



NEST-BUILDING TERMITE ASSEMBLAGES IN A WHITE-SAND AMAZONIAN FOREST FRAGMENT, LORETO- PERU

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ABSTRACT

Termites are ecosystem engineers whose nest-building activities alter soil structure and nutrient cycling. In this study, we assessed the characteristics and diversity of nest building termite assemblages in a white-sand forest fragment near Iquitos, Loreto, Peru. We surveyed ten 30 × 30 m plots in the forest to quantify nest density, taxonomic composition, nest-type, botanical substrates, nest coloration, and spatial variation in nest abundance. A total of 156 nests were recorded, representing five genera: *Nasutitermes*, *Embiratermes*, *Coptotermes*, *Constrictotermes*, and *Termes*. The most common botanical substrates associated with nest building belonged to the families Euphorbiaceae, Moraceae, and Fabaceae, particularly *Alchornea triplinervia*. Most nests were arboreal (58,0%) and dark brown in color (57,05%). Nest abundance increased significantly with greater distance from the road. In conclusion, despite the low nutrient availability, the white-sand forest fragment supports a dense and diverse assemblage of nest building termites.

KEYWORDS: Amazonian, ecological characteristics, interactions, social insects

ENSAMBLAJES DE TERMITAS CONSTRUCTORAS DE NIDOS EN UN FRAGMENTO DE BOSQUE AMAZÓNICO DE ARENA BLANCA, LORETO-PERÚ

RESUMEN

Las termitas son ingenieras del ecosistema cuyas actividades de construcción de nidos alteran la estructura del suelo y el ciclo de nutrientes. En este estudio, evaluamos las características y diversidad de las comunidades de termitas constructoras de nidos en un fragmento de bosque de arena blanca cerca de Iquitos, Loreto, Perú. Estudiamos diez parcelas de 30 × 30 m en el bosque para cuantificar la densidad de nidos, la composición taxonómica, la diversidad de tipos de nidos, los sustratos botánicos, la coloración de los nidos y la variación espacial en la abundancia de nidos. Se registró un total de 156 nidos, que representaron cinco géneros: *Nasutitermes*, *Embiratermes*, *Coptotermes*, *Constrictotermes* y *Termes*. Los sustratos botánicos más comunes asociados con la construcción de nidos pertenecían a las familias Euphorbiaceae, Moraceae y Fabaceae, particularmente *Alchornea triplinervia*. La mayoría de los nidos eran arbóreos (58,0%) y de color marrón oscuro (57,05%). La abundancia de nidos aumentó significativamente con el aumento de la distancia desde la carretera. En conclusión, a pesar de la baja disponibilidad de nutrientes, el fragmento de bosque de arena blanca estudiado alberga un conjunto denso y diverso de termitas constructoras de nidos.

PALABRAS CLAVE: Amazonía, características ecológicas, interacciones, insectos sociales

INTRODUCTION

Termites are essential ecosystem engineers that modified the physical and biological environments (Bignell & Eggleton, 2000; Holt & Lepage, 2000; Luke *et al.*, 2014; Oliveira *et al.*, 2021; Wijas & Atkinson, 2021). Termite nests are conspicuous structures whose architecture and material composition confer critical ecological functions across a wide range of biomes (Noirot & Darlington, 2000). Their functions includes the modification of soil structure, nutrient cycling, vegetation distribution and drainage patterns (Ackerman *et al.*, 2007; Apolinário & Martius, 2004; Bonachela *et al.*, 2015; Muvengwi & Witkowski, 2020; Mees *et al.*, 2021; Alves *et al.*, 2022). In the Amazon forest, studies suggest that nest-building termites drives soil formation, regulate hydrology and create fertile islands that enhance plant recruitment and heterogeneity (Ackerman *et al.*, 2007; Apolinário & Martius, 2004; Duran-Bautista *et al.*, 2020).

White-sand forests of the eastern Amazon constitute nutrient-poor ecosystems characterized by low soil fertility and specialized plant assemblages (Zárate *et al.*, 2013). These habitats are increasingly fragmented by deforestation, climate-driven droughts and expanding road networks, all of which undermine key ecological processes and reshape patterns of biodiversity (Moulatlet *et al.*, 2021).

For example, roads fragment continuous forest and generate novel microclimatic gradients, hydrological flow and vegetation structure at the forest boundary (Nunes *et al.*, 2022). However, despite their ecological importance, nest-building termite assemblages in Amazonian white-sand fragments remain poorly characterized with most studies focused on species inventories in central Amazonia, with a limited integration of nest architecture, botanical substrates or landscape-scale spatial patterns in relation to road

disturbance (Casalla & Korb, 2019; Vasconcellos *et al.*, 2010).

Most studies on the relative abundance and spatial distribution of nest types (e.g., epigeal, arboreal, and subterranean) have focused on várzea floodplains, agroforestry systems, or terra firme forests (Bezerra-Gusmão *et al.*, 2013; Martius, 1994). The selection of nest construction substrates, which is shaped by a complex interplay of biotic and abiotic factors, including plant species composition, soil physicochemical properties, and microclimatic conditions, has received limited attention (Bronstein *et al.*, 2006; Muvengwi & Witkowski, 2020). Additionally, traits such as nests coloration, which are closely linked to material composition, and the decline in nests and termite diversity due to habitat fragmentation in Amazonian ecosystems remains unexplored, leaving a substantial gap in our understanding of termite nesting ecology (Almeida *et al.*, 2017; Sales *et al.*, 2018).

In this study, we characterized nest-building termite assemblages in a white-sand forest fragment near Iquitos, Loreto, Peru. We quantified nest density, assessed taxonomic composition and nest-type diversity, documented the botanical substrates and color variation, and evaluated the variation in nest abundance along a disturbance gradient linked to forest-edge proximity.

