

4.6 CONCLUSION

Although there is a tendency for the k -value of jabon wood to be higher during the dry season than the rainy season, and vice versa for tusam wood, and a tendency for the k -value of both wood samples to be higher in the broadleaf forest than in Pine forest, the data show high disparity even within the same season and forest community. The results of the statistical analysis show that most of the data are not normally distributed. This is due to the high diversity of decomposing agents and environmental factors in the tropics, where they work in very complex reciprocal associations. Environmental factors such as rainfall and soil chemistry can affect the k -value directly and individually or indirectly and collectively through the activity of decomposing agents at different levels. The results of many controlled experimental studies conducted in the laboratory may be able to show how a single decomposing agent affects the rate of decomposition, but this may not be the case in the field. Therefore, field research on various forest communities in the tropics is still needed to determine the accumulative working patterns of decomposing agents and the influence of environmental factors on the rate of decomposition of wood litter.

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CHAPTER 5

SEASONAL DIVERSITY AND DISTRIBUTION OF DECOMPOSING MACROFUNGI IN THREE FOREST COMMUNITIES: WHY DO THEY DIFFER?

5.1 ABSTRACT

This study aimed to reveal the inter-seasonal diversity of macrofungal species in three forest communities in South Sulawesi: Karst forest, Lowland forest, and Pine forest. Field surveys were carried out twice (i.e. in the wet and dry seasons) in 25 units plots measuring 10 m x 10 m which were systematically spread in an area of approximately 1 ha in each forest community. The macrofungi found in each plot were recorded by the species name, photo, and the area of cover that measured using Crown Diameter Method to analyse the area of cover. In total there were found 130 species of macrofungi from 38 families across forest communities both in wet and dry seasons. The highest number of macrofungi species was found in the Lowland forest (67 species), followed by Karst forest (65 species), and the lowest was in Pine forest (42 species). Some species are specialists in specific forest communities. Given that most species of macrofungi are monophagous that specialist to an only litter of one tree species, the difference in the diversity of macrofungi among forest communities is likely related to the difference in tree species diversity among forest communities. In addition, microhabitat conditions were found in line with the diversity of macrofungal species inter-seasons and inter-forests.

Keywords: Cover area, Diversity, Karst forest, Lowland forest, Pine forest

5.2 INTRODUCTION

Fungi are organisms that digest food externally and absorb nutrients directly through their cell walls (Carris et al., 2012). Most fungi produce fleshy fruiting bodies with sexual reproductive structures, however, some also have asexual reproductive structures (Tang et al., 2015). As heterotrophic organisms, fungi can be distinguished based on their size: microfungi and macrofungi. In general, people can easily recognize macrofungi because they have a macroscopic life phase in the form of a fruiting body which people call it mushroom (Putra, 2020; Yusran et al., 2021)

Ecologically, macrofungi can be classified into three major groups: saprophytes, parasites, and symbiotic species (Tang et al., 2015; Nur et al., 2020). Almost all terrestrial macrofungi are saprophytes and mycorrhizal symbionts, but some of them are plant pathogens. Saprophytic fungi obtain nutrients through dead plants or animals for growing (Carris et al., 2012). While symbiotic mycorrhizal fungi and parasites obtain their nutrition from a living host (plant or animal) (Dighton, 2009; Tang et al., 2015). Through symbiotic associations, mycorrhizal fungi obtain carbohydrates (plant-produced sugars) from plants, and in return the plant obtain

minerals from the fungi (Dighton, 2009). Parasitic fungi, on the other hand, obtain their nutrition by killing the living cells of their host (Blanc, 2008).

Macrofungi have now attracted people's interest because of their broadly important role they play in an ecosystem: i.e. as agents for decomposing organic matter (Tang et al., 2015), foodstuffs, pharmaceuticals, and even biocontrol agents used in many industries (Duarte et al., 2006; Dai et al., 2009; Royse, 2014; Hyde et al., 2019). However, behind these benefits, an understanding of macrofungi is still insufficient due to difficulties in studying them, especially those that grow naturally in the field. This is due to its sporadic and short-lived nature, as well as its growth and distribution pattern which depend on several environmental factors. Hence, they have been mainly neglected and overlooked in nature conservation both at the national and international levels.

Macrofungi are cosmopolitan species, but they require certain environmental conditions to grow. Each macrofungal species requires a different habitat, different substrates, and different climatic conditions to grow (Halbwachs and Simmel, 2018). Naturally, most macrofungal species grow during the wet season, but there are also several species that grow during the dry season (Van Dijk et al., 2003; Andrew et al., 2013). Mahmud et al. (2018) revealed that environmental conditions that mainly affect the growth of fungi are temperature, humidity, and CO². Hu et al. (2022) added that the emergence of macrofungi is strongly influenced by the type of vegetation. Humidity, rainfall, and wind speed are other environmental factors reported by Hu et al. (2022) which was also found to have a significant impact on the occurrence of macrofungi.

The number of macrofungal species in the world is estimated at about 1.5 million, of which only approximately 120,000 species are known to date (Hawksworth, 2001; Hawksworth and Lücking, 2017). Among the 120,000 known species, 16,000 are found in the Indonesian archipelago, particularly on island of Java (Darajati et al., 2016). Meanwhile, data on the presence and diversity of macrofungi from outside Jawa is lacking.

The lack of data on the macrofungi diversity is also a particular problem for Sulawesi, the largest island in the Wallacea region, which is known biogeographically for its unique biodiversity (Lohman et al., 2011). This study aims to compare seasonally the differences in the diversity of macrofungi in three forest communities with different habitats and species composition: a 47-year-old secondary broadleaf karst forest, a 56-year-old secondary broadleaf lowland forest,

and a 60-year-old *Pinus merkusii* plantation forest. Given that each species of macrofungi is usually associated with a particular tree species as its host (Tapwal et al., 2013), we predict that most macrofungi species found in each forest community vary according to differences in tree species composition. The results of this study will enrich the lack of information about macrofungi in Sulawesi and become a database to support conservation efforts and sustainable use of macrophytes in the future.

5.3 MATERIAL AND METHODS

5.3.1 Study Site

This study was carried out in 2021 in three secondary forest communities on the southern peninsula of Sulawesi Island, Indonesia. The three secondary forest communities are 47-old broadleaf karst forest (119°44'14.9" E, 05°01'46.8" S, hereafter referred to as Karst forest), 56-old broadleaf lowland forest (119°46'35.0" E, 04°58'06.9" S, hereafter referred to as Lowland forest), and 60-old *Pinus merkusii* plantation forest (119°45'56.7" E, 05°00'17.3" S, hereafter referred to as Pine forest). The Karst forest is located within the Karaenta forest complex of the Bantimurung Bulusaraung National Park, while Lowland and Pine forests are located in the Education Forest of Hasanuddin University. To reveal the habitat characteristics of each forest community, vegetation analyses were carried out in each forest community by Putra et al. (2023), as shown in Table 5.1. *Pinus merkusii* dominates 88% of the total basal area of the Pine forest.

Table 5.1. Description of the research location.

Description	Karst	Lowland	Pine
Altitude	271	563	501
Soil Type	Rendzina with clay texture and exposed limestone rocks	Cambisol with silty clay mixed with small, medium, and large stones	Luvisol with loamy texture
Number of Tree Species / ha	94	61	46
Tree Density / ha	1,125	1,672	1,273
Basal Area of Trees cm ² / ha	295,555.91	467,459.63	600,070.03
Ten Most Dominant Tree Species	<i>Kleinhovia hospita</i> , <i>Cananga odorata</i> , <i>Pterospermum celebicum</i> , <i>Dracontomelon dao</i> , <i>Diospyros celebica</i> , <i>Garcinia balica</i> , <i>Samanea saman</i> , <i>Albizia splendens</i> , <i>Cordia myxa</i> , and <i>Ficus racemosa</i>	<i>Areca catechu</i> , <i>Arenga pinnata</i> , <i>Palaquium obovatum</i> , <i>Diospyros celebica</i> , <i>Mangifera</i> sp., <i>Aleurites moluccana</i> , <i>Artocarpus heterophyllus</i> , <i>Lancium domesticum</i> , <i>Dracontomelon dao</i> , and <i>Gymnacranthera paniculata</i>	<i>Pinus merkusii</i> , <i>Arthrophyllum diversifolium</i> , <i>Cinnamomum iners</i> , <i>Neolitsea cassiaefolia</i> , <i>Alstonia scholaris</i> , <i>Coffea liberica</i> , <i>Schima wallichii</i> , <i>albizia chinensis</i> , <i>Dracontomelon dao</i> , and <i>Flacourtia rucam</i>

5.3.2 Climate and Environmental Factors

Rainfall data for the study site for 2021 were obtained from the Indonesian Agency for Meteorology, Climatology, and Geophysics that located in Maros City (Figure 5.1). According to Andrew et al. (2013), microhabitat conditions affect the growth of macrofungi. For this reason, we measured several factors of microhabitat conditions, including temperature, soil moisture, and soil pH every 1st to 2nd of each month during the study period. Temperature data was measured by installing a maximum-minimum thermometer on a tree trunk at the height of about 1 m from the ground. Soil moisture and pH measurements were carried out using the Takemura Dm-5 Soil pH and Moisture Tester in 10 systematically selected plots. Meanwhile, the measurement of light intensity was only carried out once in the entire plots using a Lux meter type LX-100. Measurements were made during the day between 11.00 – 13.00 in cloudless conditions.

