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A mis padres: Anita y José Manuel
Mis tías: Vilma y Olga

Por su amor y apoyo incondicional.

“If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos.”

Edward O. Wilson

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Resumen

Estructura funcional de los ensamblajes de termitas asociados con sistemas productivos de caucho en el noroeste de la Amazonía Colombiana.

La ganadería extensiva en la amazonia ha causado deforestación y degradación en el suelo, con consecuencias negativas en la biodiversidad y servicios ambientales. Mientras el establecimiento de plantaciones de caucho ha surgido como una alternativa productiva y de restauración para suelos degradados por la ganadería. Este estudio evaluó las diferencias en los ensamblajes y la estructura funcional de las termitas en tres diferentes cultivos de caucho como una forma indirecta de evaluar la restauración de la diversidad del suelo. Tres sistemas de cultivos de caucho fueron muestreados: campos clonales (CF), plantaciones comerciales (CR) y plantaciones mixtas (MX). Adicionalmente, pasturas ganaderas (PA) y bosques naturales (NF) sirvieron como ecosistemas de referencia. Las termitas se muestrearon usando el método de transecto. De las 80 especies colectadas, 3.8% correspondía a la familia Rhinotermitidae y el 96.2% a la familia Termitidae. El bosque natural fue el uso de la tierra con mayor riqueza (54 especies) y ocurrencia de especies (437 ocurrencias). En los sistemas de cultivo de caucho fue 39% mayor que en pasturas e incluyeron el 72% del total de especies encontradas en los bosques naturales. Los usos de suelo fueron agrupados de acuerdo con su diversidad: grupo I de alta diversidad (CR y NF) y grupo II de baja diversidad (CF, MX y PA). Dentro de las 14 variables de suelo que se evaluaron, carbón orgánico, densidad aparente y conductividad eléctrica fueron las variables que más influenciaron sobre las comunidades de termitas. Las termitas consumidoras de suelo estuvieron asociadas con usos de suelo de baja diversidad y las xilófagas estuvieron asociados con usos de suelo de alta diversidad. Pasturas y MX presentaron la diversidad más baja, pero sus estructuras funcionales fueron diferentes en sí. Por otro lado, la estructura funcional de CR fue similar a la de NF. Nuestros resultados demostraron que recuperar la diversidad y la estructura funcional de las termitas es posible y dependerá de las prácticas de manejo del cultivo de caucho.

Palabras clave: Campo clonal, carbón orgánico, consumidores de suelo, especies indicadoras, usos del suelo.

Abstract

Functional structure of termite assemblages associated with productive rubber crop systems in the northwestern Colombian Amazon

Livestock production extension in Amazon has caused deforestation and soil degradation, with negative consequences on biodiversity and environmental services. While the rubber plantations establishment has arisen as a productive and restoration alternative degraded livestock soils. This study evaluated differences in termite assemblage and functional structure in three different rubber crop systems as an indirect way of evaluating soil diversity restoring. Three rubber crop systems were sampled: clonal fields (CF), traditional commercial rubber plantations (CR), and mixed plantations (MX). Additionally, livestock pastures (PA) and natural forest relicts (NF) were compared to rubber crop systems, to serve as reference habitats. Termites were sampled using the transect method. From 80 species collected, 3.8% corresponded to Rhinotermitidae family, and 96.2% to Termitidae family. The natural forest was the land use with the highest richness (54 species) and species occurrence (437 occurrences). Species richness in rubber crop systems were 39% higher than in pastures and included 72% of the termite species found in natural forests. The land uses were clustered according to their diversity: group I of high diversity (CR and NF) and group II of low diversity (CF, MX and PA). Among the 14 soil variables that were evaluated, organic carbon, bulk density and electrical conductivity were the variables that most influenced the termite communities. Soil-feeders termites were associated with less diverse land uses and wood-feeders were associated with high diverse land uses. Pastures and MX presented the lowest values in diversity, but each functional structure was different. Elseways, functional structure of CR was similar to the natural forests. Our results demonstrate that termite diversity and functional structure recovery is possible and will depend on the rubber crop system selected.

Keywords: Clonal field, indicator species, land uses, organic carbon, soil-feeders.

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Introduction

Insects contribute significantly to vital ecological functions such as pollination, biological control, food provisioning, wildlife maintenance, nutrient recycling, and decomposition of organic matter (Costanza *et al.* 1997; Crespo-Pérez *et al.* 2020), indicating them as one of the main ecosystem services providers (Dangles & Casas 2019). However, knowledge about the ecosystem services of insects is still scarce and skewed due to their high diversity of taxonomic and functional groups (Noriega *et al.* 2018). The influence of insects on agriculture, human health, and natural resources, highlights the importance of these animals for biodiversity conservation (Losey & Vaughan 2006; Scudder 2017). However, human activities, such as landscape and land cover transformation, can affect arthropod communities in different ways and, consequently, affect the ecosystems balance (Benito *et al.* 2004; Decaëns *et al.* 2004; Mathieu *et al.* 2005; Rossi *et al.* 2006). Disturbance in arthropod communities reflects on their taxonomic richness, abundance, and species composition, and measuring these variables can provide an indication of the degree of disturbance in different landscapes (Bellamy *et al.* 2018; Lamarre *et al.* 2016).

Termite assemblages are considered good biodiversity indicators in tropical regions because these insects are key organisms in soil organic matter cycling and influence significantly soil composition and structure (Bignell 2005; Lavelle 1997; Lima *et al.* 2018; Siebers *et al.* 2015). Additionally, their species diversity is not negligible and they represent a significant portion of the total soil biomass in the tropics, being one of the most abundant soil organisms in these ecosystems (Barros *et al.* 2002; Eggleton *et al.* 1996; Jones *et al.* 2003).

When the natural forest is modified and/or the land use is intensified, termite richness and abundance often decrease (Ackerman *et al.* 2009), and species composition may also change (Carrijo *et al.* 2009). The importance of these insects, as well as the effect of anthropic activity in their community, have been studied in the Amazon region under different conditions, such as agricultural landcovers implementation (Ackerman *et al.* 2009; Duran-Bautista *et al.* 2020a); natural, disturbed and fragmented forests (Bandeira *et al.* 2003; Bourguignon *et al.* 2011a; De Souza & Brown 1994); pastures (Bandeira 1989); elevation gradient (Palin *et al.* 2011); and road-associated edge effects (Dambros *et al.* 2013).

Termites feed on almost the entire lignocellulosic decomposition spectrum, from sound wood to the organic matter of humus/soil (Eggleton & Tayasu 2001). Regarding this gradient, they are usually categorized into functional or feeding groups (Constantino & Acioli 2006). Because of their capacity to assimilate cellulose as food, termites are among the main decomposers of plant material (Tokuda & Watanabe 2007), and they play important roles in Nitrogen and Carbon cycles in most tropical ecosystems (Jouquet *et al.* 2011). Also, their functional groups are influenced in different ways by landscape disturbance and can be used to understand human impact in the environments (Davies *et al.* 2003; De Souza & Brown 1994).

Termites can thrive in a variety of hostile environments and contribute to the distribution of natural resources in the soil, such as water and nutrients, and help soil rehabilitation and vegetation coverage regeneration (Jouquet *et al.* 2011; Mando *et al.* 1996; Mando & Miedena 1997). Plantations with native or introduced species established in lands previously used for extensive livestock farming show advantages from an environmental point of view, and one example of these advantages is the conservation of some soil fauna, including termites, and the natural resources they provide (Decaëns *et al.* 1999; Marichal *et al.* 2014; De Souza *et al.* 2016).

In Amazonian soils, where the fertility and recovery capacity are low, the use of termites as bioindicators of degraded ecosystems has been studied to determine the impact of land use on soil degradation and organic matter cycling (Ackerman *et al.* 2009; Bandeira *et al.* 2003; Barros *et al.* 2002; Davies *et al.* 2003). Given the sensitivity on the termite community assemblages to the disturbance and availability of soil organic matter (LeClare *et al.* 2020; Siebers *et al.* 2015), it is important to study the role of these insects in natural and anthropic ecosystems, to better understanding the soil dynamics associated with land usage. One way to do that is to correlate the diversity, abundance, and functional structure of termite communities with the soil physicochemical composition in these ecosystems under different land usages.

Currently, in the Colombian Amazon, projects for the implementation of rubber-based production systems are being carried out, where rubber production has been detected as a fundamental support for the economic development of the agricultural and industrial sector (Castellanos *et al.* 2009; Sterling & Rodríguez 2012). Given the wide establishment of rubber plantations in the country, ecological studies of termite communities in these kind of land use are still scarce (Duran-Bautista *et al.* 2020a; b; Pinzón *et al.* 2012). However, studies from other regions suggest that these insects are useful biological indicators, providing taxonomic, functional, and ecological information of the alterations that have occurred during the transformation of a field into a rubber plantation (Hidayat *et al.* 2018; Liu *et al.* 2019). Tree plantations with either native or introduced species may be better to supply resources and conserve soil fauna than extensive livestock pastures (Decaëns et al. 1999; Marichal et al. 2014; De Souza et al. 2016). Trees can increase soil organic matter availability through increasing inputs above- and below-ground, improving soil quality, and enhancing biological activity.

Considering termite assemblages as biological indicators of soil quality and the wide use of rubber-based production systems in Colombia, the current study aims to evaluate the termite diversity and functional structure in three different rubber crop systems that have been established in the Colombian Amazon in areas previously used for livestock production and compare them with two reference ecosystems: pastures (PA) still used for extensive livestock production, and natural forest relicts (NF). The three rubber crop systems evaluated are mixed plantations (MX), clonal fields (CF), and commercial plantations (CR).

The following research question is posed: How termite species richness, abundance, and functional structure are influenced by different productive systems of natural rubber in areas previously occupied by pastures and by the soil physicochemical properties, in the northwestern Colombian Amazonian basin?

The following hypotheses are raised from the bibliographic review of this thesis:

i. Natural forests have higher values in termite species richness and abundance, followed by rubber plantations, and the pasture have the lowest values.
ii. A higher abundance of termites is expected in soils that show an increment in bio-available nutrients (K, Mg, and P), organic carbon, and pH.
iii. The functional structure of the termite community in productive rubber systems is more similar to natural forests than to pastures.

Objectives

General objective

Characterize the assemblages of termites according to their diversity and functional structure in three productive systems of *Hevea brasiliensis* with respect to their previous use, as pastures, and to undisturbed natural forests, in the Caquetá state, Colombia.

Specific objectives

1. Estimate the species richness and relative abundance of termites in three rubber productive systems, natural forest, and pastures.
2. Analyze the influence of the physicochemical variables of the soil on the termite communities, in each one of the studied habitats.
3. Characterize the functional structure of termites in each of the studied habitats.

Chapter 1: Termite diversity in three rubber crop systems, natural forests, and pastures

1.1. Introduction

Termites are one of the most abundant and dominant groups in tropical forests (Barros *et al.* 2006; Hölldobler & Wilson 1990), and play an important role in the ecosystem directly influencing the organic matter decomposition, soil composition, soil structure, and nutrient cycling (Bignell 2005; Jones *et al.* 1994; Lavelle 1997).

When the natural forest is modified and/or the land use by humans is intensified, termite richness and abundance often decrease (Ackerman *et al.* 2009), and species composition and function diversity may change (Carrijo *et al.* 2009). Termite assemblages respond to changes in land use, where the abundance and species richness are influenced by the soil disturbance, which has been explored in agrosystems, forestry plantations, pastures and intervened natural covers, as well as altitudinal gradients and natural restoration (Cancello *et al.* 2014; Coulibaly *et al.* 2016; Eggleton *et al.* 1997; Jones *et al.* 2003; Oliveira *et al.* 2013; Palin *et al.* 2011).

The importance of termites, as well as the effect of anthropic activity in their communities, have been studied in the Amazon region under different conditions such as agroforestry systems, disturbed forest and natural forest (Bandeira *et al.* 2003; Barros *et al.* 2002; Bourguignon *et al.* 2011a; Palin *et al.* 2011). Studies on non-timber forest plantations established in deforested forest soils, such as natural rubber production, have reported that plantations harm the termite diversity (Barros *et al.* 2004; Liu *et al.* 2019), but the effect on rubber plantations established in degraded soils such as pastures have not been evaluated for this crop.

Nevertheless, forest crops can host a high number of termite species in Neotropical areas (Beltrán-Díaz & Pinzón-Florián 2018; Junqueira *et al.* 2009; Sanabria *et al.* 2016; De Souza *et al.* 2016). Besides, commercial tree plantations can harbor wildlife, serve as biological corridors, and recover degraded areas (Keenan *et al.* 1999; Lamb 1998).

Rubber plantations in the Amazon region have been proposed as an alternative to recover degraded soils by extensive livestock farming, which is one of the main causes of deforestation (Castellanos *et al.* 2009), in addition to having been identified as beneficial for the physical-chemical soil properties (Cherubin *et al.* 2019). Furthermore to the ecological benefits, plantations presents economic and social advantages for local rural development (Ramírez *et al.* 2018).

1.1.1. Role of the rubber plantations (*Hevea brasiliensis*) in the recovery of degraded Amazon soils

The rubber tree [*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Muell.-Arg.] is a native species of South America in the Amazon and Orinoco plains, but currently this tree species present a wide distribution throughout the Neotropics (Compagnon 1998). Rubber trees grow in tropical climates with an average temperature of 28° C and an annual rainfall of 1500 to 4000 mm (Sanjeeva Rao *et al.* 1998), which has facilitated the establishment of this crop in tropical areas in Asia and Africa (Ali *et al.* 2021), where 90% of global rubber production is concentrated (Fox & Castella 2013).

The rubber tree exploitation aims to obtain latex, which is used in the industry as a raw material, and its main destination is the automotive industry for tires manufacture (Compagnon 1998). Non-timber forest plantations represent 30% of forest plantation, moreover, it has been shown that the use of rubber tree wood, in addition to latex, can increase the profitability of rubber plantations by up to 40% (Shigematsu *et al.* 2013).

In Colombia, large-scale exploitation of rubber began in the second half of the 19th century. During this period, mainly in the Amazon region, there was a phenomenon called "the rubber fever", which entailed many socio-territorial problems. At the end of the Second World War “the fever” had its decline (Sierra 2011), but a second upswing occurred after 1960, where the national government promoted the rubber establishment, when not only large producers have been encouraged, but there was also a significant support for small producers (Ramírez *et al.* 2018).

Currently, rubber plantations are established in 17 states of Colombia, concentrated in five productive centers: Cordón cauchero cacaotero (Antioquia, and Córdoba), Magdalena centro (Caldas, Cundinamarca, and Tolima), Magdalena medio (Santander y Norte de Santander), Amazonía (Putumayo, Caquetá, and Guaviare), and Orinoquia (Meta y Vichada) In total. The total area of plantations in the country was calculated in 53,223 ha in 2015. The productive center of the Amazonía (Amazon) is the third largest with an area of 6,616 ha, and the Caquetá state is the fourth state with the largest rubber area planted with a total of 4,534 ha (CCC 2016).

Besides, the Caquetá state accounts for 22% of Colombia's deforestation and ranks third in CO_2 emissions, and the land-use change from natural forest to pastures or crops/plantations represents 84% of the state's emissions (IDEAM *et al.* 2016). However, rubber plantations have also been used as an alternative to mitigate carbon emissions: not in the traditional way, changing the land use from forest to plantations, but changing pastures into plantations (Ramírez *et al.* 2018).

Nevertheless, productive traditional rubber plantations have lost productivity in Colombia (Castellanos *et al.* 2009), increasing susceptibility to the South American leaf blight of the Rubber tree produced by the fungus *Microcyclus ulei* (P. Henn.) V. Arx, the main threat to the establishment of new rubber plantations in Latin America (Gasparotto *et al.* 2012). Therefore, It is necessary to expand the rubber genetic base, to increase tolerance to the fungus, through large-scale clonal fields with new introduced clones to the country with successful results in the origin countries (Sterling *et al.* 2011b, 2021). The rubber genetic base expansion has not only been carried out with the traditional monoculture model, also it has dabbled with agroforestry arrangements with Amazonian fruit trees (Sterling Cuéllar & Rodríguez León 2014).

The implementation of rubber-based production systems in degraded pastures helps to capture carbon through the input of litter biomass in soils poor of organic material, and also contributes to the conservation of native biodiversity, and to recover the activity of wildlife (Guillaume *et al.* 2016; Piotto *et al.* 2020). In addition to the ecological benefits, rubber production gives fundamental support for the development of the agricultural and industrial economic sector in the region (Castellanos *et al.* 2009; Sterling & Rodríguez 2012).

1.1.2. State of knowledge of termite diversity in Colombia

Colombia is a highly biodiverse country, especially because of its geographical position, with great number of ecosystems and biomes (Sánchez-Cuervo *et al.* 2012). In the country, many taxonomic groups have their diversity well studied, and ants are one example among the insects (Fernández 2003; Fernández *et al.* 2019). Termites, on the other hand, are still poorly studied, and most of the information regarding their diversity and taxonomy in the country has been published in recent years.

The first records of termites in Colombia from the literature are from the middle 19th century descriptions of the species *Anoplotermes ater* (Hagen 1858)*,* and *Heterotermes tenuis* (Hagen 1858). In this period, *Syntermes spinosus* (Latreille, 1804) was also documented as part of the diet of the indigenous communities of the Amazon rainforest (Weidner 1980). At the beginning of the 20th century, new records were also part of the description of new species from different parts of the country (Krishna & Emerson 1962; Snyder 1924, 1949).

During the 80s and 90s, some works on the ecological aspects of economic importance of termites in urban areas of Colombia were published (Galvis 1984; Galvis *et al.* 1991; Galvis & Flórez 1991). Subsequently, the first records of termites as pests in forest plantations were published in a study that used termites as indicator insects in a change of land use (Decaëns *et al.* 1994).

Since 2000, the study of termites has developed in increasing numbers. In 2005, Vargas-Niño and collaborators provided a comprehensive list of genera of the Termitidae family of Colombia (Vargas-Niño *et al.* 2005). Many studies focused on forest plantations and fruit crops, the termite species records in eucalyptus, rubber, and citrus crops from the Caribbean and Orinoco region (Abadía. *et al.* 2013; Abadía & Arcila 2009; Gutiérrez *et al.* 2004; Pinzón *et al.* 2012). More recently, ecological studies focused on ecosystem services, in addition to providing ecological data on natural and intervened land covers, provided checklists that enriched the knowledge of Colombia termite diversity in the Caribbean (Casalla & Korb 2019a; b) Orinoco (Lavelle *et al.* 2014; Sanabria *et al.* 2016), and Amazon region (Duran-Bautista *et al.* 2020b; a). The Andean and Pacific regions remain the least explored to date.

