Effects of agricultural Landscape of the Colombian Llanos on Ecosystem Services and assemblages of soil engineers

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École doctorale 227 MNHM-UPMC « Sciences de la Nature et de l'Homme : évolution et écologie »

Thèse préparée à l'Institute d'écologie et des Sciences de l'Environnent de Paris (UMR 7618)

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Dirigée par Dr. Sébastien BAROT et Dr. Florence DUBS

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To the beautiful eastern plains of Colombia and its ants…
That this work serves to encourage their conservation.

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Abstract

Tropical savannas are highly important for agricultural production and many other ecosystems services. In Colombia, these savannas have been traditionally managed through extensive livestock production and low-input agriculture. The current conversion of these natural systems to intensified agriculture can have devastating impacts on belowground and aboveground biodiversity. Soil macrofauna represents an important part of agroecosystem biodiversity and some groups have received considerable attention as ecosystem engineers. The general goal of the thesis is to evaluate and analyze the impacts of agricultural landscapes on soil engineer communities and soil ecosystem services in the Colombian Llanos. Three main questions were addressed: (1) What is the impact of agricultural management on ant communities and is it possible to identify ant species that could be used as indicators of soil-based ecosystem services? (2) What is the impact of land uses on ant and termite communities and is this impact associated with modifications of soil physical and chemical properties? (3) Do the ecological and morphological traits of ants respond to land uses and soil properties?

The results of this thesis confirm that ant communities are highly sensitive to land use changes and constitute good early indicators of soil-based ecosystem services. More accurately, annual crops have shown to be detrimental to ant and termites communities and this is probably due to the application of chemical inputs, as well as to tillage and pesticides. All land uses (Savannas, rubber or oil palm plantations, improved pastures and annual crops) have a particular soil fauna, but some species have particular habitat requirements for nest sites, food, refugees, etc. Some species are more generalist and are particularly adapted to disturbed environment. The presence of all land uses within a landscape contributes to a certain extent to

the total diversity. It was found that sites with a tree cover protect rare, sometimes inconspicuous and perhaps fragile species.

Résumé

Les savanes tropicales sont très importantes pour la production agricole et de nombreux services écosystémiques. En Colombie, ces savanes ont été traditionnellement gérées par l'élevage extensif et l'agriculture à faible intrants. La conversion actuelle de ces systèmes naturels en agriculture intensive peut avoir des effets dévastateurs sur la biodiversité du sol et au-dessus du sol. La macrofaune du sol représente une part importante de la biodiversité des agroécosystèmes et certains groupes ont reçu une attention considérable en tant qu'ingénieurs des écosystèmes. L'objectif général de la thèse est d'évaluer et d'analyser les impacts des paysages agricoles sur les communautés d'ingénieurs des sols et les services écosystémiques fournis par le sol dans les Llanos colombiens. Trois questions principales ont été abordées: (1) Quel est l'impact de la gestion agricole sur les communautés de fourmis et est-il possible d'identifier des espèces de fourmis qui pourraient servir d'indicateurs des services écosystémiques basés sur le sol? (2) Quel est l'impact de l'usage des sols sur les communautés de fourmis et de termites et cet impact est-il lié aux modifications des propriétés physiques et chimiques des sols? (3) Les traits écologiques et morphologiques des fourmis répondent-ils aux usages du sol et aux propriétés du sol?

Les résultats de cette thèse confirment que les communautés de fourmis sont très sensibles aux changements d'usage de sols et constituent de bons indicateurs précoces des services écosystémiques basés sur les sols. Plus précisément, les cultures annuelles se sont révélées le plus préjudiciables aux communautés de fourmis et de termites, et cela est probablement dû à l'application d'intrants chimiques, ainsi qu'au travail du sol et aux pesticides. Tous les usages du sol (savanes, plantation de caoutchouc ou palmiers à huile, pâturages améliorés et cultures

annuelles) ont une faune particulière, mais certaines espèces ont des besoins particuliers en termes d'habitat pour leurs nids, leur nourriture, ou des refuges. Certaines espèces sont plus généralistes et particulièrement adaptées aux environnements perturbés. En ce sens, la présence de toutes les utilisations du sol dans un paysage contribue dans une certaine mesure à la diversité totale. On a constaté que les usages des sols avec une couverture arborée permettent le maintien d'espèces rares, discrètes et souvent avec exigences de habitat particulaires.

Chapter 1: General Introduction

1.1 General context

1.1.1 Importance of Soils and the ecosystem services they provide

Soils are dynamic and diverse natural systems composed by minerals, soil organic matter, living organism, gas and water. They are also considered as critical ecosystems service providers (Schoonover and Crim, 2015). To describe soils, pedologists have used different concepts such soil components and soil properties. A soil component is defined as a biogeochemical species (e.g. nitrate NO_3-) or an aggregation of biogeochemical species (e.g. clays, sand, and silt) that makes up soils. In general, soils are composed of four major categories of components: mineral, organic, liquids, and gases. Soil properties are the physical (e.g. porosity, texture), chemical (e.g. pH, readily available phosphate), and biological (e.g. microbial biomass) characteristics of soils and are often measurable quantities that allow soil scientists to classify soils (Dominati et al., 2010) (Figure 1).
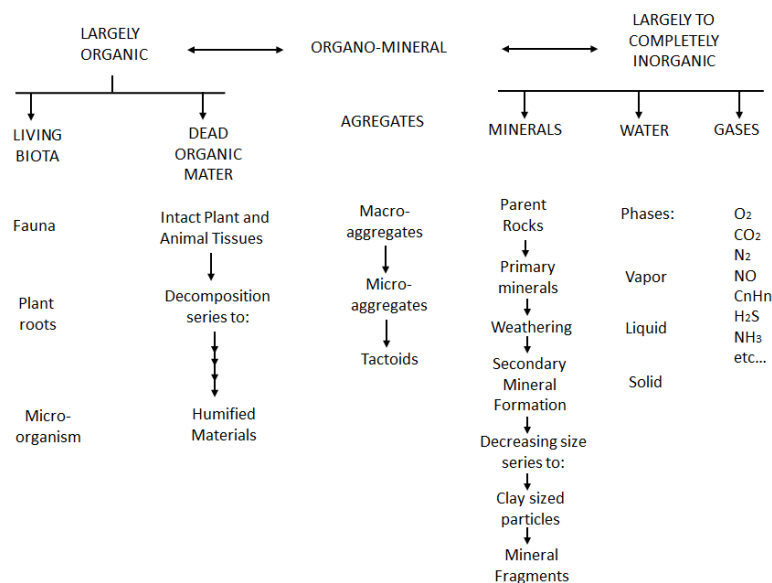
Figure 1. Ecological classification of soil components Source: (Lavelle and Spain, 2001)