MATERIALS AND METHODS

STUDY AREA

The study area was a forest fragment at Centro de Investigación y Enseñanza Forestal – CIEFOR, Puerto Almendra, Iquitos, Loreto, Perú (3°49'40" S, 73°22'30" W) at 122 m a.s.l., of the Universidad Nacional de la Amazonia Peruana- UNAP, covering 1 000 ha of secondary forest. The average of annual precipitation is 2979.3 mm; the average annual temperature is 26.4 °C; the annual

average maximum and minimum temperatures reach 31.6 °C and 21.6 °C respectively and the average of annual relative humidity is 82.1%. The botanical assemblages in the study area are similar to those described by Zarate *et al.* (2013). The sampled area is bordered by the Zungarococha road (Figure 1).

SAMPLING AND DATA COLLECTION

We established ten 900 m² plots, each measuring 30x30 m. The initial plots were located at distances of 130 m from the Zungarococha road (Figure 1), followed by subsequent plots each 30 m: 160 m, 190 m, 220 m, 250 m, 280 m, and 310 m. Sampling was conducted from 8:00 am to 12:00 pm between July and August 2023.

We detected the termite nests in each plot by visual surveys. We identified the termite species to genus using the key of Constantino (1999). The taxonomic identification of botanic substrate (family and species) of each termite nests was made in situ by an Amazonian botanic specialist of the Instituto de Investigaciones de la Amazonia Peruana- IIAP. We obtained the followed data from each nest: type (arboreal, epigeum and galleries- Figure 2); substratum (arboreum, shrub, fall tree and liana) and color (dark brown, brownish, light brown and greyish). To detect changes in the spatial variation in nests abundance we obtained the linear distance (in m) between the middle of each plot to the Zungarococha road edge (Figure 1).

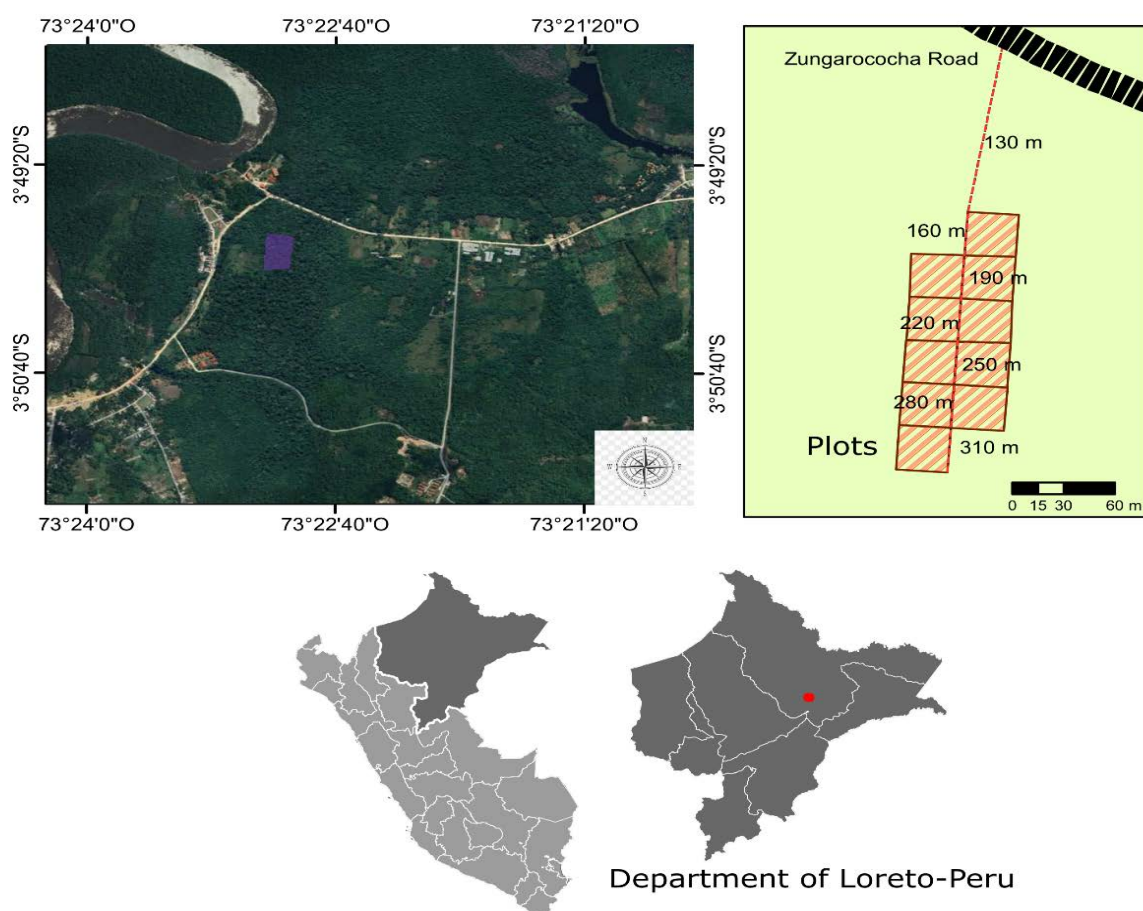


Figure 1. Map of geographic sampling for data collection in a white sand forest fragment in the department of Loreto, Perú. Purplish square is the sampling area.