Finally, there was a remarkable increase in the description of new species from Colombia in the last few years (Casalla *et al.* 2016; Castro *et al.* 2018, 2020; Castro & Scheffrahn 2019; Pinzón *et al.* 2019). These works indicate that there is still a large number of undescribed species that keep in the national biological collections, as well as from unidentified species reported in the above-mentioned ecological studies.

Currently, two different number of species recorded for Colombia are available. The first one is reported by Dr. Reginaldo Constantino's termite catalog with 60 species (Constantino 2021), the second one is the total species reported in the published literature to date, that recorded 106 species for Colombia. The Amazon region reports the highest number of species in Colombia, comprising 70% of the reported species for the country (Castro Unpublished data).

The objective of this chapter is to assess the termite diversity in three different types of rubber production systems present in the region, compared to neighboring pastures and natural forests, and analyze the influence of these crops establishing in degraded areas from a biological point of view.

1.2. Materials and methods

1.2.1. Study area

The study was conducted in the Caquetá state, of the northwestern Amazon region of Colombia (Figure 1-1), in four rubber farms located at the municipalities of San Vicente del Caguán (F1) (2°02'21.9'' N; 74°55'02.86'' W), Florencia (F2) (1°25'45.43'' N; 75°30'59.24'' W), Belén de los Andaquíes (F3) (1°20'14.04'' N; 75°48'34.19'' W), and Albania (F4) (1°14'17.75'' N, 75°52'55.13'' W). The farms were located in the Andean-Amazon pedemont with an altitudinal range between 245 to 420 m. The rainy seasons are from April to July, and October to December, with an annual rainfall of 2179mm and an average annual temperature of 23.9ºC.

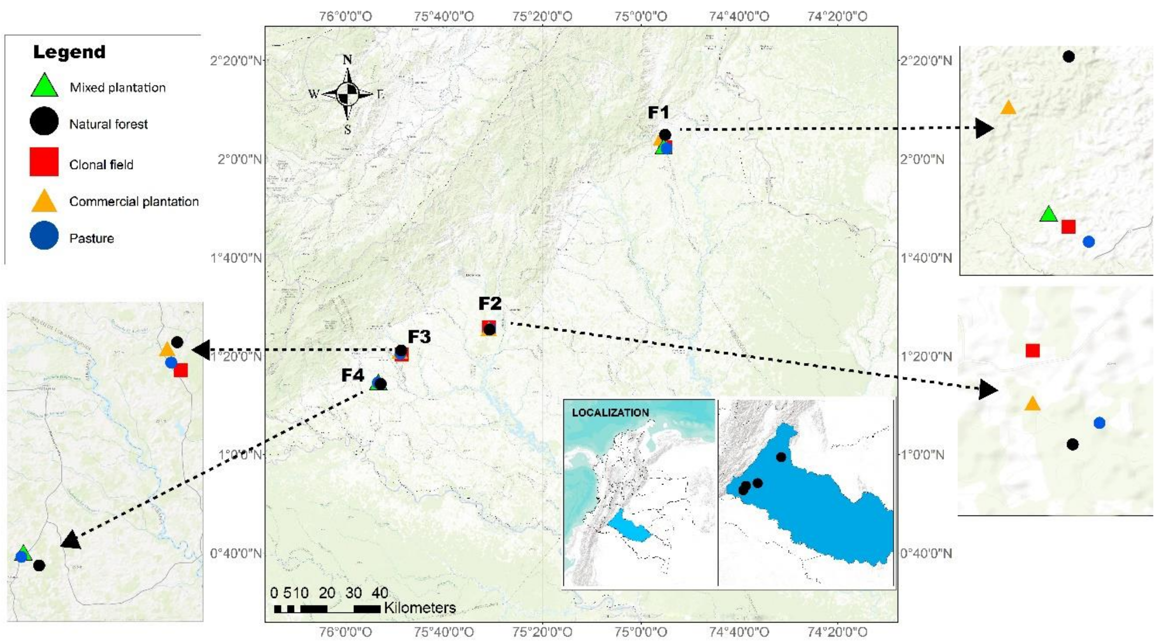


Figure 0-1: Location map of the study areas. Rubber farms: F1= San Vicente del Caguán, F2= Florencia, F3= Belén de los Andaquíes, F4= Albania.

Five different land uses were sampled: three different productive rubber systems: mixed plantations (MX), clonal fields (CF), and traditional commercial rubber plantation (CR) (Table 1). MX corresponds to rubber fields intercropped with copoazu (*Theobroma grandiflorum* (Willd. ex Sprengel) Schumann, family Sterculiaceae) fruit trees; CF are rubber monocultures with different rubber clones, and CR are rubber monocultures with one rubber clone. Pastures (PA) and natural forest relicts (NF) were evaluated as controls. PA corresponds to overgrazed fields for more than ten years by the livestock production. PA was used as a control to evaluate the previous conditions of the soil before the productive rubber system had been implemented. The NF corresponds to natural forest relicts without human intervention for at least 50 years, they have been left when the area was deforested and made into the pasture. These areas have between 5 and 15 hectares and, although not being continuous forests, they compose well-preserved patches.

Areas of PA and NF were sampled in all four farms, and the rubber systems were sampled as follows: CF, CR, and MX in San Vicente del Caguán farm (F1); CF and CR in Belen de los Andaquíes (F3) and Florencia farms (F2); and MX in Albania farm (F4). In total, two of MX, three CF and CR, and four of PA and NF were sampled (Figure 1-1). The different habitats in each farm are within a maximum distance of 1 km one another, being connected in farms F2, F3, and F4; in F1 the CR and NF habitats are not connected with the other habitats. The above-mentioned farms have practiced similar agricultural management to rubber fields (Table 1).

Table 0-1: Description of the three sampled rubber crop systems and their silvicultural management.

Rubber crop system	**Mixed plantation**	**Clonal field**	**Commercial rubber plantation**
Acronym	**MX**	**CF**	**CR**
			
Farm	F1, F4	F1, F2, F3	F1, F2, F3
General description	Mixed plantation of rubber trees from elite progeny and copoazu (*Theobroma grandiflorum*) trees.	Plantations with rubber clones from regional elite genotypes.	Mature plantations with no elite rubber clones and more than 20 years of continuous latex production.
Seedtime	July and August, 2011.	July and August, 2009.	Between 1986 and 1990.
Phytosanitary controls	Malathion insecticide (five times per year) and Mefenoxam fungicide (10 times per year).	Not applied.	Not applied.
Fertilization	Organic fertilization every six months.	Two fertilizers [N, P_2O_5, K_2O, CaO, and $S\text{-}SO_4$] and [N, P_2O_5, CaO, MgO, S, B, Cu, Mo, and Zn], every six months.	Not applied.
Labor practices	Weeds and tree pruning, waste removed mechanically every three months. Chemical control for weeds every four months.	Weeds and tree pruning waste removed mechanically every three months.	Not applied

1.2.2. Termite sampling

Sampling was carried out in April 2018, at the beginning to the rainy season. Termites were sampled following a standard transect protocol (Jones & Eggleton 2000) with modifications. The protocol used consists of tree sub-transects of five plots of 7 m x 3 m each, 15 plots in total per area (Figure 1-2), data will be analyzed by plots and transects (study sites). In the rubber systems (MX, CF and CR) the transects were spaced 7 m among them (Figure 1-2B). In the controls (NF and PA), plots of each transect were settled in a zig-zag disposition (Figure 1-2A), because these areas presented irregular forms and short linear distance. Two trained collectors sampled each plot for 30 minutes (7.5 hours per transect).

A total of 45 plots were sampled for CF and CR, 30 plots for MX, and 60 plots for each control (PA and NF). Termites were actively searched with axes and garden trowels in litter, stumps, nests, pieces of wood, twigs, fallen branches, and in six random soil monoliths of 10 x 10 x 15 cm depth. Representative samples of termites (around 10 individuals of each termite caste present for a total of around 30 individuals, as long as the individuals number found per colony allows it) were extracted with entomological tweezers and placed within 1.5-2.0 ml vial with 85% ethanol,

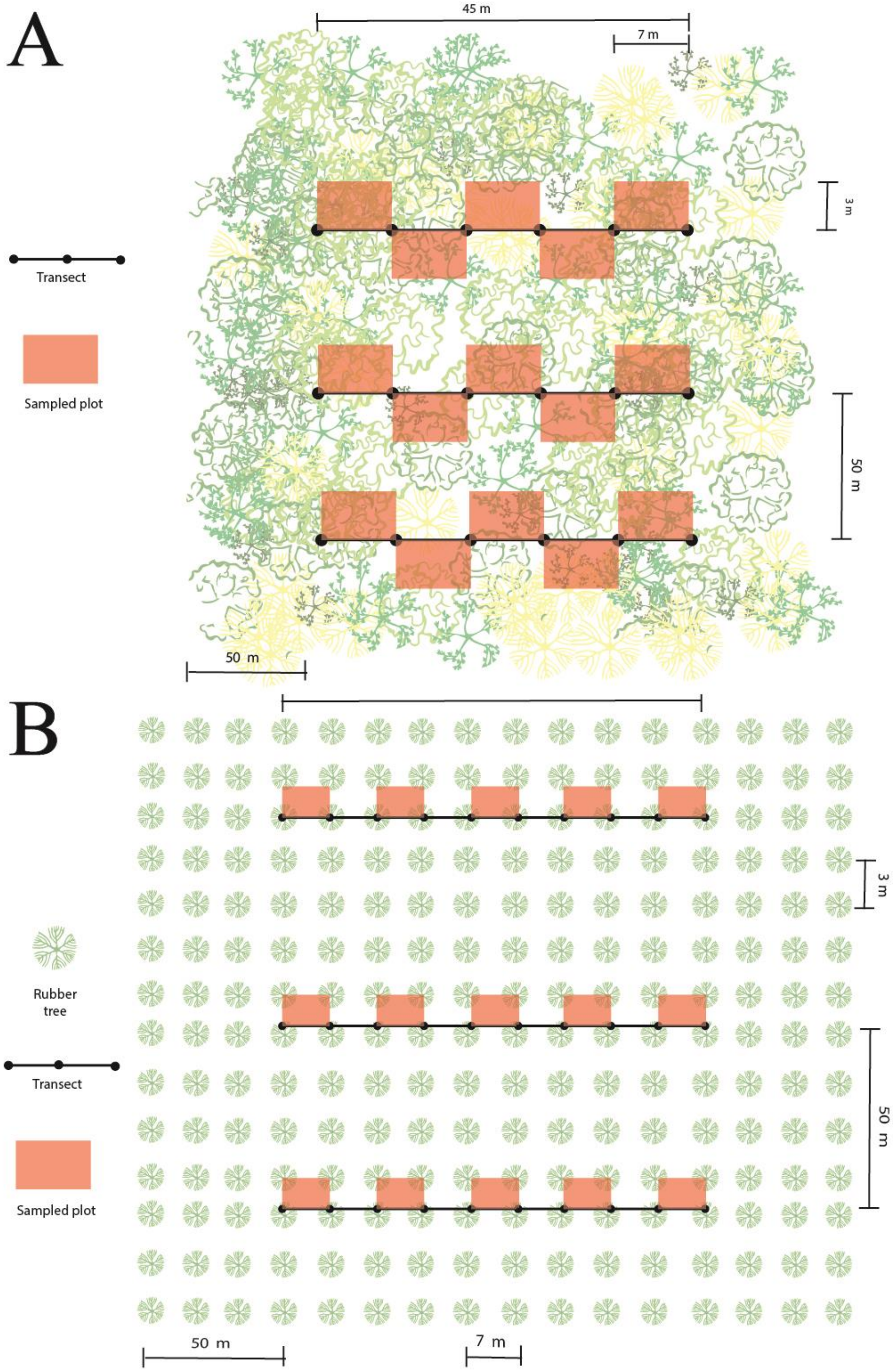


Figure 1-2: Termite sampling method. **A.** Forests and pastures. **B.** Rubber systems.

1.2.3. Termite identification

Morphological characteristics of the soldiers were used to identify all termites, except the subfamily Apicotermitinae, which lacks the soldier caste in Neotropical species. Termite species were identified in the Laboratory of Biotechnology of the Instituto Amazónico de Investigaciones Científicas SINCHI in Bogotá, following the key for termite genera published by Constantino (2002) and complemented with descriptions of recent genera (Bourguignon *et al.* 2010, 2016a; Castro *et al.* 2020; Rocha *et al.* 2012; Scheffrahn *et al.* 2017). Several keys, revisions, and original descriptions of termite species were also employed (Cancello & Cuezzo 2007; Castro & Scheffrahn 2019; Constantini & Cancello 2016; Constantino 1991, 1995, 1998, 2000; Constantino *et al.* 2006; Constantino & De Souza 1997; Emerson 1925; Krishna 2003; Krishna & Araujo 1968; Mathews 1977; Rocha & Cancello 2009; Scheffrahn 2013).

For soldierless termites (subfamily Apicotermitinae), the enteric valve (EV) morphology was used as key diagnostic character, complemented with the morphology of the mandibles and digestive tract described in keys and recent species descriptions (Bourguignon et al. 2010, 2016a; Scheffrahn 2013; Scheffrahn *et al*. 2017; Pinzón *et al*. 2019; Castro *et al*. 2020).

Soldier caste microphotographs of termite species were taken as multi-layer montages using an Olympus SZ61 stereomicroscope, and EV soldierless microphotographs were taken using an Olympus BX53 microscope, coupled to a digital camera Olympus DP27, and controlled by the Olympus Stream Basic software 2 (Supplementary material B).

Specimens were deposited in the “Colección de Artrópodos Terrestres de la Amazonía Colombiana – CATAC”, of Instituto Amazónico de Investigaciones Científicas SINCHI, Leticia, Amazonas. The collections were carried out based on "Articulo 2 del decreto 309 de 2000" that exempts the entities attached to the SINA from collecting permission.

1.2.4. Data analysis

The relative abundance was calculated by the presence or absence of a species in each plot along the transect. Therefore, if a species was present in all plots of a site, it received a relative abundance value of 15. For this study, the encounters per transect mentioned by Jones & Eggleton (2000) will be taken as the relative abundance values.

Rarefaction and extrapolation curves were generated from the species relative abundance data based on sample size and coverage, and extrapolating the rubber systems to 60 sampling units for each type of land use (Chao *et al.* 2014), facilitating comparison between sites with different numbers of plots. Curves were performed with 100 replications and with a 95% confidence interval with software R (R Core Team 2020) using the package “iNEXT 2.0.20” (Hsieh *et al.* 2016).

The β-diversity was estimated with the Jaccard dissimilarity index, which was calculated based on a termite species composition matrix grouping all plots of each study area, with the R package “Vegan 2.5-7” (Oksanen *et al.* 2019). A hierarchical cluster analysis with the Jaccard distances and the agglomeration method Ward.D2 was performed (Murtagh & Legendre 2014). The clusters was obtained using the *hclust* function and R package “dendextend 1.15.1” (Galili 2015).

To understand which species are high correlated to one or more types of land use, the Indicator Value, *IndVal* (De Cáceres *et al.* 2012, 2020) was employed. The indicator species analysis is based on the "indicator value" index (De Cáceres & Legendre 2009) which tests whether termite species can be representative of particular land use and/or land-use group. Values closer to 1 indicate higher fidelity and specificity of the indicator species concerning land use. The p-values were reported after 999 permutations, with $p < 0.01$ as significant. *Indval* analysis was performed using the *multipatt* function from the R package “indicspecies 1.7.9” (De Cáceres *et al.* 2020).

1.3. Results

Overall, 80 species belonging to 41 genera were collected across the five land uses considered (Table 1-2) in 1.101 samples. All species belong to two families: Termitidae, with 83% of total relative abundance (occurrences), and Rhinotermitidae with 17%. Apicotermitinae (26%) was the most common Termitidae subfamily, followed by Nasutitermitinae (23%), Termitinae (20%), and Syntermitinae (13%). *Nasutitermes* was the genus with the highest number of species (12), followed by *Neocapritermes* (five) and *Anoplotermes*, with four species. Thirty genera had a single species reported. Ten species belonging to the subfamily Apicotermitinae could not be identified at the genus level; evidence from the enteric valve (EV) and overall morphology suggest that they might belong to undescribed genera and species (Supplementary material B).

NF presented the highest species richness with 67.5% of species (54 spp). CR had 49% (39 spp), and CF had 31% (25 spp). MX had only 15% of the overall species reported (12 spp), with similar species richness to PA (18% of the total species, 15 spp). Relative abundance showed almost the same pattern of species richness, but MX had a greater number of occurrences than PA.

Table 0-2: Termite species and species collected, and their relative abundance in all the land uses assessed. Feeding group (guilds): W = Wood feeder, In = Intermediate, L = Leaf litter feeder, S = Soil feeder.