In general, is known that soils drive life on earth. Therefore soil functioning affects global warming, carbon sequestration, the quantity and quality of fresh water, the productivity and

nutritional value of plants growing in soil, the success of invasive organisms, the health of bays and estuaries and the availability of new medicines for human health. Soils are key drivers of the global cycles of carbon, water, nitrogen, phosphorus and sulfur. They are considered to be one of the most diverse and least understood reservoirs of biodiversity in the biosphere (Decaëns et al., 2001; Lavelle and Spain, 2001). Threats to this biodiversity are a source of concern both for the intrinsic value of soil biodiversity and for the dependence of soil functioning and soil ecosystem services.

In soil science the term "ecosystem function" has been used as a synonym for "ecosystem process. Ecosystem functions are not directly beneficial for humans. Soil functioning is based on many functions: e.g. mineralization, nitrification, etc. (Wallace, 2007). The existing literature on ecosystem services tends to focus exclusively on the ecosystem services rather than holistically linking these services to the natural capital base from which they arise. To avoid this, ecosystem services are defined here as the beneficial flows arising from natural capital stocks and fulfilling human needs. For soil ecosystem services, the stock correspond to soil characteristics, e.g. soil structure or soil organic matter content, allowing soils to provide services. The argument is that ecosystem services are not processes but flows (amount per unit time), as opposed to stocks (amount) (Dominati et al., 2010). In that sense, ecosystem services have been defined as "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly" and grouped these functions into four primary categories: regulation, habitat, production and information functions. Some authors detailed goods and services (Constanza et al., 1997), functions (de Groot et al., 2010), have classified specific roles or services provided by natural systems that support economic activity (MEA, 2005)

Additionally, the Millennium Ecosystem Assessment (MEA, 2005) took up this idea in a "framework of ecosystem services". It assessed the consequences of ecosystem change for human well-being, defining ecosystem services as "the benefits people obtain from ecosystems" (MEA, 2005). It classified ecosystem services in four categories: provisioning, regulating, cultural and supporting services. The first three categories of services directly affect people, whereas the supporting services maintain the other services. The concept of ''ecosystem'' highlights the importance of interactions between elements of biodiversity—at a range of scales—and interactions between living species and the non-living environment.

Table 1. Type of services provided by soils (Source (Dominati et al., 2010)

Role	Description
Fertility	Soil nutrient cycles ensure fertility renewal and the delivery of nutrients to plants, therefore contributing to plant growth.
Filter and reservoir	Soils fix and store solutes passing through and therefore purify water. They also store water for plants to use and take part in flood mitigation.
Structural	Soils provide physical support to plants, animals and human infrastructures.
Climate regulation	Soils take part in climate regulation through carbon sequestration and greenhouse gases (N_2O and CH_4) emissions regulation.
Biodiversity conservation	Soils are a reservoir of biodiversity They provide habitat for thousands of species regulating for instance pest control or the disposal of wastes.
Resource	Soils can be a source of materials like peat and clay.

Soil ecosystem services depend at the local scale on the activities of soil organisms. These activities are very influential for most soil functions: mineralization, stabilization of organic matter, nitrogen cycling and creation of soil structure. This corresponds to the indirect value of

soil fauna (besides their intrinsic value as component of the biodiversity). Through these processes soil organisms support the provision of soil services and benefit humans through primary production, agricultural productivity and regulatory services including carbon sequestration and control of greenhouse gas fluxes. The direct value of soil animals should not be overlooked (Gullan and Cranston, 2014)

1.1.2. Importance of soil macrofauna for soil functioning

The term macrofauna refers to invertebrates larger than 2 mm, such as Oligochaeta, Termites, Isopoda, Hymenoptera, Chilopoda, Diplopoda, Isoptera, Coleoptera, Araneae, and Gastropoda (Lavelle and Spain, 2001; Rousseau et al., 2013). All groups of soil macrofauna influence soil functioning and some studies have used them as indicators of soil quality and disturbance (Baretta et al., 2014; Lobry de Bruyn, 1999; Rousseau et al., 2013).

Figure 2: Diverse groups of soil macrofauna (Photos from varied sources of Internet)

These organisms break up plant litter, mix soil, create soil aggregates (e.g. fecal pellets or casts), build galleries (creation of pores in the soil that increase gas exchange, water infiltration, nutrient movement, root penetration and dispersal of other soil biota spatial) and locally

concentrate organic matter and mineral nutrients. Soil fauna also stimulates the mineralization of organic matter at least partially through the stimulation of microorganism (Lal, 1988; Lavelle and Spain, 2001).

