Original Article

Available online at
www.heca-analitika.com/ljes

Leuser Journal of Environmental Studies

Vol. 4, No. 1, 2026

Patterns of Termite Diversity and Their Ecological Associations with Dipterocarpaceae in the Soraya Research Station, Leuser Ecosystem, Indonesia

Iqbar Iqbar [1,2], Djufri Djufri [3,*], Syaukani Syaukani [2], and Darusman Darusman [4]

[1] Graduate School of Mathematics and Applied Sciences, Universitas Syiah Kuala, Banda Aceh 23111, Indonesia; iqbar@usk.ac.id (I.I.)
[2] Biology Department, Faculty of Mathematics and Natural Sciences, Universitas Syiah Kuala, Banda Aceh 23111, Indonesia; syaukani@usk.ac.id (S.S.)
[3] Biology Department, Faculty of Education and Teacher Training, Universitas Syiah Kuala, Banda Aceh 23111, Indonesia; djufri_bio@usk.ac.id (D.D.)
[4] Department of Soil Science, Faculty of Agriculture, Universitas Syiah Kuala, Banda Aceh 23111, Indonesia; darusman@usk.ac.id (D.D.)

* Correspondence: djufri_bio@usk.ac.id

Article History

Received 13 February 2026
Revised 5 April 2026
Accepted 16 April 2026
Available Online 26 April 2026

Keywords:
Isoptera
Coarse wood debris
Natural resistance
Forest recovery
Bioindicators

Abstract

This study aimed to assess termite diversity and habitat distribution at the Soraya Research Station (SRS), analyze ecological associations between termite species and Dipterocarpaceae, and identify key interaction types and their ecological roles in forest succession. Termite sampling was conducted using a standardized belt transect method across 50 subplots (0.5 ha). A total of 48 termite species from 2 families and 17 genera were recorded, with Termitidae (43 species) being the dominant family. Termite distribution was strongly associated with decomposing substrates, particularly fallen logs, while living trees showed high resistance to colonization. Despite the dominance of Dipterocarpaceae, only 10.4% of termite taxa interacted directly with these trees, and 92,1% of examined Dipterocarpaceae structures showed no active colonization. Specific interactions identified included neutral associations (*Hospitalitermes hospitalis),* opportunistic pest (*Nasutitermes roboratus),* and specialized decomposers *(Coptotermes curvignathus, Macrotermes malaccensis,* and *Pericapritermes samarangi*). The high termite diversity indicates significant ecological recovery at SRS. Termite-host interactions are primarily governed by substrate quality and decomposition stages rather than host identity, highlighting the effective structural and chemical defenses of living Dipterocarpaceae in secondary tropical forests.

1. Introduction

Tropical lowland Dipterocarp/Dipterocarpaceae forests are among the most biodiverse globally and play a crucial role in maintaining ecological stability, carbon storage, and biodiversity conservation [1]. The Soraya Research Station (SRS), located within the Leuser Ecosystem, is a secondary lowland Dipterocarp Forest undergoing natural regeneration following historical logging. Over the past three decades, protection efforts have enabled forest recovery, although structural changes remain evident, particularly in the reduced abundance of large trees [2, 3].

Termites are recognized as key ecosystem engineers in tropical forests, contributing significantly to decomposition processes, nutrient cycling, and soil formation. By breaking down wood, litter, and other

DOI: 10.60084/ljes.v4i1.397

organic materials, termites accelerate carbon turnover and enhance soil fertility, thereby supporting forest regeneration [4–6]. In Dipterocarp-dominated ecosystems, termites interact with both living and dead trees, influencing vegetation dynamics and ecosystem processes [7–9]. Termite termitaria, for example, increased soil and forest diversity in dry Dipterocarps Forest by enriching cation exchange and counteracting alkaline erosion [9–11].

Recent studies have highlighted the importance of termites in tropical ecosystems, demonstrating their contribution to decomposition and ecosystem resilience under environmental stress. A 2019 study in Malaysian tropical forests showed that termites mitigate drought effects by increasing soil moisture. In Indonesia, a 2021 survey in Kalimantan found high termite diversity in post-logging forests, supporting nutrient cycling, while a 2023 study in Central Java linked termite diversity to soil factors in Dipterocarp forests. However, most studies have focused on general diversity patterns or ecological functions, while species-specific interactions with Dipterocarps remain poorly documented, particularly in Southeast Asia [12–16].

In the Leuser Ecosystem, previous studies have reported termite diversity and their role in supporting wildlife, including the Sumatran orangutan (*Pongo abelii*), which utilizes termites as a protein source [2, 17–19]. Research from 2021-2022 at SRS confirmed orangutan feeding behaviors that include arboreal termites from the Dipterocarpaceae [2, 20]. Nevertheless, detailed information on termite infestation patterns in Dipterocarpaceae, particularly across different substrate conditions (living trees, dead trees, stumps, and logs), is still limited.

Therefore, this study aims to: (1) Assess termite diversity and habitat distribution in Soraya Research Station; (2) Analyze ecological associations between termites species and Dipterocarpaceae; (3) Identify key interaction types and their ecological roles in forest succession. This study provides new empirical data on termite-Dipterocarpaceae interactions and contributes to a better understanding of ecosystem functioning in tropical secondary forests.

2. Materials and Methods

2.1. Study Area

The research was conducted in Soraya Research Station (SRS), Subulussalam, Aceh, Indonesia, located at coordinates (02°55’30.1” N and 97°55’42.5” E (Figure 1). The area represents a lowland Dipterocarps forest with an elevation up to 350 m above sea level. The climate is characterized by annual rainfall ranging from 196.9 to 245 cm, average temperatures 25.3 to 26.6°C, and relative humidity around 87% [21].

2.2. Sampling Design

Field sampling was conducted in two randomly selected main plots totaling 0.5 ha, which were divided into 50 subplots (10 m x 10 m). The plots were randomly created to capture habitat variability [9, 22, 23].

2.3. Termite Sampling

Termites in the Soraya Research Station (SRS) were surveyed across 50 established subplots using a standardized belt transect sampling method, widely applied in tropical termite studies. All potential termite habitats within each subplot were systematically examined through direct observation and active colony searching. The surveyed substrates include living trees, dead standing trees, and stumps from both Dipterocarpaceae and non-Dipterocarpaceae species, as well as fallen logs, litter, and soil mounds.

Particular attention was given to trees with a diameter at breast height (DBH) ≥ 10 cm. Each tree was carefully inspected from the base, including the surface and buttress roots, and extended upward along the trunk to a height of approximately 2 m. Smaller vegetation was only recorded when termite activity was observed.

Termite specimens were collected manually with forceps to represent both worker and soldier castes, with approximately 10-20 individuals per caste to ensure reliable identification using diagnostic morphological characteristics. Specimens were carefully extracted and preserved in vials containing 70% ethanol, labeled with complete location data for identification [9, 24].

2.4. Identification

All collected termite specimens were identified to the species level whenever possible; when species-level identification was not feasible, specimens were identified to the genus level. The identification process was conducted at the Biosystematics Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Syiah Kuala, where specimens were also curated as reference collections.

Termite identification was based on detailed morphological examination, including key diagnostic characters such as the antennae, mandibles, pronotum, labrum, postmentum, and head capsule. Observations were performed using a LEYBOLD™ stereomicroscope with 10× ocular magnification.