Family/ Subfamily/ Species	**Natural Forest (NF)**	**Pasture (PA)**	**Commercial Plantation (CR)**	**Clonal Field (CF)**	**Mixed Plantation (MX)**	**Total**	**Feeding group**
Sampling effort (# plots)	**60**	**60**	**45**	**45**	**30**	**255**	
Rhinotermitidae	**27**	**24**	**39**	**85**	**16**	**191**	
Coptotermes testaceus (Linnaeus, 1758)	3					3	W
Heterotermes tenuis (Hagen, 1858)	21	24	39	85	16	185	W
Dolichorhinotermes longilabius (Emerson, 1924)	3					3	W
Termitidae	**410**	**50**	**267**	**117**	**66**	**910**	
Apicotermitinae	**70**	**30**	**52**	**76**	**57**	**285**	
Anoplotermes banksi Emerson, 1925	39	6	10	7		62	S
Anoplotermes janus Bourguignon & Roisin, 2010	1					1	S
Anoplotermes meridianus Emerson, 1925	7	2	6	11	4	30	S
Anoplotermes parvus Snyder, 1923	1		10			11	S
Aparatermes thornatus Pinzon & Scheffrahn, 2019	1					1	L
Apicotermitinae sp.1			4			4	S
Apicotermitinae sp.2				3		3	S
Apicotermitinae sp.3			2	1	2	5	S
Apicotermitinae sp.4	2	1			1	4	S
Apicotermitinae sp.5				2		2	S
Apicotermitinae sp.6				1		1	S
Apicotermitinae sp.7			1			1	S

Apicotermitinae sp.8					2	2	S
Apicotermitinae sp.9			2			2	S
Apicotermitinae sp.10			1			1	S
Compositermes vindai Scheffrahn, 2013				2		2	S
Disjunctitermes insularis Scheffrahn, 2017		2	2	8	16	28	S
Humutermes krishnai Bourguignon & Roisin, 2016		8	1	7		16	S
Hydrecotermes arienesho Bourguignon & Roisin, 2016			4	1		5	S
Hydrecotermes kawaii Bourguignon & Roisin, 2016	9		1		4	14	S
Patawatermes nigripunctatus (Emerson, 1925)			1			1	S
Patawatermes turricola (Silvestri, 1901)			1	5	12	18	S
Rubeotermes jheringi (Holmgren, 1906)	4	1				5	S
Rustitermes boteroi Constantini, Castro & Scheffrahn, 2020	6	10	6	28	16	66	S
Nasutitermitinae	**130**	**4**	**105**	**15**	**7**	**261**	
Agnathotermes crassinasus Constantino, 1990	1					1	S
Angularitermes pinocchio Cancello & Brandão, 1996	1					1	S
Araujotermes parvellus (Silvestri, 1923)			1	1		2	In
Atlantitermes cf. *oculatissimus* (Emerson, 1925)			2	1		3	In
Caetetermes taquarussu Fontes, 1981	1					1	L
Coatitermes clevelandi (Snyder, 1926)	2		4			6	In
Constrictotermes cavifrons (Holmgren, 1910)	2					2	In
Ereymatermes rotundiceps Constantino, 1991	3					3	S
Nasutitermes acajutlae (Holmgren, 1910)	7					7	W

Nasutitermes banksi Emerson, 1925	16		2			18	W
Nasutitermes brevipilus Emerson, 1925	1					1	W
Nasutitermes nr. *comstockae* Emerson, 1925					3	3	W
Nasutitermes corniger (Motschulsky, 1855)	2		5	5		12	W
Nasutitermes gaigei Emerson, 1925					4	4	W
Nasutitermes guayanae (Holmgren, 1910)	49		79	6		134	W
Nasutitermes octopilis Banks, 1918	4					4	W
Nasutitermes similis Emerson, 1935	13					13	W
Nasutitermes sp.1			2			2	W
Nasutitermes sp.2	3					3	W
Nasutitermes surinamensis (Holmgren, 1910)	2	3				5	W
Paraconvexitermes cf. *nigricornis* (Holmgren, 1906)	1					1	In
Rotunditermes bragantinus (Roonwal & Rathore, 1976)	7		3			10	L
Subulitermes baileyi (Emerson, 1925)	1	1	2			4	S
Triangularitermes triangulariceps Mathews, 1977	12		5	2		19	W
Velocitermes cf. *uniformis* (Snyder, 1926)	2					2	L
Syntermitinae	**83**	**14**	**33**	**11**		**141**	
Cyrilliotermes angulariceps (Mathews, 1977)	7		6			13	S
Embiratermes ignotus Constantino, 1991	7		2			9	In
Embiratermes neotenicus (Holmgren, 1906)	33	8	15	10		66	In
Embiratermes robustus Constantino, 1993	2					2	In
Labiotermes labralis (Holmgren, 1906)	2					2	S
Rhynchotermes diphyes Mathews, 1977	1					1	L

Silvestritermes euamignathus (Silvestri, 1901)	8	5	10			23	In
Silvestritermes heyeri (Wasmann, 1915)	3			1		4	In
Silvestritermes minutus (Canter, 1968)	19					19	In
Syntermes aculeosus Emerson, 1945	1					1	L
Syntermes molestus (Burmeister, 1839)		1				1	L
Termitinae	**127**	**2**	**77**	**15**	**2**	**223**	
Cavitermes parvicavus Mathews, 1977	1					1	S
Cavitermes tuberosus (Emerson, 1925)	1					1	S
Crepititermes verruculosus (Emerson, 1925)		1	1			2	S
Cylindrotermes flangiatus Mathews, 1977	7		2			9	W
Cylindrotermes parvignathus Emerson, 1949	65		60	2		127	W
Microcerotermes arboreus Emerson, 1925	3					3	W
Neocapritermes pumilis Constantino, 1991	2		1			3	In
Neocapritermes talpa (Holmgren, 1906)			4	7		11	In
Neocapritermes talpoides Krishna & Araujo, 1968			1			1	In
Neocapritermes taracua Krishna & Araujo, 1968	1		5	1		7	In
Neocapritermes utiariti Krishna & Araujo, 1968	18					18	In
Orthognathotermes humilis Constantino, 1991			2			2	S
Planicapritermes planiceps (Emerson, 1925)	11		1			12	W
Spinitermes trispinosus (Hagen, 1858)				1		1	S
Termes nigritus (Silvestri, 1901)	7					7	In
Termes fatalis Linnaeus, 1758	6	1		4	2	13	In
Termes hispaniolae (Banks, 1918)	5					5	In
Total Abundance (hits)	**437**	**74**	**306**	**202**	**82**	**1101**	

Total Richness	**54**	**15**	**39**	**25**	**12**	**80**

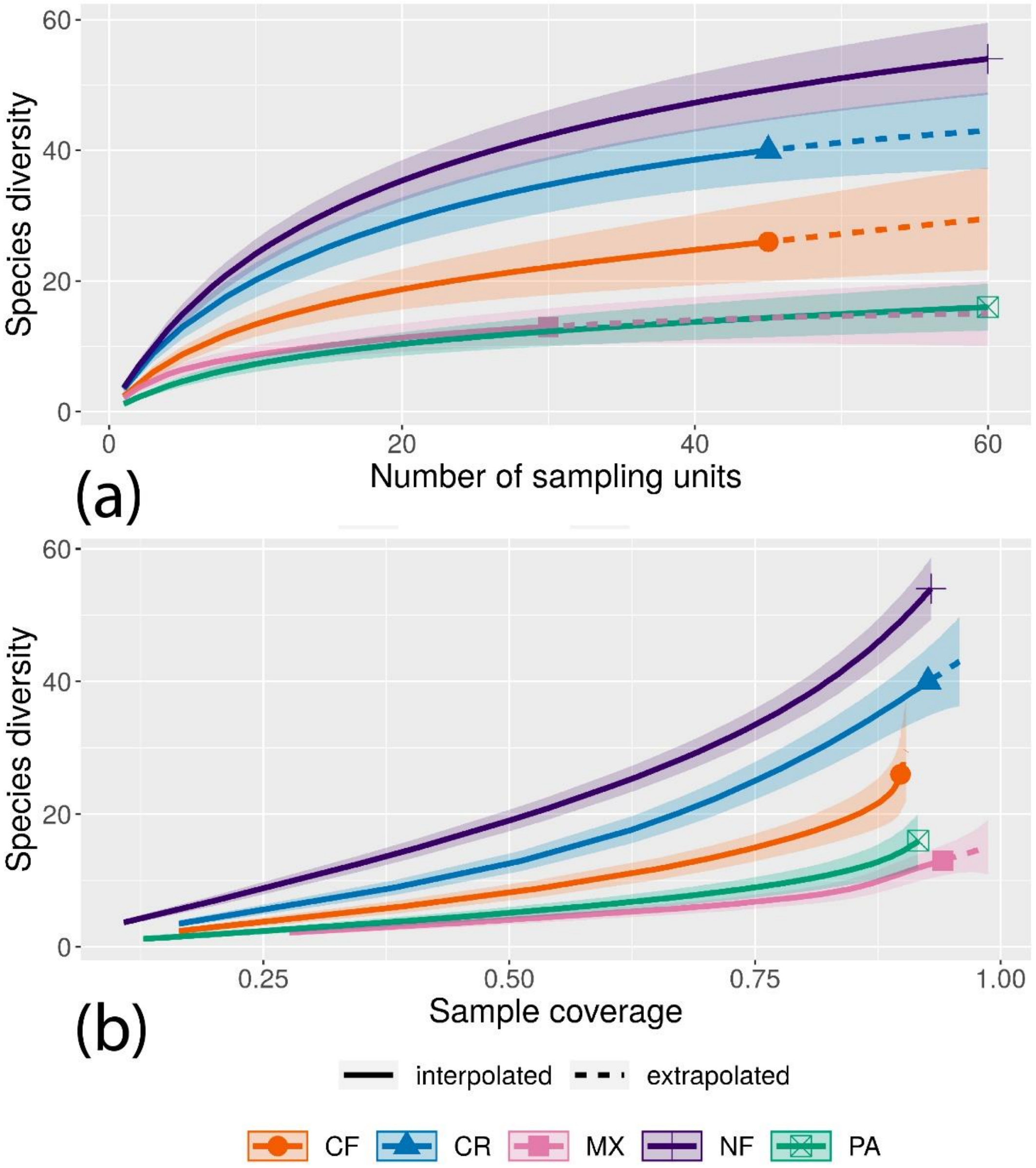


Figure 0-3: Sample size-based rarefaction and extrapolation sampling curves (a), and coverage-based rarefaction and extrapolation sampling curves (b) for each type of land use in the Northwestern region of the Colombia Amazon. Shaded areas are the 95% confidence intervals (based on a bootstrap method with 100 replications). Land uses: MX= mixed plantation, CF= clonal field, CR= commercial plantation, NF= natural forest relict, and PA= pasture.

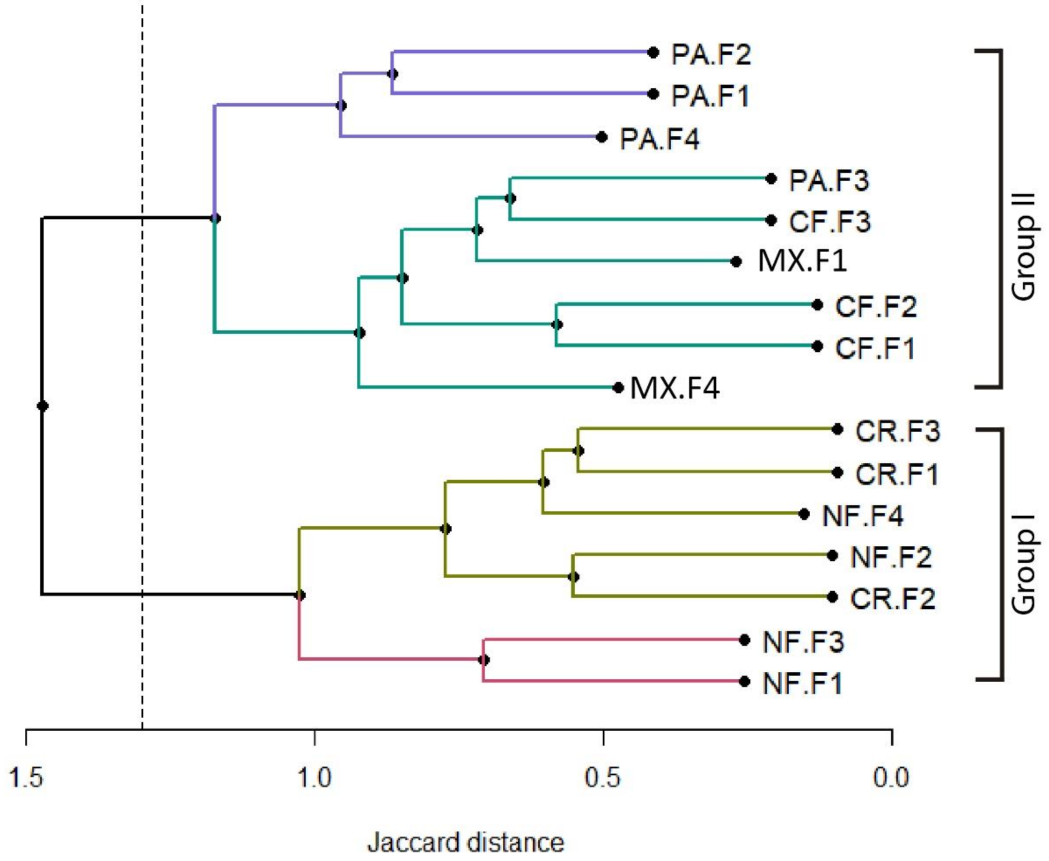


Figure 0-4: Hierarchical clustering constructed with Jaccard dissimilarity index and the Ward.D2 method (K=4, X intercept=1.2), to group the species composition in each farm (F) per land uses (five types) in the Northwestern region of the Colombian Amazon. Farms: F1= San Vicente del Caguán farms, F2 = Florencia farms, F3 = Belán de los Andaquíes farms, F4 = Albania farms. Land uses: MX= mixed plantation, CF= clonal field, CR= commercial plantation, NF= natural forest relict, and PA= pasture. Colors defined groups clustered by K=4 at Ward.D2 method. Diversity groups= Group I: NF and CR; Group II = CF, MX and PA:

The β-diversity using species composition based on the hierarchic clustering of each area found two main groups (Figure 1-4): Group I) with all NF and CR areas, and Group II) including the areas with CF, MX, and PA. In Group I, NF from the farms located in San Vicente (F1) and Belén (F3) were the most diverse and presented a high similarity (lower Jaccard distance) in species composition. NF from Florencia (F2) and Albania (F4) were grouped with CR, which also had a high diversity, similar to the NF. In Group II, two subgroups were found: the first one includes F1, F2, and F4 pastures with the lowest diversity, and the second included the other types of land use: MX and CF, along with PA.F3 (Figure 1-4).

Five indicator species were found in NF and two in MX (Table 1-3). In the single combination CR, CF, and PA indicator species were not found. Seven combinations of land use reported indicator species and a total of 15 indicator species were found with a significance *p-value* (< 0.01). The species *Cylindrotermes parvignathus* Emerson, 1949 and *Nasutitermes guayanae* (Holmgren, 1910) were considered good indicators (high significancy) for the areas of diversity Group I (Figure 1-4), and *Rustitermes boteroi* Constantini, Castro & Scheffrahn, 2020 of diversity Group II (Figure 1-4).

Table 0-3: Results of termite indicator species analysis from five land uses from the northwestern Colombian Amazon.

Land use / Land use group	Indicator species	IndVal.g	Stat	*p*-value
MX	*Disjunctitermes insularis*	0.668	0.489	0.005**
	Patawatermes turricola	0.762	0.467	0.005**
NF	*Neocapritermes utiariti*	1	0.504	0.005**
	Nasutitermes banksi	0.859	0.400	0.005**
	Silvestritermes minutus	1	0.391	0.005**
	Planicapritermes planiceps	0.893	0.369	0.005**
	Nasutitermes similis	1	0.368	0.01**
CF + CR	*Neocapritermes talpa*	1	0.316	0.01**
CF + PA	*Humutermes krishnai*	0.947	0.397	0.005**
CR + NF	*Cylindrotermes parvignathus*	0.982	0.819	0.005**
	Nasutitermes guayanae	0.952	0.696	0.005**
MX + CF + PA	*Rustitermes boteroi*	0.872	0.503	0.005**
CR + NF + PA	*Anoplotermes banksi*	0.872	0.535	0.005**
MX + CF + CR + PA	*Heterotermes tenuis*	0.919	0.756	0.005**
CF + CR + NF + PA	*Embiratermes neotenicus*	1	0.463	0.005**

IndVal.g: indicator value. Land uses: MX= Mixed plantation, CF= clonal field, CR= commercial plantation, NF= natural forest relict, and PA= pasture. Significances: * < 0.05; ** <0.01; *** < 0.001

1.6. Discussion

The termite richness found in this study (80 species) was, so far, the highest recorded for Colombia, with more than 50% of the species reported in studies in the Caribbean and Orinoquia regions (Casalla & Korb 2019b; Pinzón *et al.* 2017). Our results, along with previous studies, corroborate the high diversity of termite species that exist in the Amazon basin (Bourguignon *et al.* 2011a; Davies *et al.* 2003). A large number of species not yet described were identified, and this result demonstrates that much more taxonomic work remains to be done for termites in Colombia, so we can have a better picture of the diversity of these organisms in the Amazon region (Bourguignon *et al.* 2016b; Castro *et al.* 2020).

Rarefaction curves indicate that termite sampling seems to be well-represented in this study (Figure 1-3). Sampling units were sufficient to find the extrapolated number of species for all land-use types. Sample size and coverage-based curves followed the same pattern of species diversity in CF and CR. The sites with the lowest diversity were PA and MX, in this order; the diversity of CR and CF could be limited by the numbers of sampling units (Figure 1-3a). Although MX had the lowest sampling effort, the extrapolation data shows it with the same pattern as PA, with the sample coverage even higher in MX than PA (Figure 1-3b).

Furthermore, they could differentiate natural forest from pastures, and rubber crop systems; nevertheless, mixed plantations and pastures present similar curves (Fig. 1-3). Similar patterns regarding differentiation on land uses has been reported in eucalyptus, pine, and teak plantations studies done in other tropical regions (Attignon *et al.* 2005; Beltrán-Díaz & Pinzón-Florián 2018; Junqueira *et al.* 2009), where old plantations were more diverse than youngest plantations. The plantation aging and agricultural practices, such as insecticide use, weeds removal, and tree pruning removed from the system, probably influenced termite diversity and species composition. MX and CF were the youngest areas and had their waste removed from the system periodically, and both areas exhibited similar species composition to pastures (PA). CR was the oldest plantation and the most similar area to NF. In the same way, MX was the youngest and the only system where they employed insecticides, and showed the lowest diversity, along with PA.

Termite assemblage is a valuable indicator of disturbance or recovery of landscapes (Dosso *et al.* 2013; Eggleton *et al.* 1996). NF was the most diverse environment for termites, followed by CR and CF. Different authors reported that transformations of all natural vegetations into pastures in the Neotropics have resulted in local extinction of termite populations (Barros *et al.* 2006; Carrijo *et al.* 2009). Our results showed an important reduction of termite diversity when forest relicts (NF) were compared with pastures (PA) and evidenced a partial recovery of termite diversity with the establishment of some types of rubber crop systems in areas previously occupied by pastures. However, α and β termite diversity in rubber plantations was still lower when compared to natural relict forests, indicating that some termite species might be very sensitive to any kind of disturbance (as the five indicator species in NF), or take long of recolonization of the areas (see discussion below). Our results are in agreement with previous studies that have shown that rubber plantations cannot recover all termite diversity lost due to disturbances in a natural environment (Hidayat *et al.* 2018; Liu *et al.* 2019). In this same direction, a recent comparisons of termite communities in rubber plantations, natural regeneration, and silvopastoral systems used to improve soil quality in the Colombian Amazon revealed, that rubber plantations sustained the lowest diversity (Duran-Bautista *et al.* 2020b).

Furthermore, it is important to highlight those agricultural practices (pruning waste, pesticides, fungicides and chemical fertilization) among different rubber crop systems have remarkable influence in the soil fauna diversity (Letourneau & Altieri 1999; Souty-Grosset & Faberi 2018). Our results showed higher number of species in commercial plantations (CR) and clonal fields (CF), corroborating that the plantation age tends to influence the termite diversity (Beltrán-Díaz & Pinzón-Florián 2018; Liu *et al.* 2019; Luke *et al.* 2014), additionally these were the rubber crop with less agricultural practices carried out (Table 1-1). Also, greater species richness and abundance were found in mature plantations of CR (more than 28 years) compared to newer ones: MX (7 years) and CF (9 years), indicating that recovery of termite diversity requires long time (Coulibaly *et al.* 2016; Eggleton *et al.* 2002); and where in MX the agricultural practices was intensives.