In particular, earthworms, termites and ants are very important components of soil macrofauna due there abundance, their diversity and the influence of their activities. Because they strongly influence the physical and chemical properties of soils they have been designated as ecosystem engineers (Jones CG, Lawton JH, 1994; Lavelle and Spain, 2001). They create long-lived biogenic structures (BS) with different physicochemical properties according to the species and the soil where they carry on their activities (Blanchart et al., 1997; Decaëns et al., 2001). This has detectable effects on habitat structure and constitutes an important source of soil heterogeneity with relevant consequences for soil functioning (Brussaard et al., 2007). It changes the composition and the structure of biological communities, especially through the introduction of exotic species, and exclusion of native species.

In tropical regions, soil macroinvertebrates play an important role in the provision of many ecosystem services through their action on soil processes (Fragoso and Lavelle, 1995; Lavelle et al., 1997). Some studies have used macrofauna as indicators of soil quality and disturbance (Marichal et al., 2014; Rousseau et al., 2013; Sanabria et al., 2016). They participate in the regulation of decomposition and nutrient cycling processes (Lavelle et al., 1997) and in the maintenance of soil physical properties suitable for plant growth (Blanchart et al., 1997). They modulate the mineralization rate of soil organic matter by selectively activating several functional groups of microflora in the soil, at distinct temporal and spatial scales (Lavelle et al., 1997). However, these processes highly depend on the composition of soil macrofauna and its diversity, and understanding the effects of human activities on these communities is therefore

of utmost importance. The relationship between biodiversity and ecosystem functioning has generated intensive research and controversy in recent years (Brussaard et al., 1997; Ekschmitt and Grif, 1998; Pinto et al., 2014). Other studies focus on the relationship between soil fauna diversity and primary productivity, the stability of primary productivity and nutrient cycling. Most of these studies focus on the influence of decomposer diversity largely neglecting how changes in predator diversity may affect ecosystem function. However, there are several ways in which changes in animal diversity could change trophic interactions and ecosystem functions (Duffy, 2002). The invertebrate assemblages of tropical savanna soils are especially species-rich (Vasconcelos et al., 2008), are functional diverse (Barrow and Parr, 2008) and have high value in conservation (Gonçalves-Alvim and Fernandes 2001, Silva and Bates 2002).

The decrease of soil macrofauna abundance and diversity is often observed. This can be explained by their vulnerability to disturbance, but may also result from changes to soil properties, especially soil chemistry, and/or from the removal or reduction of niche heterogeneity and from severe modifications of microclimates (Barros et al., 2002; Decaëns et al., 2001; Laossi et al., 2008). Examples of impacts on soil fauna are known for tillage, soil properties, microclimate, food availability and pesticide application, both in Colombia and elsewhere (Barros et al., 2003; Lavelle et al., 2014; Sanabria et al., 2016).

1.1.3. The role of termite communities

In particular, Termites (Isoptera) are arguably the most important soil ecosystem engineers (Bignell, 2006a) in tropics. Their functional domain is designated the termitosphere (Jouquet et al., 2011; Lavelle and Spain, 2001). In most lowland tropical habitats, where termites are especially abundant, the termitosphere comprises a large part of the soil column, challenged only by the functional domain of earthworms. Termites have the abilities to forage over long

distances and to partially control their own living environments through the creation of nest structures where the humidity and temperature remain constant throughout all seasons.

As soil engineers, termites play a key role in the functioning of many tropical and subtropical ecosystems, which contribute to the provision of many ecosystem services. Termites are amongst the main macroinvertebrate decomposers and exert additional impacts through the creation of biostructures (mounds, galleries, etc) with different soil physical and chemical properties. They influence the distribution of natural resources such as water, organic matter mineral nutrients in the landscape and consequently the diversity of soil microbes, plants and animals, which is a mark of their strong effect on the whole functioning of tropical ecosystems (Bignell 2006, Eggleton et al. 2008, Jouquet et al. 2011)

Figure 3. Diverse species of Termites found in this work.

1.1.4. The role of ant communities

Ants are classified in a single family, the Formicidae, within the order Hymenoptera, and are social insects (Hölldobler and Wilson 1990). They consist of more than 14,000 described species (AntBase, 2015). However, the number of species still remaining to be discovered and described is incredibly high (Hölldobler and Wilson, 1990) The imperfect classification of some ant groups (especially due to the presence of sibling species) complicates the assessment of

their biodiversity. The Neotropical and African areas have the greatest number of endemic ant genera. Despite this fact, ant taxonomy is still poorly studies in these areas (Hölldobler and Wilson, 1990). Among the insects, ants are an abundant group Ants, bees, wasps and termite comprise 75% of the total insect biomass (Hölldobler and Wilson, 1990).

Furthermore, several authors consider ants as soil ecosystem engineers. Through their nesting habits, ants are agents of bioturbation, mixing soil horizons and creating avenues for water and gas exchange through the tunnels and chambers that make up their nest architecture (Folgarait, 1998). These activities result in soil production and altering soil chemical, physical, and biotic profiles (de Bruyn and Conacher, 1990; Lavelle and Spain, 2001). Their movement of materials from above and below ground concentrates nutrients and minerals in the nest and associated soil. The above ground nest structure is engineered as well. By creating soil or other mound structures, the ants may change soil temperature and moisture profiles. Because of this soil engineering, the occurrence, abundance, and spatial pattern of soil organisms and therefore the soil community are significantly different in areas with ant nests and those without (Brussaard, 1997; Folgarait, 1998; Gotelli and Ellison, 2002).

Several ecological factors may influence ant diversity. Species may lack a preferred size, type, or species of nesting site (Armbrecht et al., 2004; Torres and Snelling, 1997) or particular species, size, or composition of shade tree necessary for nesting. Ants may also be affected by the type, the number, and the height of microhabitat, or food availability (Armbrecht et al., 2006; Philpott and Foster, 2009; Philpott et al., 2000) presumably related to microbial populations and food webs in litter (Kaspari et al., 2001). Ecological interactions that impact or have the potential to impact ant diversity include invasions of exotic ants (Holway et al., 2002), competitive exclusions by aggressive ant species frequently abundant in intensive agricultural

habitats, predation by army ants (Kaspari, 1996) predation by birds (Philpott et al., 2005). They may act as effective seed dispersers (i.e myrmecochory) (Douglas et al 1993, Rico-Gray and Oliveira 2007), pollinators, predator and are involved in various mutualisms (Blatrix et al., 2009), that have broad effects on the arthropod community affecting dynamics and interactions (Gotelli and Ellison, 2002; Holway et al., 2002).