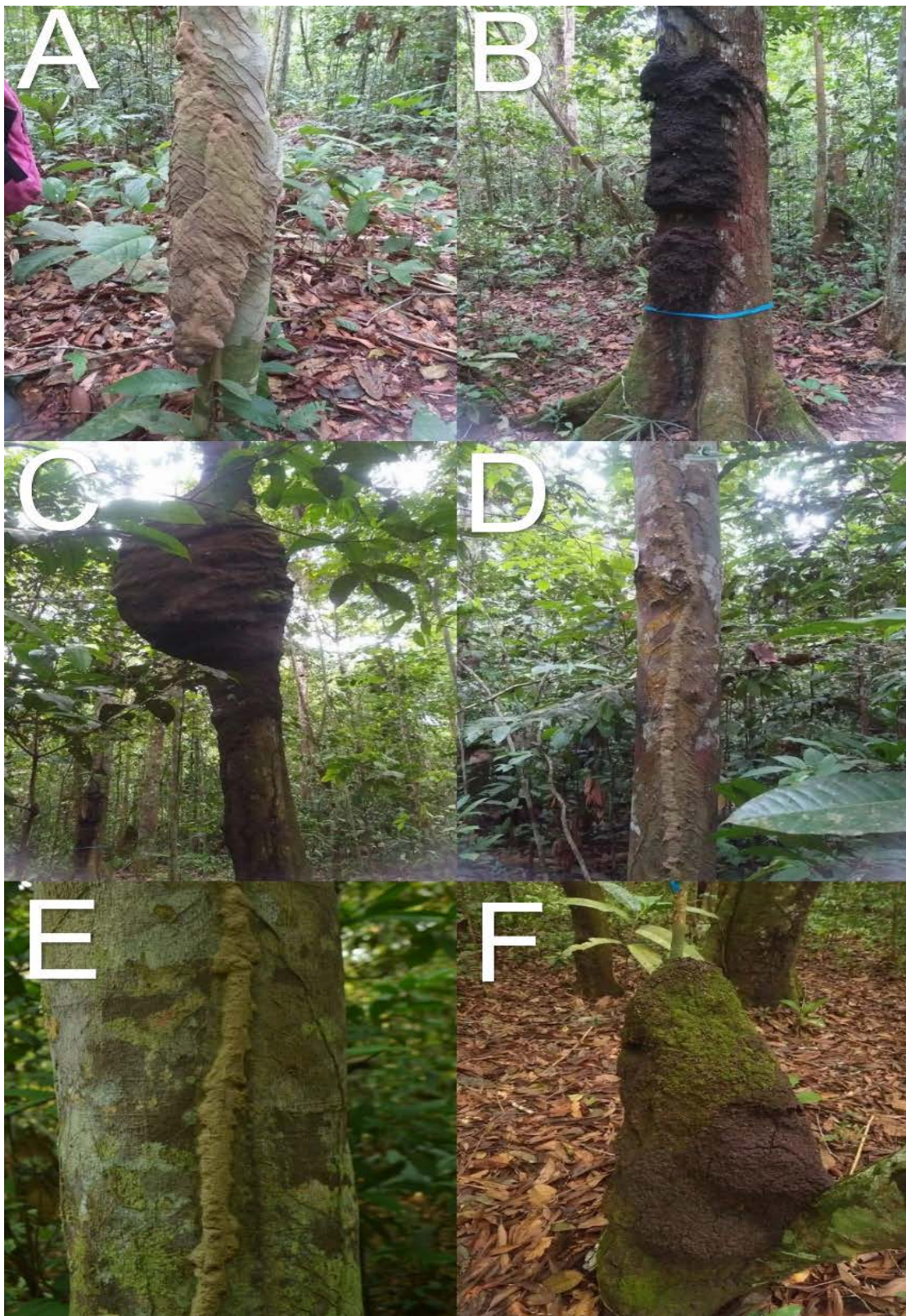


Figure 2. Classification of termite nest types detected in 10 plots of 30x30 m in a forest fragment in Loreto, Peru: A-C= Arboreum type; D-E= Galleries type; F= Epigeum.

DATA ANALYSIS

We determined the total and relative abundance of termite nests by total area and per square meter. We calculated the percentage of occurrence of nests by botanical family and their presence by plant species. We performed a chi-squared test to determine the statistical significance between plant species and termite genus. We assessed the occurrence percentage of termite nest types, substratum, and color. We performed a linear regression analysis of the $\log_{10}$ of the distance from the road to each plot versus the $\log_{10}$ of the number of nests in each plot. We performed a chi-squared test to determine the statistical significance of the occurrence of termite genus occurrence across plot distances.

For data analysis, we treated the presence of each nest as an independent sample. However, termites can often extend their nests through subterranean galleries and emerge as other mounds in different locations. All analyses were performed using standard package of R software v.4.2.1. (R Core Team, 2015).

RESULTS

We detected a total of 156 nests in 900 m² of sample area of five termite genus: *Coptotermes*, *Constrictotermes*, *Nasutitermes*, *Embiratermes* and *Termes*, four sub-Families: Coptotermitinae, Nasutitermitinae, Syntermitinae and Termitinae and two Families: Rhinotermitidae and Termitidae. The relative abundance of mounds in was 0,17 mounds/m².

The genus *Nasutitermes* was the most abundant (60,90% of occurrence, n= 95), followed by *Embiratermes* (33,33% of occurrence, n=52); *Coptotermes* (3,85% of occurrence, n= 3,85); *Constrictotermes* (1,28% of occurrence, n=2) and *Termes* (0,64% of occurrence, n= 1) (Table 1) (Supplementary Material 1).