Finally, mixed plantations (MX) did not recover termite diversity, even when compared to those of similar age (CF), MX had similar termite diversity values to PA. Although other mixed plantations, with different arrangements of trees, such as palm, rubber, guava, copoazu, banana, and cocoa trees in the northwestern Colombian Amazon have been reported to improve the soil physical quality in areas previously occupied with pastures

(Cherubin *et al.* 2019). Our results must be looked at with caution, however, because pesticides affect regional biodiversity, including the soil fauna (Beketov *et al.* 2013; Ghosal & Hati 2019; Zaller & Brühl 2019), and agricultural practices on MX likely affected the recovery of termite diversity (Table 1-1).

Two species of soil-feeding termites were identified as species indicators for MX: *Patawatermes turricola* (Silvestri, 1901) and *Disjunctitermes insularis* Scheffrahn, 2017, positively influencing soils due to their feeding habits (Bourguignon *et al.* 2009, 2015). The three land uses with the lowest diversity (Group II, fig. 3), presented *Rustitermes boteroi* Constantini, Castro & Scheffrahn, 2020, a soil-feeding termite as a species indicator. These results support that these species are common in soils with low organic matter availability (OC and N, Table S.1), which it is the case in young plantations or young successional coverings. Our results are not in agreement with several other studies that have shown soil-feeding termites as the most affected by anthropic disturbance (Eggleton *et al.* 2002; De Souza & Brown 1994; Viana *et al.* 2014) (see also chapter 3 of this Thesis).

In the same way, two xylophagous species, *Cylindrotermes parvignathus* and *Nasutitermes guayanae*, were considered good indicators for the areas with higher diversity (Group I, fig. 3). The species *C. parvignathus* is widely reported in forests of northern South America (Davies *et al.* 2003; Pinzón *et al.* 2012; Rocha & Cancello 2007), and *N. guayanae* is also abundant all along the Amazon forest (Constantino 1992; Pinzón *et al.* 2017; Roisin *et al.* 2006). *Nasutitermes guayanae* is abundant in Colombia in citrus crops (Abadía. *et al.* 2013), and is also reported as an indicator of macroinvertebrate diversity in Amazonian soils (Duran-Bautista *et al.* 2020a). Both species are abundant in natural areas and oldest rubber plantation areas (CR). These species were not reported in young plantations, probably taking time for recolonization and establishment.

Another xylophagous species, *Heterotermes tenuis* (Hagen, 1858), was identified as an indicator species for all non-natural land uses. *H. tenuis* has been reported in high abundances from different agrosystems (Ackerman *et al.* 2009; Beltrán-Díaz & Pinzón-Florián 2018; Junqueira *et al.* 2009), and it is sometimes identified as a pest in Neotropical systems (Mill 1992; Constantino 2002b).The indicator species of natural forests (NF) have been commonly found in natural forests of the Amazon basin such as *Neocapritermes* *utuariti*, *Sikvestritermes minutus*, *Planicapritermes planiceps*, and *Nasutitermes banksi* (Ackerman *et al.* 2009; Bandeira 1989; Bourguignon *et al.* 2011a; Constantino 1992).

The first hypothesis of this thesis was corroborated for the abundance values, the natural forest was the land use with the highest values, followed by the tree rubber crop systems: commercial plantations, clonal fields and mixed plantations; and pastures had the lowest abundance values. however, the hypothesis assumed that species richness values would behave same as the abundance values. But the hypothesis was not corroborated for the species richness value, because the land use with the lowest values of species richness was not pastures but mixed plantations, although the highest values were from the NF followed by CR and CF. Our results demonstrate that termite diversity recovery will depend on the farming system selected and possibly with the agricultural practices implemented in the field, with some rubber crop systems recovering termite diversity better than others.

Chapter 2: Influence of the soil physicochemical variables on termite community

2.1. Introduction

The Amazon rainforest is one of the most important biomes on earth, hosting a high biological diversity (Charity *et al.* 2016). With a total area of 477,274 km^2, the Colombian Amazon comprises 5.71% of the Amazon Basin (Gutierrez *et al.* 2003). The 89% of Colombian Amazon is on natural covers, mainly as natural primary forests (Murcia *et al.* 2014). The Amazon basin harbor a great diversity of termites (Ackerman *et al.* 2009; Bourguignon *et al.* 2011a; Constantino & Cancello 1992; Palin *et al.* 2011), and it is estimated that the Colombian Amazon is one of the most diverse bioregion of the country (Duran-Bautista *et al.* 2020a).

The Colombian Amazon soils are characterized by low fertility (Peña-Venegas *et al.* 2006), but micro and macro soil organisms play fundamental roles in the transformation of organic matter, mineralization and nutrient fluxes (Barros *et al.* 2004; Marichal *et al.* 2014; Peña-Venegas *et al.* 2015, 2019). Termites are one the main groups of organisms contributing to these transformations, since they are considered to be one of the major decomposers in tropical forests (Eggleton *et al.* 1996; Jouquet *et al.* 2014; Lavelle 1997), and harbor a high soil biomass (Dahlsjö *et al.* 2014; Fittkau & Klinge 1973), being one of the most abundant soil organisms in tropical ecosystems (Barros *et al.* 2002; Eggleton *et al.* 1996; Jones *et al.* 2003).

In Colombia, the ecological studies of the termite fauna have been limited to its diversity and lists of species, leaving aside other important ecological aspects such as functional ones (Beltrán-Díaz & Pinzón-Florián 2018; Pinzón *et al.* 2012, 2017; Pinzón & Castro 2018;

Vargas-Niño *et al.* 2005). In recent years, however, the ecology of these insects in Colombia is becoming more relevant than their importance as pests (Casalla & Korb 2019a; b; Duran-Bautista *et al.* 2020a). Soil-termites relationship changed with soil physicochemical properties, such as in soils with poor quality (such as low fertility) there are lower numbers of termite species (Duran-Bautista *et al.* 2020b). In order to contribute to the understanding of the changes in the termite community according to soil quality, in this chapter, changes in termite communities related to soil physicochemical properties were evaluated in the three rubber production systems, pastures, and natural forests.

2.1.1. The role of termites in the ecosystems

Termites are social insects that live in nests or colonies, and they are easy to differentiate from other groups of insects because all their castes present distinctive morphologies (Eggleton 2011). Termites belongs to the order Blattodea, infraorder Isoptera, phylogenetically related to cockroaches of the family Cryptocercidae, with which they share their functional role as decomposers (Inward *et al.* 2007; Legendre *et al.* 2008, 2015).

Each colony of termites is composed of morphological castes that, specialize in different functions. Reproducers (“queens” and “kings”) are responsible for colony establishments. The queen lay eggs, which hatch into larvae and then they will transform into sterile “workers” are responsible for the construction and maintenance of tunnels and galleries, food foraging, and parental care; and “soldiers” are in charge of the protection of the colony (Eggleton & Tayasu 2001). The soldier caste is absent in the Apicotermitinae subfamily in the Neotropics, also, there are polymorphisms in soldiers and workers in some termite species (Rocha *et al.* 2019; Roisin 1996).

There are approximately 3000 living species of termites described, 612 of which are from the Neotropics, being the third most diverse world region after the Oriental region (1,154 species) and the Ethiopian regions (757 species) (Constantino 2021). Some termites species are recognized for their economic importance as urban and agricultural pests, only 371 species (12.4%) have been reported as destructive, and only 104 (3.4%) are considered serious threats (Krishna *et al.* 2014). Nevertheless, these insects are fundamental for most tropical ecosystems (Jankielsohn 2018).

Termites are considered good indicators of biodiversity and soil quality because their relation with soil organic matter cycling, and their influence in soil composition and structure (Bignell 2005; Lavelle 1997; Siebers *et al.* 2015). The structures created by termites such as nests, soil sheetings, foraging holes, etc. and their foraging activities improve soil aeration, water uptake, and carbon fluxes and storage, influencing long-term soil fertility (Jouquet *et al.* 2011, 2014). Due to modifying their environment and influence the soil composition and structure, termites are considered "ecosystem engineers" likewise ants and earthworms (Jones *et al.* 1994; Lavelle 1997).

Because of their importance, termite communities are used as bioindicators to explore the ecosystem services in different land uses in Colombia, mainly in the Caribbean, Orinoco, and Amazon regions (Beltrán-Díaz & Pinzón-Florián 2018; Casalla & Korb 2019b; Duran-Bautista *et al.* 2020b; a; Pinzón *et al.* 2017; Sanabria *et al.* 2016). These studies showed that termite diversity have a direct relationship to the soil quality, and also responds to different impacts in land covers, such as deforestation and establishment of agrosystems (Bourguignon *et al.* 2015; Davies *et al.* 2003; Sanabria *et al.* 2016), demostred that the termite assemblage are influenced by pH, moisture, cation exchance capacity, macronutrients (Mg, Ca, Na, and K), micronutrients (Fe, Cd, and Fe), carbon, nitrogen and organic matter . In in this chapter, the changes in termite communities in relation to some soil physicochemical properties were evaluated for the three rubber production systems, including commercial rubber plantations (CR), clonal fields (CF), mixed plantations (MX), and also pastures, and natural forests. Our hypothesis state that higher abundance of termites is expected in soils that show an increment in bio-available nutrients (K, Mg, and P), organic carbon, and pH.

2.2. Materials and methods

Termite collecting and sample processing are explained in the materials and methods section of chapter 1.

2.2.1. Measurement of soil physicochemical properties

In each study area from the five use land during termite sampling, one soil sample of 500g from 0-15cm soil depth (45 samples in total from all study) was extracted to evaluate the following 14 soil variables: i) pH (1:1 in water); ii) electrical conductivity (ED) using a saturated soil paste (Corwin & Yemoto 2017); iii) organic carbon (OC) using the NTC 5403 Walkley - Black method (Walkley & Black 1934); iv) cation exchange capacity (CEC) calculated based in base cations and acid cations; texture variables v) sand, vi) clay, and vii) silt was calculated by Bouyoucos method (Bouyoucos 1936); viii) bulk density (AD) was calculated by the cylinder volume method; ix) potassium (K), x) calcium (Ca), and xi) magnesium (Mg) using extraction with ammonium acetate method NTC 5349 (ICONTEC 2016a); xii) phosphorus (P) using colorimetric method NTC 5350 (ICONTEC 2016b); xiii) iron (Fe) using the acid Mehlich solution NTC 5526 (ICONTEC 2007); xiv) total nitrogen (N) calculated from organic carbon. Soil samples were analyzed in Agrilab laboratories SAS in Bogotá D.C.

2.2.2. Data analysis

A Pearson correlation analysis was carried out to determine the soil physicochemical variables highly correlated. The correlation index (ci) was estimated, and they range between -1 (perfect negative coefficient) and +1 (perfect positive coefficient), and a correlation heat-map was plotting for illustrate the clustering correlation groups. The normality was test for each variable with the "shapiro.test" R function (≥0.05), and visual inspection of the data normality was carried out with Q-Q plots (quantile-quantile plots) using the R package "ggpubr 0.4.0" (Kassambara 2020); all soil variables fulfilled the normality assumptions to apply the Pearson correlation test. In addition, a principal component analysis (PCA) was performed with the physicochemical variables to determine variables with the highest contribution to the two principal components. By using these two analyses, it was possible to refine correlated variables that were explaining the same thing and variables that do not present any importance for the results of the study.

Furthermore, a second PCA was performed to visualize associations between land use, termite composition and the principal soil variables identified. The Pearson correlation was performed using the "*cor*" R function, and the correlation heat-map was plotting using the R package "corrplot" (Wei & Simko 2017), and the PCAs were carried out using the R packages "FactoMineR" (Husson *et al.* 2020; Lê *et al.* 2008), and "factoextra" (Kassambara & Mundt 2020).

To find linear changes between termite species and the most explanatory soil variables (from PCA), a constrained ordination test was performed to see the relationships between the species composition matrix and soil variables. To know which test to apply a direct gradient analysis was used due to the nature of the data, where the distribution of species composition along gradients of important edaphic factors was analyzed. A Detrended correspondence analysis (DCA) was performed to obtain the gradient lengths of the occurrence matrix of species composition (occurrences from all species) matrix. The gradient obtained by the DCA showed a short gradient (<4) which reflected that the termite data were not heterogeneous and a linear method was the better choice (Braak & Smilauer 2002; Legendre & Legendre 2012). For this reason, a Redundancy analysis (RDA) was performed to evaluate the direct gradient of termite assemblage in relation to soil variables. A Hellinger transformation was applied to the occurrence data, due to its heterogeneity (Legendre & Gallagher 2001).

The RDA was carried out to find linear combinations between termite species with the principal soil variables obtained from PCA (Figure 2-3) and the five land uses, representing the largest variance between the variables as possible. The significance of the association between each principal soil variables with occurrences for each plot and land uses, and variation in termite community were tested by a Monte-Carlo test (999 permutations). All statistical analyses were conducted employing the R package “vegan” (Oksanen *et al.* 2019) in the software R project (R Development Core Team 2021).

2.3. Results

Three clusters of soil variables could be recognized with positive correlations in the Pearson correlation matrix of the 14 soil variables evaluated, two with high values (ci ≥ 0.75) and one with average value (ci ≥ 0.5) (Figure 2-1). The two clusters that presented a high interdependence were organic carbon (OC) with nitrogen (N), and the bulk density (AD) with sand. The third cluster have a positive correlation but not so strong correlation was that of calcium (Ca) with magnesium (Mg). On the other hand, clay with AD and sand was found with negative correlations of high values (ci ≤ −0.75). It was also observed a high negative correlation between iron (Fe), OC, and N with the CEC, showing a correlation in variables that influence soil fertility (OC, N, and Fe).

The first two dimensions (components) of the PCA explained 53.8% of the total variance, with 10 variables (out of 14) explaining most of the variation of these two dimensions (Figure 2-2a). Five variables, including two physical (CEC and Silt) and three chemicals (OC, N, and FE), presented a high correlation with Dim1, and another five variables, including two chemicals (pH and Ca) and three physicals (AD, Clay, and Silt), presented a high correlation with Dim2 (Table 2-1).

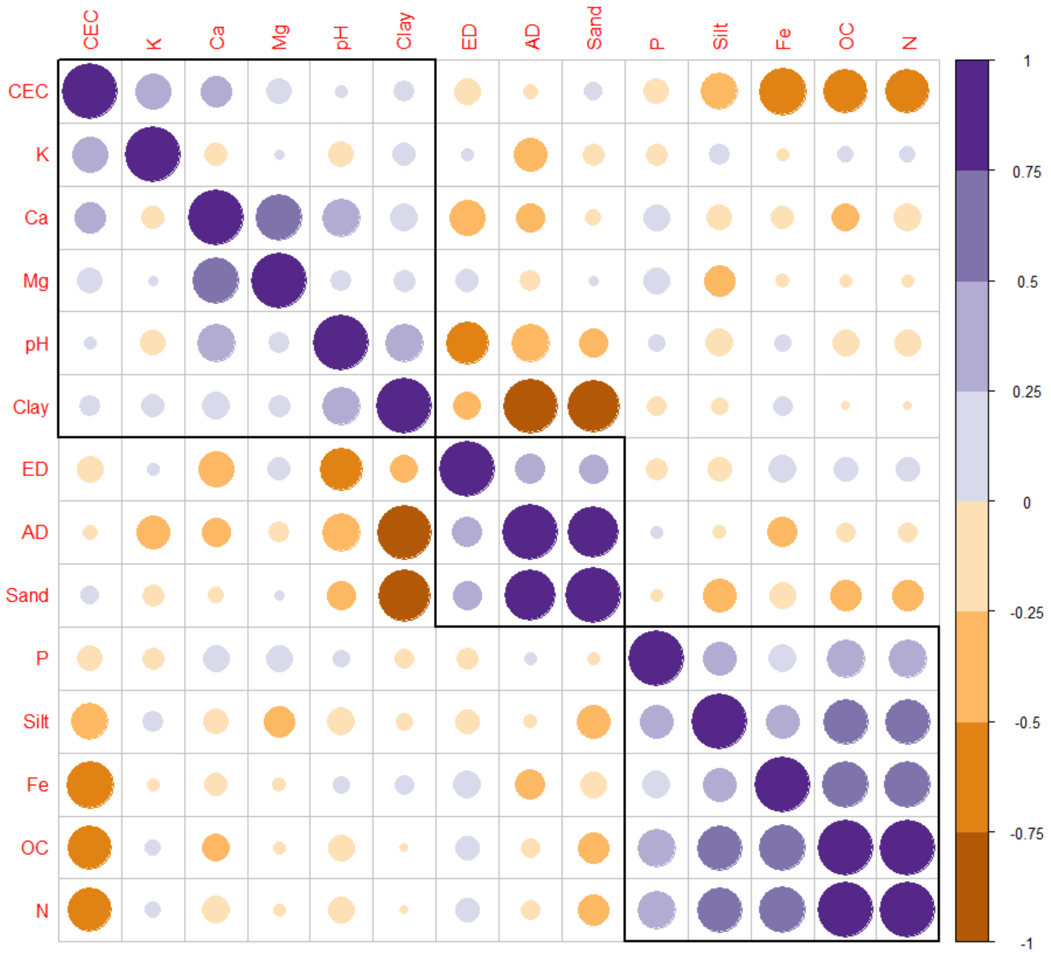


Figure 0-1: Correlation heat-map of 14 soil properties consolidated through clustering and ensemble-averaged. A small positive or negative correlation coefficient between two parameters suggests small interdependence. Soil properties abbreviations: CEC=Cation exchange capacity; K= potassium; Ca=Calcium; Mg=Magnesium; ED=Electrical conductivity; AD=Bulk density; P=Phosphorus; Fe=Iron; OC=Organic carbon; N=Total nitrogen.

These correlation values are well represented by the contributions that the variables have to the PCA dimensions. As seen in figures 2-2b and 2-2c, where the significant contributions to the frist and second dimension of the PCA are the same that are significantly correlated with the dimensions, demonstrating that the significant variables in the sampled soils are the 10 mentioned above, being five physical and five chemical properties of the soil.