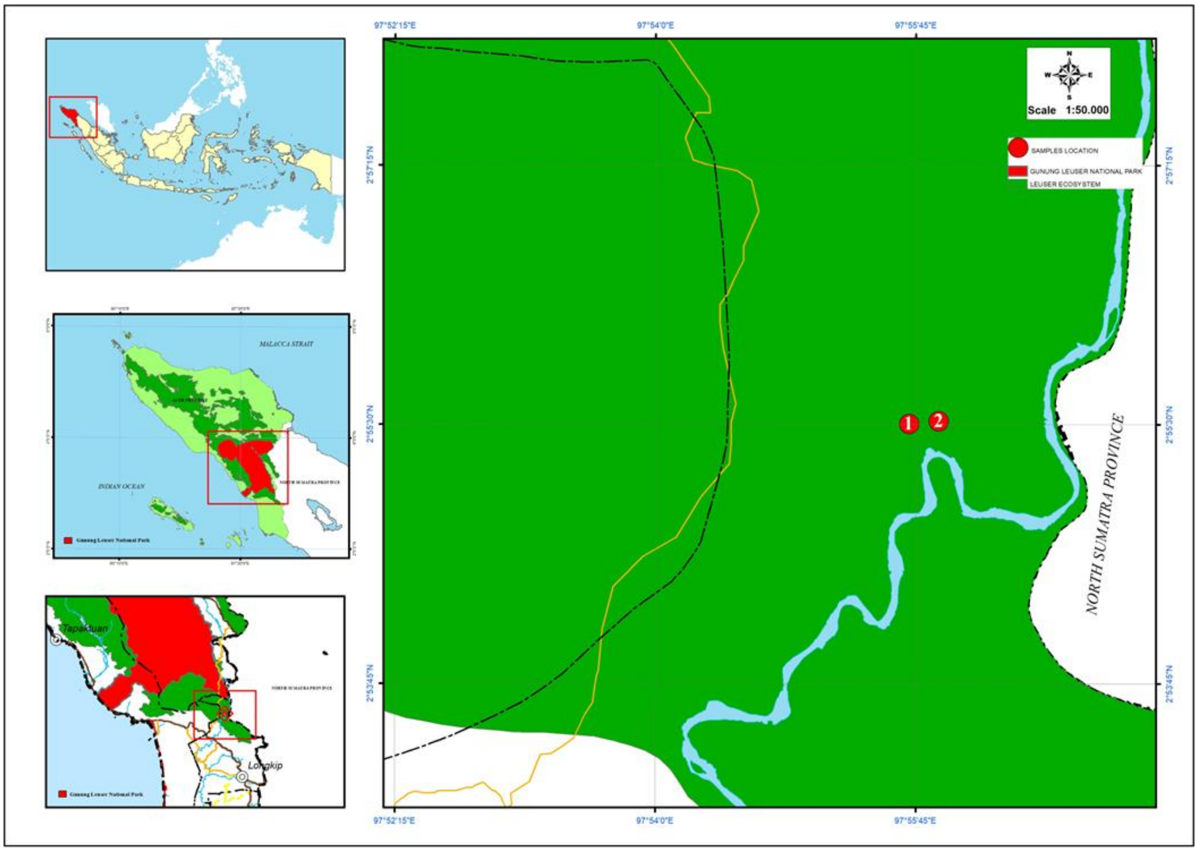

Figure 1. Termite research locations at the Soraya Research Station Forest.

Identification procedures followed established taxonomic references [25–33], including works by Roonwal and Chhotani, Krishna et al., Ahmad, Wang et al., Syaukani, and Rocha et al.

In parallel, all plant individuals within the sampling subplots were identified to the species level, regardless of termite presence. For dead trees, stumps, and logs colonized by termites, plant species were identified whenever morphological characteristics allowed. Plant identification was supported by regional floras and verified using digital plant identification platforms such as Plant Net and Plant.id [34].

2.5. Data Analysis

Termite diversity was assessed using taxa richness (S), defined as the total number of species or morphospecies recorded across all sampling units. This metric was selected to provide a baseline characterization of community composition in the study area, particularly given the focus on habitat associations rather than comparative diversity indices. The distribution of taxa across sampling subplots was also examined to identify patterns of occurrence and spatial heterogeneity [35, 36].

Habitat associations were evaluated using frequency-based analysis, in which the occurrence of each termite species was quantified across substrate types, including living trees, dead trees, stumps, logs, litter, and soil. Frequencies were calculated as the number of occurrences of each species in each habitat category, enabling identification of dominant substrates and preferred ecological niches. This approach enabled comparison of habitat use among species and functional groups, particularly with respect to decomposition stages and substrate conditions [37, 38].

Correspondence Analysis (CA) was used to examine the relationships between termite species and habitat types. CA was performed using a species-by-habitat contingency matrix in PAST (Paleontological Statistics) version 5.2. CA, based on chi-square distances, allows the simultaneous ordination of species and habitat variables in a reduced-dimensional space. The resulting biplots were used to identify patterns of habitat association, ecological gradients, and niche differentiation among termite species [39].

3. Results and Discussion

3.1. General Termite Diversity and Habitat Distribution

The survey at the Soraya Research Station (SRS) successfully documented 48 termite species distributed across 2 families, 6 subfamilies, and 17 genera. The taxonomic breakdown reveals a significant dominance of the family Termitidae (43 species) over Rhinotermitidae

(5 species). Overall, termite occurrence was strongly associated with decomposing substrates, particularly dead wood, stumps, and soil, while interactions with living trees were relatively limited (Table 1).

This relatively high level of diversity in a forest that has undergone approximately three decades of secondary succession suggests a substantial degree of ecological recovery [40]. Compared to other forest systems in Indonesia, termite diversity at SRS is notably higher; for example, studies in West Sumatra reported only 13 species [41], while monoculture *Eucalyptus pellita* plantations in Riau recorded as few as 8 species [42]. These comparisons highlight the importance of structural complexity and habitat heterogeneity in supporting diverse termite assemblages.

In terms of habitat distribution, termite occurrence was strongly associated with decomposing substrates, particularly dead standing trees, stumps, and fallen logs. Among these, logs supported a considerable number of colonies (41 occurrences), underscoring their importance as both sources and nesting substrates. In contrast, living trees (DLT and OLT) and litter supported fewer colonies, indicating lower suitability or higher resistance to colonization. Notably, termites were absent from approximately 70% of the examined potential habitats (329 out of 470 observations), suggesting a high degree of habitat selectivity or natural resistance in certain substrates.

Among the recorded species, *Macrotermes malaccensis* exhibited the broadest habitat range, occurring across multiple substrate types, including dead wood, stumps, soil, and litter (Table 1). This wide ecological tolerance reflects its role as a fungus-growing termite capable of exploiting diverse organic materials [43].

Correspondence Analysis (CA) further clarified these patterns by revealing a distinct ecological gradient separating wood-based substrates (e.g., logs and litter) from soil-associated habitats (e.g., soil, stumps, and dead standing trees) (Figure 2). Most termite taxa were associated with wood and soil substrates, whereas fewer species were associated with litter or living trees, indicating clear differences in habitat preference and resource utilization.

The dominance of Termitidae in SRS is consistent with patterns reported across tropical forests in Southeast Asia, where this family typically constitutes the majority of termite assemblages due to its high functional diversity. Members of Termitidae occupy a wide range of ecological niches, including wood-feeding, soil-feeding, and fungus-growing strategies, enabling them to exploit heterogeneous environments such as secondary forests [24, 44, 45].

The strong association between termite occurrence and coarse woody debris (CWD) highlights the critical role of dead wood in sustaining termite diversity and ecosystem functioning. Dead wood provides both resources and nesting sites, particularly for wood-feeding and fungus-growing termites. These groups play a pivotal role in accelerating the decomposition of lignocellulosic material, thereby enhancing nutrient cycling and carbon turnover in tropical forest systems [46, 47].

The relatively low incidence of termites in living Dipterocarpaceae and other tree species suggests that these plants may possess inherent resistance mechanisms, such as high wood density and resin content, which limit termite colonization. As a result, termite activity in SRS appears to be predominantly associated with decomposition processes rather than direct herbivory, reinforcing their role as key decomposers in forest ecosystems. Termite attacks often occur on trees already under stress—damaged by logging, fire, or water shortages—rather than on healthy, established Dipterocarps [22, 48].

The high proportion of uncolonized habitats further indicates that termite distribution is spatially heterogeneous and environmentally constrained. Microclimatic factors at SRS—including high annual humidity (approximately 87%) and stable temperatures ranging from 25.3°C to 26.6°C—provide generally favorable conditions for termite activity. However, local variation in moisture availability, micro-topography, and canopy cover likely creates a mosaic of suitable and unsuitable habitats. Such fine-scale environmental heterogeneity has been widely recognized as a major determinant of termite distribution and community structure [49, 50].

Importantly, the separation of habitats along the CA axes indicates niche differentiation among termite taxa, suggesting that species partition available resources based on substrate type and decomposition stage. This partitioning reduces interspecific competition and supports the coexistence of diverse termite assemblages within the same landscape. Overall, these findings demonstrate that termite community structure in SRS is strongly governed by substrate-driven ecological processes, reinforcing their role as key ecosystem engineers in tropical forest recovery [51, 52].

3.2. Specific Associations with Dipterocarpaceae

A total of 63 Dipterocarpaceae structures were examined within the study plots, comprising 60 living trees (DLT)

Table 1. Detailed Incidence of termite species across various habitats at SRS.