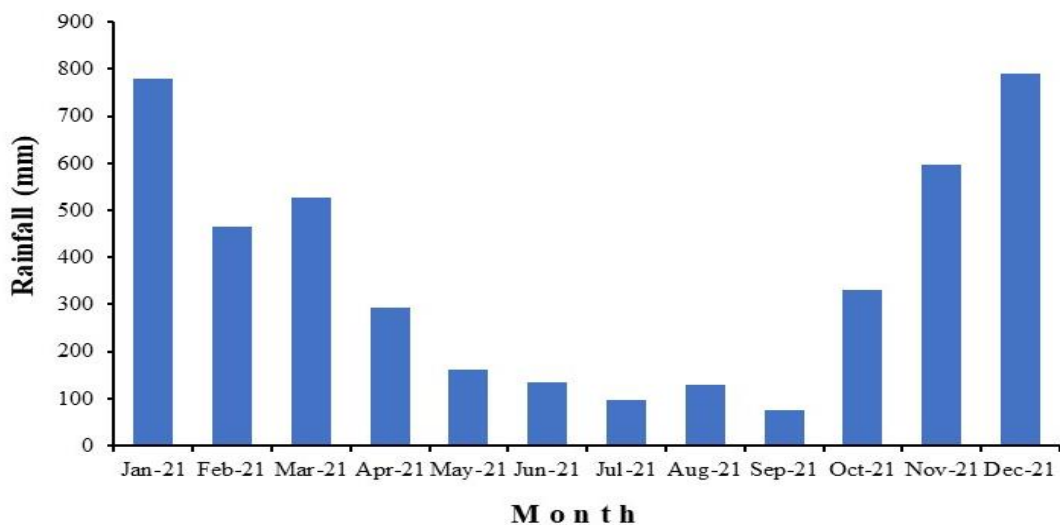


Figure 5.1. Monthly total rainfall during the study period (Source: Indonesian Agency for Meteorology, Climatology, and Geophysics in Maros City).

5.3.3 Macrofungal Diversity and Distribution

Observations of macrofungi were carried out in 25 plots measuring 10 m x 10 m which were systematically distributed over an area of approximately 1 ha in each forest community. Observations on macrofungi included the identification of species, area of cover, and type of substrate. Identification of species in the field

was carried out using a macrofungal field manual. All macrofungal species found were photographed. When identification could not be carried out directly in the field using a field guidebook, species identification was carried out in the laboratory through several online identification manuals. For each macrofungal colony that we found in each plot, we measured the colony diameter using the Crown Diameter Method (Mueller-Dombois and Ellenberg, 1974). According to this method, the diameter of an imperfect circle is measured four times from different directions, and the diameter used is the average of the four measurements. In addition, the type of substrate on which macrofungi grew was also recorded, such as litter (leaves, twigs, fruits), decayed wood, living tree trunks and roots, cow dung, soil, and rocks. Observations of macrofungi were made twice: first in the wet season (March 2021) and second in the dry season (September 2021).

5.3.4 Data Analysis

The area of cover of each colony of macrofungal species in the three forest communities, we analysed using the following formula: (Odum, 1993).

$$Cover Area = \frac{1}{4} \times \pi \times d^2$$

Where: π = Constants (3.14)

$$d = Diameter \left(\frac{Diameter\ 1 + Diameter\ 2 + Diameter\ 3 + Diameter\ 4}{4} \right)$$

We used the Analysis of Variance (ANOVA) with Tukey Honest Significant Difference (HSD) method to detect the differences in (a) the soil moisture among the forest communities in the wet and dry seasons; (b) the soil pH among the forest communities in the wet and dry seasons; (c) the Light Intensity among the forest communities. All statistical analyses were performed using the R version 4.2.1 application (Team R Studio, 2021).

5.4 RESULTS AND DISCUSSION

5.4.1 Environmental Conditions During the Wet Season and Dry Season

Different macrofungal species grow in different microclimatic environmental tolerance ranges (Lee et al., 2002; Parveen et al., 2017). Among the three forest communities studied, the highest temperature maximum during the wet season was recorded in the Pine forest, while the lowest was recorded in the Karst forest (Table 5.2). However, during the dry season, the maximum temperature did not show a difference among the three forest communities. The same result was also recorded for the minimum temperature during the wet season, the highest minimum temperature was recorded in the Pine forest, while the lowest minimum temperature was recorded in the Karst forest. Minimum temperature during the dry season did not differ between the Karst forest and the Pine forest but was lower in the Lowland forest.

For the soil moisture during the wet season, the highest value was noted in the Karst forest, followed by the Lowland forest, and lowest in the Pine forest ($P < 0.001$). In the dry season, the mean soil moisture was significantly highest in the Lowland forest, followed by the Karst forest, and lowest in the Pine forest ($P < 0.001$). The mean pH during wet season was not significantly different between the Karst and Lowland forests but was much lower in the Pine forest ($P = 0.0016$). Meanwhile, the mean pH during the dry season was significantly highest in the Lowland forest, followed by the Karst forest, and lowest in the Pine forest ($P < 0.001$). For the mean light intensity, the highest value was noted significant in the Pine forest, followed by the Karst forest, and lowest in the Lowland forest ($P = 0.0012$).

Boddy et al. (2013) stated that among the microhabitat factors, temperature, soil moisture, and light intensity are ecologically the most important environmental factors for fungal growth. Macrofungi generally grow in a range of temperature intervals between 25 °C – 35 °C (Kapoor and Sharma, 2014) and soil moisture at an interval range of 70% - 90% (Daud et al., 2021). Relative high soil moisture is strongly associated with high rainfall (Afolabi et al., 2009). On the other hand, the higher the intensity of sunlight in a habitat, the lower the diversity of macrofungi species because in such habitat conditions, the temperature increases which then triggers evaporation so that soil moisture decreases. Yusef and Allam (1967)

revealed that high irradiation intensity would inhibit the growth of macrofungi populations because it would inhibit the formation of reproductive organs and fungal spores.

Table 5.2. Microhabitat conditions in the three forest communities.

Variable	Forest Communities					
	Karst		Lowland		Pine	
	Wet	Dry	Wet	Dry	Wet	Dry
Tem. Max (°C)	25.5	30	27	30	28	30
Tem. Min (°C)	18.9	20	19	19	19.5	20
Soil Moisture (%)	95.3 ^a	65.3 ^A	78.5 ^b	73.5 ^B	57 ^c	28.3 ^C
Soil pH	6.33 ^e	6.23 ^E	6.28 ^e	6.51 ^F	5.90 ^f	5.95 ^G
Light Intensity (Lux)	94.16 ^{ij}		69.84 ⁱ		134.08 ^j	

Different lowercase letters after the mean values of soil moisture, soil pH, and light intensity in a row indicate significant differences between forest communities during the wet season (a, b, c for soil moisture, e, f for soil pH, and i, j for light intensity), while different uppercase letters after the mean values of soil moisture and soil pH in a row indicate significant differences between forest communities during the dry season (A, B, C for soil moisture and E, F, G for soil pH).

5.4.2 Seasonal Diversity of Macrofungi in the Three Forest Communities

The total species of macrofungi found both in the wet and dry seasons were 130 species from 38 families (Figure 5.2). Three families with the largest number of species were Polyporaceae (19 species), Marasmiaceae (17 species), and Ganodermataceae (12 species). Prasetyaningsih and Rahardjo (2015) reported that, families from the Order of Polyporales, especially Polyporaceae and Ganodermataceae, were less affected by changes in physical environmental factors. Their large and hard fruit body allows them to adapt well in various habitats, both in wet and dry habitat conditions (Lestari and Febrianti, 2018). Meanwhile, although their fruiting bodies are relatively more minor and have a smoother appearance, species from Marasmiaceae have the ability to survive the dry season by wrinkling their fruiting body, then quickly returning to their normal state in the following wet season (Seasons, 2021).

Of the 130 species of macrofungi found, 81 species were recorded in the wet season, 22 species were recorded in the dry season, and 27 other species were recorded in both the wet and dry seasons (Table 5.3). The highest number of species was recorded in the Lowland forest (67 species), the second highest in the Karst forest (65 species), and the lowest in the Pine forest (42 species). During the

wet season, the largest number of macrofungal species was recorded in the Karst forest and the lowest number was in the Pine forest, while during the dry season, the largest number was recorded in the Lowland forest, and the lowest number was in the Karst forest. For macrofungal species that were found in both seasons, the largest number of species was found in the Lowland forest while the lowest was in the Pine forest.