PLANT SUBSTRATES

Termite nests were identified in 34 botanical families. The family Euphorbiaceae had the highest occurrence (15,30%), followed by Fabaceae (13,50%), Moraceae (9,40%), Rubiaceae (7,10%), Lauraceae (5,90%), and Myristicaceae (5,30%) (Figure 3A), *Alchornea triplinervia* was the species with the most mound occurrences (14,70%), followed by *Brosimum utile* (7,10%), *Iryanthera ulei* and *Ocotea oblonga* (4,70%), *Eschweilera coriacea* and *Remijia peruviana* (4,10%), and *Pourouma tomentosa* and *Protium* sp., (3,50%) (Figure 3B). The chi-squared test revealed significant differences between plant species (X-squared = 285,27; df = 244; p-value = 0,035). The occurrence of plant species by termite genus is detailed in Supplementary Material 2.

TYPE, SUBSTRATUM, AND COLOR OF NESTS

The most abundant type was arboreum (58% occurrence), followed by epigeum (37% occurrence) and galleries (5% occurrence), The predominant substratum was tree (62,3%), followed by shrub (28,2%), fall tree (7,7%), and liana (1,9%), The most common color was dark brown (57,05%), followed by brownish (32,05%), light brown (5,77%), and grayish (5,13%) (Table 2, Figure 4) (Supplementary Material 3).

NESTS ABUNDANCE SPATIAL VARIATION

The linear regression analysis revealed a positive edge effect between road distance and plot distance (p-value = 0,01), with a coefficient of determination (R²) of 0.53 for the relationship between mound abundance and road distance (Figure 5A). The percentage of termite genus increased with the distance from the road (Figure 5B). The chi-squared test determined significant

Table 1. Termite nests abundance in a white sand fragment forests in the department of Loreto, Perú.

Family	Sub Family	Genus	Nest abundance	Relative abundance (Nest/total nests)	Relative abundacen (Nest/900 m ² *)	Percentage (%) of nest occurrence in 900 m ²
Rhinotermitidae	Coptotermitinae	<i>Coptotermes</i>	6	0.04	0.0067	3.85
		<i>Constrictotermes</i>	2	0.01	0.0022	1.28
	Nasutitermitinae	<i>Nasutitermes</i>	95	0.61	0.1056	60.90
		<i>Embiratermes</i>	52	0.33	0.0578	33.33
	Termitinae	<i>Termes</i>	1	0.01	0.0011	0.64

Table 2. Percentage (%) of occurrence of nest by type, substratum and color in 900 m² in a white sand fragment forests in the department of Loreto, Perú. (-) represent not occurrence.

Genus	Type of mound			Mound substratum				Mound color			
	Arboreum	Epigeum	Galleries	Tree	Fallen Tree	Shurb	Liana	Greyish	Brownish	Dark Brown	Ligth Brown
<i>Constrictotermes</i>	100	-	-	100	-	-	-	100	-	-	-
<i>Coptotermes</i>	50	33,33	16,66	50	16,66	33,33	-	-	20	80	-
<i>Embiratermes</i>	38,46	53,84	7,69	53,84	11,53	34,61	-	4,16	25	62,50	8,33
<i>Nasutitermes</i>	68,42	28,42	3,15	66,31	5,26	25,26	3,15	2,17	38,04	54,44	5,43
<i>Termes</i>	-	100	-	100	-	-	-	-	-	100	-

differences in termite genus relative to plot distances (X-squared = 118,65; df = 36; p-value = 0,001).

DISCUSSION

Our results revealed a surprisingly robust nest abundance for an edaphically harsh environment. We recorded five genera, *Nasutitermes*, *Embiratermes*, *Coptotermes*, *Constrictotermes* and *Termes*, in 0.9 ha. Our termite nest density (156 per 0.09 ha) substantially exceeds the 79 mounds reported by Ackerman *et al.* (2007) across 0.104 ha of secondary forest in Brazil. However, it was lower than the 275 nests and six subfamilies reported by Dambros *et al.* (2013) in a fragmented terra firme forest in Central Amazonia.

Our observed generic richness is comparable to that in earlier studies of termite assemblages in forest fragments. For example, Fonseca de Souza & Brown (1994) recorded six genera (nine species) in a central Amazonian remnant, Junqueira & Diehl (2009) reported seven genera in a successional forest fragment in São Paulo, Brazil; and Genet *et al.* (2001) listed eight genus in a subtropical dry forest fragment in Puerto Rico. However, our richness is lower than the values reported from Dambros *et al.* (2013), that reported six subfamilies in a fragmented terra firme forest in Central Amazonia; Constantino (2013) documented 31 genera across terra firme and Várzea ecosystems; Palin *et al.* (2011) that identified 23 genera in the Tambopata National