Consequently, after analyzing the correlation analysis (Figure 2-1) and the PCA of the soil variables (Figure 2-2), seven variables, that did not explain variance or were redundant, were eliminated. Variables that were discarded for lack of explanatory variance were Mg, K, P, and Clay. Among the highly correlated variables the following were eliminated based on the highest correlation value with PCA dimensions (Table 2-1): between AD and Sand, Sand was discarded, between OC, Fe, and N, Fe and N were discarded. Therefore, these variables were not considered for ordering the species and sampling sites concerning the edaphic variables and the variance increase. This was evidenced in Figure 2-3, where once these seven variables were eliminated, the explained variance increased by 12.7%.

Table 0-1: Pearson correlation coefficient describing the relationship between each soil variable to the principal components. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$. PCA dimensions: Dim1 = dimension 1 (axis 1); Dim2 = dimension 2 (axis 2).

Soil variable	**Code**	**Dim1**	**Dim2**
pH		-0.222	0.668**
Electrical conductivity	ED	0.199	-0.525*
Cation exchange capacity	CEC	-0.762***	0.148
Organic carbon	OC	0.943***	0.024
Bulk density	AD	-0.726***	0.304
Clay		-0.436	0.030
Sand		-0.350	-0.798***
Silt		0.732**	0.036
Potassium	K	0.016	0.169
Calcium	Ca	-0.377	0.503*
Magnesium	Mg	-0.222	0.258
Total nitrogen	N	0.942***	0.022
Iron	Fe	0.778**	0.144
Phosphorus	P	0.425	0.084

The soil variable that more explain the variance of the model was electrical conductivity (*p*-value = 0.0005). The first principal component axis (Dim1) explained 42.2% of the total variance, and the second axis (Dim2) 20.4%; together, they explained 62.6% of the total variability (Figure 2-3). Group I and II from the analysis of β-diversity (Chapter 1) were also correlated with the soil variables. Group I (NF + CR) was correlated with higher values of ED, and CEC. Group II (MX + CF + PA) was correlated with higher values of pH and Ca. Silt, OC and AD not showed a higher correlation with some particular group.

In soil properties PCA (Figure 2-2), OC was the variable most explanatory of the model and was significantly correlated with the two axes of the PCA (Dim1 *p*-value= 0.003; Dim2 *p*-value= 0.007). Silt and ED also had a high variance, followed by pH and AD, and CEC. The variable with the lowest explanation of termite species composition was Ca. Macronutrients did not present higher variances, where calcium (Ca) was the only macronutrient selected for this analysis even if presented the lowest contribution.

The study areas were ordered creating an evident difference between the termite composition of each diversity group obtained from chapter 1, with group I distributing bellow X-axis and group II above X-axis (Figure 2-3). Nearer points to each other in the right side to X-axis represent the CF and CR sites that share edaphic characteristics and similar species composition, typical of mature tree plantations.

Considering the termite assemblage across all land uses, RDA shows that the edaphic variables explained 64.1% of the termite assemblage variation considered in dimensions 1-2. The variation explained by these two dimensions is highly significant (Table 2-2). Organic carbon (OC) was the only variable that did not significantly explain the termite assemblage with a high variation; likewise, the other variables explaining the highest variance were pH, ED, AD, Silt, CEC, and Ca (Table 2-3). The highest correlation values with Dim1 are related to ED, AD, OC, and Ca, while the highest correlations in Dim2 were related to CEC, Silt, and pH.

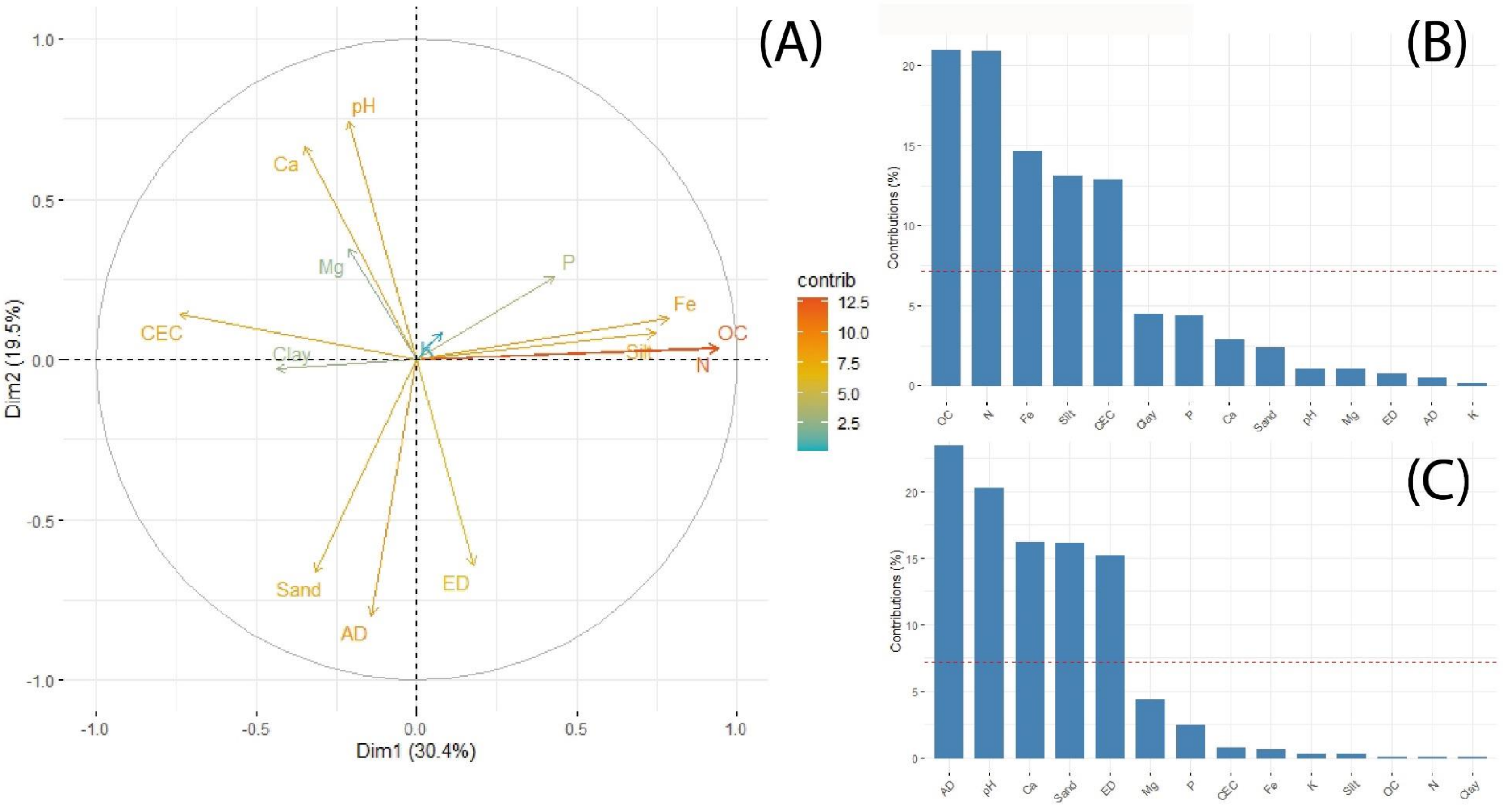


Figure 0-2: A) Ordering plot derived from the principal component analysis of the 14 physicochemical properties from the study areas. Percentage (%) on axes Dim1 and Dim2 indicate variance cumulative percentage in the original data matrix. B) Contribution of soil variables to Dim1. C) Contribution of soil variables to Dim2. contrib = contributions to the principal axes.

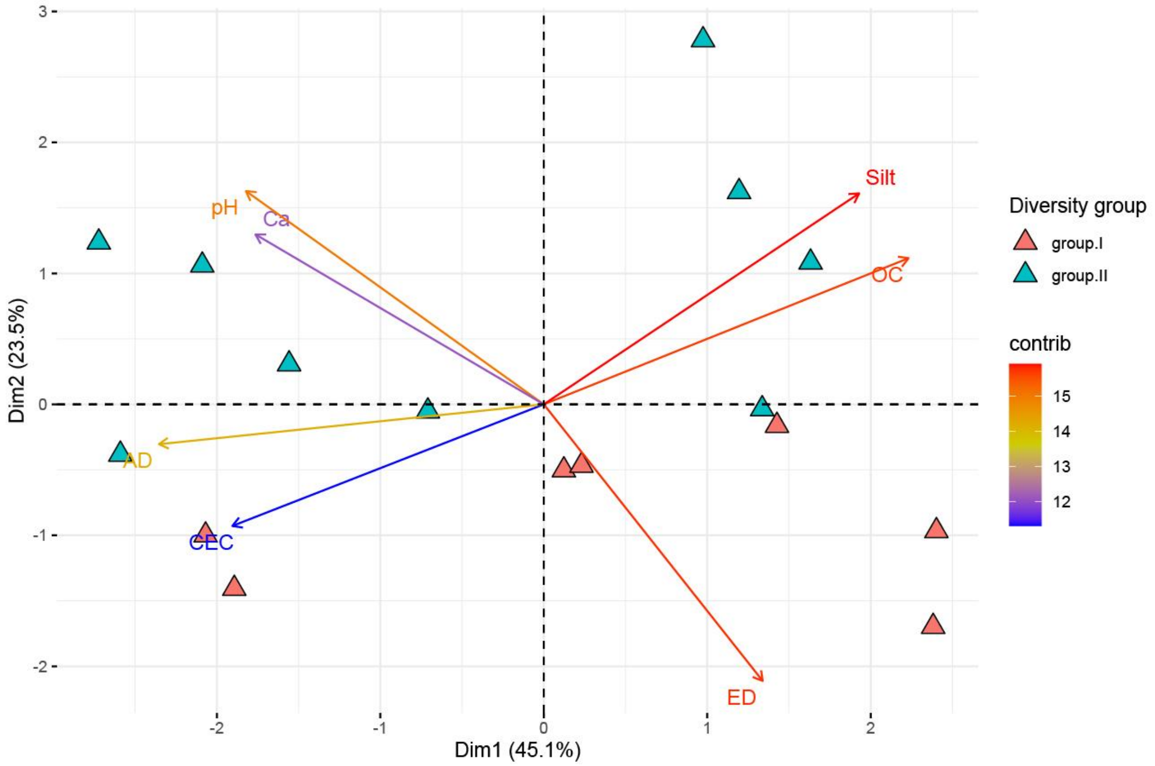


Figure 0-3: Principal component analysis (PCA) of termite diversity group and soil variables. Percentage (%) on axes Dim1 and Dim2 indicate variance cumulative percentage in the original data matrix. contrib = contributions to the principal axes. Diversity groups from β-diveristy analysis.

Table 0-2: Significance values of RDA axes forward selection to test the changes of principal soil variables on termite species. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

Axes	**df**	**Variance**	**F**	***p*-value**	**Significance**
RDA1	1	0.6719	18.2416	0.001	***
RDA2	1	0.2414	6.5547	0.001	***
RDA3	1	0.1663	4.5163	0.001	***
RDA4	1	0.1162	3.1547	0.020	*
RDA5	1	0.0642	1.7420	0.318	
RDA6	1	0.0510	1.3850	0.384	
RDA7	1	0.0352	0.9567	0.454	
Residual	202	7.4401			

Table 0-3: Results of redundancy analysis (RDA) forward selection to test the changes of principal soil variables on termite species. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

Soil variables	**df**	**Variance**	**F**	***p*-value**	**Significance**
pH	1	0.1899	5.1546	0.001	***
Electrical conductivity (ED)	1	0.3712	10.0780	0.001	***
Cation exchange capacity (CEC)	1	0.2083	5.6558	0.001	***
Organic carbon (OC)	1	0.0622	1.8568	0.030	*
Bulk density (AD)	1	0.0171	5.0018	0.001	***
Silt	1	0.0154	4.6229	0.001	***
Calcium (Ca)	1	0.2046	5.5558	0.001	***

RDA indicated pairwise correlations between soil variables and termite assemblage structure in different land uses. Figure 2-4 shows the ellipses that represent each land use, where the grouping explained in the diversity β is clear (Figure 1-4). CR and NF presented were clustered being on the positive side of the Y-axis (group I), on the other hand, CF, PA, and MX being ordered on the negative side of the Y-axis (group II).

Termite species best representing assemblages concerning soil uses and edaphic variables were distributed further from the point cloud of the lowest correlated species. *Rustitermes boteroi* was clustering with the least diverse uses MX and PA, in addition to it was grouped with the soil’s calcium available. Likewise, was *Heterotermes tenuis* was clustered with group II and represented in CF and PA.

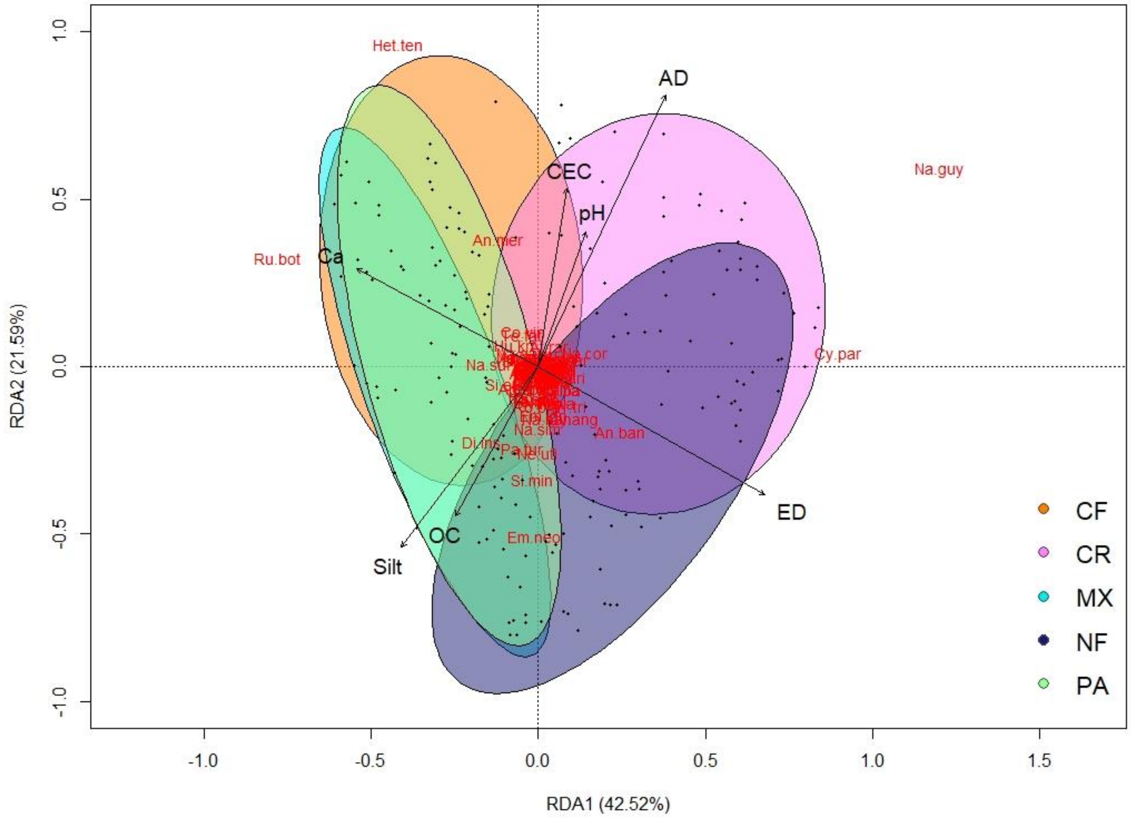


Figure 0-4: RDA Ordination bi-plot of termite assemblage composition and significant soil variables in the five land uses. Physicochemical soil variables are shown by arrows. Land uses are represented with ellipses with a confidence level of 0.90. Black points represent the sampled plots. Acronym species: An.ban *Anoplotermes banksi*; An.mer: *Anoplotermes meridianus*; At.rar: *Atlantitermes raripilus*; Cy.par: *Cylindrotermes parvignathus*; Co.vin: *Compositermes vindai*; Di.ins: *Disjunctitermes insularis*; Em.neo: *Embiratermes neotenicus*; Het.ten: *Heterotermes tenuis*; Hum.kri: *Humutermes kishnai*; Na.cor: *Nasutitermes corniger*; Na.guy: *Nasutitermes guaynae*; Na.sim: *Nasutitermes similis*; Na.sur: *Nasutitermes surinamensis*; Ne.uti: *Neocapritermes utiariti*; Pa.tur: *Patawatermes turricola*: Ru.bot: *Rubeotermes boteroi*; Si.eua: *Silvestritermes euamignathus*; Si.min: *Silvestritermes minutus*; Te.fat: *Termes fatalis*.

2.4. Discussion

Changes in the species composition of termite communities were influenced by soil physicochemical properties (Figure 2-3). The correlation analysis (Figure 2-1) for eliminating redundant and non-explanatory soil variables, showed positive results as the co-inertia analysis presented a significant positive association between the termite diversity groups (group I and II, Figure 1-4), and the seven explanatory variables. The correlation analysis and the soil properties PCA favored significative co-inertia association, which in some cases has not been evidenced when soil variables are not depurated concerning termite assemblage (Sanabria *et al.* 2016).

The two soil variables that presented a higher contribution to the variance in Dim1 were OC and N (Figure 2-2b). The main source of soil N is the organic matter, and the termite activity liberates organic carbon and inorganic nitrogen into the soils, increasing the availability of nitrogen in the form of NH_4+ and NO_3− (Ashton *et al.* 2019; Evans *et al.* 2011; Ndiaye *et al.* 2004; Yamada *et al.* 2006), however, there are other soil organisms that also positively influence the N availability in soils, such as soil microorganisms (Lu *et al.* 2020; Veresoglou *et al.* 2012). . Additionally, more OC and N availability favor the formation of microhabitats for a wide variety of soil organisms (Begon *et al.* 2007). The OC and N were lower in rubber crop systems when compared to pastures (Supplementary material A). One possible explanation for this occurring would be the implementation of agronomic practices through which weeds and other plant remains are eliminated permanently from the crop systems (Letourneau & Altieri 1999; Schroth 1999).

The variables that most contributed to Dim2 were AD and pH (Figure 2-2c). The bulk density (AD) presents high values in the PA and MX land uses, in general in the diversity group II sites. Soil compaction by cattle produces low porosity in soils that directly affects the hydrological function of it, by the current intensive trampling of cattle and in MX by the trampling of cattle to which soils were subjected, since these areas were cattle pastures long before the mixed plantation establishment (Decaëns *et al.* 1999, 2004; Duran-Bautista *et al.* 2020a). Therefore, in our results, AD is directly related to the low diversity of termites.