In all forest communities, the diversity of macrofungal species was distinctly higher in the wet season than in the dry season. Ideal climate conditions during the wet season, where the relative humidity is higher, the temperature is lower, and light intensity is also lower, support fungal fruiting (Sysouphanthong et al., 2010; Boddy et al., 2013; Li et al., 2018). This finding was also supported by Tibuhwa (2011) who studied the phenology of the macrofungal community at the University of Dar es Salaam main campus in Tanzania, and by Sutjaritvorakul et al. (2017) who studied the seasonal (wet and dry season) and climatic changes on macrofungal diversity in Sai Yok District, Kanchanaburi Province, China.

This study found that the fruiting bodies of several macrofungal species from the families of Auriculariaceae, Boletaceae, Hygrophoraceae, Hymenogastraceae, Marasmiaceae, Pleurotaceae, Psathyrellaceae, Pyronemataceae, and Tricholomataceae grew in the dry season. Meanwhile, a previous study reported that in general, macrofungal species from these families are difficult to grow in the dry season because they require relatively high humidity (Daud et al., 2021). These contradictory findings may be caused by climate change which makes the dry season not completely dry, but rainfall still occurs at the study site even though with low intensity (Figure 5.1). The monthly rainfall in September 2021 was 72 mm. According to the climate classification by Schmidt and Ferguson (1951), the rainfall of 72 mm per month falls into the category of humid enough to support the growth of the saprophyte macrofungi group with soft and easily crushed fruiting bodies. Sutjaritvorakul, et al. (2017) revealed that macrofungal species that grow during the dry season or throughout the year generally come from the family of Ganodermataceae and Polyporaceae. The characteristics of hard or rigid fruiting bodies and their large size are the reasons why species of these families can grow across seasons (Noverita and LumbanTobing, 2020). The hard fruiting bodies have denser hyphal systems and thicker cell walls so as to prevent excessive evaporation (Moser, 1993; Halbwachs et al., 2016).

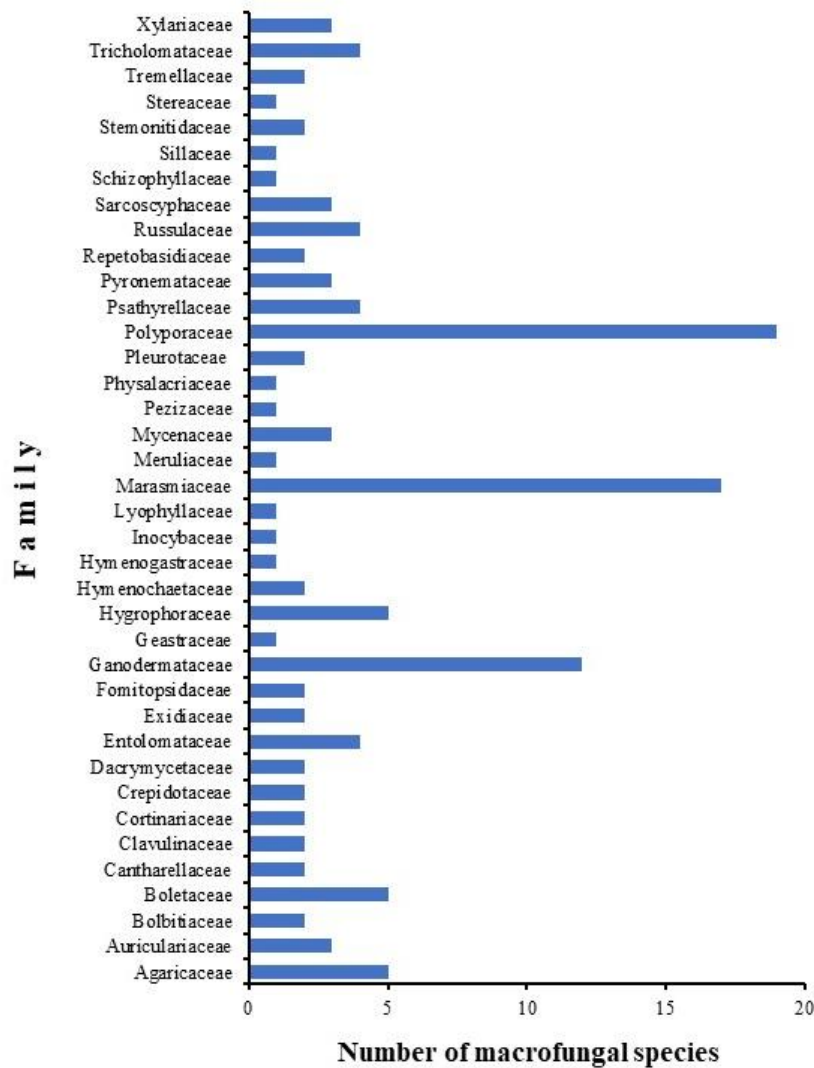


Figure 5.2. The number of species of each macrofungal family found in the three forest communities.

The variation in the diversity of macrofungal species among forest communities can be related to differences in soil moisture, light intensity, and temperature. Hu et al. (2022) and Santos-Silva et al. (2011) revealed that the combination of canopy cover and soil moisture is the main factor in supporting the growth of macrofungi in forests. Thick and large canopy cover will keep the soil moist due to the lack of intensity of sunlight penetrating into the forest floor (Hasselquist et al., 2018). In addition, the type of bedrock and soil may be related to water holding capacity and this in turn determines soil moisture.

Table 5.3. Number of species and cover area of macrofungi in the wet and dry seasons.

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
1	<i>Auricularia auricula-judae</i>	Auriculariaceae	425.86	380.49	1559.19	75.10	126.89	11.46	Lt
2	<i>Polyporus</i> sp.	Polyporaceae	14.82	23051.35					Lt
3	<i>Favolus</i> sp.	Polyporaceae	1.99	17930.00					Lt
4	<i>Fomitopsis ochracea</i>	Fomitopsidaceae	108.00	1054.29					LT
5	<i>Scutellinia</i> sp.	Pyronemataceae	37.05	2.55					Lt
6	<i>Megacollihya platyphylla</i>	Tricholomataceae	120.33	865.41	82.77			255.71	Lt, So
7	<i>Pleurotus pulmonarius</i>	Pleurotaceae	1.03	1659.18	23.13				Lt, DW
8	<i>Coprinellus disseminatus</i>	Psathyrellaceae	2154.48	346.82	5434.54				LT
9	<i>Inocybe rimosa</i>	Inocybaceae	101.67	41350.90		274.87			Lt, LT, So
10	<i>Polyporus arcularius</i>	Polyporaceae	21.68	577.97		15.83			Lt
11	<i>Marasmiellus candidus</i>	Marasmiaceae	786.28		851.31	580.13			Lt, DW
12	<i>Microporus xanthopus</i>	Polyporaceae	1424.00		895.66	40216.81	5.51		Lt
13	<i>Coprinellus</i> sp.1	Psathyrellaceae	32.52		41.24	7677.14	29.63		Lt, DW
14	<i>Clavulina cristata</i>	Clavulinaceae	13.71		1604.91	100.02	109.59		So
15	<i>Schizophyllum commune</i>	Schizophyllaceae	3069.40		3.50		3.68		Lt
16	<i>Auricularia polytricha</i>	Auriculariaceae	1396.82		46.54		468.24		Lt
17	<i>Mycena olivaceomarginata</i>	Mycenaceae	26.25		270.87		1.22		Lt, So
18	<i>Mycena galopus</i>	Mycenaceae	17.67		114.40		27.77		Lt, So
19	<i>Trametes ochracea</i>	Polyporaceae	13138.98		3478.14				Lt
20	<i>Campanella tristis</i>	Marasmiaceae	258.05		18.59				Lt
21	<i>Marasmiellus</i> sp.1	Marasmiaceae	112.33		48.29				Lt
22	<i>Scutellinia scutellata</i>	Pyronemataceae	86.82		16.01				Lt
23	<i>Crepidotus versutus</i>	Crepidotaceae	65.12		81.53				Lt