No.	**Family & Species**	**Incidence Location (Habitats)**									**No. Col**	**Percentage**
		DLT	**DDT**	**SD**	**OLT**	**ODT**	**OS**	**Log**	**Litter**	**Soil**		
I.	Rhinotermitidae											
1	*Coptotermes curvignathus*		1								1	0.2
2	*Schedorhinoterme* sp.					1					1	0.2
3	*Schedorhinotermes breavialatus*								1		1	0.2
4	*Schedorhinotermes javanicus*				1						1	0.2
5	*Schedorhinotermes sarawakensis*					2		1		1	4	0.9
II.	Termitidae											
6	*Amitermes dentatus*							1			1	0.2
7	*Bulbitermes flavicans*					1					1	0.2
8	*Dicuspiditermes nemorosus*				1			2	1	1	5	1.1
9	*Dicuspiditermes semarangi*							1			1	0.2
10	*Havilanditermes atripennis*							1			1	0.2
11	*Homallotermes eleanorae*								1		1	0.2
12	*Homallotermes foraminifer*				1						1	0.2
13	*Hospitalitermes birmanicus*								1		1	0.2
14	*Hospitalitermes hospitalis*	1			1			1			3	0.6
15	*Longipeditermes longipes*				1						1	0.2
16	*Longipeditermes mandibulatus*							1	2		3	0.6
17	*Macrotermes ahmadi*							1			1	0.2
18	*Macrotermes beufortensis*								1		1	0.2
19	*Macrotermes malaccensis*		1		1	2	2	4	3	1	14	3
20	*Macrotermes* sp.								3		3	0.6
21	*Malaysiotermes* sp.				2	1		1	2		6	1.3
22	*Microcerotermes dubius*				1						1	0.2
23	*Microcerotermes serrula*				1			1		1	3	0.6
24	*Nasutitermes johoricus*							1			1	0.2
25	*Nasutitermes longinasoides*							1			1	0.2
26	*Nasutitermes longinasus*				2	1	1	4	4	2	14	3
27	*Nasutitermes neoparvus*							1	1		2	0.4
28	*Nasutitermes proatripennis*				1	3		1	1		6	1.3
29	*Nasutitermes roboratus*	1						1		2	4	0.9
30	*Odontotermes longingnathus*					1		2			3	0.6
31	*Odontotermes mathuri*					1		1	3	3	8	1.7
32	*Odontotermes minitus*				2	1	2	3			8	1.7
33	*Odontotermes paraoblongathus*							1			1	0.2
34	*Odontotermes sarawakensis*				5		3	2	4	1	15	3.2
35	*Odontotermes* sp.							1			1	0.2
36	*Odontotermes sundaicus*								1		1	0.2
37	*Odototermes grandiceps*						1				1	0.2
38	*Odototermes oblongatus*									1	1	0.2
39	*Pericapritermes latighnathus*									1	1	0.2
40	*Pericapritermes mohri*								1		1	0.2
41	*Pericapritermes samarangi*			1				1			2	0.4
42	*Pericapritermes* sp.							2			2	0.4
43	*Pericapritermes speciosus*							1	1		2	0.4
44	*Procapritermes augustignathus*				1						1	0.2
45	*Procapritermes greeni*					1				1	2	0.4
46	*Procapritermes martyni*							2	1		3	0.6
47	*Procapritermes* sp.						2	1			3	0.6
48	*Termes propigus*									1	1	0.2
49	No Termite	58			268	3					329	70
	Total	**60**	**2**	**1**	**289**	**18**	**11**	**41**	**32**	**16**	**470**	**100**
	Percentage	**12.8**	**0.4**	**0.2**	**61.5**	**3.8**	**2.3**	**8.7**	**6.8**	**3.4**	**100.0**	

(Note: DLT=Dipterocarpaceae Living Trees; DDT=Dipterocarpaceae Dead Trees; DS=Dipterocarpaceae Stump; OLT=Other Living Trees; ODT=Other Dead Trees; OS=Other Stump; No. Col=Number of Colony)

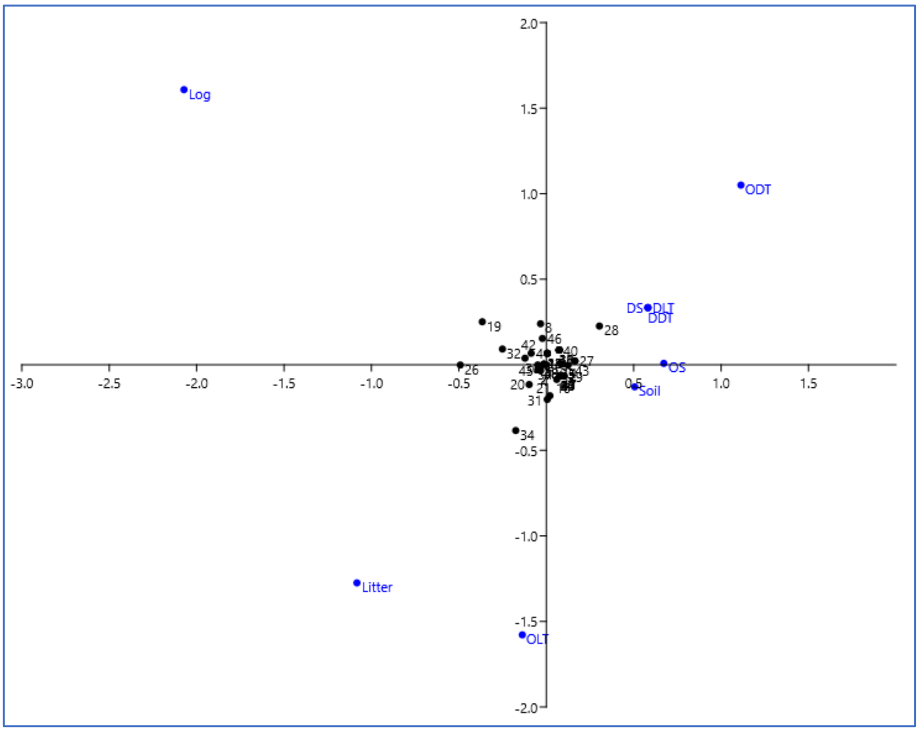

Figure 2. Correspondence analysis (CA) biplot showing associations between termite species and habitat types.

Table 2. Summarized the observed association between termite species and Dipterocarp ace substrates

No	Termite Species	Habitat in Dipterocarpaceae	Total
1	*Hospitalitermes hospitalis*	Living *Shorea multiflora* (DLT)	1
2	*Nasutitermes roboratus*	Living *Dipterocarpus humeratus* (DLT)	1
3	*Coptotermes curvignathus*	Dead *Shorea multiflora* (DDT)	1
4	*Macrotermes malaccensis*	Dead *Shorea multiflora* (DDT)	1
5	*Pericapritermes samarangi*	*Shorea multiflora* Stump (DS)	1
6	No Termite	Various (*Shorea, Dipterocarpus*, etc.)	58
Total			**63**

DLT =Dipterocarpaceae Living Trees; DDT = Dipterocarpaceae Dead Trees; DS = Dipterocarpaceae Stump; data derived from standardized 0.5 ha plots

representing ten species (*Dipterocarpus elongatus, D. grandiflorus, D. humeratus, Dryobalanops oblongifolia, Shorea dasyphylla, S. johorensis, S. lepidota, S. multiflora, S. leprosula, and S. palembanica*), as well as two dead standing trees (DDT), and one stump (DS), predominantly belonging to *Shorea multiflora*.

Despite the dominance of Dipterocarpaceae in the forest structure, termite associations were notably limited. Only five termite species representing 10.4% of the total recorded taxa (n=48) were observed to interact directly with Dipterocarpaceae, accounting for five incidences (7.9% of examined structures). These included *Hospitalitermes hospitalis* and *Nasutitermes roboratus* on living trees, *Coptotermes curvignathus* and *Macrotermes malaccensis* on dead standing trees, and *Pericapritermes samarangi* on a stump.

In contrast, 58 structures (92,1%) showed no evidence of active termite colonization, indicating a strong pattern of avoidance or resistance. However, the presence of abandoned galleries on several individuals of *Shorea multiflora* suggests that termite colonization attempts may occur but are often unsuccessful or transient, likely due to unfavorable substrate conditions (Table 2).

The extremely low proportion of termite associations with Dipterocarpaceae (7,9% of structures) reflects a high degree of ecological selectivity, where termite colonization is strongly constrained by substrate characteristics rather than host availability. Although Dipterocarpaceae dominated the forest of Soraya Research Station (SRS), they are rarely utilized as primary substrates, indicating that abundance does not equate to ecological suitability.

The physical and chemical defenses of Dipterocarpaceae can largely explain this limited association. These trees are characterized by high wood density (commonly 0.6-1.0 g cm^{-3}) [16, 53] and lignin content, both of which reduce palatability and increase resistance to termite feeding. Experimental studies have demonstrated that wood with lignin content exceeding 33% significantly limits termite digestion efficiency and feeding activity [46]. In addition, Dipterocarpaceae produce secondary metabolites, particularly phenolic compounds such as ellagic acid and oligostilbenoids like hopeaphenol, which can inhibit termite gut symbionts and digestive enzymes [54, 55]. These structural and chemical defenses are widely recognized as key deterrents against xylophagous insects, particularly in Southeast Asian tropical forests [54]. Consequently, termite activity tends to concentrate on dead, decayed, or structurally compromised substrates, as observed in this study [56, 57].

Despite these defenses, the presence of small or termite species indicates that resistance is not absolute. Generalist and fungus-growing termites, such as *Macrotermes malaccensis,* are capable of exploiting a wide range of substrates, including partially decomposed wood, by relying on symbiotic fungi to break down lignocellulosic material. Similarly, subterranean termites such as *Coptotermes curvignathus* are well adapted to colonize moist, decaying wood in contact with soil, where microbial preconditioning facilitates decomposition [58, 59].

The distinction between living and dead substrates is therefore critical. In this study, termite interactions were predominantly restricted to dead or structurally compromised Dipterocarpaceae, while associations with living trees were rare and likely opportunistic. This supports the broader ecological consensus that termites in tropical forests function primarily as detritivores, contributing to nutrient cycling rather than acting as primary herbivores [60–63]. The high proportion of uncolonized structures (92.1%) further indicates that termite colonization is highly selective and environmentally constrained. The presence of abandoned galleries suggests that termites actively explore potential substrates but may abandon them if conditions are unsuitable, reflecting a dynamic colonization process governed by quality, moisture, and microbial interactions [44, 62, 64–66].