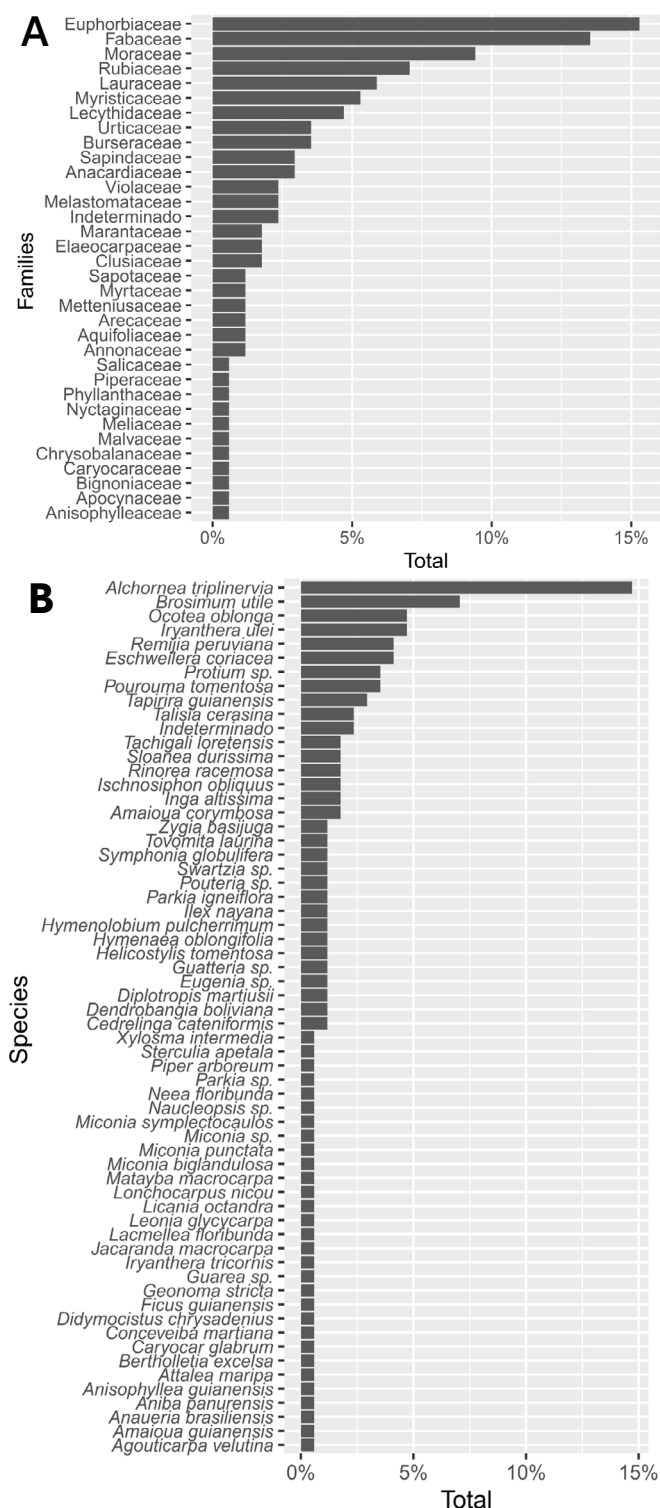


Figure 3. A: Total percent of occurrence (%) of termite nests in plant families in the sampled area. **B:** Total percent of occurrence (%) of termite nests in plant species in the sampled area.

Reserve, Peru; and Casalla & Korb (2019) that recorded 17 genera in a Colombian dry forest fragment. These discrepancies in diversity likely reflect differences in habitat continuity, soil fertility, sampling effort, plot size and taxonomic resolution (morphospecies versus genus), underscoring the need for cautious cross-study comparisons.

Our findings highlight *Nasutitermes* and *Embiratermes* as the dominant species in the white-sand fragment. These genera are known for their broad ecological amplitude and ability to inhabit urban, anthropogenic, and both disturbed and undisturbed forest environments (Bustamante & Martius, 1998; Vasconcellos *et al.*, 2010; Scheffrahn & Su, 2005; Boulogne *et al.*, 2017; Mello *et al.*, 2014; Lima *et al.*, 2018). Although terra firme and flooded forests differ markedly from white-sand in terms of soil fertility and vegetation structure, several studies have reported similar dominance of the subfamily Nasutitermitinae, especially *Nasutitermes* (Ackerman *et al.*, 2009; Pinzon *et al.*, 2017). The abundance of both genus is closely associates with forest structural and environmental parameters, particularly leaf litter biomass, woody plant basal area and mean tree diameter. These parameters exhibit strong, positive correlations with termite nests density (Davies *et al.*, 2003; Jones *et al.*, 2003; Apolinário & Martius, 2004; Vasconcellos *et al.*, 2010; Dahlsjö & Iñiguez, 2020).

We observed that termite genera exhibited non-random associations with certain botanical families. *Nasutitermes* and *Embiratermes* were frequently associated with the Euphorbiaceae family, particularly *Alchornea triplinervia*, while *Coptotermes* occurred across several plant taxa, with notable frequency in *Brosimum utile* (Moraceae). *Constrictotermes* showed higher occurrence in *Amaioua corymbosa* (Rubiaceae) and *Ilex nayana* (Aquifoliaceae). Despite these patterns, termites do not appear to respond to