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
24	<i>Hygrocybe helobia</i>	Hygrophoraceae	40.17		0.18				So
25	<i>Daldinia concentrica</i>	Xylariaceae	16.79		2.68				So
26	<i>Peziza succosa</i>	Pezizaceae	7.80		238.46				Lt
27	<i>Marasmius elegans</i>	Marasmiaceae	1.83		1.95				Lt
28	<i>Omphalina</i> sp.	Tricholomataceae	5128.71						Lt
29	<i>Bracket polypore</i>	Fomitopsidaceae	2647.81						Lt
30	<i>Perenniporia tenuis</i>	Polyporaceae	2182.38						Lt
31	<i>Trametes</i> sp.	Polyporaceae	2083.28						Lt
32	<i>Xylaria longipes</i>	Xylariaceae	1280.09						Lt
33	<i>Marasmiellus</i> sp.2	Marasmiaceae	1146.40						Lt, DW
34	<i>Amauroderma rude</i>	Ganodermataceae	277.15						Lt
35	<i>Clavulina ornatipes</i>	Clavulinaceae	245.61						LT
36	<i>Marasmius</i> sp.1	Marasmiaceae	222.41						Lt, So
37	<i>Calocera</i> sp.	Dacrymycetaceae	147.21						Lt
38	<i>Marasmius epiphyllus</i>	Marasmiaceae	120.26						Lt
39	<i>Phaeocollybia christinae</i>	Cortinariaceae	77.83						Lt, So
40	<i>Cookeina</i> sp.	Sarcoscyphaceae	74.57						Lt
41	<i>Marasmiellus dichrous</i>	Marasmiaceae	65.67						Lt, DW
42	<i>Phlebia coccineofulva</i>	Meruliaceae	62.42						Lt
43	<i>Cookeina sulcipes</i>	Sarcoscyphaceae	49.52						Lt
44	<i>Calvatia</i> sp.	Agaricaceae	29.80						So
45	<i>Stemonitis smithii</i>	Stemonitidaceae	28.74						DW
46	<i>Oudemansiella</i> sp.	Physalacriaceae	23.85						Lt, So
47	<i>Marasmius araucariae</i>	Marasmiaceae	20.64						Lt

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
48	<i>Cotylidia</i> sp.	Repetobasidiaceae	19.38						Lt
49	<i>Marasmiellus nigripes</i>	Marasmiaceae	15.56						Lt, DW
50	<i>Trogia infundibuliformis</i>	Marasmiaceae	14.67						Lt, So
51	<i>Leucocoprinus</i> sp.	Agaricaceae	12.70						Lt, LT
52	<i>Microporellus dealbatus</i>	Polyporaceae	10.53						Lt
53	<i>Entoloma</i> sp.2	Entolomataceae	5.62						Lt
54	<i>Boletus edulis</i>	Boletaceae	3.60						So
55	<i>Tremella fuciformis</i>	Tremellaceae	2.77						Lt
56	<i>Mycena</i> sp.	Mycenaceae	1.27						Lt
57	<i>Fomes fomentarius</i>	Polyporaceae	1.27						Lt
58	<i>Cotylidia diaphana</i>	Repetobasidiaceae	66.04			2.87			Lt
59	<i>Auricularia delicata</i>	Auriculariaceae		304.73					LT
60	<i>Trametes versicolor</i>	Polyporaceae		204.80					Lt, DW
61	<i>Entoloma flavidum</i>	Entolomataceae		158.86					So
62	<i>Coriolopsis</i> sp.	Polyporaceae		19.13					Lt
63	<i>Calvatia craniiformis</i>	Agaricaceae		1.27					So
64	<i>Perenniporia tephropora</i>	Polyporaceae		5725.23	430.93				DW
65	<i>Psilocybe cubensis</i>	Hymenogastraceae		278.09	4234.82	97.55			CD
66	<i>Xylaria</i> sp.	Xylariaceae			7.49	17607.59			So
67	<i>Hygrocybe</i> sp.1	Hygrophoraceae			219.45	158.58			So
68	<i>Hygrocybe miniata</i>	Hygrophoraceae			4.79	10.60			Lt, So
69	<i>Hygrocybe</i> sp.2	Hygrophoraceae			3.06	2.71			So
70	<i>Coprinopsis</i> sp.	Psathyrellaceae			1.27	1.27			Lt, DW
71	<i>Ganoderma</i> sp.1	Ganodermataceae			390.08	2845.14	52.59	22.49	Lt, DW

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
72	<i>Perenniporia</i> sp.1	Polyporaceae			13.37	370.91	147.65		DW
73	<i>Ganoderma</i> sp.2	Ganodermataceae			162.37	4.48	111.96		Lt, LT
74	<i>Elmerina</i> sp.	Exidiaceae			7506.07		430.18		Lt, LT
75	<i>Marasmius minutissimum</i>	Marasmiaceae			429.62		4.36		Lt, DW
76	<i>Ganoderma fornicatum</i>	Ganodermataceae			77.96		244.71		DW
77	<i>Geastrum saccatum</i>	Geastraceae			5.89		118.95		Lt, So
78	<i>Ganoderma</i> sp.3	Ganodermataceae			1.47		17.58		LT
79	<i>Stereum ostrea</i>	Stereaceae			711.01			8.12	Lt
80	<i>Cantharellus</i> sp.	Cantharellaceae			1829.55				LT
81	<i>Ganoderma chalconeum</i>	Ganodermataceae			1722.76				DW, LT
82	<i>Pycnoporus sanguineus</i>	Polyporaceae			639.52				DW
83	<i>Marasmius</i> sp.2	Marasmiaceae			484.97				Lt, DW, So
84	<i>Calocera cornea</i>	Dacrymycetaceae			317.01				LT
85	<i>Earliella scabrosa</i>	Polyporaceae			240.93				DW
86	<i>Collybia platyphylla</i>	Psathyrellaceae			238.25				Lt
87	<i>Coltricia perennis</i>	Hymenochaetaceae			30.96				Lt
88	<i>Microporus</i> sp.	Polyporaceae			26.64				Lt
89	<i>Marasmiellus vaillantii</i>	Marasmiaceae			18.54				Lt, So
90	<i>Boletus auripes</i>	Boletaceae			17.91				So
91	<i>Earliella</i> sp.	Polyporaceae			16.62				DW
92	<i>Inocybe</i> sp.	Inocybaceae			14.29				Lt, LT
93	<i>Cookeina tricholoma</i>	Sarcoscyphaceae			10.53				Lt
94	<i>Tremella</i> sp.1	Tremellaceae			9.82				So
95	<i>Perenniporia</i> sp.2	Polyporaceae			7.87				Lt

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
96	<i>Hygrocybe cantharellus</i>	Hygrophoraceae			2.50				DW
97	<i>Ganoderma resinaceum</i>	Ganodermataceae			2.15				So
98	<i>Cantharellus minor</i>	Cantharellaceae				478.20			Lt
99	<i>Entoloma</i> sp.1	Entolomataceae				193.01			Lt, So
100	<i>Filoboletus</i> sp.	Mycenaceae				122.72			Lt, DW
101	<i>Coprinellus</i> sp.2	Psathyrellaceae				25.80			Lt
102	<i>Conocybe</i> sp.	Bolbitiaceae				15.29			Lt, So
103	<i>Xantagaricus</i> sp.	Agaricaceae				10.90			So
104	<i>Lactarius</i> sp.	Russulaceae				9.99			So
105	<i>Russula</i> sp.	Russulaceae				7.96			So
106	<i>Trogia</i> sp.	Marasmiaceae				1.02			Lt, DW
107	<i>Boletellus emodensis</i>	Boletaceae					32.08	763.34	LT
108	<i>Coltricia cinnamomea</i>	Hymenochaetaceae					57750.71		DW, LT, So
109	<i>Ganoderma</i> sp.5	Ganodermataceae					28127.79		LT, So
110	<i>Elmerina</i> sp.2	Exidiaceae					206.80		Lt
111	<i>Ganoderma applanatum</i>	Ganodermataceae					193.47		Lt
112	<i>Boletus</i> sp.	Boletaceae					160.09		Lt, So
113	<i>Perenniporia rosmarini</i>	Polyporaceae					144.68		Lt
114	<i>Suillus luteus</i>	Sillaceae					120.42		DW, So
115	<i>Ganoderma</i> sp.4	Ganodermataceae					95.57		Lt
116	<i>Termitomyces</i> sp.	Lyophyllaceae					88.18		Lt, So
117	<i>Entoloma albidum</i>	Entolomataceae					50.66		So
118	<i>Pycnoporus</i> sp.	Polyporaceae					47.81		Lt
119	<i>Amauroderma rugosum</i>	Ganodermataceae					33.59		So

No	Species	Family	Cover Area cm ² / 0.25 ha						Substrate
			Karst		Lowland		Pine		
			Wet	Dry	Wet	Dry	Wet	Dry	
120	<i>Marasmius candidus</i>	Marasmiaceae					27.55		Lt, So
121	<i>Pleurotus</i> sp.	Pleurotaceae					9.39		So
122	<i>Stemonitis</i> sp.	Stemonitidaceae					7.96		So
123	<i>Russula fragilis</i>	Russulaceae						3033.01	So
124	<i>Ganoderma lucidium</i>	Ganodermataceae						141.18	LT
125	<i>Russula paludosa</i>	Russulaceae						45.86	So
126	<i>Baeospora myosura</i>	Marasmiaceae						13.06	So
127	<i>Crepidotus</i> sp.	Crepidotaceae						7.96	DW
128	<i>Conocybe apala</i>	Bolbitiaceae						3.18	So
129	<i>Leucocoprinus bimbaumii</i>	Agaricaceae						1.59	So
130	<i>Boletellus</i> sp.	Boletaceae						1.27	So
Total Cover Area			39549.23	93911.07	34644.36	70906.49	88997.26	4308.25	
Total Number of Species			65		67		42		
Number of Species Found in the Wet Season			48		41		29		
Number of Species Found in the Dry Season			7		12		10		
Number of Species Found in Both Season			10		14		3		