The patterns observed in SRS are consistent with findings from other tropical regions. In Sumatra, termite assemblages in both natural and managed systems show a strong preference for necromass rather than living wood, with Termitidae dominating disturbed environments [42]. Similarly, studies within the Leuser Ecosystem report termite activity concentrated on decaying *Shorea* species, with limited infestation on living trees.

In Kalimantan, logged Dipterocarp forests support high termite diversity but maintain low infestation rates on living Dipterocarpaceae, indicating persistent mechanisms. However, contrasting cases exist; for example, *Shorea leprosula* has been reported as susceptible to *Coptotermes* spp. in Kalimantan, where infestations are characterized by soil sheeting on the bark. The absence of such interactions in SRS suggests that termite-host relationships are context dependent, influenced by local termite assemblages and the availability of alternative food resources [61, 67, 68].

Across Southeast Asia, termite-Dipterocarpaceae interactions reflect long-term coevolutionary processes. Dipterocarps have evolved strong structural and chemical defenses, while termites have diversified into functional groups that exploit different ecological niches. This results in selective, rather than generalized, interaction, with most termite activity concentrated on decomposing substrates [61, 69].

3.3. Analysis of Key Termite-Dipterocarpaceae Host Interactions

While overall associations were limited, species-specific interactions reveal distinct ecological roles that contribute to ecosystem functioning. These interactions range from neutral relationships to active decomposition and opportunistic exploitation.

3.3.1. Neutral Association: Hospitalitermes hospitalis

At SRS, *Hospitalitermes hospitalis* exhibited a strictly neutral association with *Shorea multiflora,* constructing spherical arboreal nests at 30 cm above ground (Figure 3). Nest placement at the intersection of Dipterocarp saplings and thorny rattan (*Myrialepsis paradoxa*) suggests a structural defense strategy in which physical barriers reduce predation risk.

Ecologically, this behavior reflects a non-wood-feeding functional group, in which termites use trees only as architectural support while foraging. This pattern is consistent with recent studies showing that arboreal termites in tropical forests often function as surface foragers rather than wood consumers, redistributing organic matter rather than directly decomposing host trees [70–72].

Such a neutral association is important because it demonstrates that not all termite-plant interactions are exploitative. Instead, they reflect commensal ecological relationships, which increase habitat complexity without imposing physiological stress on the host. This supports broader ecological frameworks in which termite functional diversity contributes to multilayered

Figure 3. Nest of *H. hospitalis:* (A. Ball-Shaped arboreal nest, B. Thorny rattan for nest reinforcement, C. *S. multiflora* sapling.

ecosystem processes, including canopy-level nutrient cycling and microhabitat formation [37, 73].

3.3.2. Pest and Decomposer: Nasutitermes roboratus

In contrast to the neutral associates, *Nasutitermes roboratus* demonstrated a dual ecological role as both an opportunistic pest and a primary decomposer [74–76]. In living *Dipterocarpus humeratus* (pole stage), this species constructed thin, soil-covered nests that extended up to 5 meters toward the trunk (Figure 4). Unlike *Hospitalitermes, N. roboratus* consumes the wood of the living tree while simultaneously building its arboreal nest. This behavior is consistent with other *Nasutitermes* species, such as *N. matangensis,* which are known to attack and eventually kill trees in industrial plantations as their populations grow and nests enlarge [42, 61]. By attacking both living wood and rotten logs, *N. roboratus* facilitates nutrient cycling but also poses a potential threat to timber health in succession forests [77, 78].

Recent studies in Southeast Asian forests have shown that *Nasutitermes* species can shift from benign to damaging depending on colony size and resource competition, highlighting the importance of population dynamics in determining ecological outcomes [79]. Thus, the presence of *N. roboratus* in SRS reflects a transitional ecological role, particularly relevant in secondary forests where resource heterogeneity is high [80–82].

3.3.3. Subterranean Decomposer: Coptotermes curvignathus

Coptotermes curvignathus was the only representative of the subfamily Coptotermitinae found in SRS, specifically associated with the dead wood of *Shorea multiflora* (Figure 5)*.* It was indicating a primarily decomposer role in this system. Although widely recognized as a destructive pest in plantation ecosystems, its ecological function in natural forests is more nuanced [83]. Subterranean termites such as *Coptotermes* play a crucial role in the early stages of wood decomposition, particularly in dense hardwood systems such as Dipterocarpaceae. Their ability to penetrate and degrade structurally resistant wood facilities, subsequent colonization by fungi and other invertebrates [84, 85].

Recent ecological syntheses emphasize that termite-driven decomposition is a key component of the tropical carbon cycle, with termite processing a substantial proportion of dead biomass and influencing soil structure and nutrient dynamics [86]. The confinement of *C. curvignathus* to dead substrates in SRS suggests that host defenses remain effective in living trees, while decomposing wood provides an accessible resource. This reinforces the concept that termite activity is strongly governed by substrate conditions rather than by the taxonomic identity of the host [80–82].

3.3.4. Generalist Foraging Decomposer: Macrotermes malaccensis

Macrotermes malaccensis exhibited characteristics of a generalist decomposer, with broad habitat distribution but limited association with Dipterocarpaceae to recently fallen trees (Figure 6). As a fungus-growing termite, this species relies on symbiotic fungi to degrade lignocellulosic material, allowing efficient utilization of

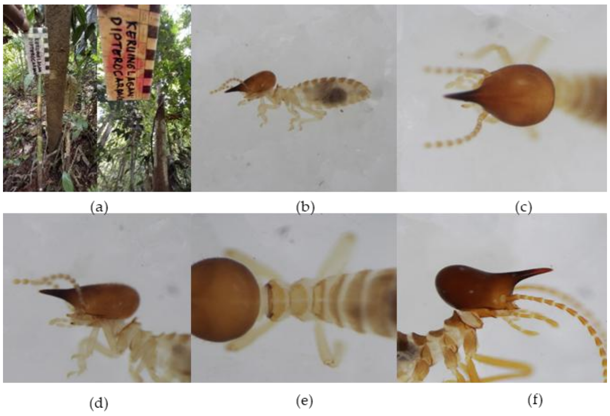

Figure 4. Attack of *Nasutitermes roboratus* on Dipterocarpaceae: (a) *Dipterocarpus humeratus* (pole stage) attacked by *N. roboratus*; (b-f) Various views of *N. roboratus.*

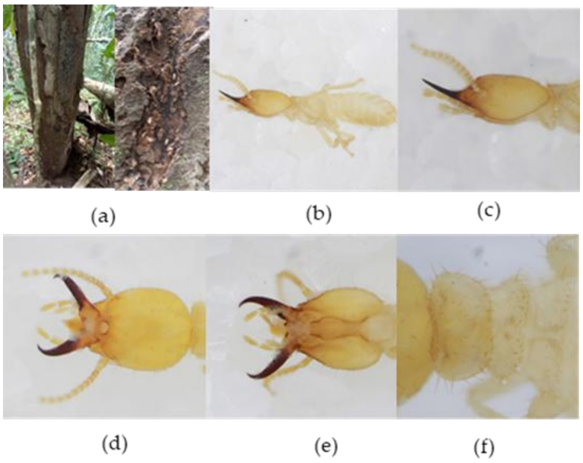

Figure 5. *Coptotermes curvignathus* termites: (a) *Shorea multiflora* dead after being attacked by termites; (b-f) various views of *C. curvignathus.*

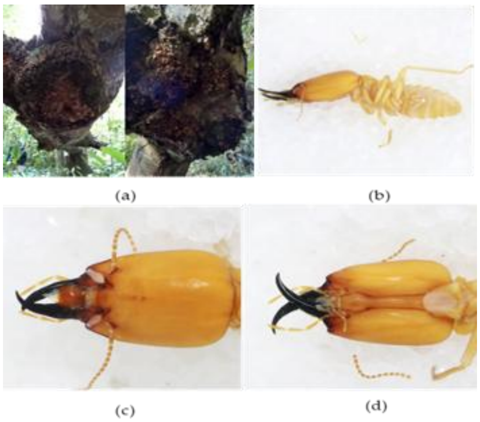

Figure 6. *Macrotermes malaccensis* termites: (a) *Shorea multiflora* dead and fallen after being attacked by termites; (b-d) various view of *M. mallaccensis.*

complex plant biomass. This symbiosis is considered one of the most advanced decomposition systems among insects, enabling a near-complete breakdown of organic substrates [87, 88].