Organic carbon (OC) was the variable that most contributed explaining the variance of termite communities (Figure 2-3). Sites that present most OC favor the activity and stability of organisms in the soil (De Souza *et al.* 2016). On the other hand, electrical conductivity (ED) presented the lowest values in plantations and agroforestry systems in the northwest of the Colombian Amazon (Arévalo-Gardini *et al.* 2015), such as MX and CF. When the high ED values increased, the number of ions and cations in the soil increases, meaning greater fertility (Officer *et al.* 2004). In our results the high ED values were highly correlated with the group I of termites (Figure 2-3). The ED increase has been apparent in areas with epigeal termite nests against pastures without nests (Fallah *et al.* 2017). Compared to the areas of diversity group II, CR and NF showed higher numbers of these nests, which explains how termites may be contributing to increase ED values in CR and NF soils, influencing their fertility.

A larger diversity of termite species was reported in low pH soils within Amazonian Forest. Amazonian soils have always low pH, favoring the transformation of large amounts of organic material (Bourguignon *et al.* 2016b; Davies *et al.* 2003; LeClare *et al.* 2020). Soil pH is probably the most important variable affecting the availability of base cations and aluminum and iron saturation, and therefore the fertility of the Amazonian soils (Lemos *et al.* 2021; Moreira *et al.* 2009). Aluminum tends to remain in mineral forms, blocking the polar sites, where basic cations released from organic matter can be fixed (Quesada *et al.* 2010). Then, even if the pH was less acidic in pastures (PA) or mixed plantations (MX) and, therefore, the aluminum saturation is reduced, soil fertility is not improved. Additionally, in these two land uses, the input of organic matter into the soil is low, which explains the low termite species richness and abundance. This, in turn, may affect the soil physical stabilization and its capacity to storing nutrients (Culliney 2013; Jones 1990).

The silt was the soil structure variable most correlated with termite communities; also high concentrations of clay correlated with high termite abundance (Barros *et al.* 2003). Clay and silt textures tend to hold more organic matter and minerals than sand textures, favoring the presence of termites. This explains why high percentages of sand in soils do not explain termite assemblages (Viana *et al.* 2014).

Embiratermes neotenicus was correlated with MX, PA, and NF, in addition to being correlated with the variables OC and Silt. This species was found as an indicator of low chemical fertility in Amazonian soils (Duran-Bautista *et al.* 2020a), therefore, has populations naturally in the forest and can be adapted to resist the MX and PA soils, but they do not adapt in mature plantations such as CR and CF with better chemical fertility. Futhermore, *Cylindrotermes parvignathus* and *Anoplotermes banksi* which appeared in mature CR plantations, and presented fair similarity with natural forests, are also reported as extremely abundant in neotropical natural forests (Bourguignon *et al.* 2011a). Additionally, in our results, these two species presented a high correlation with the variable ED.

Some indicator species retrieved in the analysis presented in chapter 1 were also considered to be explanatory in the RDA ordination (Table 1-3). Likewise, it is the case of *Nasutitermes guayanae*, that was abundant (26% of total abundance) in commercial plantations (CR), and the RDA bi-plot clustered this species with CR and NF (Figure 2-4), thereby supporting the result of our analysis as an indicator for these two land uses. However, *N. guyanae* was a more dominant species in CR. Although this species has been reported in Colombia as a pest on other crops (Arcila *et al.* 2013), in natural forests is abundant (Pinzón *et al.* 2017), as was evident in our results. Its high abundance may not necessarily be a threat to crops, if optimal conditions for their populations are present, as those offered by the NF.

Two species very explanatory in the RDA and present as indicators were *Heterotermes tenuis* and *Rustitermes boteroi.* The first one had a high abundance in places where it is an indicator species, as already I discussed it in chapter 1. Moreover *R. boteroi* was clustered with the land uses of group II, and correlated with the calcium variable, being this element a fundamental nutrient to plant growth and essential for structuring its roots (Bizuti *et al.* 2018; White 1998). Calcium was also the most influential macronutrient in younger plantations. It is noteworthy that *R. boteroi* was retained as a species resistant to disturbance and common in open areas. This is a species recently described for science, and possibly has an important role in the recovery of degraded soils.

High numbers of leaf litter arthropods are usually favored by high levels of soil macronutrients (Barros *et al.* 2002), however, only was calcium the macronutrient correlated with the termite community structure. Nevertheless, it has been reported that macronutrient aggregations are higher in mounds than soils (Lima *et al.* 2018; Schaefer *et al.* 2016). This second hypothesis was corroborated in this work where the abundance of termites was greater in sites with high K, Mg, P, OC and pH. However, there was a greater correlation of the abundance of termites with the variables AD, ED and the macronutrient Ca. From this study we can conclude that four physical (one structure), and three chemical, soil properties influenced termite communities. Pastures and mixed plantations presented the lowest values in soil variables that represent fertility. On the other hand, commercial plantations of the rubber crops presented the most consistent similarity to natural forests in relation to their soil properties.

Chapter 3: Functional structure of termite assemblages

3.1. Introduction

In the tropics termites play an important role in the decomposition process of plant material in the soil through interacting with other organisms (Cabrera & Crespo 2001; Davies *et al.* 2015; Roisin & Leponce 2004). Termites are predominant animals in the soil macrofauna, their ecological importance and sensitivity to changes in land use allow to correlate the taxonomic composition and functional role of termites with edaphic factors within the plantations and natural ecosystems (Barros *et al.* 2004; Cabrera 2012; Liu *et al.* 2019; Velásquez *et al.* 2012).

Termites constitute an important group of organic matter decomposers, thanks to symbiotic microorganisms inside their guts, they are able to digest cellulose (Higashi *et al.* 1992; König *et al.* 2013). Their diet is mainly based on dead plant material (Lima & Costa-Leonardo 2007). Those attributes allow to group them into functional or feeding groups (guilds) based on their diet (Eggleton & Tayasu 2001).

Previous studies have suggested changes in the structure of termite guilds among different land uses and environmental gradients (Eggleton *et al.* 1995; Jones *et al.* 2003; Luke *et al.* 2014; Roisin *et al.* 2006). These changes can also be followed by functional traits, such as size or morphological characters of worker mandibles (Liu *et al.* 2019). Guilds composition is usually more similar into natural forests related to old-growth restoration areas (Bandeira *et al.* 2003; Junqueira *et al.* 2009; de Paula *et al.* 2016); furthermore, change in termite functional diversity is also greater in areas at lower elevation compared to areas at high elevation (Cunha *et al.* 2020; Inoue *et al.* 2006; Palin *et al.* 2011).

Termites have been poorly studied in Colombia, being more recognized as pests in agroecosystems, with their ecological role usually being ignored (Abadía. *et al.* 2013;

Abadía & Arcila 2009; Gutiérrez *et al.* 2004). Termite studies in rubber crops in Colombia have been carried out on the incidence of damage and management of pest species (Leon *et al.* 2009; Pinzón *et al.* 2012; Sterling *et al.* 2011a).

In recent years, classic termite diversity studies have been able to explore the impact of land-use change on the diversity of these insects in Colombia (Beltrán-Díaz & Pinzón-Florián 2018; Casalla & Korb 2019b). Nevertheless, some approaches to characterize the functional structure in natural areas was carried out in the Orinoco region (Pinzón *et al.* 2017). Likewise, ecosystem services of termite communities have been evaluated, highlighting the importance of termite conservation in disturbed ecosystems (Duran-Bautista *et al.* 2020a; Sanabria *et al.* 2016). However, changes in the functional structure studies in termites from different land uses has not yet been a subject studied extensively in Colombia, a lot less in the Amazon region.

3.1.1. Termite functional groups (guilds)

Termites play an important role in plant material degradation and nutrient cycling (Bignell 2005), and different termite groups feed on a variety of substrates, from living plants to organic matter with mineral soil (Eggleton 2011; Eggleton & Tayasu 2001). Termite ability to assimilate lignocellulose as food is possible due to cellulosic enzymes produced by both, the termite and their intestinal microbiota, and this capacity makes them as part of the main decomposers of plant material (Tokuda *et al.* 1997; Tokuda & Watanabe 2007).

A wide variety of food resources used by termites have been identified: live wood, dead wood, decomposed wood, grass, litter, fungi, manure, carcass, humus; and lichens (Lima & Costa-Leonardo 2007). Due to these different diets among termite species, they can be separated in guilds according to their feeding or functional groups.

In addition, termites have been classified according to the degree of which their nesting and feeding behaviors overlap, even though this classification comes out with difficulties (Abe 1987). Some species are confused in their nest type with a feeding substrate, because they can be collected in a substrate in which they live, or forage but not feeding. Other classifications have been proposed based on direct field observations on their feeding habits (Eggleton *et al.* 1997; De Souza & Brown 1994).

One of the most used classifications recognizes five feeding groups of termites based on their phylogeny, and morphological characters, such as the digestive tube, mandibular molar plate morphology, and the apical tooth size (Donovan *et al.* 2001). Yet, another classification has been proposed by superimposing life-type groups, and the groups by internal morphology and gut content, obtaining up to eight different groups (Eggleton & Tayasu 2001). This last classification seems to give more accurate results, However, differences have been identified between the groups established with the niches of some Neotropical species (Bourguignon *et al.* 2011b).

In this chapter, we assess the variation of the taxonomical and functional composition of termites in three rubber production systems established in the northwestern Colombian Amazon, compared to neighboring pastures and natural forests.

3.2. Materials and methods

Termite samples were collected and identified as explained in chapter 1. Soil physicochemical variables were collected and analyzed as explained in chapter 2.

3.2.1. Determination of the termite functional groups

Termite feeding groups were assigned by genus based on the literature (Carrijo *et al.* 2009; Davies 2002; Oliveira *et al.* 2013; De Souza & Brown 1994) and unpublished data regarding each species, further field notes (life-types and substratum were individuals were collected) and descriptions of the worker mandibles and gut anatomy were included. Species were classified in the following four feeding groups: (i) Soil feeders, that feed on mineral soil and humus, ii) intermediaries, that feed on the soil-wood interface, iii) xylophages, that feed on wood, and iv) leaf-litter feeders, that feed on litter and small pieces of wood.

3.2.2. Data analysis

A constrained ordination test was performed to find linear changes between the termite functional groups with the principal soil variables obtained from chapter 2 (Figure 2-3) and the five land uses, were termite functional groups were the dependent variables, and soil properties were the independent variables. A direct gradient analysis was used, allowing the sites comparison with difference of sampling units. A short gradient (<4) was also obtained in the DCA analysis with the matrix of functional groups (species occurrence of each functional group). The same methodology used to analyze the RDA of the species composition was performed as explained in chapter two.

3.3. Results

Wood-feeding termites was the most abundant feeding group, representing 53% of the samples (567 occurrences), followed by soil-feeding termites, with 27% (315 occurrences), intermediates termites, with 18% (204 occurrences), and finally leaf-litter feeder termites with 1.5% (17 occurrences). Wood-feeders were more abundant in natural forests, clonal fields, and commercial rubber plantations, while soil-feeders were more abundant in mixed plantations and pastures (Figure 3-1). Soil-feeding termites were the richest feeding group, with 34 species (43% of the species), while wood and intermediate feeders represented 25% each (Figure 3-2).

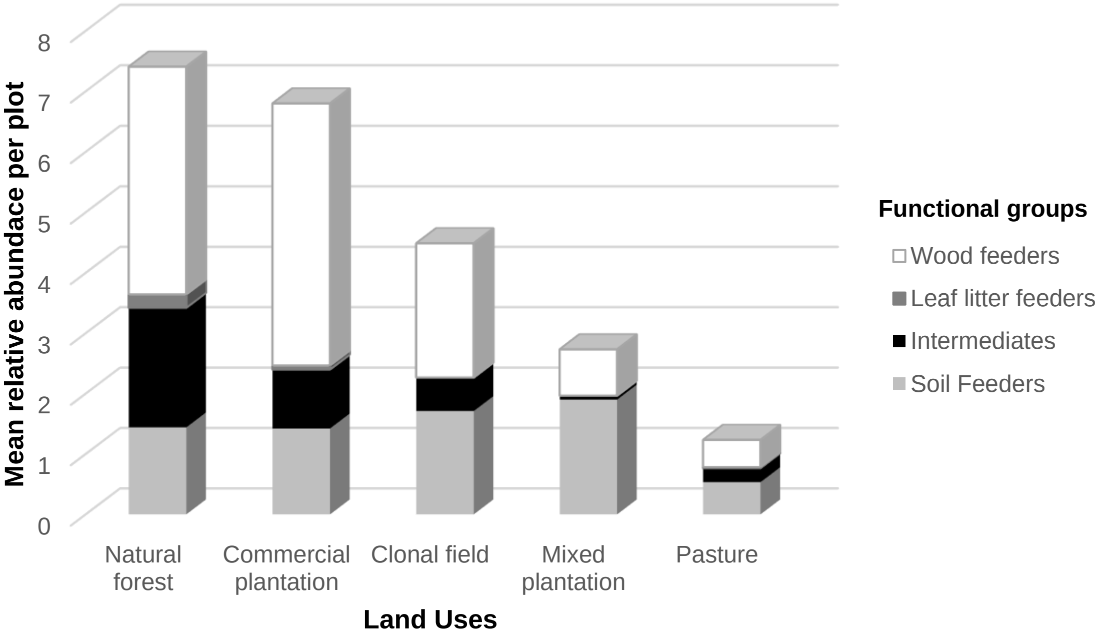


Figure 0-1: Mean relative abundance of termite functional groups per plot in the five land uses.

Leaf-litter feeder termites were the least abundant group and with the lowest species (seven species) representation and these were absent in CF. The intermediates termites showed low values of richness and abundance in MX, with two occurrences and only one species, even when compared with CF (25 occurrences and seven species), and PA (14 occurrences and tree species), that were the areas with the second and third lower values of richness and abundance for this group. Mean abundance per plot and species richness of the four functional groups per plot have the same pattern in all land uses (Figure 3-1; 3-2).

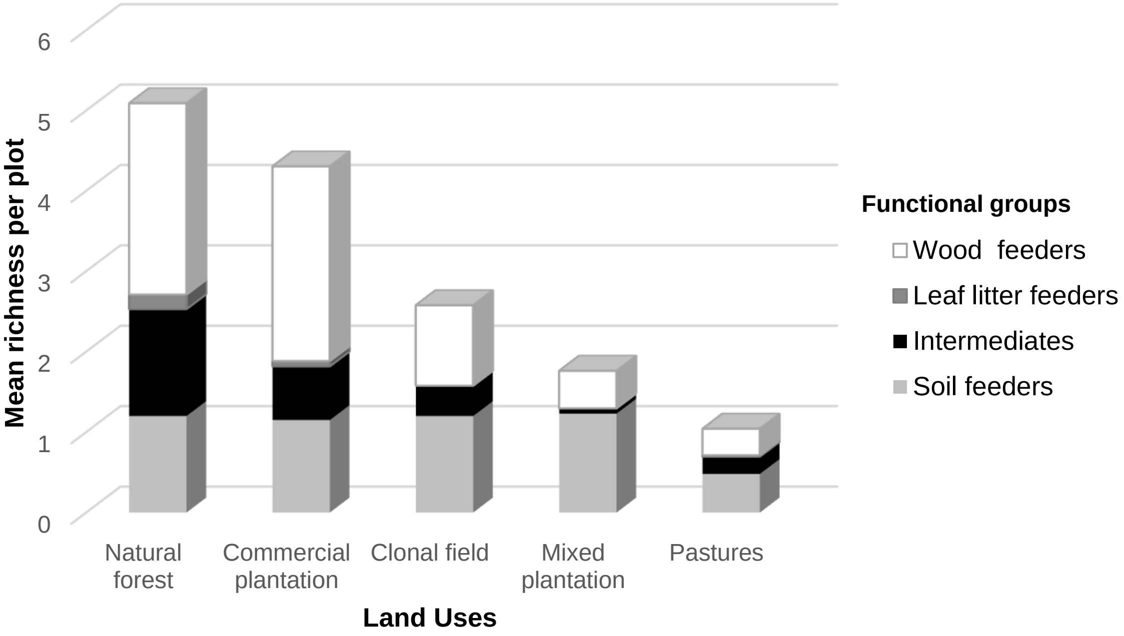


Figure 0-2: Mean species richness of termite functional groups per plot in the five land uses.

Considering the termite functional groups across all land uses, RDA shows that the edaphic variables explained 93.6% of the termite functional structure variation of the all-land-uses comprised in dimensions 1-2. The variation explained by these two dimensions is highly significant, being the only two significant dimensions because Dim1 and Dim2 explain almost all the variation (Table 3-1).

All the edaphic variables evaluated in the RDA ordination presented a significant effect on the functional groups. The variables that presented higher significance were CEC, ED, AD, and Ca, the same variables that were significant with the species assemblage (Table 2-2). Organic carbon (OC), Silt, and pH were the least significant variables; however, they still have a significant effect (*p*<0.01) on functional groups (Table 3-2).