Note for the Substrate: Lt = Litter; DW = Decayed Wood, LT = Living Tree; CD = Cow Dung; So = Soil

Data from this study indicate that in the wet season, soil moisture was significantly the highest in the Karst forest, the second highest was in the Lowland forest, and the lowest was in the Pine forest. Meanwhile, in the dry season the highest soil moisture was observed in the Lowland forest, followed by the Karst forest and the lowest was also in the Pine forest. Rendzina soil with a clay texture on porous limestone bedrock in Karst forest is likely to be able to hold more water during the wet season compared to Cambisol soil with dusty clay mixed with small, medium and large stones in the Lowland forest. However, during the dry season, denser canopy cover in the Lowland forest, characterized by lower light intensity, can better retain moisture under the forest stand, causing soil moisture in the Lowland forest to be higher than Karst forest. Low soil moisture in Pine forests compared to Karst forests and Lowland forests can be caused by the needle cover of Pine forests which allows a lot of sunlight to reach the forest soil surface (North et al., 2005; Park et al., 2022), as well as caused by the higher transpiration rate of Pine forest stands compared to broadleaf forest stand (Swank and Douglass, 1974). In general, data on variations in inter-forest microhabitat conditions were consistent with macrofungal species' inter-forest diversity. More species of macrofungi were found in forests with higher soil moisture, lower light intensity, and higher soil pH.

Macrofungi cover area in the wet season was largest in the Pine forest, followed by the Karst forest, and lowest in the Lowland forest. Meanwhile in the dry season, the cover area of macrofungi showed the largest value in the Karst forest, followed by Lowland forest and the lowest was in Pine forest. *Trametes ochracea*, *Elmerina* sp. and *Coltricia cinnamomea* were macrofungal species with the largest cover area respectively in Karst, Lowland, and Pine forests during the wet season. Meanwhile, in the dry season, *Inocybe rimosa*, *Microporus xanthopus*, and *Russula Fragilis* were the species with the largest cover area respectively in Karst, Lowland, and Pine forests.

The distinct difference in the cover area of macrofungi between forest communities, either in the wet or the dry season, is apparently related to the cover area (colony size) of species unique to certain forest communities in a certain season. For example, two macrofungal species (*Coltricia cinnamomea* and *Ganoderma* sp.5) that were only found in Pine forest in the wet season have large colony size covering up to 85878.50 cm² or 94% of the total cover of all macrofungal species in this forest community. While in the dry season, the

existence of *Polyporus* sp, *Favolus* sp., and *Inocybe rimosa* with large colony size (82332.25 cm² or 88% of the total cover area of macrofungi in this forest) only in Karst forest made the total cover area of macrofungi in this forest became the largest. Thus, the diversity of macrofungal species must not always be in line with the cover area since each species performs a different size of fruiting body and colony size.

Most of the macrofungal species found in this study were saprophytic and growing on litter or soil substrate, while some species were ectomycorrhiza fungi, (Table 5.3). Litter was the substrat most supported the growth of macrofungal species (81 species), followed by soil (46 species), weathered wood (25 species), and living trees (17 species). One species was found to grow on cow dung. As to the substrate on which they grow, saprotrophic fungi are generally monophagous, using only the litter of a single tree species as a substrate (Tibuhwa, 2011). Only a few species can grow on different substrate types. This is related to the differences in carbon and nutrient requirements for each macrofungal species, which are determined by the chemical properties of the substrate, such as the ratio of lignin, hemicellulose, cellulose, and pH (Grinhut et al., 2007). Therefore, differences in the diversity of macrofungal species among forest communities are inseparable from the type of forest community. This is because different forest communities are composed of and dominated by different tree species. Shay (2016) further stated that the diversity of macrofungi has a strong correlation with the diversity of tree species that compose forest stands, especially in tropical habitats.

Several species of macrofungi were found to be specialists only in a certain forest community (Table 5.3). Differences in the successional stage and environmental conditions may cause differences in the structure and species composition among forest communities. This enables one tree species to grow in a certain forest community but not in other forest communities. Given that most fungi are monophagous, it is not surprising that there are species of macrofungi that are only found in certain forest communities, along with their host plants that are only found in that forest community.

When compared between broadleaf forests and pine forests, the data from this study show that the diversity of macrofungal species in the broadleaf forests (Karst and Lowland forests) is distinctly higher compared to Pine forest. This appears to be due to the higher diversity of three species in broadleaf (Table 5.1). In addition, microclimatic conditions such as high soil moisture, lower light intensity,

and higher soil pH in the broadleaf forest are more favorable for the growth of many macrofungal species than those in Pine forests. The acidic pH will affect the quality of carbon needed by macrofungi to grow (Andersson et al., 2000; Kemmitt et al., 2006). Rousk et al. (2009) revealed that the soil pH gradient often correlates with the vegetation structure, which will indirectly form the colonization of different fungal species.

5.5 CONCLUSION

In total, we found 130 species of macrofungi in the three forest communities identified in 38 families. Seasonally, more species were found during the wet season in all forest communities, and some species were found to be adaptable to both seasons. Among the forest communities, more species were found in broadleaf forests than in Pine forests. This study reveals that the season, species structure and composition of the forest community, and some microhabitat conditions in particular soil moisture, light intensity, and soil pH determine the diversity and distribution species of macrofungi across the three forest communities studied.

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CHAPTER 6

DIFFERENCES IN THE VEGETATION DYNAMIC PATTERNS OF THREE TROPICAL SECONDARY FORESTS IN SOUTH SULAWESI, INDONESIA

6.1 ABSTRACT

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: succession, population, tree density, basal area, species composition

6.2 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.

6.3 MATERIAL AND METHODS

6.3.1 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 6.1, 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.

Table 6.1. 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>Pinus 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 loamy texture
Altitude (m asl)	271	563	501

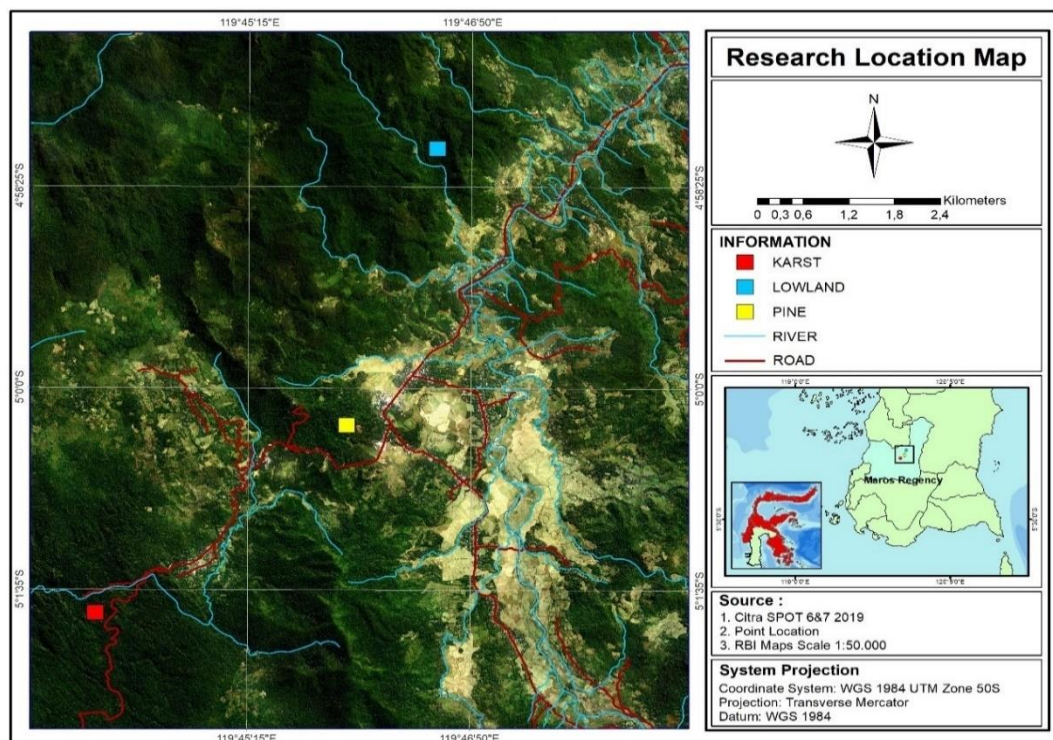


Figure 6.1. Map showing the locations of the three forest types studied. (Source: Putra et al., 2023).