The way and intensity of soil use can also change the richness and composition of ant communities. Thus, habitats with disturbed soils or with humidity or mineral concentration modified by farming or mining activities are likely to differ from undisturbed habitats with respect to ant species richness and composition. Moreover, environments at different succession stages can also host different ant communities (Andersen and Majer 2004, Osorio-Pérez et al. 2007, Schmidt and Diehl 2008, Schmidt et al. 2013).

Studies of ant communities in agroecosystems have contributed to the knowledge of the influence of agriculture activities on natural environments (Lobry de Bruyn, 1999; Schmidt et al., 2013) and also helped to identify ant species with potential for biological control in several types of crops (Castro and Queiroz., 1987). Ants have a high sensibility to environmental changes and are easily sampled (Silva and Brandao, 2010) making these insects useful to evaluate the impacts or changes of agriculture on natural environments, such as agroecosystem intensification (Andersen et al., 2002; De la Mora et al., 2013; Philpott et al., 2000).

Figure 4. Some species of ants found in this work. *Centromyrmex alfaroi*, *Neivamyrmex punctaticeps* and *Ectatomma tuberculatum* (Source Alex Wild© www.myrmecos.net)

1.1.4. Impacts of agriculture practices on soil fauna

Various anthropogenic activities create patchworks of modified land use types that exhibit similar patterns throughout the world. Thus, there is an urgent need to develop methods to recognize the effects of these activities on biodiversity and, where possible, to minimize adverse effects (Andersen et al., 2004). In that sense agriculture is considered as one of main agents of changes in biodiversity (Schmidt and Diehl, 2008).

The disruptive impact of agriculture in species richness and abundance may be caused by the reduction of canopy cover litter depth, and soil volume (Carvalho and Vasconcelos, 1999). Another serious consequence of agriculture expansion is forest fragmentation, which leads to several abiotic and biotic changes mainly due to area reduction and border extension of fragments. Fragmentation severely impacts the ecosystem by disrupting species richness and composition(Armbrecht and Perfecto, 2003), population and community dynamic, trophic interactions, and ecological processes (Laurance and Vasconcelos, 2009).

Another serious consequence of agriculture expansion is forest fragmentation, which leads to several abiotic and biotic changes mainly due to area reduction and border extension of fragments. Fragmentation severely impacts the ecosystem by disrupting species richness and composition (Armbrecht and Perfecto, 2003), population and community dynamic, trophic interactions, and ecological processes (Gascon et al., 1999; Marichal et al., 2014). Agroforestry, pasture agriculture, and crops have been shown to alter species composition and reduce species richness (Majer et al., 1997; Marinho et al., 2002; Vasconcelos, 1999).

Tillage in some form has been employed since the dawn of human agriculture. This prepares the soil for planting. However, depending on the practices employed, tillage can degrade the soil environment to a point where it may no longer support cropping systems (Lal, 1993). Important characteristics such as soil structure, resistance to wind and water erosion, cycles of water, nutrients and organic matter may be disrupted in a manner that is very difficult to rectify (Lal, 1993). This practice can cause rapid nutrient turnover, reduced water and oxygen availability, compaction, aggregate disruption, increased desiccation and exposure to UV (Franzluebbers, 2002; Pagliai et al., 2004). Despite the fact that tillage is used in part to increase soil porosity for root penetration, increases in porosity can be quite short-term as tilled soil is less structurally stable due to the reduction in organic matter and biological activity associated with it (Liiri et al. 2012). Additionally, the reduction in soil biodiversity associated with conventionally tilled systems leads to a reduction in biopores (tunnels and chambers) created by soil engineers such as earthworms, ants, termites and other invertebrates (Decaëns et al., 2001; Lavelle and Spain, 2001; Lavelle et al., 2014; Pagliai et al., 2004). These biopores are important to plant growth because they have a high degree of connectivity and allow for easy root penetration and water movement (Pagliai et al., 2004).

Pesticides are also one factor of impact. It is the most cost-effective means of pest and weed control allowing the maintenance of current yields and so contribute to economic viability. Concern about the environmental impact of repeated pesticide use has prompted research into the environmental fate of these agents, which can emigrate from treated fields to air, other land and water bodies. How long the pesticide remains in the soil depends on how strongly it is bound by soil components and how readily it is degraded. It also depends on the environmental conditions at the time of application, *e.g.*, soil water content. Pesticide use must ensure public

safety and environmental protection with regards to both the chemical itself and their potentially harmful metabolites (Arias-Estévez et al., 2008).

1.2. The case of Colombian Llanos

The Llanos or Altillanura Plana of Colombia, extends northeast from the Meta Department to the Venezuelan border and is bounded to the north by the Andean Cordillera Oriental. Atroughly 200 m in elevation, climate is characterized by distinct wet and dry seasons, with very little rainfall between December and March and average annual temperatures around 26∘C. Soils are mainly Oxisols with low fertility and high acidity and Al saturation (IGAG, 2004; Lascano and Estrada, 1989).