Recent research in Southeast Asian Dipterocarp forests shows that *Macrotermes* species contribute significantly to soil heterogeneity, nutrient availability, and vegetation patterns, particularly through mound-building and organic matter processing [9, 89]. The preference of *M. malaccensis* for dead rather than living Dipterocarpaceae reflects an energy-optimization strategy, in which termites exploit substrates that are already partially decomposed and energetically favorable. This behavior is consistent with broader ecological models of termite

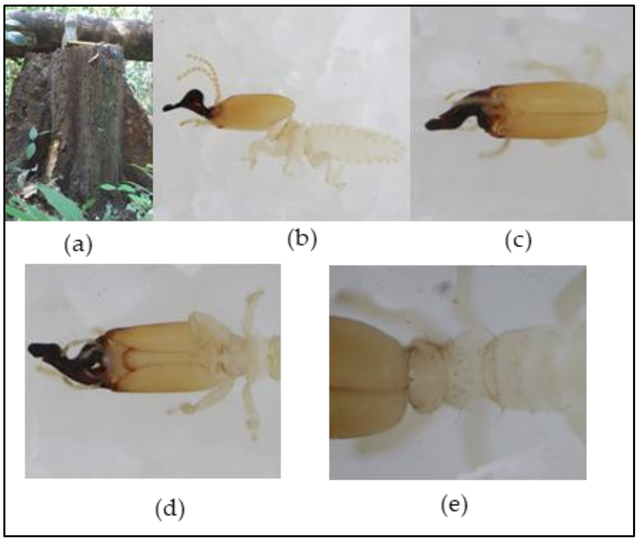

Figure 7. *Pericapritermes samarangi* termites: (a) *Shorea multiflora* dead and fallen after being attacked by termites; (b-e) various views of *P. samarangi.*

foraging, in which resource accessibility determines substrate selection [23, 90].

3.3.5. Soil-Interface Decomposers: Pericapritermes samarangi

Pericapritermes samarangi functioned as a specialized soil-interface decomposer at SRS, occurring exclusively in stumps and highly decomposed wood of *Shorea multiflora* (Figure 7). This species belongs to a group of termites that feed on organic-rich soil and humified material rather than fresh wood. Such termites are critical to the final stage of decomposition, in which organic matter is mineralized and reintegrated into the soil. Their activity contributes to nutrient recycling, soil aggregation, and improved soil structure [91].

Recent studies have highlighted that soil-feeding termites significantly influence belowground biodiversity and soil ecosystem processes, acting as key drivers of pedogenesis and nutrient redistribution in tropical forests. Moreover, the presence of *Pericapritermes* is often associated with low disturbance and high soil quality, making it a useful bioindicator of ecosystem recovery. Its occurrence in SRS suggests that the forest has reached a relatively advanced stage of ecological succession, with well-developed soil organic layers [4, 92].

3.4. Synthesis and Ecological Implications

Taken together, the results from sections 3.1-3.3. reveal that termite communities in SRS are structured along a substrate-driven functional gradient, rather than simple taxonomic associations with Dipterocarpaceae hosts. Although Dipterocarpaceae dominate the forest vegetation, termite interactions with these trees remain highly selective, with most species preferentially exploiting dead, decaying, or soil-associated substrates.

This pattern reflects a fundamental ecological mechanism in tropical forests, where termite activity is governed primarily by resource quality, decomposition stage, and accessibility, rather than host identity. The species-specific interactions further demonstrate a clear functional differentiation, ranging from neutral arboreal associations (*Hospitalitermes) to facultative herbivory (Nasutitermes)* and progressive decomposition processes *(Coptotermes, Macrotermes,* and *Pericapritermes).*

Importantly, these findings suggest that Dipterocarpaceae possess effective structural and chemical defenses that limit termite colonization in living tissues, thereby reducing herbivory pressure. At the same time, termite communities play a critical role in processing necromass, facilitating nutrient cycling, and contributing to soil development during forest recovery.

From an ecosystem perspective, termites function as key decomposers and ecosystem engineers, supporting the resilience of secondary forest by maintaining biogeochemical cycles. The coexistence of multiple functional groups ensures that organic matter is processed across successive stages of decomposition, reinforcing ecosystem stability.

Overall, this study highlights that termite-Dipterocarpaceae interaction in SRS are best understood with a functional ecological framework, where the balance between resistance (host traits) and utilization (termite feeding strategies) shapes community dynamics in regenerating tropical forests.

4. Conclusions

This study provides critical empirical insight into the functional dynamics of termites in the secondary forests of the Leuser Ecosystem, particularly at the Soraya Research Station (SRS). A total of 48 termite species were recorded, reflecting substantial ecological recovery after three decades of succession, with communities dominated by the family Termitidae and exhibiting strong habitat selectivity for coarse woody debris, such as fallen logs and stumps, which serve as essential nesting and foraging substrates. Ecological associations with Dipterocarpaceae were minimal and highly selective, as 92.1% of observed structures remained uncolonized, likely due to inherent resistance mechanisms such as high wood density and defensive secondary metabolites.

The study further identified a gradient of interaction types, ranging from neutral associations that enhance habitat complexity to opportunistic species with transitional roles to specialized decomposers that break down lignocellulosic material and soil-interface decomposers that act as indicators of advanced succession and high soil quality. Overall, termites function as essential ecosystem engineers driven by substrate availability, preferentially utilizing necromass over living tissues, thereby supporting nutrient cycling and long-term forest stability.

Based on these findings, future research should emphasize long-term monitoring, integration of molecular and functional approaches, expanded spatial comparisons across forest types, and closer linkage with soil and carbon dynamics. At the same time, conservation strategies should recognize termite diversity as a key component of sustainable forest management and support the use of Dipterocarpaceae in restoration efforts.

Author Contributions: Conceptualization, I.I., S.S. and D.D.; methodology I.I., S.S. and D.D.; software, I.I.; validation, S.S., D.D. and D.D.; formal analysis, I.I. and S.S.; investigation, I.I. and S.S.; resources, I.I. and S.S..; data curation, I.I.; writing—original draft preparation, I.I.; writing—review and editing, S.S. and D.D.; visualization, I.I. and S.S.; supervision, D.D. and D.D.; project administration, I.I.; funding acquisition, S.S. All authors have read and agreed to the published version of the manuscript.

Funding: This study was partly funded by the Dissertation Research Grant (PDD), DRPM of the Indonesian Government to Syaukani (FY-2023) No. 671/UN11.2.1/PT.01.03/DRPM/2023.

Ethical Clearance: Entry permit letter for the Soraya research station forest area No. 522.91/5002.V from the Head of the Environment and Forestry Service, Aceh, dated August 31, 2022.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data related to this research can be accessed by contacting the corresponding author, subject to applicable data protection and privacy policies.

Acknowledgments: We would like to express our gratitude to the Aceh Provincial Environment and Forestry Service, the Aceh Region VI Forest Management Unit, and the Leuser Conservation Forum for their research permits. We also extend our sincere thanks to the Manager and Staff of the Soraya Research Station, and especially to the Termite Research Team of the Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Syiah Kuala (Rahmadani, Via Anjelia, and Muhammad Azzanie Bessania) for their invaluable assistance during the research.

Conflicts of Interest: All the authors declare no conflicts of interest.

References

1. Brearley, F. Q., Banin, L. F., and Saner, P. (2016). The Ecology of the Asian Dipterocarps, *Plant Ecology & Diversity*, Vol. 9, Nos. 5–6, 429–436. doi:10.1080/17550874.2017.1285363.
2. Mahyana, Widayati, K. A., and Rianti, P. (2023). Activity Budget and Diet in Sumatran Orangutan (Pongo Abelii) at Soraya Research Station, Aceh, *HAYATI Journal of Biosciences*, Vol. 30, No. 4, 653–661. doi:10.4308/hjb.30.4.653-661.
3. Harnelly, E., Fitri, I., Iqbar, Yunita, and Kusuma, H. I. (2025). Assessing Dipterocarp Diversity at Soraya Research Station, Leuser Ecosystem, *Jurnal Penelitian Pendidikan IPA*, Vol. 11, No. 4, 1–9. doi:10.29303/jppipa.v11i4.10599.
4. Jouquet, P., Bottinelli, N., Shanbhag, R. R., Bourguignon, T., Traoré, S., and Abbasi, S. A. (2016). Termites: The Neglected Soil Engineers of Tropical Soils, *Soil Science*, Vol. 181, Nos. 3–4, 157–165. doi:10.1097/SS.0000000000000119.
5. de Souza, H. J., and Delabie, J. H. C. (2021). Ecosystem Engineers: Ants and Termites, *Encyclopedia of Social Insects*, Springer International Publishing, Cham, 347–352. doi:10.1007/978-3-030-28102-1_186.
6. Wijas, B. J., Flores-Moreno, H., Allison, S. D., Rodriguez, L. C., Cheesman, A. W., Cernusak, L. A., Clement, R., Cornwell, W. K., Duan, E. S., Eggleton, P., Rosenfield, M. V., Yatsko, A. R., and Zanne, A. E. (2024). Drivers of Wood Decay in Tropical Ecosystems: Termites versus Microbes along Spatial, Temporal and Experimental Precipitation Gradients, *Functional Ecology*, Vol. 38, No. 3, 546–559. doi:10.1111/1365-2435.14494.
7. Bucek, A., Šobotník, J., He, S., Shi, M., McMahon, D. P., Holmes, E. C., Roisin, Y., Lo, N., and Bourguignon, T. (2019). Evolution of Termite Symbiosis Informed by Transcriptome-Based Phylogenies, *Current Biology*, Vol. 29, No. 21, 3728-3734.e4. doi:10.1016/j.cub.2019.08.076.
8. Oberst, S., Lai, J. C. S., Martin, R., Halkon, B. J., Saadatfar, M., and Evans, T. A. (2020). Revisiting Stigmergy in Light of Multi-Functional, Biogenic, Termite Structures as Communication Channel, *Computational and Structural Biotechnology Journal*, Vol. 18, 2522–2534. doi:10.1016/j.csbj.2020.08.012.
9. Kaewfoo, M., Bunyavejchewin, S., Marod, D., Wiwatwittaya, D., Baillie, I. C., Davies, S. J., and Hallett, S. H. (2024). Termitaria Enhance Soil and Forest Diversity in Deciduous Dipterocarp Forest, Northern Thailand, *Journal of Tropical Ecology*, Vol. 40, e5. doi:10.1017/S0266467423000342.
10. Messer, A., McCormick, K., Sunjaya, Hagedorn, H. H., Tumbel, F., and Meinwald, J. (1990). Defensive Role of Tropical Tree Resins: Antitermitic Sesquiterpenes from Southeast Asian

Dipterocarpaceae, *Journal of Chemical Ecology*, Vol. 16, No. 12, 3333–3352. doi:10.1007/BF00982102.