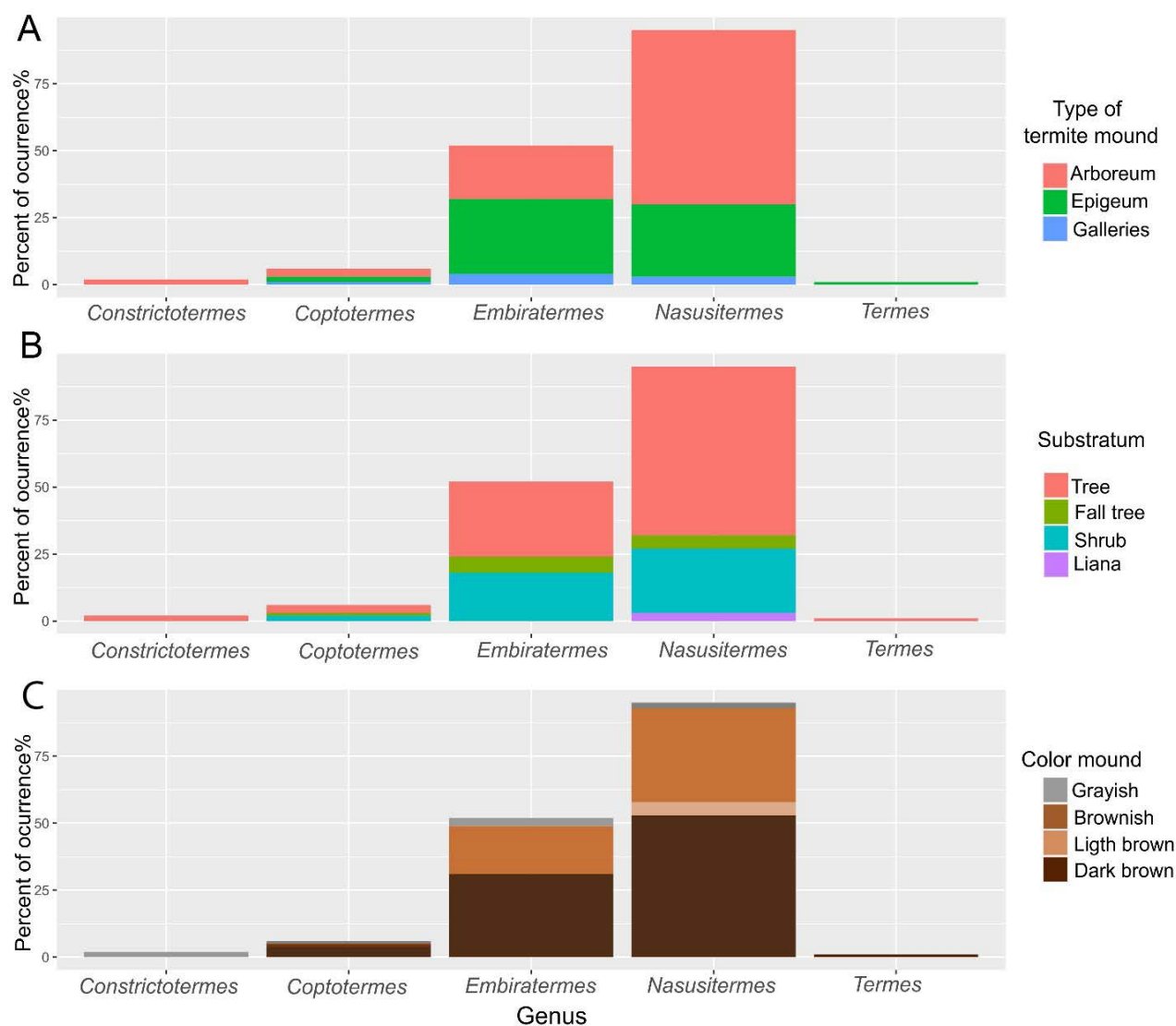


Figure 4. Percentage of occurrence of termite nest by genus in the sampled area. A= types; B= substratum and C= color of nests.

specific environmental cues such as botanical identity; instead, mound placement likely reflects stochastic dispersal via alate flight, followed by nest construction in structurally accessible substrates rather than selective ones (Araújo *et al.*, 2010). The predominance of dark-brown color in nests (57%) suggests incorporation of humic-rich organic material. Such pigmentation may enhance solar absorption, mitigate thermal fluctuations and stabilize internal nest temperatures (Noirot & Darlington, 2000; Paejaroen *et al.*, 2021). Furthermore, the predominance of

arboreal nests (58%) underscores the importance of above-ground vegetation architecture in substrate selection. Termites appear to exploit buttresses and low-lying branches to access drier, better-aerated microhabitats within an otherwise saturated soil matrix.

Although our sampling represents a single unit and modest spatial extent, the clear gradient in nest abundance and genus (Figure 5) from the road into the forest appears to reflect an edge effect. Microclimatic shifts created by the edge, including higher temperatures, lower humidity,