6.3.2 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 6.2). 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.

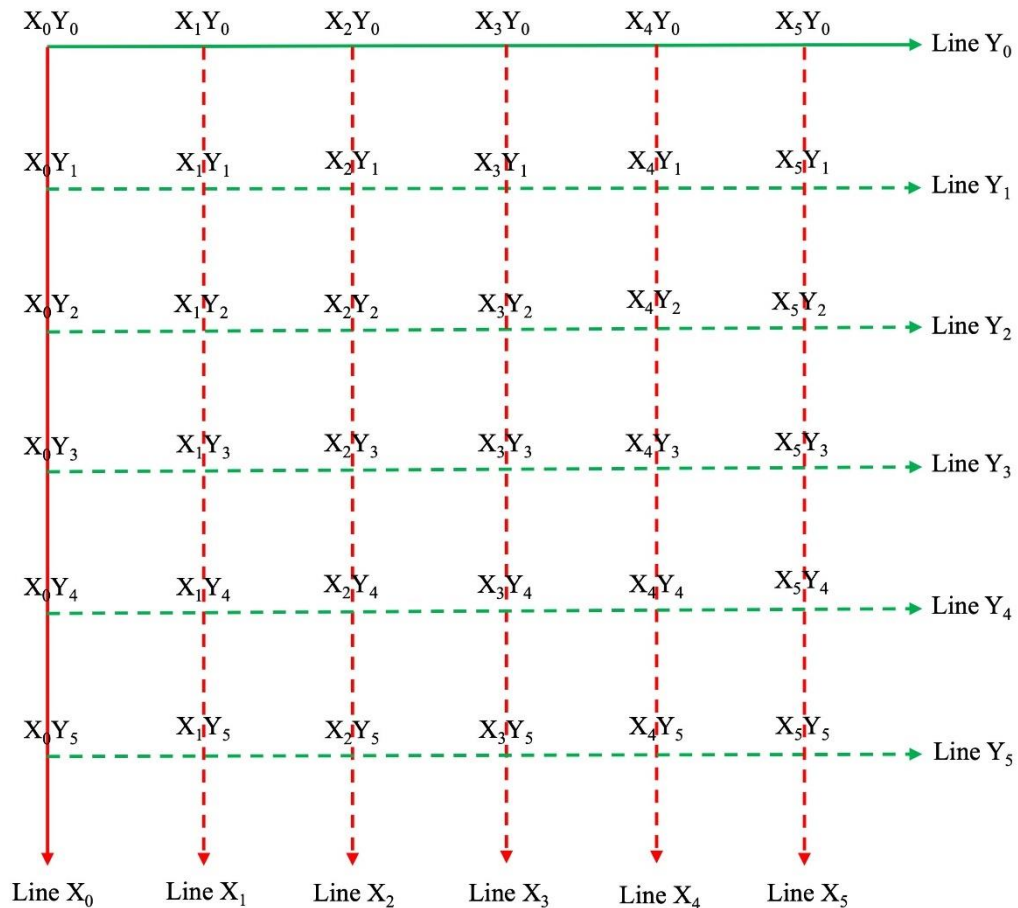


Figure 6.2. Sketch of the steps for setting a permanent plot.

6.3.3 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.

6.3.4 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).

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

Where BA = basal area, π = constant 3.14, r = trunk girth 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 m^2/ha for the BA).

6.4 RESULTS

6.4.1 Dominant Species Composition and Structure

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, *Arthrophyllum 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 6.2. 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.	Cluciaceae	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>Arthrophyllum 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		29.75	46.89	60.60
Total Species		90	61	42

6.4.2 Dynamics of BA and Density of the Karst Forest

The density of trees ≥ 5 cm in diameter was reduced year over year (Figure 6.3 left) 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 6.3 right). The total BA grew from 29.75 m^2/ha in 2019 to 30.24 m^2/ha in 2020. In 2021, the BA again increased to 31.05 m^2/ha , and it rose to 31.63 m^2/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.

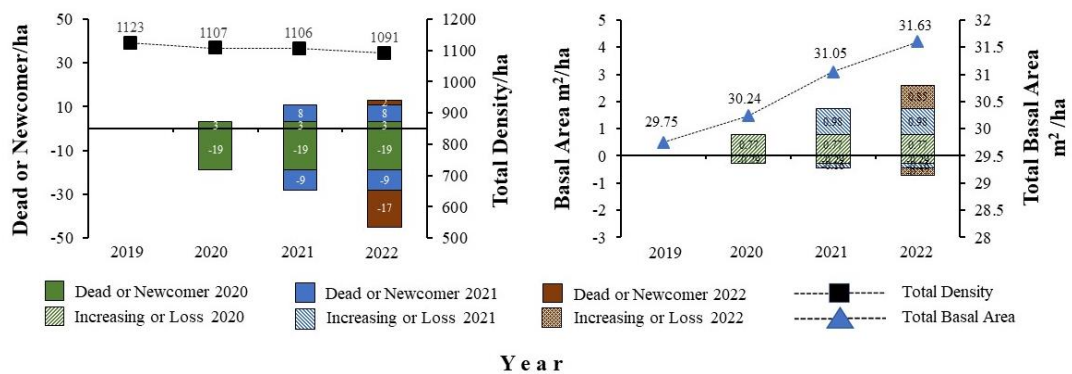


Figure 6.3. The dynamics of forest structure based on total density (left) and total basal area (right) in the Karst forest over four years (2019 to 2022).

6.4.3 Dynamics of BA and Density of the 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 6.4 left). 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 6.4 right). In the first year of observation in 2019, the total BA was 46.89 m^2/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.

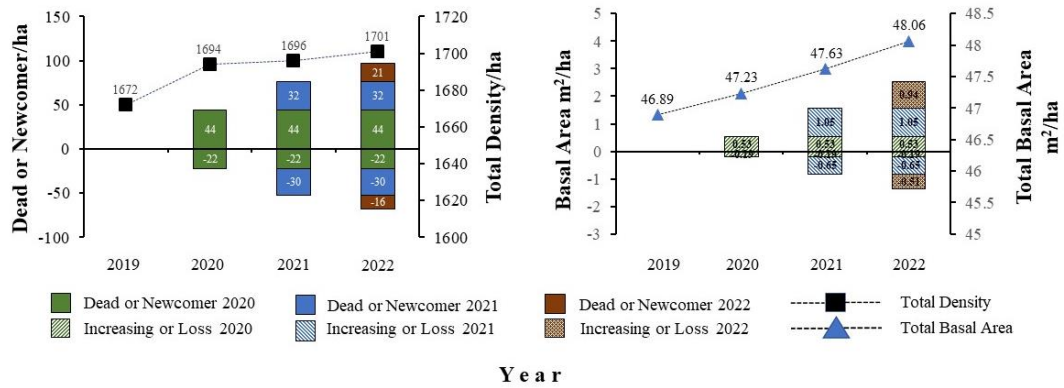


Figure 6.4. The dynamics of forest structure based on total density (left) and total basal area (right) in the Lowland forest over four years (2019 to 2022).

6.4.4 Dynamics of BA and Density of the Pine Forest

In the Pine forest, the total density of trees with a diameter of ≥ 5 cm showed a different pattern each year (Figure 6.5 left). 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.

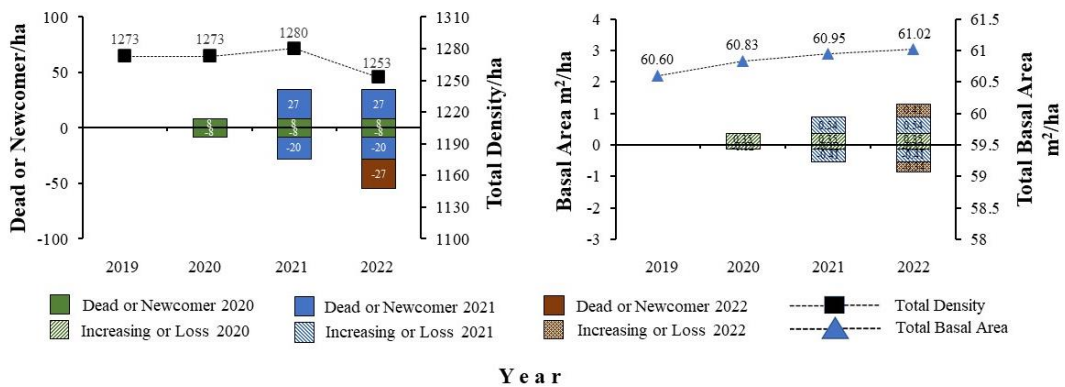


Figure 6.5. The dynamics of forest structure based on total density (left) and total basal area (right) in the Pine forest over four years (2019 to 2022).

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 6.5 right). 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.