11. Ashton, L. A., Griffiths, H. M., Parr, C. L., Evans, T. A., Didham, R. K., Hasan, F., Teh, Y. A., Tin, H. S., Vairappan, C. S., and Eggleton, P. (2019). Termites Mitigate the Effects of Drought in Tropical Rainforest, *Science*, Vol. 363, No. 6423, 174–177. doi:10.1126/science.aau9565.

12. Arif, A., Muin, M., Putri, G., and Hidayah, M. (2021). Termites (Insecta: Isoptera) Diversity in Forest Consecciion Areas of PT Inhutani I, Indonesia, *IOP Conference Series: Earth and Environmental Science*, Vol. 886, No. 1, 012129. doi:10.1088/1755-1315/886/1/012129.

13. Govorushko, S. (2018). Economic and Ecological Importance of Termites: A Global Review, *Entomological Science*, Vol. 22, No. 1, 21–35. doi:10.1111/ens.12328.

14. Sugio, K., Miyaguni, Y., and Yoshimura, T. (2020). Colony Structure and Caste Distribution in Living Trees of the Ryukyu Drywood Termite, Neotermes Sugioi (Blattodea: Kalotermitidae) in Okinawa Island, *Journal of Asia-Pacific Entomology*, Vol. 23, 853–862. doi:10.1016/j.aspen.2020.07.013.

15. Evans, T. A. (2021). Predicting Ecological Impacts of Invasive Termites, *Current Opinion in Insect Science*, Vol. 46, 88–94. doi:10.1016/j.cois.2021.03.003.

16. Rana, A., Chandel, R. S., Verma, K. S., and Joshi, M. J. (2021). Termites in Important Crops and Their Management, *Indian Journal of Entomology*, Vol. 83, No. 3, 486–504. doi:10.5958/0974-8172.2021.00001.8.

17. Sutekad, D., Jannah, M., Fitri, L., and Fauziah, F. (2022). Daily Behavioral Research on Sumatran Orangutan (Pongo Abelii) Mothers and Offsprings at Suaq Balimbing Research Station, Gunung Leuser National Park, Aceh Province, Indonesia, *Biodiversitas*, Vol. 23, No. 10, 5108–5121. doi:10.13057/biodiv/d231018.

18. Yanti, L. A., Moulana, R., Limbong, B. M. B., Syafruddin, S., Iqbar, I., Siregar, A. W., Rosita, I., Jamilah, M., and Ar-Rasyid, U. H. (2024). Identification of Food Type and Feeding Behavior of Sumatran Orangutans (Pongo Abelii) at the Ketambe Research Station in Gunung Leuser National Park, *IOP Conference Series: Earth and Environmental Science:The 5th International Conference on Agriculture and Bio-Industry 11/10/2023 - 12/10/2023 Hybrid* (Vol. 1297), IOP Publishing, 12096. doi:10.1088/1755-1315/1297/1/012096.

19. Riegger, T., Weibel, R., and Schuppli, C. (2022, August 1). *Impact of Food Availability on Ranging Behaviour of the Sumatran Orangutans (Pongo abelii) at the Suaq Balimbing Population*University of Zurich, Zurich.

20. Iqbar, I., Safriana, R., and Fauziah, F. (2024). Feeding Behavior and Diet Preferences of Sumatran Orangutans (Pongo Abelii Lesson 1827) at Soraya Research Station, Mount Leuser National Park, Indonesia, *Biodiversitas*, Vol. 25, No. 4, 1788–1796. doi:10.13057/biodiv/d250449.

21. Soraya Research Station. (2022). *Periodically Climatology Report of Soraya Research Station*Subulussalam.

22. Saud, O. R., Harmonis, Mardji, D., Erwin, Budi, A. S., and Arung, E. T. (2025). Investigation of Species and Patterns of Termite Attacks on Dipterocarpaceae Stands in Samarinda Forest Areas, East Kalimantan, Indonesia, *IOP Conference Series: Earth and Environmental Science* (Vol. 1562), Institute of Physics. doi:10.1088/1755-1315/1562/1/012021.

23. Calderón-Cortés, N., Escalera-Vázquez, L. H., and Oyama, K. (2018). Occurrence of Termites (Isoptera) on Living and Standing Dead Trees in a Tropical Dry Forest in Mexico, *PeerJ*, Vol. 6, e4731. doi:10.7717/peerj.4731.

24. Muarrif, S., Samadi, S., Jauharlina, J., and Syaukani, S. (2023). Description of the Termite Genus Prohamitermes (Termitinae) with New Characters from the Leuser Ecosystem, Sumatra, Indonesia, *Biodiversitas*, Vol. 24, No. 11, 6119–6125. doi:10.13057/biodiv/d241133.

25. Roonwal, M. L., and Chhotani, O. B. (1989). *Fauna of India and Adjacent Countries-Isoptera (Termites)Vol I*, (the D. Z. S. of India, Ed.), Goverment of India, Calcutta-India.

26. Krishna, K. (1965). Termites (Isoptera) of Burma, *American Museum of Novitates*, Vol. 2210, 1–34.

27. Krishna, K. (2020). Termite. Encyclopedia Britannica.

28. Krishna, K., Grimaldi, D. A., Krishna, V., and Engel, M. S. (2013). *Treatise on the Isoptera of The World*, *Bulletin of the American Museum of Natural History* (Vol. 1), American Museum of Natural History (BioOne sponsored). doi:10.1206/377.1.

29. Krishna, K., Grimaldi, D. A., Krishna, V., and Engel, M. S. (2013). Treatise on the Isoptera of the World: Termitidae (Part Two), *Bulletin of the American Museum of Natural History*, Vol. 2013, No. 377, 1495–1989.

30. Krishna, K., Grimaldi, D. A., Krishna, V., and Engel, M. S. (2013). Treatise on the Isoptera of the World: Termitidae (Part One), *Bulletin of the American Museum of Natural History*, Vol. 2013, No. 377, 973–1495.

31. Krishna, K., Grimaldi, D. A., Krishna, V., and Engel, M. S. (2013). Treatise on the Isoptera of the World: Neoisoptera Excluding Termitidae, *Bulletin of the American Museum of Natural History*, Vol. 2013, No. 377, 627–971.

32. Krishna Kumar, Grimaldi David A., and Krishna Valeri E. (2013). Treatise on the Isoptera of the World: Neoisoptera Excluding Termitidae, *Bulletin of the American Museum of Natural History*, Vol. 2013, No. 377, 623–973.

33. Krishna, K., Grimaldi, D. A., Krishna, V., and Engel, M. S. (2013). Treatise on the Isoptera of the World: Introduction, *Bulletin of the American Museum of Natural History*, Vol. 2013, No. 377, 1–200. doi:10.1206/377.1.

34. Argent, G., Saridan, A., Campbell, E. J. F., Wilkie, G., Fairweather, G., Hadiah, J. T., Middleton, J. T., Pendry, C., Pinars, M., and Warwick, MYulisa, K. S. (1998). *Manual of The Larger and More Importand Non Dipterocarpaceae of Central Kalimantan, Indonesia* (Vol. 2), Samarinda, Indonesia.

35. Ramos-Merchante, A., and Prenda, J. (2017). Macroinvertebrate Taxa Richness Uncertainty and Kick Sampling in the Establishment of Mediterranean Rivers Ecological Status, *Ecological Indicators*, Vol. 72, 1–12. doi:10.1016/j.ecolind.2016.07.047.

36. Jamil, N., Wan Ismail, W. N., Abidin, S. S., Amaran, M. A., and Hazali, R. (2017). A Preliminary Survey of Species Composition of Termites (Insecta: Isoptera) in Samunsam Wildlife Sanctuary, Sarawak, *Tropical Life Sciences Research*, Vol. 28, No. 2, 201–213. doi:10.21315/tlsr2017.28.2.15.

37. Madonsela, Z., and Magagula, C. N. (2024). Termite Species and Functional Diversity as Determined by Vegetation and Edaphic Characteristics in a Savanna Ecosystem, *The Journal of Basic and Applied Zoology*, Vol. 85, No. 1, 5. doi:10.1186/s41936-024-00356-y.