Although it was not possible to get clear information on the age and history of the cultivated plots, some general information could be collected. Humans have long impacted the original savanna with a clear management intensity gradient from Carimagua, where the most preserved savannas with rather dense tree cover could be found, to Puerto Lopez where all trees had been eliminated and grazing pressure was high. Improved pastures were rather heterogeneous, since the oldest ones may have been installed some 10–15 yr ago and are degraded with relatively high densities of weeds and heavily compacted soils. Transitory crops are always recently implemented systems since cropping is usually maintained for a few cycles, during 2–4 yr before perennial tree crops are installed. Rubber and oil palm had been installed 3–10 yr prior to samp.ling in all cases. While these systems are typically installed in fields following annual crops, some rubber plots in Carimagua had been directly converted from savanna (Baptiste, 2006; Lavelle et al., 2014).
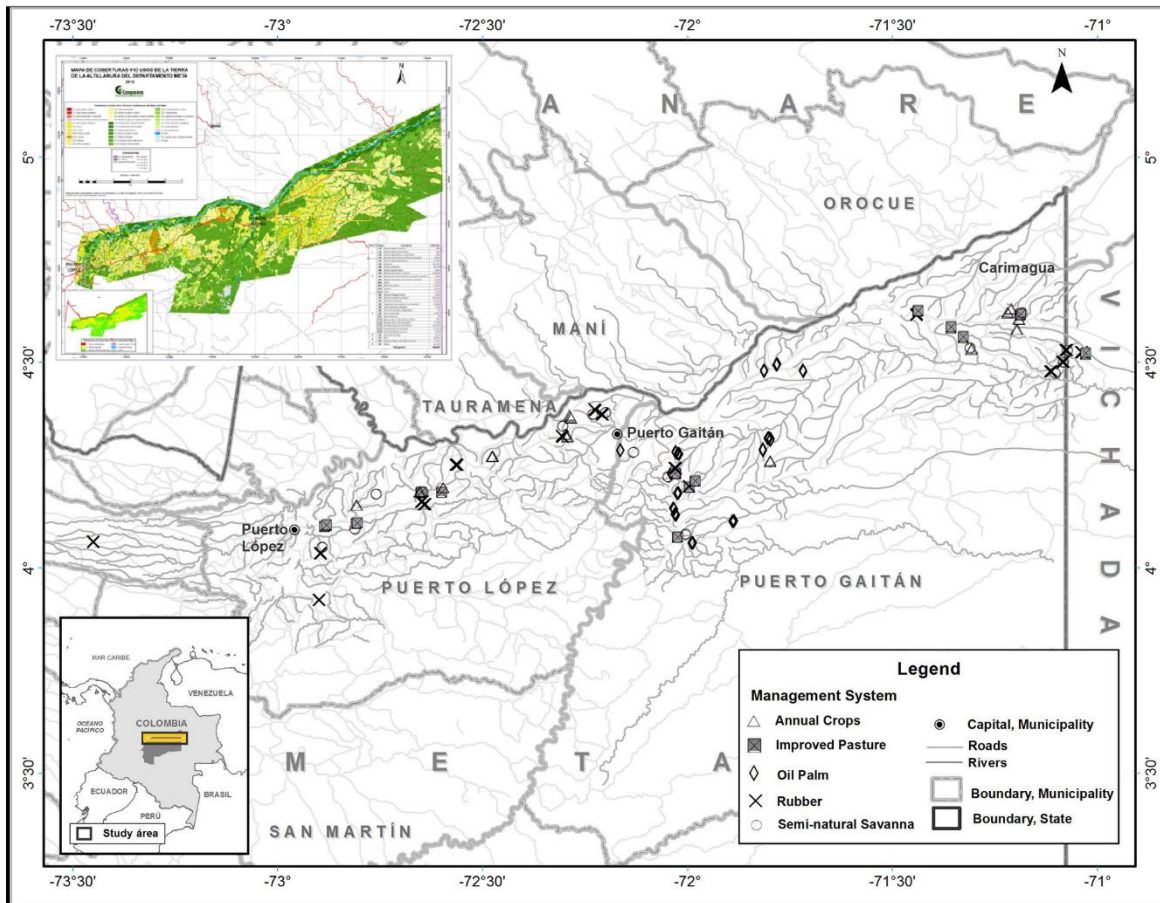
Figure 5. Map of location of the 75 plots and associated land cover/land uses of the Meta department - Colombia. (Source : (Rodriguez 2011, Sanabria et al. 2014)

Politically, the Llanos region has been transformed from a neglected frontier into a zone of primary national significance and high hopes have been placed on the region to provide future economic growth. Recent investment in the region has focused on large-scale agricultural intensification involving the conversion of semi-natural savanna to annual crops of rice, maize and soybean, perennial crops such as oil palm and rubber, and improved pastures (typically sown with *Brachiaria* species and fertilized every few years). This conversion usually involves high inputs of fertilizer and lime combined with deep and rather intensive tillage. Such intensification has generated much concern, as soils and ecosystems of the region are generally fragile and comprise a patchwork of agricultural land uses mixed with semi-natural savanna

and riparian forests. These types of vegetation are both critical landscape components for the regulation of regional water quality and biodiversity (Baptiste, 2006; Lavelle et al., 2014).

Figure 6. Panoramic of the Llanos Region at the municipality of Puerto Lopez (Meta-Colombia). Source Ciat Flickr (www.flickr.com/photos/ciat).

The soils of the Llanos were developed on a thick mantle of clay-muddy alluvial sediments from the eastern Andean cordillera. They have typical characteristics of a formation due to conditions of high and continuous temperature, to excess humidity in rainy season, high concentration of Iron (Fe) and Aluminum (Al) oxides that provide them certain characteristics of acid soils. They are susceptible to degradation: they often lose some of their physical, chemical and biological properties because of an inadequate human intervention, which decreases soil fertility and threaten agricultural sustainability (Rippstein et al., 2001).

Tropical savannas are dynamic, highly productive and biodiverse ecosystems (Andersen et al., 2004; Grace et al., 2007; Melo et al., 2013), comprising heterogeneous mosaics of grass dominated vegetation types and a sparse and discontinuous stratum of trees or shrubs.