6.4.5 Population Dynamics

In the first year of observation (2019) in the Karst forest, 90 species were found in a plot of 0.75 ha. Of the 90 species, 25 species experienced the dynamics of the number of individuals over the four years of observation. 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.).

In the first year of observation, 61 species were found in the Lowland forest plot. Of the total number of species, 27 species experienced dynamics in the number of individuals during the four years of research. Twelve species saw growth in the number of individuals (*A. catechu*, *D. celebica*, *Garcinia celebica* L., *C. iners*, *D. dao*, *Lansium domesticum*, *G. paniculata*, *Horsfieldia bivalvis* Merr., *Anacolosa frutescens* Blume, *Melicope lunu-ankenda* (Gaertn.) T.G.Hartley, *Diospyros* cf. *Sundaica* Bakh., and *Syzygium* sp.), and 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.

Of 42 species found 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*, *Neolitsea cassiaefolia*, *Schima wallichii*, *D. dao*, *F. rukam*, and *Coffea 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 the number of 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*, which is a broadleaf species that has a small tree habitus.

6.5 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 coffasus*, *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).

6.6 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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CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1 DISCUSSION

The elements that make up a forest ecosystem are diverse and can be broadly divided into abiotic elements (soil, climate components, altitude, elevation and the chemical environment) and biotic elements (flora and fauna and the organic materials they produce) (Cleland et al., 1997; Britannica, 2023). These elements interact within a very complex system to determine the rate and direction of the development of forest communities until they reach a stable condition called climax (Zhou et al., 2021). Forests are cybernetic ecosystems where trees are the primary autotrophic organisms that produce organic material for life in subsequent tropical structures (Munawar et al., 2011; Baltzinger et al., 2012). Only a small part of the forest tree's production is utilised by organisms at the higher tropical levels, and most of the remainder accumulates on the ground surface as litter. Litter that accumulates on the surface of the forest floor decomposes and produces nutrients for the soil.

Apart from being influenced by the extrinsic environment (both abiotic and biotic elements), the production of a forest ecosystem is also influenced by intrinsic factors such as the composition and structure of the species that make up the forest stand (Park et al., 2019). Forest stands of different ages consist of different tree species with different stand structures; they produce litter in different quantities and qualities and decompose at different rates (Salim and Budiadi, 2014). The production and decomposition of litter produced by a forest stand determines the input of nutrients into the soil, which are then reused by the trees that make up the forest stand as they grow (Yang et al., 2004; Giweta, 2020). The greater the production and rate of decomposition of litter in a forest stand, the faster the development of the forest ecosystem.

In secondary forests, at the succession stage, the composition of the litter produced by the forest stand is essential in understanding its ecological properties given that the diversity of plant species is related to biomass production and the availability of nutrients in the soil; it also provides information about their relationship with soil organisms (Michopoulos et al., 2019; Dong et al., 2022). The results of this study show that of the three forest communities studied, the highest cumulative annual litter production was recorded in the Lowland forest, followed by the Pine forest and then the Karst forest. Leaves were the most abundant litter component produced by the three forest communities, followed by reproductive

organs and twigs, except in the Karst forest, where the twig component was higher than the reproductive organs. Specific separation of litter components is essential because it can provide information about phenology and nutrient cycling patterns (Van et al., 2002; Ferreira et al., 2014). According to Vitousek (1984), young forests have a higher leaf turnover than old forests, which may be an adaptation for ecosystem restructuring. The results of this study indicate that less leaf litter was produced in the Karst forest than in the older Lowland forest. When compared with the stand age, the tree density and basal area cover appear to have a positive influence on the leaf litter production.

Seasonally, Karst and Pine forests produce more litter in the dry season than in the wet season, but in the Lowland forest, the litter production did not significantly differ between seasons. Different phenological patterns between tree species that form forest stands could be the cause of this. Such as the dominance of pioneer species in the Karst forest, some of which shed their leaves during the dry season (Ishida et al., 2013), due to reduced soil moisture during that season. The same thing also happens in the Pine forest, where pine trees that have a high transpiration rate are susceptible to drought, so they shed many of their leaves in the dry season to reduce transpiration (Poyatos et al., 2013; Jacquet et al., 2014). The high level of defoliation in most tree species in the Karst and Pine forests affects the reproductive phenology cycle. The reproductive period begins before the peak of the dry season, and the fruit reaches maturity in the dry season and falls at the same time as the leaves fall. Tree species in the Karst forest and *P. merkusii* in Pine forest will try to ripen their fruit before dropping all or most of their leaves in the dry season because, without leaves, they can no longer carry out photosynthesis to produce carbohydrates to enlarge their fruit. Orthodox seeds produced by pioneer tree species do not have to germinate immediately after being dropped because they can remain dormant for decades in the soil (Solberg et al., 2020; Matilla, 2022), so there is no problem with fruit dropping in the dry season.

Climax tree species produce fleshy fruits with large seeds that require a relatively longer growing time to ripen (Susanto et al., 2016; Rungrojtrakool et al., 2021). These seeds are dormant for a short time and must germinate immediately under the canopy of dense forest stands after being dropped from the parent tree (Obroucheva et al., 2016). This species of tree ripens and drops its fruit during the wet season because the wet soil conditions during the wet season support the growth of the newly germinated seeds. Therefore, climax tree species must retain

their leaves to preserve their fruit during the dry season by developing water-saving transpiration (Boonkorkaew et al., 2012). This may explain our finding of why litter production in the Lowland forest dominated by climax species did not differ between the dry and wet seasons.

Litter production, decomposition, and nutrient cycling have been studied in various forest types worldwide (Van et al., 2002; Pandey et al., 2007; Chakravarty et al., 2019; Wongprom et al., 2022). Some researchers (Yang et al., 2004; Demessie et al., 2012) believe that broadleaf forests with high litter production will have a high decomposition rate. If attention is paid to the amount of biomass decomposed (biomass loss), the results of this study show the same trend as reported by Yang et al. (2004) and Demessie et al. (2012). However, if the k -value of the decomposition rate is considered, it can be seen that the Karst forest, which has much lower total litter production than the Lowland forest, shows a higher k -value. This is possible given that the k -value is relative to the total amount of litter produced. The higher k -value in the Karst forest compared to the Lowland forest is caused by the total litter production in the Karst forest being lower than in the Lowland forest, which makes the k -value in the Karst forest proportionally higher. If broadleaf forests are compared with needle-leaf forests, the total litter production in the Pine forest is not significantly different from that of the Karst and Lowland forests, but the decomposition rate in the Pine forest is much slower than in the Karst and Lowland forests. Thus, the results of this study explain that the rate of decomposition does not always have to be directly or inversely proportional to litter production. Depending on the combined influence of the intrinsic and extrinsic factors, the litter production and decomposition rates can vary between forest communities.

Leaves are the litter components that are easily decomposed compared to wood. According to Cao et al. (2020), about half of the net primary productivity of forest ecosystems is returned to the soil through leaf litter decomposition. However, leaf litter from different tree species has different decomposition rates. For example, needle leaves of *Pinus* spp. are known to have a prolonged decomposition rate compared to broad leaves (Prescott et al., 2000; Sheffer et al., 2015). The relatively high lignin content in *Pinus* spp. leaves could be the main factor inhibiting decomposition (Talbot and Treseder, 2012). However, the results of this study show different results, where the decomposition rate of tusam (*P. merkusii*) needle leaves was faster than that of ebony leaves in broadleaf forest communities (Karst

and Lowland forests). This may be caused by the lower content of secondary metabolites such as phenolics, tannins, and resins in tusam needle leaf litter compared to ebony leaf litter. High secondary metabolite content can indirectly be toxic to decomposing agents (Cameron and LaPoint, 1978; Heil et al., 2002; Salminen et al., 2011). In addition, the high diversity of decomposing agents in broadleaf forests, most of which are lignin decomposers, is the reason why the decomposition rate of tusam leaves is faster than ebony leaves in broadleaf forest communities.

Apart from leaves, wood is a component of litter, which contributes significantly to restoring forest soil fertility. Although the wood decomposition process takes longer than leaves, the contribution of wood litter to C turnover is comparable to leaf litter (Gill and Jackson, 2000). Like leaf litter, wood from different tree species will contain different chemical compounds. The results of the research show that jabon wood decomposes more quickly in the dry season than in the wet season, while the opposite trend occurs for tusam wood. The high abundance of *Odontotermes* sp. in the dry season shows a significant relationship to the mean *k*-value of Jabon wood in the season. Tusam wood contains more hemicellulose than Jabon wood. Hemicellulose significantly improves water absorption behavior, potentially reducing wood's resistance to attack by microorganisms (Zhang et al., 2011; Hosseinaei et al., 2012). This research shows that there is a significant positive correlation between the number of bacterial species and the mean *k*-value of tusam wood decomposition for one year, starting at the beginning of the wet season. Macrofauna *Odontotermes* sp. have a stronger influence than microorganisms in determining the wood decomposition rate at the beginning of the decomposition process (see also Collins, 1981). However, in a longer decomposition process, physical environmental factors can influence microbial activity more effectively than macrofauna, both directly and indirectly (Hu et al., 2021).