38. Heriza, S., Buchori, D., Harahap, I. S., and Maryana, N. (2022). Decomposition of Wood by Termites in Different Types of Land Use, *Jurnal Perlindungan Tanaman Indonesia*, Vol. 26, No. 1, 21. doi:10.22146/jpti.69322.

39. Pratiknyo, H., Ahman, I., and Budianto, B. H. (2018). Diversity and Abundance of Termites along Altitudinal Gradient and Slopes in Mount Slamet , Central Java , Indonesia, *Biodiversitas*, Vol. 19, No. 5, 1649–1658. doi:10.13057/biodiv/d190508.

40. Iqbar, Djufri, Darusman, Rahmadani, Anjelia, V., Bessania, M. A., and Syaukani. (2024). Termite Attack on Succession Forest Plants at Soraya Research Station, Leuser Ecosystem, Sumatra, *IOP Conference Series: Earth and Environmental Science* (Vol. 1359), Institute of Physics. doi:10.1088/1755-1315/1359/1/012120.

41. Handru, A., Herwina, H., and Henny Herwina, C. (2016). Termite Species Diversity at Four Nature Reserves in West Sumatra, Indonesia, *~ 682 ~ Journal of Entomology and Zoology Studies*, Vol. 4, No. 5, 682–688.

42. Prastyaningsih, S. R. I. R., Hardiwinoto, S., Musyafa, and Koranto, C. A. D. (2020). Diversity of Termites (Isoptera) on Industrial Forest Plantation of Eucalyptus Pellita Stands of Tropical Ecosystem in Riau, Indonesia, *Biodiversitas*, Vol. 21, No. 11, 5498–5505. doi:10.13057/biodiv/d211158.

43. Vesala, R., Niskanen, T., Liimatainen, K., Boga, H., Pellikka, P., and Rikkinen, J. (2017). Diversity of Fungus-growing Termites (*Macrotermes*) and Their Fungal Symbionts (*Termitomyces*) in the Semiarid Tsavo Ecosystem, Kenya, *Biotropica*, Vol. 49, No. 3, 402–412. doi:10.1111/btp.12422.

44. Li, H., and Greening, C. (2022). Termite-Engineered Microbial Communities of Termite Nest Structures: A New Dimension to the Extended Phenotype, *FEMS Microbiology Reviews*, Vol. 46, No. 6. doi:10.1093/femsre/fuac034.

45. Syaukani, S., Thompson, G. J., Yamasaki, T., Othman, A. S., Muarrif, S., Sarong, M. A., Djufri, D., and Eguchi, K. (2019). Taxonomy of the Genus Longipeditermes Holmgren (Termitidae, Nasutitermitinae) from the Greater Sundas, Southeast Asia, *Zoosystematics and Evolution*, Vol. 95, No. 2, 309–318. doi:10.3897/zse.95.31636.

46. Ci, H., Guo, C., Sai, B., Tuo, B., Zhao, W., Qin, H., Zhang, T., Yan, E., and Cornelissen, J. H. C. (2025). The Wood Economics Spectrum Modulates the Positive Effects of Termite Foraging Intensity on Deadwood Invertebrate Diversity, *Functional Ecology*, Vol. 39, No. 6, 1498–1509. doi:10.1111/1365-2435.70021.

47. Beránková, T., Arora, J., Romero Arias, J., Buček, A., Tokuda, G., Šobotník, J., Hellemans, S., and Bourguignon, T. (2024). Termites and Subsocial Roaches Inherited Many Bacterial-Borne Carbohydrate-Active Enzymes (CAZymes) from Their Common Ancestor, *Communications Biology*, Vol. 7, No. 1, 1449. doi:10.1038/s42003-024-07146-w.

48. Zamir Rasib, K., Shehzad, K., and Muhammad Tariq, H. (2023). Feeding Preferences and Responses of Subterranean Termite on Different Commercial Timbers, *Journal of Dairy, Veterinary & Animal Research*, Vol. 12, No. 1, 13–17. doi:10.15406/jdvar.2023.12.00316.

49. Mirabile, G., Torta, L., Lamendola, M., Rizzo, M. C., and Manachini, B. (2024). Attacks of Kalotermes Flavicollis Fabricius (1793) and Associated Aspergillus Micheli Ex Haller (1768) Species, *Insects*, Vol. 15, No. 11, 899. doi:10.3390/insects15110899.

50. Martinka, M., and Tuf, I. H. (2025). The Relationship Between Abundance and Actual Spatial Distribution of Terrestrial Isopods (Oniscidea), *Diversity*, Vol. 17, No. 11, 790. doi:10.3390/d17110790.

51. Pulla, S., Suresh, H. S., Dattaraja, H. S., and Sukumar, R. (2017). Multidimensional Tree Niches in a Tropical Dry Forest, *Ecology*, Vol. 98, No. 5, 1334–1348. doi:10.1002/ecy.1788.

52. Yang, H., Jing, M., Sheng, H., Liu, M., Yang, W., Lu, K., and Zhu, J. (2025). Temporal Niche Differentiation of Rhythmic Taxa Enhances Microbial Network Stability in a Subtropical Reservoir, *Environmental Research*, Vol. 287, 123056. doi:10.1016/j.envres.2025.123056.

53. Phillips, O. L., Sullivan, M. J. P., Baker, T. R., Monteagudo Mendoza, A., Vargas, P. N., and Vásquez, R. (2019). Species Matter: Wood Density Influences Tropical Forest Biomass at Multiple Scales, *Surveys in Geophysics*, Vol. 40, No. 4, 913–935. doi:10.1007/s10712-019-09540-0.

54. Ali, D. E., Abd el-Aziz, M. M., Ibrahim, S. S. A., Sheta, E., and Abdel-Sattar, E. (2023). Gastroprotective and Anti-Helicobacter Pylori Potentials of Essential Oils from the Oleoresins of Araucaria Bidwillii and Araucaria Heterophylla, *Inflammopharmacology*, Vol. 31, No. 1, 465–483. doi:10.1007/s10787-022-01112-w.

55. Susilowati, A., Rachmat, H. H., Elfiati, D., Hidayat, A., Hadi, A. N., Zaitunah, A., Nainggolan, D., and Ginting, I. M. (2021). Floristic Composition and Diversity at Keruing (Dipterocarpus Spp.) Habitat in Tangkahan, Gunung Leuser National Park, Indonesia, *Biodiversitas*, Vol. 22, No. 10, 4448–4456. doi:10.13057/biodiv/d221038.

56. Abrão, F., Silva, T. S., Moura, C. L., Ambrósio, S. R., Veneziani, R. C. S., de Paiva, R. E. F., Bastos, J. K., and Martins, C. H. G. (2021). Oleoresins and Naturally Occurring Compounds of Copaifera Genus as Antibacterial and Antivirulence Agents against Periodontal Pathogens, *Scientific Reports*, Vol. 11, No. 1, 4953. doi:10.1038/s41598-021-84480-7.

57. Leandro, L. M., De Sousa Vargas, F., Barbosa, P. C. S., Neves, J. K. O., Da Silva, J. A., and Da Veiga-Junior, V. F. (2012). Chemistry and Biological Activities of Terpenoids from Copaiba (Copaifera Spp.) Oleoresins, *Molecules*, Vol. 17, No. 4, 3866–3889. doi:10.3390/molecules17043866.

58. Martha, R., Mubarok, M., Darmawan, W., Syafii, W., Dumarcay, S., Gerardin Charbonnier, C., and Gerardin, P. (2021). Biomolecules of Interest Present in the Main Industrial Wood Species Used in Indonesia-A Review, *Journal of Renewable Materials*, Vol. 9, No. 3, 399–449. doi:10.32604/jrm.2021.014286.

59. Jusselme, M., Cezard, L., Baumberger, S., Robert, A., Lapierre, C., Diouf, M., and Miambi, E. (2020). Changes in the Phenolic Fraction of Protobind 1000 and Bacterial Microbiota in the Gut of a Higher Termite, Nasutitermes Ephratae, *Open Access Journal of Microbiology & Biotechnology*, Vol. 5, No. 3, 1–11. doi:10.23880/oajmb-16000169.

60. Fajar, A., Himmi, S. K., Latif, A., Tarmadi, D., Kartika, T., Guswenrivo, I., Yusuf, S., and Yoshimura, T. (2021). Termite Assemblage and Damage on Tree Trunks in Fast-Growing Teak Plantations of Different Age: A Case Study in West Java, Indonesia, *Insects*, Vol. 12, No. 4, 295. doi:10.3390/insects12040295.

61. Saud, O. R., Harmonis, Mardji, D., Erwin, Budi, A. S., and Arung, E. T. (2025). Investigation of Species and Patterns of Termite Attacks on Dipterocarpaceae Stands in Samarinda Forest Areas, East Kalimantan, Indonesia, *IOP Conference Series: Earth and Environmental Science*, Vol. 1562, No. 1, 012021. doi:10.1088/1755-1315/1562/1/012021.

62. Woon, J. S., Boyle, M. J. W., Ewers, R. M., Chung, A., and Eggleton, P. (2019). Termite Environmental Tolerances Are More Linked to Desiccation than Temperature in Modified Tropical Forests, *Insectes Sociaux*, Vol. 66, No. 1, 57–64. doi:10.1007/s00040-018-0664-1.