Significant turnover in species and communities occur at both local and regional scales (Marques and Schoereder, 2014).

The Colombian savannas cover approximately 15% of the total land area and are considered as the second largest savanna system with approximately 17 million hectares (Rippstein et al., 2001). Since the early twentieth century Colombian savannas were used in a traditional way to produce goods and services for local communities by fishing, hunting and harvesting activities (Etter et al., 2006). The need to increase agricultural production for food and energy resources is driving agricultural frontiers into the last remaining arable lands (Hubert et al., 2010). In the 80s diverse changes occurred through the establishment of large-scale intensive agriculture and it is estimated that over 50,000 ha has been converted in the last 20 years. This has turned the region into one of the most threatened ecosystems in Colombia (Romero-Ruiz et al., 2012).The whole process has been reinforced by the clear intention of the Colombian government to ensure the agricultural development of the Llanos (Rippstein et al., 2001).

This region is rapidly being converted from semi-natural systems, dedicated largely to extensive cattle ranching (Baptiste, 2006; Romero et al., 2009; Romero-Ruiz et al., 2012), and low-input traditional agriculture, to highly intensified commercial production of annual crops (rice, soybean, maize), biofuels (sugar cane and oil palm) and tree crops such as rubber. Intensive exploitation affects the integrity of biodiversity and changes the structure of biological communities (Altieri and Nicholls, 2003). Even if these ecosystems have a critical importance for agricultural production they have received limited conservation attention in comparison to the better known ecosystems such as the Amazon and Andes forests (Ribas et al., 2003). Actually, a wide range of factors are impacting the functioning of natural ecosystems of the region: overall expansion of road infrastructure, petroleum activities, mining, monocultures and illicit crops, expansion of the agriculture frontier (Baptiste, 2006). All these factors influence

the functioning of soil and impact their biodiversity. For example, the structure and dynamics of insect communities (Baptiste, 2006) and, in particular, ant communities are impacted by agriculture intensification (De la Mora et al., 2013; Lach et al., 2010; Philpott et al., 2006).
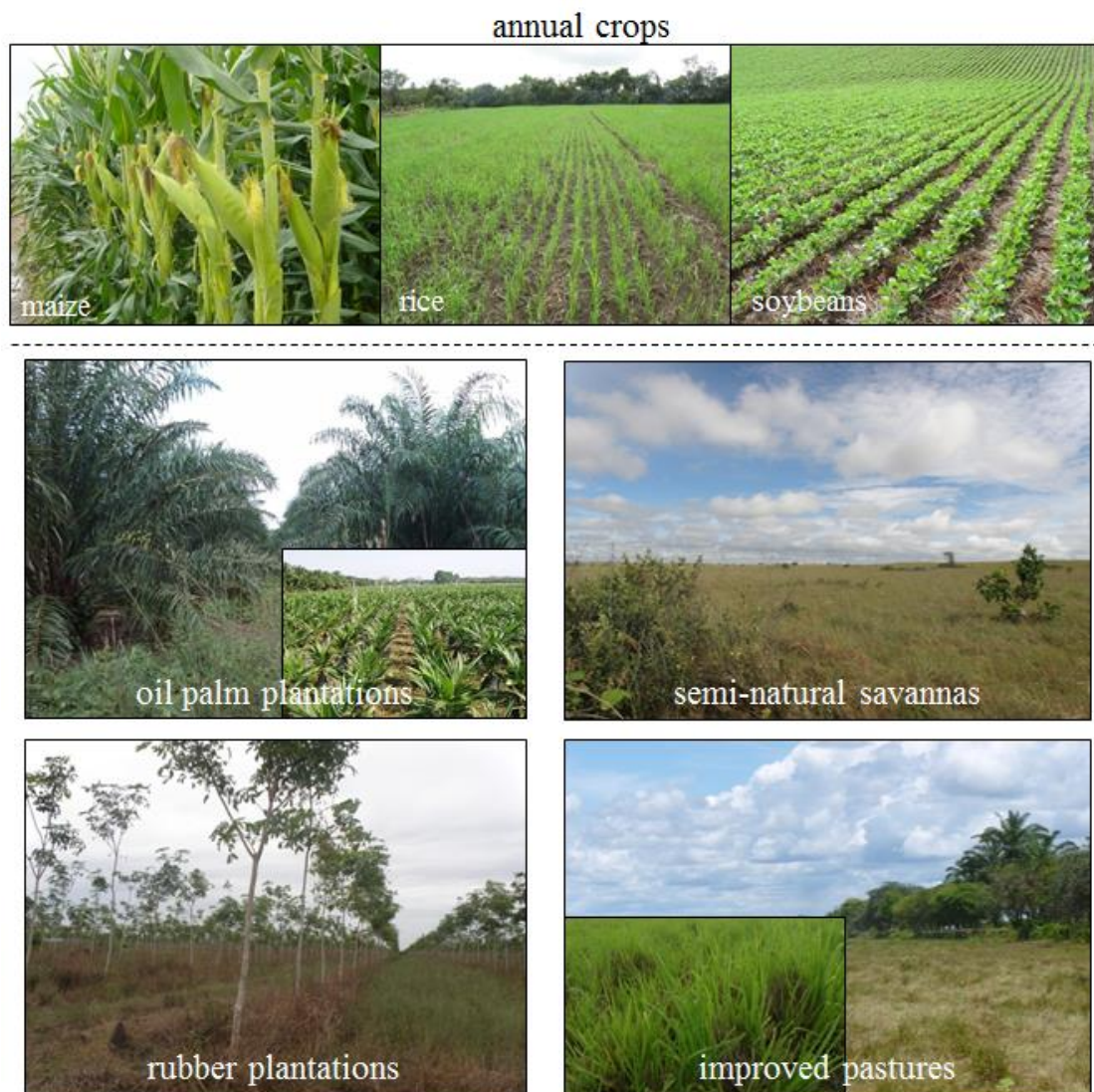
Figure 7. Types of land uses sampled in the Llanos region.