Table 0-1: Significance values of RDA axes forward selection to test the effects of principal soil variables on termite functional groups. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

Axes	**df**	**Variance**	**F**	***p*-value**	**Significance**
RDA1	1	0.037581	28.8210	0.001	***
RDA2	1	0.019250	14.7629	0.002	**
RDA3	1	0.003005	2.3043	0.763	
RDA4	1	0.000861	0.6607	0.999	
Residual	205	0.267312			

Table 0-2: Results of redundancy analysis (RDA) forward selection to test the effects of principal soil variables on termite functional group. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

Soil variables	**df**	**Variance**	**F**	***p*-value**	**Significance**
pH	1	0.004643	3,5088	0.033	*
Electrical conductivity (ED)	1	0.010103	7,6349	0.001	***
Cation exchange capacity (CEC)	1	0.011703	8,8437	0.001	***
Organic carbon (OC)	1	0.004405	3,3288	0.030	*
Bulk density (AD)	1	0.013470	10,3865	0.001	***
Silt	1	0.006236	4,7123	0.007	**
Calcium (Ca)	1	0.017749	13,4125	0.001	***

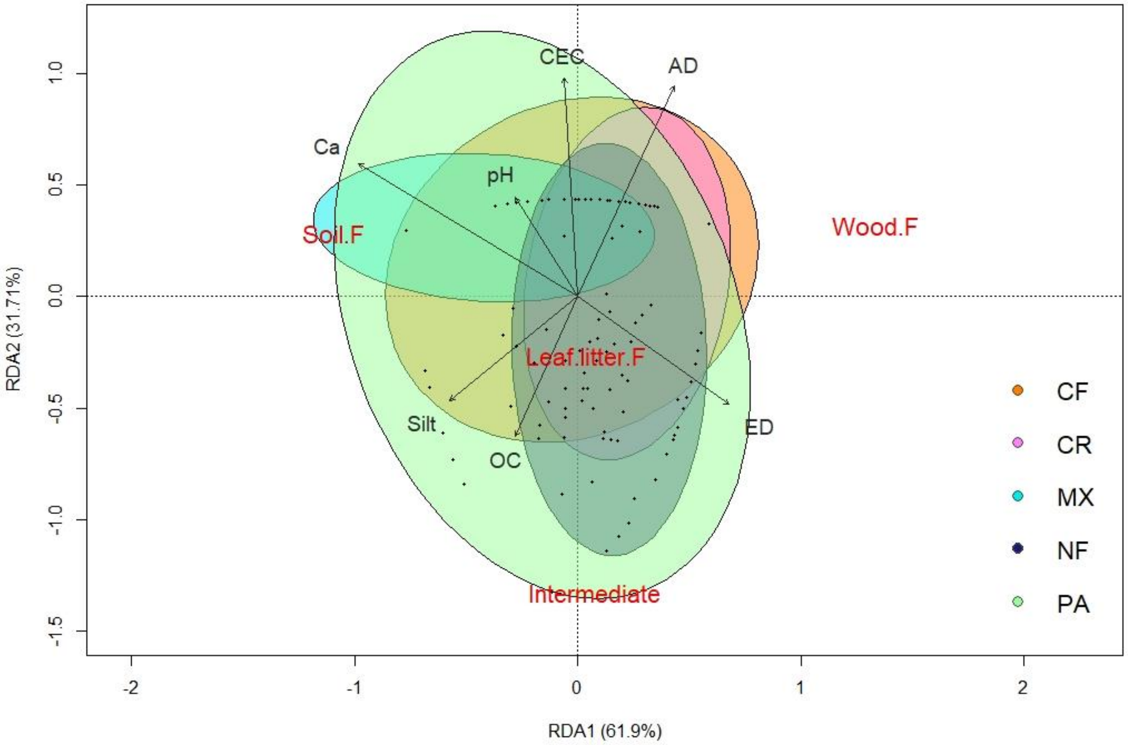


Figure 0-3: RDA Ordination bi-plot of termite functional group abundance and significant soil variables in the five land uses. Physicochemical soil variables are shown by arrows: OC = organic carbon, ED= electrical conductivity, CEC= cation exchange capacity, AD= bulk density, Ca= calcio. Land uses are represented with ellipses with a confidence level of 0.90. Black points represent the sampled plots.

The RDA bi-plot shows that each functional group distanced itself from the others, defining a functional structure of the termites with respect to the five land uses. The termite functional group abundances influenced their mapping order of each functional group (Figure 3-3).

Soil feeders were the only group clustering to the left side of the axis-Y, associated with the least diverse sites (MX and PA), and correlating positively with calcium availability in soil. Leaf litter feeders were grouped in the center of the ordering map, being overlap with CR, NF, and PA in low incidence, the only land uses where this functional group was found.

Intermediate termites were correlated with both PA and NF. This is evident to NF, since this land use presented the highest abundance and richness of this group. Although PA does not present such high values of abundance and diversity, the proportion (%) of intermediate termites compared to wood and soil feeders was higher in this land use than in any other.

Both leaf litter feeders and intermediates termites were highly correlated to organic carbon (OC).

The wood-feeders were highly correlated with mature CF and CR plantations. Wood feeders are the most abundant and diverse group in this study (Figure 3-1; 3-2), and this influenced that all the land use ellipses tend to be ordered in the wood feeder quadrant. These termites were highly correlated with bulk density (AD).

The MX ellipse has a structure of mostly soil-feeders, followed by wood-feeders, and not correlated with leaf-litter feeders and intermediates termites. CF is highly correlated with soil feeders, wood feeders, and, to a lesser extent, to intermediate termites. The CR is highly correlated with wood feeders, intermediates, and leaf litter feeders, and show a low (but still significant) correlation with the soil feeders. The NF presented a similar correlation to CR, but the influence of the intermediates termites was higher and the NF ellipse was closer to the soil feeders than the CR ellipse. The functional structure of NF and CR were the most similar among land uses (Figure 3-4).

3.4. Discussion

Our results showed that the termite functional structure changes with respect to land uses, in addition to termite functional groups respond to soil variables. The rubber crop systems presented different proportions on the functional groups termite assemblages, although in the most mature and most diverse plantation (CR) the structure was similar to that of a natural forest (NF), as it has been reported in other agroecosystems in the central Amazon (Ackerman *et al.* 2009). On the other hand, the Clonal field, another type of mature plantation was lacking of litter consumers, and the mixed plantation had a more similar functional structure with pastures than with the other crops (da Cunha & Orlando 2011; Houston *et al.* 2015; de Paula *et al.* 2016), this seems to be related to agricultural practices that are more intensive in these two crop systems than in CR.

The functional groups ordering shows a clear differentiation between them, and the ellipses of the rubber crops and natural forest are more defined in relation to the abundance of the groups found than pastures. It should be noted that the pasture large ellipse corresponds to a high correlation with the following three guilds: soil-feeders, wood-feeders, and intermediate termites. Although the area of its ellipse is large, PA has a lower abundance and diversity. For instance, intermediate termites present 14 occurrences of only three species, representing 20% of the total species found in this land use. In the case of wood feeders, only two species were found, with *Heterotermes tenuis* representing 32.5% of the total abundance of termites in PA. This species seems to adapt well to conditions of little shade and high soil compaction, being the main consumer of dead wood available in pastures (Beltrán-Díaz & Pinzón-Florián 2018).

Wood-feeding termites were dominant in natural forest and mature rubber plantations (CR and CF), being both mature plantations, with high availability of tree pruning waste (Table 1). Possibly, soil organic matter availability seems to be a factor influenced by the wood-feeding termite diversity, since these termites digests the wood and enriches the soil with organic matter (Jones *et al.* 2003; Luke *et al.* 2014; Neoh *et al.* 2018). Therefore, if the available organic carbon is low, the wood-feeder termite diversity will also be low, as well as the availability of organic matter. Similar results were reported in other rubber plantation studies (Liu *et al.* 2019; Pinzón *et al.* 2012). In the case of the mixed plantations (MX), where other crops, such as fruit trees are intercropped with rubber, additional agricultural practices are implemented to secure fruit production, and these practices are probably affecting termite communities as well.

The high values of bulk density (AD) in PA and MX seems to directly affect termite diversity by physical limitations (Jones *et al.* 2003; De Souza *et al.* 2016), and favoring the colonization of a few species capable of living in these conditions. This variable presented a high correlation with soil-feeders, which were more common in land uses with low organic carbon and higher pH (MX and PA). Our results, however, contradicts previous studies that found that most soil feeders species are sensitive to disturbed areas, strongly decreasing their species number and abundance compared to natural areas (Bandeira *et al.* 2003; Davies 2002; Eggleton *et al.* 2002; Jones *et al.* 2003).

In our results, soil-feeders, mainly the Apicotermitinae subfamily, presented a high abundance in all land uses, and particularly they are dominant in sites of group II. Besides, in CR and NF (group I) soil-feeders termite species of Nasutitermitinae and Syntermitinae increased their abundance and diversity, suggesting that the soil-feeders of these subfamilies do not adapt well to young plantations and disturbed sites (Ackerman *et al.* 2009; Beltrán-Díaz & Pinzón-Florián 2018). Some soil-feeders termite species that were capable of colonizing these environments are the Apicotermitinae *Rustitermes boteroi* and

Disjunctitermes insulares, both abundant in PA and MX. Other species of "ecosystem engineers", such as earthworm *Pontoscolex corethrurus*, were also reported as abundant in compacted soils of Colombia and the Amazon (Gutierrez-Sarmiento & Cardona 2014; Marichal *et al.* 2010; Pisco *et al.* 2013). Besides, it has been reported that termite mounds of soil-feeders present high fractions of silt and clay (Brauman 2000). In our results, Silt was the soil texture variable showing high correlation with termite assemblage (Table 3-2).

The group of leaf-litter feeders was the most notably influenced by young plantations and degraded soils, since they were absent in CF and MX, and in PA the only occurrence was *Syntermes molestus* (Table 1-2), however in the Orinoco region in young plantations leaf-litter feeders were more abundant (Pinzón *et al.* 2012). It would be expected in pastures to have a high number of occurrences and species of leaf-litter feeders for the presence of grass and shrub plant species that create a food supply for this group of termites (Beltrán-Díaz & Pinzón-Florián 2018; Davies 2002), which are non-existent in CF and MX by the weed and tree pruning activity that eliminates the availability of food. However, in the PA sampled in this study, leaf-litter termites were not diverse or abundant.

Intermediate termites, such as *Embiratermes neotenicus* and *Silvestritermes euamignathus*, had relatively high abundances in the pastures, compared to the other termite species found in this land use. These species were found commonly in epigeal mounds and were also found in abundance in CF and CR (Davies *et al.* 2003; Duran-Bautista *et al.* 2020a). However, the only intermediate termite species found in the mixed plantations was *Termes fatalis*. Interestingly, although it is known that this species builds epigeal nests (Constantino 1992), the application of insecticide and mechanical removal of weeds seems to be eliminating their visible mounds. This would imply that *T. fatalis* presents nest plasticity, and this silvicultural management is probably selecting populations of subterranean nest builders. Intermediate species are highly abundant and diverse in NF, CR, and to a lesser extent in CF, this corroborated the reported by Pinzón *et al.* (2012) were intermediate termites were found in old rubber plantations. They have also a significant part of the termite composition of PA, what made their ellipse in figure 3-4 with such a large area. We suggest that this pattern was due to intermediate termites having influenced PA because this group is relatively abundant and diverse in this land use. However, these values are much lower than those found in CF and NF, which indicates that the functional structure of PA is not very concise and its wide-area infers a weak and poorly defined structure.

Soil tillage has an impact on soil organism's sensitive to changes in soil structure. In pasture covers, the tillage is non-existent, and in some cases, it causes a high soil fauna abundance and richness in comparison to agricultural soils with high soil tillage (Carneiro *et al.* 2009). This may also explain why PA was more diverse and presented a broader functional structure than MX, where the soil structure had more agricultural management activities than the other cropping systems (Table 1-1).

Wood-feeders termites comprise a large part of termite composition in communities of natural forests. Naturally, this proportion is also present in rubber crop systems, due to the high wood supply produced by rubber trees (Figure 3-1; 3-2). But the high presence of these termites did not represent a concern in typical overpopulations of agricultural pests (Abadía. *et al.* 2013), since the presence of this group is, instead of consuming living trees, probably helping the cellulose degradation and contributing to the natural processes carbon cycling (Dosso *et al.* 2013; Junqueira *et al.* 2009; Pinzón *et al.* 2012).

The hypothesis put forward for this chapter was corroborated, the pasture functional structure was the least defined and, on the other hand, the CR crop system presented a functional structure very close to NF structure, and CF structure also presented characteristics close to NF structure. Although MX structure was the one that presented the functional structure furthest from NF of the three rubber crop systems, it was more defined than the PA functional structure. We can conclude that the rubber productive systems evaluated present a different functional structure. The commercial plantation presented a functional structure similar to the natural forest, which can be inferred that rubber crops can help to recover, in addition to diversity, the functional structure of termites in the ecosystem, which has been lost by extensive livestock.

Conclusions and recommendations

4.1. Conclusions

Rubber crops in areas of degraded pastures may promote soil fauna recover and, improve the soil physicochemical properties. However, the implementation of rubber crop systems to restore degraded pastures previously used for extensive livestock farming does not necessarily increase termite diversity. The type of rubber crop system implemented will significantly determine the recovery of the termite diversity expected. Our results also suggest that some agricultural practices can affect termite recovery, which influences the way in which plantations are currently managed in the region.

The functional structure of the termite assemblage changes concerning the type of land use. Functional groups are more diverse when plantations are more mature; and the physicochemical soil properties such as bulk density, organic carbon, electrical conductivity, cation exchange capacity, and pH are appropriate. On the other hand, in areas such as pastures, which are the most affected by soil compaction and low fertility, the termite assemblage does not present a stable functional structure; and in the lowest diverse rubber crop system (mixed plantations), termite functional structure was reduced when was compared with commercial rubber and clonal field. The natural forest showed the most diverse and abundant and compex while the commercial rubber plantations was the rubber system with the most similar structure to this natural non-disturbed land use.

4.2. Recommendations

There is a clear influence of the mixed plantations in soil variables, with variables such as bulk density, pH, and organic carbon with values typical of highly degraded and compacted soils. Rubber plantations with fewer silviculture management (CF and CR), helps to recover the soil fauna, and may serve as biological connectors between natural forest patches. Because of that, we recommended to incorporate these practices into the plans of local restoration.

In addition, the clonal fields and commercial plantations help to recover the functional structure in the ecosystem soil organisms, as evidenced by termites. However, termite functional structure in these plantations will not be the same as a natural forest. The establishment and exploitation of mature plantations, such as those evaluated in this study, could be an alternative to recover degraded soils and promote an economic activity for the region.

In this study, I did not directly evaluate the effect of silviculture management on termite communities, so it is suggested that studies should be conducted to evaluate the effects of agrochemicals and other agricultural practices applied to rubber crop systems might affect termite diversity and different edaphic fauna.

In this work, I corroborated the usefulness of studying termite communities to analyze the effects of changes in land uses, the impact of agricultural practices in the soil, and the state of diversity in soils. Therefore, I recommend using the responses of assemblages of termite communities for ecological studies in the country, taking advantage of this still underestimated insect group, especially in Colombia.

The establishment of rubber crops with adequate agricultural practices have a positive impact on recovering soil biological diversity and forest conservation. This activity, presenting a high contribution to the recovery and conservation of soils, is also an economic activity that generates employment and social development continuously for a long time and, being an alternative for the region development, stopping deforestation and recovering the productivity of the soils.

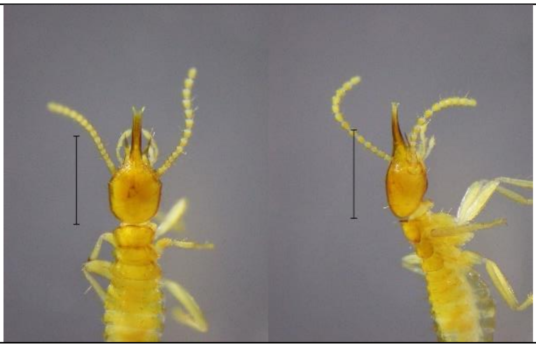
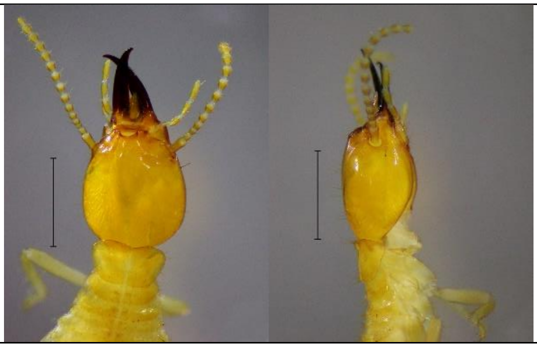
A. Supplementary material: Soil physicochemical properties from five different land uses in the Northwestern Colombia Amazon

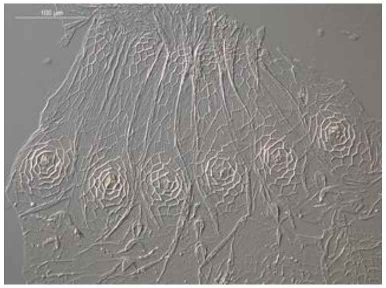
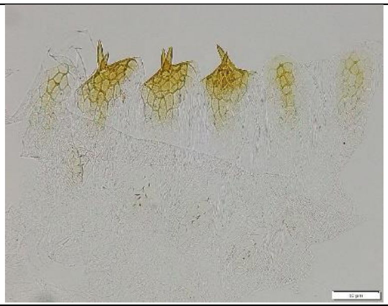
Soil property	Mixed plantation (n = 2)	Clonal Field (n = 3)	Commercial rubber (n = 3)	Pastures (n = 4)	Natural forest (n = 4)
pH	4.68 ± 0.21	4.47 ± 0.15	4.77 ± 0.07	4.77 ± 0.18	4.37 ± 0.139
ED (dS/m)	0.07 ± 0.014	0.086 ± 0.025	0.1 ± 0.02	0.065 ± 0.017	0.102 ± 0.009
CEC (meq/100g)	5.935 ± 1.958	8.056 ± 2.80	6.15 ± 1.84	6.2 ± 1.97	6.06 ± 2.167
OC (%)	1.169 ± 0.298	1.150 ± 0.314	1.006 ± 0.4	1.297 ± 0.41	1.31 ± 0.191
AD (g/cm^3)	1.375 ± 0.091	1.38 ± 0.069	1.46 ± 0.072	1.345 ± 0.068	3.77 ± 4.883
Clay (%)	49 ± 1.414	49.33 ± 3.055	50.66 ± 2.3	48.5 ± 2.51	47.25 ± 1.64
Sand (%)	41 ± 7.071	39.33 ± 9.865	45.33 ± 2.309	41.5 ± 1.91	42.75 ± 1.92
Silt (%)	10 ± 5.656	8 ± 2	4 ± 0	10 ± 2.82	10 ± 1.63
K (mg/kg)	38.6 ± 11.5965	49.866 ± 16.919	33.26 ± 11.5	33.5 ± 6.59	41 ± 18.24
Ca (mg/kg)	274 ± 63.639	238 ± 24.269	231.33 ± 43.98	256.5 ± 19.67	215.75 ± 21.82
Mg (mg/kg)	46 ± 7.07106	34 ± 3.605	39.66 ± 12.74	33.5 ± 7.59	35.25 ± 9.91
N (%)	0.0975 ± 0.0247	0.095 ± 0.026	0.0836 ± 0.03	0.108 ± 0.033	0.109 ± 0.016
Fe (mg/kg)	174 ± 46.669	173.66 ± 48.644	246.33 ± 121.62	233.75 ± 109.72	234.25 ± 102.94
P (mg/kg)	1.085 ± 0.0494	0.73 ± 0.511	0.59 ± 0.63	1.07 ± 0.058	1.07 ± 0.103