63. Godoy D. Plaza, T. (2025). Feeding Patterns of Termites (Isoptera), *Advances in Termite, Bee and Wasp Biology - Ecology, Physiology, and Integrated Management*, IntechOpen. doi:10.5772/intechopen.1002364.

64. Chen, C., Singh, A. K., Yang, B., Wang, H., and Liu, W. (2023). Effect of Termite Mounds on Soil Microbial Communities and Microbial Processes: Implications for Soil Carbon and Nitrogen Cycling, *Geoderma*, Vol. 431. doi:10.1016/j.geoderma.2023.116368.

65. Luo, Y., Wu, D., Weng, C., Zhou, W., Yu, M., and Zhang, A. (2024). Competitive Exclusion Drives Termite Community Assembly Process on Islands, *Landscape Ecology*, Vol. 39, No. 9, 161. doi:10.1007/s10980-024-01922-z.

66. Nakashima, M., and Matsuura, K. (2025). Termite Antimicrobial Defense through Interaction with Symbiotic Microorganisms in Nest Materials, *Scientific Reports*, Vol. 15, No. 1, 23391. doi:10.1038/s41598-025-07667-2.

67. Ngatiman, N., and Fernandes, A. (2015). Coptotermes Sp. Termite Attacks in Some Locations of Red Meranti (Shorea Leprosula Miq.) Plantation, *In ICBS Conference Proceedings, International Conference on Biological Science, KnE Life Sciences* (Vol. 3), Knowledge E, 141–146. doi:10.18502/kls.v3i4.698.

68. Fernandes, A., and Ngatiman. (2015). Patterns of Coptotermes Sp . Termite Attack on Shorea Leprosula Miq IN KHDTK Sebulu, East Kalimantan, *The 3rd International Conference on Biological Science 2013*, KnowledgeE Publishing Services, 544–548. doi:10.18502/kls.v2i1.213.

69. Salam, D. M., Laksmita, A. N., Salam, D. M., Fernandes, A., and Maharani, R. (2024). Chemical Characteristics of Dipterocarps Resins for Functional Usage, 060004. doi:10.1063/5.0184567.

70. Guo, C., Tuo, B., Ci, H., Yan, E., and Cornelissen, J. H. C. (2021). Dynamic Feedbacks among Tree Functional Traits, Termite Populations and Deadwood Turnover, *Journal of Ecology*, Vol. 109, No. 4, 1578–1590. doi:10.1111/1365-2745.13604.

71. Law, S., Eggleton, P., Griffiths, H., Ashton, L., and Parr, C. (2019). Suspended Dead Wood Decomposes Slowly in the Tropics, with Microbial Decay Greater than Termite Decay, *Ecosystems*, Vol. 22, No. 6, 1176–1188. doi:10.1007/s10021-018-0331-4.

72. Oberst, S., Lai, J. C. S., Martin, R., Halkon, B. J., Saadatfar, M., and Evans, T. A. (2020). Revisiting Stigmergy in Light of Multi-Functional, Biogenic, Termite Structures as Communication Channel, *Computational and Structural Biotechnology Journal*, Vol. 18, 2522–2534. doi:10.1016/j.csbj.2020.08.012.

73. Castro, D., and Fernández, F. (2025). Cohabitation Networks: Exploring How Termites and Ants Share Nests in Amazonian Forests, *Neotropical Biology and Conservation*, Vol. 20, No. 3, 221–246. doi:10.3897/neotropical.20.e154485.

74. Syaukani. (2014). Biosystematics of Hospitalitermes Hospitalis Holmgren (Isoptera) From Borneo, *Proceedings of The 4th Annual International Conference Syiah Kuala University (AIC Unsyiah)* (Vol. 4), 154–159.

75. Hapukotuwa, N. K., and Grace, J. K. (2012). Coptotermes Formosanus and Coptotermes Gestroi (Blattodea: Rhinotermitidae) Exhibit Quantitatively Different Tunneling Patterns, *Psyche*, 1–7. doi:10.1155/2012/675356.

76. Saputra, A., Halim, M., Jalaludin, N.-A., Hazmi, I. R., and Rahim, F. (2017). Effects of Day Time Sampling on The Activities of Termites In Oil Palm Plantation at Malaysia-Indonesia, *Serangga*, Vol. 22, No. 1, 23–32.

77. Hidayat, M. R., Endris, W. M., and Dwiyanti, Y. (2018). Effect of a Rubber Plantation on Termite Diversity in Melawi, West Kalimantan, Indonesia, *Agriculture and Natural Resources*, Vol. 52, No. 5, 439–444. doi:10.1016/j.anres.2018.10.016.

78. Jalaludin, N. A., Rahim, F., and Yaakop, S. (2018). Termite Associated to Oil Palm Stands in Three Types of Soils in Ladang Endau Rompin, Pahang, Malaysia, *Sains Malaysiana*, Vol. 47, No. 9, 1961–1967. doi:10.17576/jsm-2018-4709-03.

79. Lee, C.-Y., and Lee, S.-H. D. (2025). Termite Baiting—How It Changed the Landscape of the Pest Management Industry and Termite Research in Southeast Asia, *Journal of Economic Entomology*, Vol. 118, No. 3, 1029–1037. doi:10.1093/jee/toaf081.

80. Hassan, B., and Morrell, J. J. (2021). Termite Testing Methods: A Global Review, *Journal of Testing and Evaluation*, Vol. 49, No. 6, 4607–4636. doi:10.1520/JTE20200455.

81. Subekti, N., Priyono, B., and Aisyah, A. N. (2018). Biodiversity of Termites and Damage Building in Semarang, Indonesia, *Biosaintifika: Journal of Biology & Biology Education*, Vol. 10, No. 1, 176–182. doi:10.15294/biosaintifika.v10i1.12832.

82. Heriza, S., Buchori, D., Harahap, I. S., and Maryana, N. (2021). Response of Termite Communities to Natural Forest Conversion, *Biodiversitas Journal of Biological Diversity*, Vol. 22, No. 11. doi:10.13057/biodiv/d221147.

83. Kirton, L. G., and Wong, A. H. H. (2000). The Economic Importance and Control of Termite Infestations in Relation to Plantation Forestry and Wood Preservation in Peninsular Malaysia - An Overview, *Sociobiology*, Vol. 37, No. 2, 325–349.

84. Kamarudin, M. A., Abdullah, S., and Lau, W. H. (2022). Efficacy of Soil-Borne Entomopathogenic Fungi against Subterranean Termite, Coptotermes Curvignathus Holmgren (Isoptera: Rhinotermitidae), *Egyptian Journal of Biological Pest Control*, Vol. 32, No. 1, 44. doi:10.1186/s41938-022-00536-4.

85. Kutana, A. N., Nandika, D., and Arinana, A. (2025). Feeding Preferences of Subterranean Termite Schedorhinotermes Javanicus on Tusam (Pinus Merkusii) Wood, *Jurnal Sylva Lestari*, Vol. 13, No. 1, 45–59. doi:10.23960/jsl.v13i1.1063.

86. Bignell, D. E. (2019). Termite Ecology in the First Two Decades of the 21st Century : A Review of Reviews, *Insects*, Vol. 10, No. 60, 1–10. doi:10.3390/insects10030060.

87. Wisselink, M., Aanen, D. K., and van 't Padje, A. (2020). The Longevity of Colonies of Fungus-Growing Termites and the Stability of the Symbiosis, *Insects*, Vol. 11, No. 8, 527. doi:10.3390/insects11080527.

88. Ahmad, F., Yang, G., Liang, S., Zhou, Q., Gaal, H. A., and Mo, J. (2021). Multipartite Symbioses in Fungus-growing Termites (Blattodea: Termitidae, Macrotermitinae) for the Degradation of Lignocellulose, *Insect Science*, Vol. 28, No. 6, 1512–1529. doi:10.1111/1744-7917.12890.

89. Subekti, N., and Mar'ah, R. (2019). Estimating Population Size for Macrotermes Gilvus Hagen (Blattodea: Termitidae) in Indonesia, *Journal of Physics: Conference Series*, Vol. 1321, No. 3, 032050. doi:10.1088/1742-6596/1321/3/032050.

90. Rahmadani, R., Rizki, A., Novita, N., and Syaukani, S. (2025). Inventory and Ecology of Termites (Blattodea) Attacking Plants at Ketambe Research Station, Mount Leuser National Park, Sumatra, *International Journal of Applied Science and Engineering Review*, Vol. 06, No. 02, 41–58. doi:10.52267/IJASER.2025.6204.

91. Subi, S., and Sheela, A. M. (2020). Review on Termite Mound Soil Characteristics and Agricultural Importance, *Journal of Agriculture and Ecology Research International*, 1–12. doi:10.9734/jaeri/2020/v21i730152.

92. Pribadi, T., Raffiudin, R., and Harap, I. S. (2011). Termites Community as Environmental Bioindicators in Highlands: A Case Study in Eastern Slopes of Mount Slamet, Central Java, *Biodiversitas Journal of Biological Diversity*, Vol. 12, No. 4. doi:10.13057/biodiv/d120409.