1.3. Structure of the thesis and goals

This thesis is based on data from the project: "Indicators of efficiency in the use of biophysical, socioeconomic and environmental resources (Eco-Efficiency) of productive systems of the Altillanura plana Orinocense" carried on in Colombia between 2011 and 2012. The principal aim of that project was assessing to the impact of the soil perturbation on biodiversity, ecosystem services and other elements of the natural capital using them as a tool for designing sustainable management options in the region.

To address this goal, soil macro invertebrate communities and soil-based ecosystem services (climate regulation, hydrologic functions, soil stability provided by macro aggregation and nutrient provision potential) were evaluated in four major production systems: improved pastures, annual crops (rice, corn and soy bean), oil palm and rubber plantations, and compared them to the semi natural savanna. In total fifteen plots of each system were sampled, in 2011, along a 200 km natural gradient of soil and climatic conditions. In each plot, climate regulation by measuring greenhouse gas emissions (N_2O, CH_4 and CO_2) and C storage in above ground plant biomass and soil (0–20 cm) were assessed. Soil biodiversity (macro invertebrate communities, with particular detail on ants and termites) and three other soil-based ecosystem services, were assessed using sets of 12–20 relevant variables associated with each service and synthesized via multivariate analyses into a single indicator for each ecosystem function (See: (Lavelle et al., 2014; Sanabria et al., 2014)

The general goal of the thesis is to evaluate and analyze the impacts of agricultural landscapes on soil engineer communities and soil ecosystem services in the Colombian Llanos. The thesis is composed of three chapters written as articles for international scientific journals. The two first chapters have already been published. The third one has been submitted.

Chapter 2. **Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos** (*Published in Applied Soil Ecology 84 (2014) 24–30*). In this chapter we start from the fact that ants are a group sensitive to land management and serve as important regulators of key soil processes and we sought to understand the impacts of agricultural management on ant communities in the eastern Colombia and to identify species that could be used as indicators of soil-based ecosystem services. As expected, land management was found to greatly influence ant communities. Improved pastures showed the highest species richness and semi-natural savanna the greatest abundance of ants. Within each of these fields a suite of soil and agroecosystem characteristics were measured and combined into synthetic indicators of five soil-based ecosystem services (nutrient provision, water storage and regulation, maintenance of soil structure, climate regulation services and soil biodiversity and biological activity). Ant species were then associated with these synthetic indicators using the IndVal method to identify indicator species for each of the five consolidated ecosystem services measured. Fourteen indicator species were identified and found to be significantly associated with either the high or low provision of each of the five services.

Chapter 3. Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos (*Published in European Journal of Soil Biology 74 (2016) 81-92*). In this chapter the aim was to evaluate the impact of land use on ant and termite communities in Colombian savanna landscapes, and to assess whether this impact is associated with the modification of soil physical and chemical properties. The multivariate analysis used revealed that termite communities significantly differed among land uses, but not between regions. We also found that ant communities differed between regions and land uses. The between group analyses determined that termite communities are distributed in three groups of land use: one formed by semi-natural savannas and improved

pastures, the second by oil palm plantations and annual crops and the third by rubber plantations. Through general linear models applied separately to each species we found 19 significant associations of soil physical or chemical properties, land uses or regions with 15 ant species and 14 significant associations with 6 termite species. The strong association between land use and ant or termite communities is likely due to changes in ant and termite habitats resulting from agricultural practices such as tillage, fertilization, and lime addition. These results suggest that annual crops are the most detrimental land use for termites and ants, because their communities are highly sensitive to vegetation cover and agricultural practices such as tillage.

Chapter 4. Do the traits respond to agricultural changes? The case of ground dwelling ants in Colombian Llanos (*Sanabria C., Barot S., Fonte S., Lavelle P. and Dubs F., 2016 in preparation*). Despite many methods to predict the impacts of agricultural activities on biodiversity have been developed, predictions are generally restricted to species that have been thoroughly studied. The trait approach could allow overcoming this problem. Knowledge on the trait of species can be used to analyze the impact of land use changes on communities and find general rules that could allow predicting these impacts. In five land uses (annual crops rubber plantations, oil palm plantations, improved pastures and semi-natural savannas) from the region of the Colombian Llanos we have tested the existence of a relation between morphological and ecological traits of ants, and whether those traits respond to soil properties and land uses. We found a correlation between morphological and ecological traits. A RLQ analysis showed a significant common structure among species distribution, environmental factors, and species attributes with ecological traits but not with morphological traits. This analysis allowed to distinguish a gradient of tree cover, from annual crops and improved pastures to rubber plantations and semi-natural savannas. Land uses with trees are associated to

ants with specialized diets and linked to nest localization. Taken together ecological traits can be used to predict the structure of ant communities along a tree cover gradients.

1.4 References

Altieri, M.A., Nicholls, C.I., 2003. Soil fertility management and insect pests: Harmonizing soil and plant health in agroecosystems. Soil Tillage Res. 72, 203–211. doi:10.1016/S0167-1987(03)00089-8

Andersen, A.N., Fisher, A., Hoffmann, B.D., Read, J.L., 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecol. 29, 87–92.

Andersen, A.N., Hoffmann, B.D., Müller, W.J., Anthony, D., Mullert, W.J., Griffiths, A.D., 2002. Using ants as bioindicators in land management : simplifying assessment of ant community responses 39, 8–17.

Andersen, A.N., Majer, J.D., 2004. Ants show the way Down Under: Invertebrates as Bioindicators in Land Management. Front. Ecol. Environ. 2, 291–298.

AntBase, 2015. AntBase [WWW Document]. www.antbase.org.

