conditions, including soil conditions, greatly influence the abundance of species and families as well as the population structure in a landscape area. To understand this, the PCA was conducted. PCA of the secondary natural forest at the study site showed the relationship between environmental factors and the structure of the plant community that developed after disturbance. PCA graphs indicated that soil pH, dust content, C%, and clay had significant relationships with the distribution of species associated with advanced stages of succession. Species that are more adaptive to environments with high organic matter content tend to favor the growth of climax species, which have slower growth but are more competitive in denser shade environments. In contrast, factors such as sand, P, N, and K contribute to different plant community structures that favor pioneer species. The presence of these nutrients is often found in the early stages of succession, where fast-growing, light-tolerant plant species dominate before climax species begin to gradually replace them (Mukharomah, 2021).

From the perspective of secondary forest succession, this pattern suggests that soil conditions strongly influence the course of forest regeneration after exploitation or disturbance. The predominance of sand and higher nutrient content early in succession allows pioneer species such as *C. scabra*, *M. malabathricum*, and *P. aduncum* to develop rapidly, forming an initial vegetation layer that then contributes to the increase of organic matter in the soil. As time goes on, the buildup of litter will lead to more organic carbon and a more stable soil, which will make it easier for climax species like *A. marginata* and *P. quercifolium* to thrive. These species need a more closed environment and more stable resources. Therefore, the results of this analysis confirm that the recovery of secondary forest ecosystems is not only determined by species availability but also by soil factors that shape natural regeneration dynamics. This understanding is important in forest management and conservation strategies, especially in efforts to accelerate ecosystem recovery after exploitation by HPH in the past (Binkley & Fisher, 2019).

The comparison between climax species and pioneer species in the research plot area also reveals ecosystem recovery. This can indicate the status of its ecological succession. Based on the ecological index analysis, the comparison between pioneer species and climax species in the secondary natural forest ecosystem shows a regeneration pattern that reflects the dynamics of succession. Of the total of 30 species identified in the table, 16 species are classified as climax species, while the other 14 species are pioneer species. The presence of pioneer species such as *C. scabra*, *M. malabathricum*, and *P. aduncum* indicates that this ecosystem is still in the early to middle stages of recovery after disturbance; for example, due to exploitation by HPH, pioneer species are characterized by fast growth and high tolerance to extreme environmental conditions, such as nutrient-poor soils and high sunlight exposure. However, over time, climax species such as *A. marginata*, *G. maluensis*, and *P. quercifolium* began to dominate. Climax species have slower growth rates but are more competitive in more closed forest conditions with soil rich in organic matter. The almost balanced ratio between pioneer and climax species suggests that this forest is in a transitional phase towards more stable conditions but has not yet fully reached the climax stage (Zhang et al., 2025).

The balance between pioneer and late-successional (climax) species observed in the secondary forest of Tamboke Village provides a critical basis for defining appropriate restoration strategies. The relatively high proportion of pioneer species, together with moderate species diversity, indicates that the forest is in a transitional phase of succession rather than a degraded or stable climax condition. Pioneer species play an essential role in early recovery by rapidly occupying open spaces, improving microclimatic conditions, and facilitating soil recovery through litter input. However, if pioneer dominance persists for extended periods, it may constrain the recruitment and establishment of shade-tolerant climax species, thereby slowing the development of structurally complex and resilient forest ecosystems (Souza, 2021). From a management perspective, this pioneer–climax balance suggests that neither full reliance on natural succession nor intensive planting across the entire area is optimal. Instead, restoration strategies should aim to maintain pioneer species as facilitators of early succession while actively promoting the establishment of climax species. Pioneer species such as *C. scabra* should be retained to stabilize canopy cover and soil conditions, but their dominance may need to be regulated through selective thinning where they suppress late-successional recruitment. This approach allows managers to harness the ecological benefits of pioneer species without compromising long-term successional trajectories (Holl & Aide, 2011).

The presence of a substantial number of climax species in the regeneration pool indicates that the ecosystem retains a natural recovery potential that can be enhanced through targeted interventions. Enrichment planting of late-successional species should focus on species with high structural and ecological value, such as *A. marginata*, *P. quercifolium*, and *Lithocarpus* spp., particularly in microsites with favorable soil conditions. By aligning management actions with the observed pioneer–climax balance, forest managers can accelerate succession, improve biodiversity outcomes, and guide secondary forests toward more stable and functional ecosystem states. This adaptive, succession-based strategy is widely recognized as an effective framework for managing post-logging secondary forests in the tropics(Williams et al., 2024).

Furthermore, the PCA graphs showed that environmental factors such as soil pH, organic carbon content, and dominance of the clay fraction were more closely correlated with climax species, while sand content and macronutrients (P, N, and K) were more related to pioneer species. This indicates that pioneer species are more dependent on soils with lower fertility, while climax species are more dominant on soils that have improved structure and increased organic matter content due to successional processes. This transition process is important in the recovery of forests previously degraded by HPH exploitation, where natural regeneration can take place without major intervention if environmental conditions are favorable. In the context of forest management, an understanding of this ecological index based on species comparisons is essential for determining more effective rehabilitation strategies. Strengthening natural succession by maintaining pioneer species until climax species are able to thrive will accelerate ecosystem recovery and increase the stability and sustainability of biodiversity in secondary natural forests (Mukharomah, 2021).

Conclusion

The vegetation structure of the secondary natural forest in Tamboke Village reflects an ecosystem in an early- to mid-successional phase, characterized by moderate species diversity and the dominance of pioneer taxa during regeneration. While pioneer species dominate the early growth stages, the occurrence of late-successional species indicates a continuing transition toward structural and compositional stability. These patterns suggest that natural regeneration remains effective under current environmental conditions; however, successional progression is likely sensitive to disturbance and changes in soil properties. Maintaining low disturbance levels and monitoring species turnover across growth stages are therefore critical to sustaining long-term forest recovery and biodiversity development in this landscape.

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