Several previous studies have shown that the decomposition rate in coniferous forests is lower than that of broadleaf forests (Prescott et al., 2000; He et al., 2007; Guo et al., 2007; Lorenz et al., 2004). In general, the results of this study support those of previous studies, but they are not fully consistent. For example, the decomposition rate of jabon wood (a broadleaf species) in the dry season is higher in the Pine forest than in the Lowland forest. The decomposition rate of tusam wood (a coniferous species) did not show significant differences

among the three forest communities in the dry season experiment and the decomposition rate of the ebony leaves (a broadleaf species) in the Lowland forest during the wet season was not significantly different from that of the Pine forest.

Whitten et al. (1987) explain that in contrast to forest ecosystems in other tropical regions, the forest ecosystem in Sulawesi is characterised by very diverse tree compositions without a clear dominant species. This, of course, has consequences for the chemical quality of the litter produced, which varies greatly even within the same type of forest community (Pérez-Harguindeguy et al., 2000; Hättenschwiler, 2005). Given that the process of litter decomposition is influenced by intrinsic factors (litter quality) in addition to extrinsic factors (Bryant et al., 1998; Cai et al., 2021), litter of different qualities will have a different resistance to attack by decomposing agents (Chae et al., 2019; Yan et al., 2019). This study found that decomposing agent microorganisms from different forest communities, or even from different tree species within the same forest community, were generally not the same (see Chapters 3 and 5). The data from the wood decomposition experiments show an abnormal distribution, even though the number of wood samples was in the thousands. Thus, the results of this study support the theory that the decomposition process is a very complex process, involving various intrinsic and extrinsic factors whose presence can vary greatly from one place to another, even within the same habitat type (Powers et al., 2009; Austin and Ballaré, 2010; Fukasawa and Matsukura, 2021).

Suppose this study's results are compared with those reported in temperate regions. In this case, it can be seen that annual litter production in tropical forests is higher than in temperate forests (see Patrício et al., 2012; Tiwari and Joshi, 2015; Leal et al., 2023 for the litter production in temperate climates). The decomposition rate data in this study also shows values that are faster than those reported from research in forests in temperate regions (see Lorenz et al., 2004; Powers et al., 2009; Bisht et al., 2014 for the decomposition rate in the temperate climates). The year-round growing season in tropical regions can cause higher litter production than in temperate regions. In tropical regions, there is no winter when plants stop producing. The year-round growing season also allows trees in forest stands in tropical areas to grow taller and thicker, resulting in more litter (Leigh Jr et al., 2004). In contrast to temperate climates, warm temperatures throughout the year and higher humidity support the life of decomposing agent microorganisms better in tropical areas (Pietsch et al., 2019). However, in tropical

areas, decomposition also occurs very slowly in cold subalpine ecosystems on high mountain peaks, so most of the litter does not decompose and forms peat. In tropical forests, peat can also form in areas with high rainfall and falls throughout the year. This is because rainwater is acidic and can inhibit the growth of decomposing agent microorganisms (Lim et al., 2011; Shah and McCormack, 2020), which ultimately causes the litter's decomposition not to run well.

Although statistically not completely significant, which may be due to the small number of soil samples analysed, the results of this study show that, as indicators of soil fertility, the C, N and CEC were found to be the highest in the Lowland forest soils, lower in the Karst forest and lowest in the Pine forest. However, of the three forest communities studied, the highest C/N values were recorded in the Karst forest, with the lowest values found in the Pine forest. The C, N and CEC values of the soil in the three forests studied are not in line with the k -value of decomposition, which was found to be the highest in the Karst forest, lower in the Lowland forest and lowest in the Pine forest; they are, however, in line with the value of the biomass loss, which is highest in the Lowland forest, lower in the Karst forest and lowest in the Pine forest. The basal area growth rate was highest in the Karst forest, lower in the Lowland forest and lowest in the Pine forest. The mismatch in decomposition rates, soil fertility levels (C, N, C/N, and CEC) and basal area growth between the three forests does not mean that the decomposition rates and soil fertility do not affect forest growth. Rather, the difference in the dominant species between the young broadleaf secondary forest (Karst) and the old broadleaf secondary forest (Lowland) could be the cause of this mismatch. Pioneer species, fast-growing species that dominate the Karst forest, such as *Kleinhovia hospita*, *Cananga odorata* and *Pterospermum celebicum*, grow faster than primary species, such as *Palaquium obovatum*, *Diospyros celebica* and *Areca catecu* (palm species), which dominate the Lowland forest. However, when considered from a biomass perspective, it is not certain that trees that grow faster in diameter have a higher biomass growth. This is because biomass is related to specific gravity, and fast-growing pioneer species generally have low specific gravity. Unfortunately, the forest growth variable measured in this study was not the biomass but rather the basal area.

Before finally experiencing a natural succession process, the three forest communities studied had the same history of land use in the form of shifting cultivation. The Karst forest areas began to be abandoned around 1970, the

Lowland forest around 1965 and the Pine forest around 1960, at this time, these areas were in an infertile condition. The succession process not only gradually restores the forest vegetation cover, but at the same time it also restores the soil fertility through litter production and decomposition (Furey and Tilman, 2021). Older forests experience a longer process of returning nutrients than younger forests (Xiong et al., 2021; Yin et al., 2021). This could be another reason why the C and CEC values in the Lowland forest are higher than those in the Karst forest (Wang et al., 2017; Xiong et al., 2021).

The Pine forest is the oldest of the three forests; however, based on the soil fertility indicators, it has the lowest C, N, C/N and CEC values. This appears to be related to the low rate of litter decomposition in the Pine forest community. As a result, the growth rate of the basal area in the Pine forest is also slower than in the other two forest communities. Regardless of what factors cause the low rate of decomposition in the Pine forest, the results of this research support previous findings, which indicate that the rate of decomposition is directly proportional to the level of soil fertility (Soares et al., 2020); this in turn, determines the production (biomass growth) of the forest stand (Hansson et al., 2020).

7.2 CONCLUSIONS

Research on forest litter production and its decomposition rate has generally been carried out in subtropical and temperate climates. This study is one of the few that consider the relationship between the litter production, decomposition rate and forest dynamics in tropical regions. Not entirely in line with the results of research in subtropical and temperate regions, this study has revealed several new findings:

1. Seasonal litter production patterns vary greatly between forest communities, both between broadleaf forests and between broadleaf forests and needle-leaved forests. The age of the stand determines the species composition that makes up the stand, where according to the level of succession, each tree species has its own phenological adaptation pattern regarding the annual dynamics of climate elements. This, in turn, influences the seasonal litter production pattern of a forest stand and differentiates it from other forest stands.

2. The low rate of decomposition of *P. merkusii* litter under its parent tree stand is not caused by the *P. merkusii* litter containing a chemical composition that is difficult to degrade. Rather, it is due to the microhabitat conditions under the pine stands, which cause very few decomposing microorganisms to live there. This inhibits the rate of decomposition not only in *P. merkusii* litter but also in litter from broadleaf species. This is explained by data showing that *P. merkusii* litter decomposes more quickly than broadleaf litter under broadleaf forest stands. However, this study has not found the level of difference and the causes of these differences in microhabitat conditions between broadleaf forest communities and needle-leaved forest communities.
3. The decomposition rate of jabon wood tends to be higher in the dry season compared to the wet season across the three forest communities, while tusam wood samples showed the opposite trend. This difference indicates that the decomposition process in tropical forests is complex and varies at the microsite scale following the diversity of suitable decomposing agents and their complex interrelationships. The decomposition rate of either jabon or tusam wood samples was higher in broadleaf forests than in pine forests. This inter-forest difference is proportional to the difference in the diversity and abundance of decomposing agents between forest communities.
4. Decomposition rates, both seasonal and annual, do not always coincide with litter production and show wide variations between forest communities and between locations within the same forest community. These findings explain that the factors that control the course of the decomposition process are very complex and vary from one place to another, even within the same forest community.
5. The diversity of microorganisms in a forest community, on the one hand, determines the rate of decomposition, while on the other hand, the variety of microorganisms is determined by the composition of the tree species that make up the forest community. For example, one finding of this study shows that macroscopic fungi are only associated with one tree species as their host. Hence, the presence of the host tree determines its existence and only degrades the biomass of the host tree.
6. Litter production is directly proportional to the decomposition rate if seen from the biomass loss value (not the *k*-value). However, it is not entirely

proportional to the tree's basal area growth rate: the basal area growth is not always the same as the biomass growth because the basal area is only related to volume, while biomass is also associated with specific gravity apart from the basal area. Unfortunately, this research did not use biomass as a forest growth parameter.

7.3 REFERENCES

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