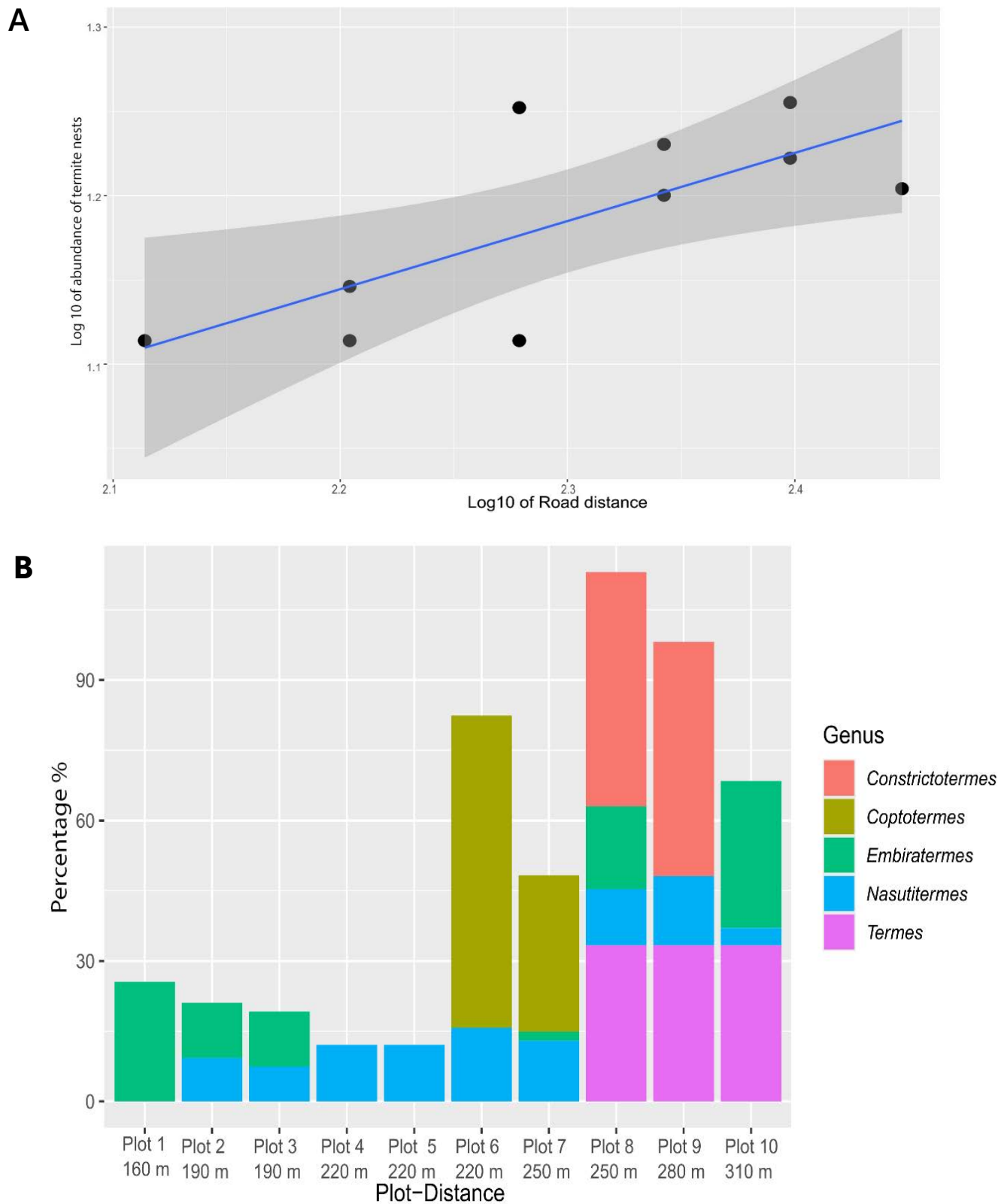


Figure 5. A: Linear regression between the distance of plots from the road edge versus the abundance of termite nests. **B:** Variation in termite genus across distance from road edge.

and variable soil moisture, alter niche availability and favor termite taxa with broader physiological tolerances (Almeida *et al.*, 2017). Comparable results have been reported in Amazonia. Fonseca de Souza & Brown (1994) and Dambros *et al.* (2013) documented reduced termite occurrence and altered community composition near forest edges. Dosso *et al.* (2017) demonstrated rapid, short-term changes in termite assemblages following slash-and-burn disturbances.

CONCLUSIONS

Our study demonstrates that even nutrient-poor white-sand forest fragments near Iquitos support dense, and taxonomically rich, nest-building termite assemblages. The predominance of nests constructed primarily on Euphorbiaceae, Fabaceae and Moraceae families, especially *Alchornea triplinervia*, and the high frequency of dark-brown nests reflect consistent substrate selection and material use strategies. The positive relationship between nest abundance and distance from the road highlights the sensitivity of termite engineers to disturbances. These findings underscore the resilience of termites in maintaining soil turnover and microhabitat heterogeneity under extreme edaphic constraints, and they emphasize the need to incorporate termite-mediated processes into conservation and management plans for fragmented white-sand ecosystems.

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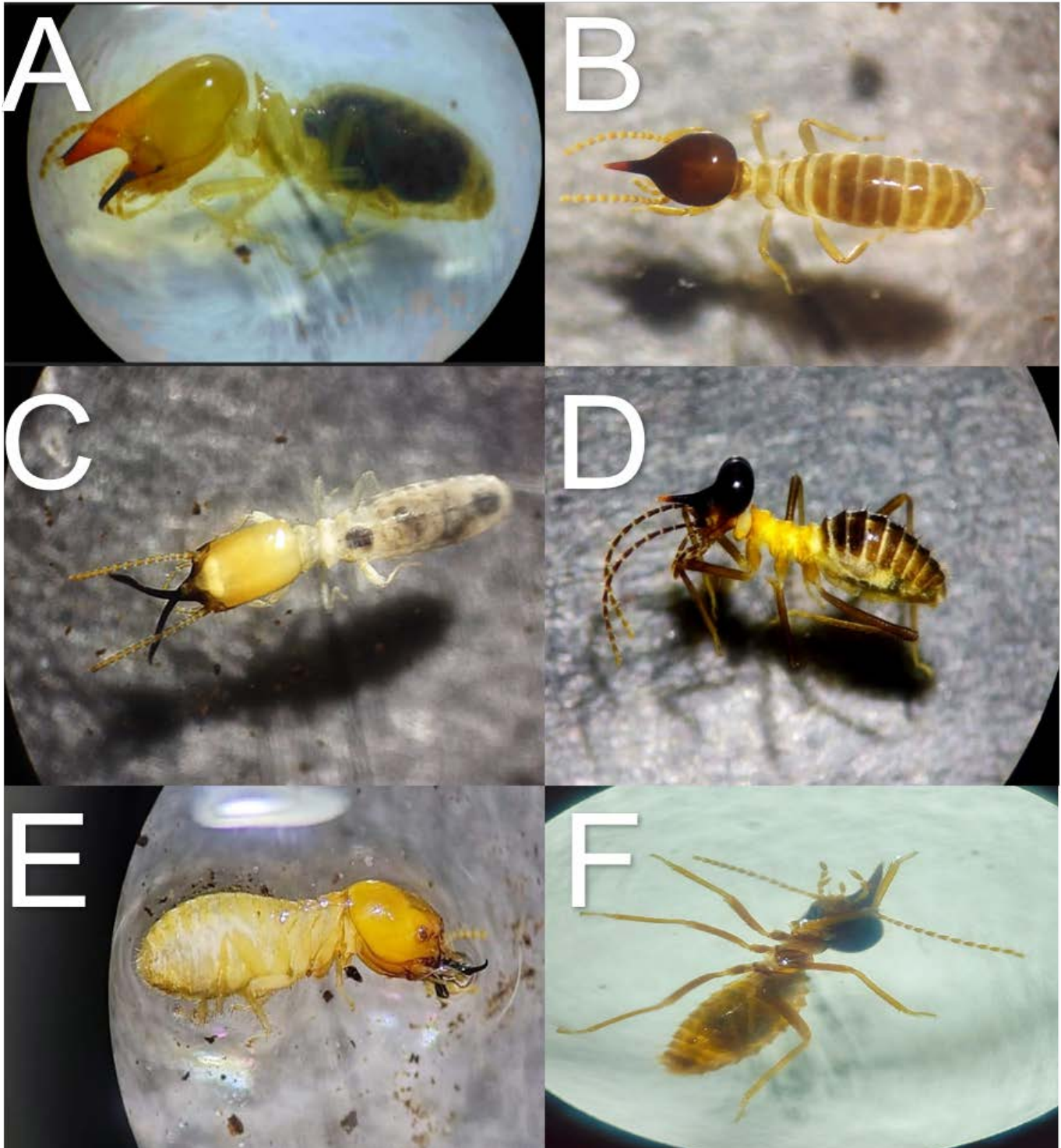
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SUPPLEMENTARY MATERIAL 1. Genus taxonomic diversity of termites reported in 10 plots of 30x30 m in a white sand forest fragment in Amazonia. **A:** Family: Termitidae; Sub- Family: Syntermitinae; Genus: Embiratermes; **B:** Family: Termitidae; Sub-Family: Nasutitermitinae; Genus: Nasutitermes. **C:** Family: Termitidae; Sub- Family: Termitinae; Genus: Termes. **D:** Family: Termitidae; Sub-Family: Nasutitermitinae; Genus: Constrictotermes; **E:** Family: Rhinotermitidae; Sub-Family: Coptotermitinae; Genus: Coptotermes. **F:** Family: Termitidae; Sub- Family: Nasutitermitinae; Genus: Nasutitermes.