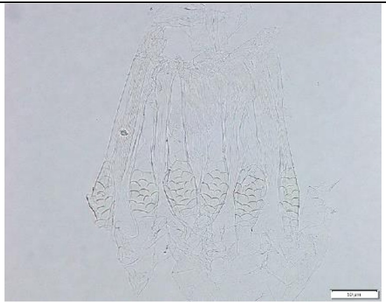
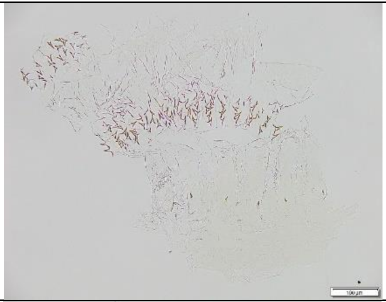
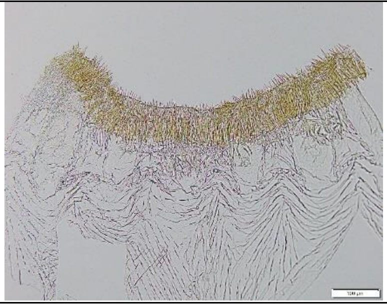
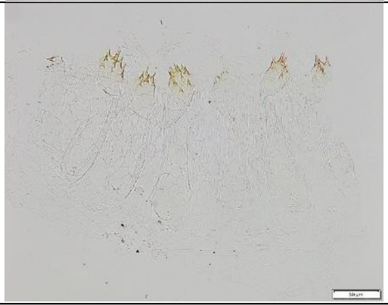
	Mixed plantation		Clonal field			Commercial rubber plantation			Pastures				Natural Forest			
	F1	**F4**	**F1**	**F2**	**F3**	**F1**	**F2**	**F3**	**F1**	**F2**	**F3**	**F4**	**F1**	**F2**	**F3**	**F4**
pH	4.83	4.53	4.30	4.60	4.52	4.68	4.80	4.83	4.63	4.95	4.59	4.91	4.20	4.50	4.32	4.47
ED	0.06	0.08	0.11	0.06	0.09	0.10	0.08	0.12	0.09	0.05	0.06	0.06	0.11	0.10	0.11	0.09
CEC	7.32	4.55	7.50	11.1	5.57	6.01	8.07	4.39	8.23	7.56	4.63	4.39	5.84	9.15	5.12	4.16
OC	0.958	1.38	1.14	0.842	1.47	0.766	0.782	1.47	1.11	0.810	1.68	1.59	1.09	1.40	1.53	1.24
AD	1.44	1.31	1.41	1.43	1.30	1.51	1.50	1.38	1.35	1.44	1.29	1.30	1.11	1.36	1.30	1.34
Clay (%)	48.0	50.0	46.0	50.0	52.0	52.0	52.0	48.0	52.0	48.0	48.0	46.0	47.0	46.0	50.0	46.0
Sand (%)	46.0	36.0	46.0	44.0	28.0	44.0	44.0	48.0	40.0	44.0	42.0	40.0	45.0	44.0	40.0	42.0
Silt (%)	6.00	14.0	8.00	6.00	10.0	4.00	4.00	4.00	8.00	8.00	10.0	14.0	8.00	10.0	10.0	12.0
K	30.4	46.8	65.0	53.0	31.6	20.0	40.4	39.4	27.4	39.4	39.0	28.2	21.2	64.8	35.0	43.0
Ca	319	229	223	266	225	269	183	242	285	254	242	245	206	244	193	220
Mg	51.0	41.0	31.0	38.0	33.0	46.0	25.0	48.0	44.0	29.0	34.0	27.0	32.0	50.0	29.0	30.0
N	0.080	0.115	0.095	0.070	0.122	0.064	0.065	0.122	0.093	0.068	0.140	0.132	0.091	0.117	0.128	0.103
Fe	141	207	195	118	208	206	150	383	184	110	280	361	126	193	249	369
P	1.12	1.05	0.140	1.05	1.00	0.246	0.211	1.33	1.12	1.12	1.01	1.03	1.02	1.01	1.23	1.05

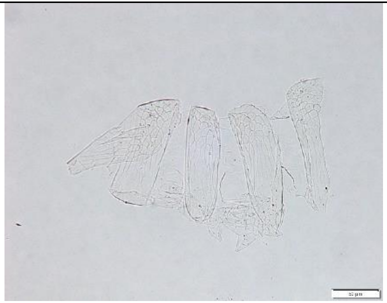
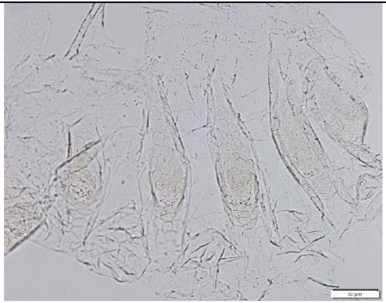
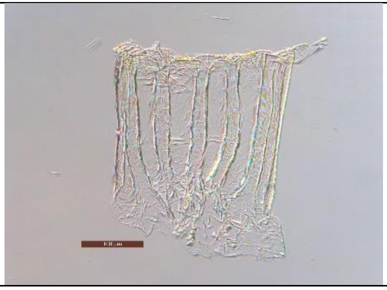
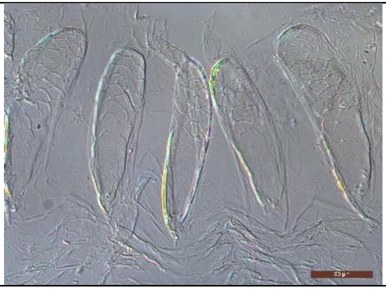
B. Supplementary material: Photographic catalog of the termite species

NOTE: species with * do not present photos in the catalog due to logistical problems with the COVID-19 pandemic. The termite specimens were in the CATAC collection located in the city of Leticia, Amazonas, where there were strict restrictions to travel, including the airport closure.

RHINOTERMITIDAE			
Dolichorhinotermes longilabius (Emerson, 1924)		*Coptotermes testaceus* (Linnaeus, 1758)	

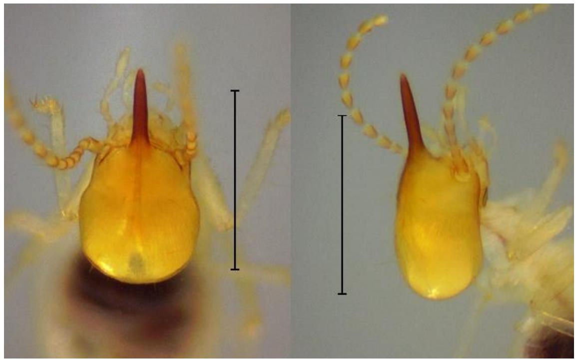
Heterotermes tenuis (Hagen, 1858)			
TERMITIDAE			
Apicotermitinae			
Anoplotermes banksi Emerson, 1925		*Anoplotermes janus* Bourguignon & Roisin, 2010	

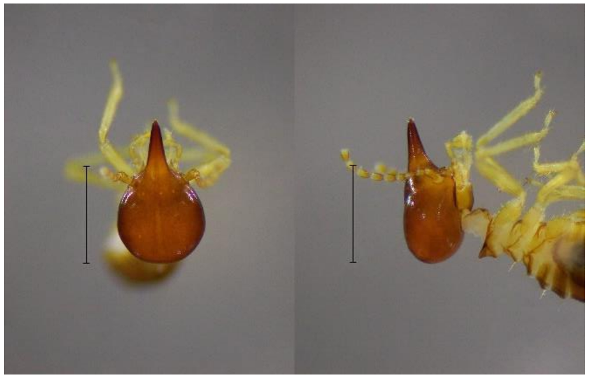
Anoplotermes meridianus Emerson, 1925		*Anoplotermes parvus* Snyder, 1923	
Aparatermes thornatus Pinzon & Scheffrahn, 2019		Apicotermitinae sp.1	
Apicotermitinae sp.2		Apicotermitinae sp.3	

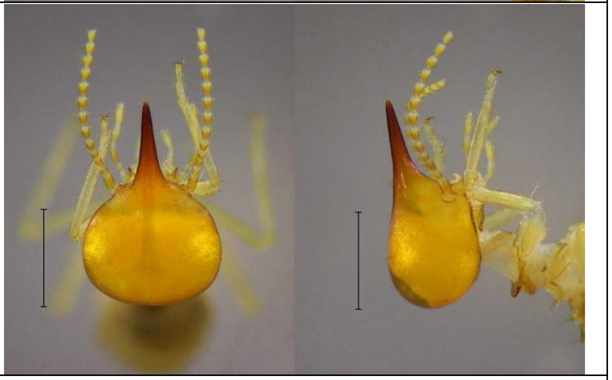
Apicotermitinae sp.4		Apicotermitinae sp.5	
Apicotermitinae sp.6		Apicotermitinae sp.7	
Apicotermitinae sp.8		Apicotermitinae sp.9	

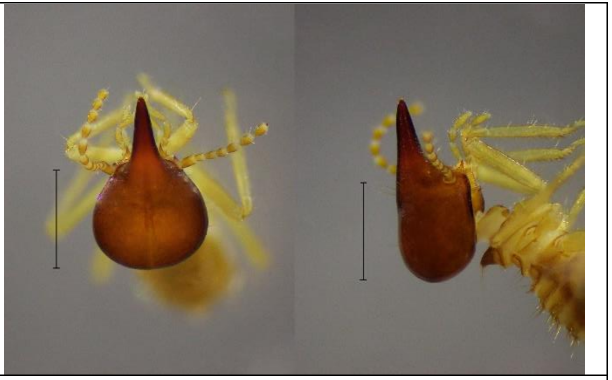
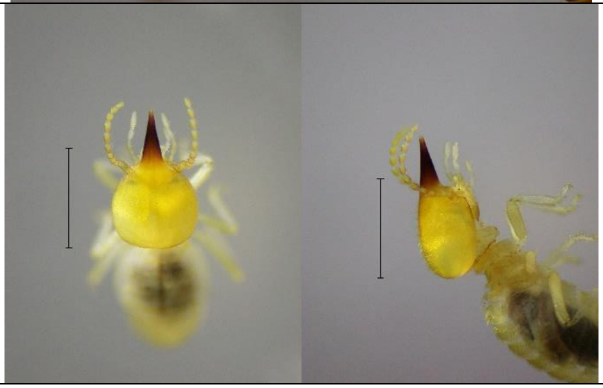
Apicotermitinae sp.10		*Compositermes vindai* Scheffrahn, 2013	
Disjunctitermes insularis Scheffrahn, 2017		*Humutermes krishnai* Bourguignon & Roisin, 2016	
Hydrecotermes arienesho Bourguignon & Roisin, 2016		*Hydrecotermes kawaii* Bourguignon & Roisin, 2016	

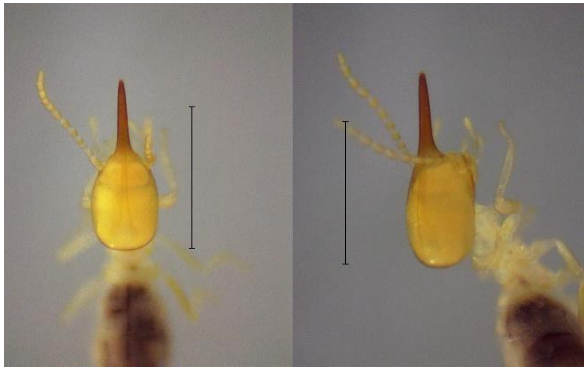
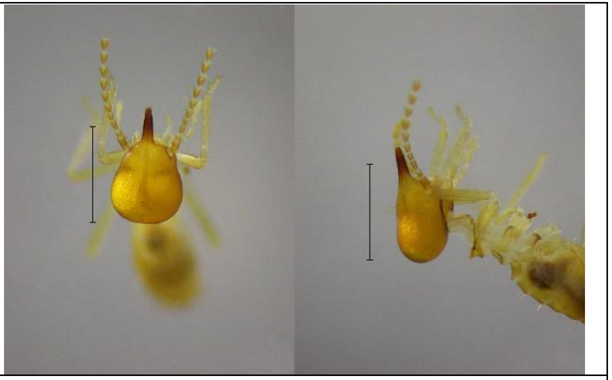
Patawatermes nigripunctatus (Emerson, 1925)		*Patawatermes turricola* (Silvestri, 1901)	
Rubeotermes jheringi (Holmgren, 1906)		*Rustitermes boteroi* Constantini, Castro & Scheffrahn, 2020	
Nasutitermitinae			
Agnathotermes crassinasus Constantino, 1990		*Angularitermes pinocchio* Cancello & Brandão, 1996	

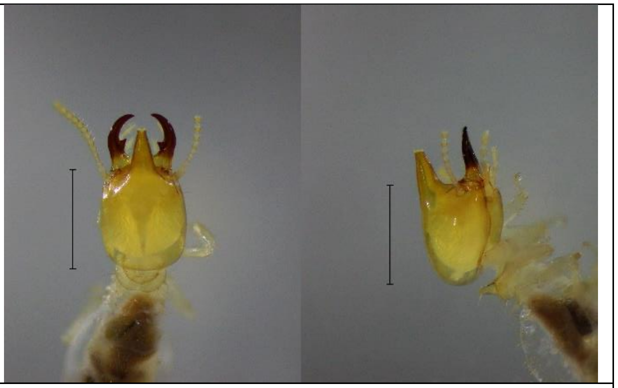
Araujotermes parvellus (Silvestri, 1923)		*Atlantitermes* cf. *oculatissimus* (Emerson, 1925)	
Caetetermes taquarussu Fontes, 1981		*Coatitermes clevelandi* (Snyder, 1926)*	
Constrictotermes cavifrons (Holmgren, 1910)		*Ereymatermes rotundiceps* Constantino, 1991*	

Nasutitermes acajutlae (Holmgren, 1910)		*Nasutitermes banksi* Emerson, 1925	
Nasutitermes brevipilus Emerson, 1925		*Nasutitermes* nr. *comstockae* Emerson, 1925	

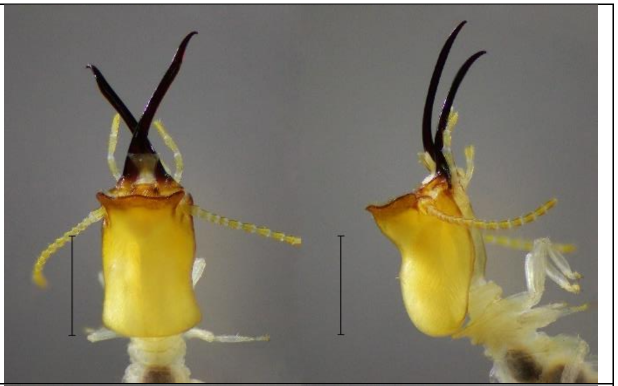
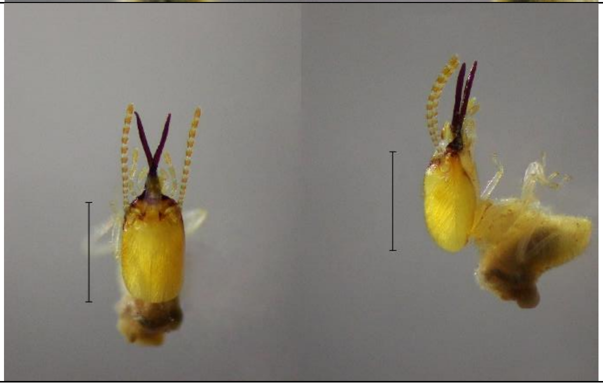
Nasutitermes corniger (Motschulsky, 1855)		*Nasutitermes gaigei* Emerson, 1925	
Nasutitermes guayanae (Holmgren, 1910)		*Nasutitermes octopilis* Banks, 1918	
Nasutitermes similis Emerson, 1935		*Nasutitermes* sp.1	

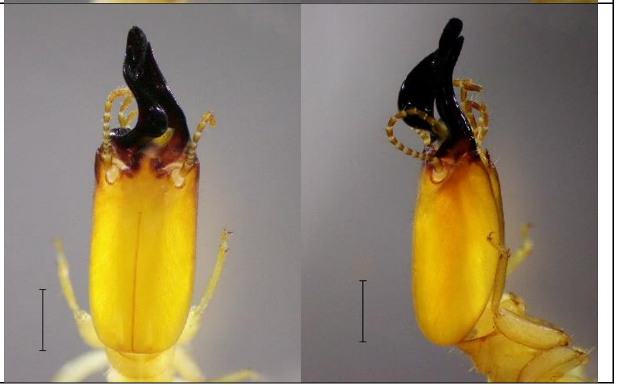
Nasutitermes sp.2		*Nasutitermes surinamensis* (Holmgren, 1910)	
Paraconvexitermes cf. *nigricornis* (Holmgren, 1906)		*Rotunditermes bragantinus* (Roonwal & Rathore, 1976)	

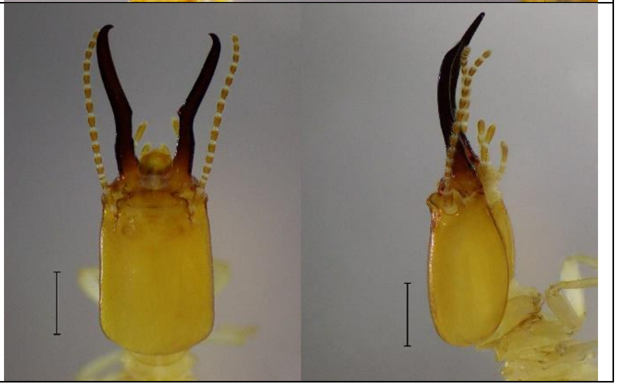
Subulitermes baileyi (Emerson, 1925)		*Triangularitermes triangulariceps* Mathews, 1977	
Velocitermes cf. *uniformis* (Snyder, 1926)			
Syntermitinae			

Cyrilliotermes angulariceps (Mathews, 1977)		*Embiratermes ignotus* Constantino, 1991	
Embiratermes neotenicus (Holmgren, 1906)		*Embiratermes robustus* Constantino, 1993*	
Labiotermes labralis (Holmgren, 1906)*		*Rhynchotermes diphyes* Mathews, 1977*	

Silvestritermes euamignathus (Silvestri, 1901)		*Silvestritermes heyeri* (Wasmann, 1915)	
Silvestritermes minutus (Canter, 1968)		*Syntermes aculeosus* Emerson, 1945*	
Syntermes molestus (Burmeister, 1839) *			
Termitinae			

Cavitermes parvicavus Mathews, 1977		*Cavitermes tuberosus* (Emerson, 1925)	
Crepititermes verruculosus (Emerson, 1925)		*Cylindrotermes flangiatus* Mathews, 1977	

Cylindrotermes parvignathus Emerson, 1949		*Microcerotermes arboreus* Emerson, 1925	
Neocapritermes pumilis Constantino, 1991		*Neocapritermes talpa* (Holmgren, 1906)	

Neocapritermes talpoides Krishna & Araujo, 1968		*Neocapritermes taracua* Krishna & Araujo, 1968	
Neocapritermes utiariti Krishna & Araujo, 1968		*Orthognathotermes humilis* Constantino, 1991	

Planicapritermes planiceps (Emerson, 1925)		*Spinitermes trispinosus* (Hagen, 1858)	
Termes nigritus (Silvestri, 1901)		*Termes fatalis* Linnaeus, 1758	

Termes hispaniolae (Banks, 1918)			

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