SUPPLEMENTARY MATERIAL 2. Total occurrence of termite nests in plant species in 900 m² in a white sand fragment forests in Iquitos, Loreto, Perú.

Plant species	Genus				
	<i>Constrictotermes</i>	<i>Coptotermes</i>	<i>Embiratermes</i>	<i>Embiratermes</i>	<i>Termes</i>
<i>Agouticarpa velutina</i>				1	
<i>Alchornea triplinervia</i>		1	6	18	
<i>Amaioua corymbosa</i>	1		1	1	
<i>Amaioua guianensis</i>				1	
<i>Anaueria brasiliensis</i>				1	
<i>Aniba panurensis</i>				1	
<i>Anisophyllea guianensis</i>			1		
<i>Attalea maripa</i>			1		
<i>Bertholletia excelsa</i>				1	
<i>Brosimum utile</i>		2		9	1
<i>Caryocar glabrum</i>				1	
<i>Cedrelinga cateniformis</i>			1	1	
<i>Conceveiba martiana</i>			1		
<i>Dendrobangia boliviana</i>				2	
<i>Didymocistus chrysadenius</i>			1		
<i>Diploctropis martiusii</i>			1	1	
<i>Eschweilera coriacea</i>			4	3	
<i>Eugenia</i> sp.				2	
<i>Ficus guianensis</i>				1	
<i>Geonoma stricta</i>				1	
<i>Guarea</i> sp.				1	
<i>Guatteria</i> sp.				2	
<i>Helicostylis tomentosa</i>				1	1
<i>Hymenaea oblongifolia</i>				2	
<i>Hymenolobium pulcherrimum</i>				2	
<i>Ilex nayana</i>	1			1	
<i>Indeterminado</i>			2	2	
<i>Inga altissima</i>			3		
<i>Iryanthera tricornis</i>				1	
<i>Iryanthera ulei</i>			3	5	
<i>Ischnosiphon obliquus</i>			1	2	
<i>Jacaranda macrocarpa</i>			1		
<i>Lacmellea floribunda</i>		1			

SUPPLEMENTARY MATERIAL 2. Continue

Plant species	Genus				
	<i>Constrictotermes</i>	<i>Coptotermes</i>	<i>Embiratermes</i>	<i>Embiratermes</i>	<i>Termes</i>
<i>Leonia glycyarpa</i>				1	
<i>Licania octandra</i>				1	
<i>Lonchocarpus nicou</i>			1		
<i>Matayba macrocarpa</i>			1		
<i>Miconia biglandulosa</i>			1		
<i>Miconia punctata</i>					1
<i>Miconia</i> sp.			1		
<i>Miconia symplectocaulos</i>			1		
<i>Naucleopsis</i> sp.				1	
<i>Neea floribunda</i>			1		
<i>Ocotea oblonga</i>			3	5	
<i>Parkia igneiflora</i>		1		1	
<i>Parkia</i> sp.				1	
<i>Piper arboreum</i>			1		
<i>Pourouma tomentosa</i>			2	4	
<i>Pouteria</i> sp.				2	
<i>Protium</i> sp.			1	5	
<i>Remijia peruviana</i>		1	2	4	
<i>Rinorea racemosa</i>			3		
<i>Sloanea durissima</i>				3	
<i>Sterculia apetala</i>			1		
<i>Swartzia</i> sp.				2	
<i>Symphonia globulifera</i>			1	1	
<i>Tachigali lorentensis</i>			1	2	
<i>Talisia cerasina</i>				4	
<i>Tapirira guianensis</i>			1	4	
<i>Tovomita laurina</i>				2	
<i>Xylosma intermedia</i>			1		
<i>Zygia basijuga</i>			1	1	

SUPPLEMENTARY MATERIAL 3. Percentage of occurrence of termite nest by genus in the sampled area. A= types; B= substratum and C= color of nests.