Arias-Estévez, M., López-Periago, E., Martínez-Carballo, E., Simal-Gándara, J., Mejuto, J.C., García-Río, L., 2008. The mobility and degradation of pesticides in soils and the pollution of groundwater resources. Agric. Ecosyst. Environ. 123, 247–260. doi:10.1016/j.agee.2007.07.011

Armbrecht, I., Perfecto, I., 2003. Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agric. Ecosyst. Environ. 97, 107–115. doi:10.1016/S0167-8809(03)00128-2

Armbrecht, I., Perfecto, I., Silverman, E., 2006. Limitation of nesting resources for ants in Colombian forests and coffee plantations. Ecol. Entomol. 31, 403–410. doi:10.1111/j.1365-2311.2006.00802.x

Armbrecht, I., Perfecto, I., Vandermeer, J., 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science 304, 284–6. doi:10.1126/science.1094981

Baptiste, G., 2006. Utilizar., in: H. Correa, S. L. Ruiz, & L. M. Arevalo (Eds.), Plan de Accion En Biodiversidad de La Cuenca Del Orinoco, Colombia. Instituto de Investigacions en Recursos Biologicos Alexander von Humboldt., Bogota, Colombia, p. 330.

Baretta, D., Luise, M., Bartz, C., Fachini, I., Anselmi, R., Zortéa, T., Duarte, C.R., Baretta, M., 2014. Soil fauna and its relation with environmental variables in soil management systems Fauna edáfica e sua relação com variáveis ambientais em sistemas de manejo do solo. Rev. Ciência Agronômica 45, 871–879. doi:10.1590/S1806-66902014000500002

Barros, E., Neves, A., Blanchart, E., Fernandes, E.C.M., Wandelli, E., Lavelle, P., 2003. Development of the soil macrofauna community under silvopastoral and agrosilvicultural systems in Amazonia. Pedobiologia (Jena). 47, 273–280.

Barros, E., Pashanasi, B., Constantino, Reginaldo; Lavelle, P., 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biol Fertil Soils 35, 338–347. doi:10.1007/s00374-002-0479-z

Barrow, L., Parr, C.L., 2008. A preliminary investigation of temporal patterns in semiarid ant communities: Variation with habitat type. Austral Ecol. 33, 653–662. doi:10.1111/j.1442-9993.2008.01832.x

Bignell, D.E., 2006a. as Soil Engineers 8 Termites and Soil Processors 6.

Bignell, D.E., 2006b. Termites as Soil Engineers and Soil Processors, in: Soil Biology. pp. 183–219. doi:10.1007/3-540-28185-1_8

Blanchart, E., Lavelle, P., Braudeau, E., Le Bissonnais, Y., Valentin, C., 1997. Regulation of soil structure by geophagous earthworm activities in humid savannas of Cote d'Ivoire. Soil Biol. Biochem. 29, 431–439. doi:10.1016/S0038-0717(96)00042-9

Blatrix, R., Bouamer, S., Morand, S., Selosse, M.-A., 2009. Ant-plant mutualisms should be viewed as symbiotic communities. Plant Signal. Behav. 4, 554–556. doi:10.1111/j.1469-8137.2009.02793.x

Brussaard, L., 1997. Biodiversity and Ecosystem Functioning in Soil. Ambio 26, 563–570.

Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., C. Fragoso, D.W. Freckman, V.S.R.V., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Ruseck, J., Söderström, B., Tiedje, J.M., Virginia., R.A., 1997. Biodiversity and ecosystem function in soil. Ambio 26, 563–570.

Brussaard, L., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233–244. doi:10.1016/j.agee.2006.12.013

Carvalho, S.K., Vasconcelos, L.H., 1999. Forest fragmentation in central Amazonia and its eff€ ects on litter-dwelling ants. Biol. Conserv. 91, 151–157. doi:10.1016/S0006-3207(99)00079-8

Castro, A.G., Queiroz., M.V.B., 1987. Estrutura e organização de uma comunidade de formigas em agroecossistema neotropical. Ann. Soc. Entomol. Bras. 16, 363–375.

Constanza, R., d'Arge, R., de Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, Jo., Raskin, R., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

De Bruyn, L.L.A., Conacher, A.J., 1990. The role of termites and ants in soil modification - a review. Soil Res. 28, 55–93.

De Groot, R.S., Alkemade, R., Braat, L., Hein, L., Willemen, L., 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecol. Complex. 7, 260–272. doi:10.1016/j.ecocom.2009.10.006

De la Mora, a., Murnen, C.J., Philpott, S.M., 2013. Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. Biodivers. Conserv. 22, 871–888. doi:10.1007/s10531-013-0454-z

Decaëns, T., Lavelle, P., Jiménez, J.J., Escobar, G., Rippstein, G., Schneidmadl, J., Sanz, J.I., Hoyos, P., Thomas, R.J., 2001. Impact of land management on soil macrofauna in the Eastern savannas of Colombia, in: Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia. Ciat, Cali-Colombia, pp. 19–41.

Dominati, E., Patterson, M., Mackay, A., 2010. A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecol. Econ. 69, 1858 − 1868.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99, 201−219. doi:10.1034/j.1600-0706.2002.990201.x

Eggleton, P., Bignell, D.E., Hauser, S., Dibog, L., Norgrove, L., Madong, B., 2008. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa 90, 189–202.

Ekschmitt, K., Grif, B.S., 1998. Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment 10, 201–215.

Etter, A., McAlpine, C., Wilson, K., Phinn, S., Possingham, H., 2006. Regional patterns of agricultural land use and deforestation in Colombia. Agric. Ecosyst. Environ. 114, 369–386. doi:10.1016/j.agee.2005.11.013

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning : a review. Biodivers. Conserv. 1244, 1221–1244.

Fragoso, C., Lavelle, P., 1995. Are earthworms important in the decomposition of tropical litter? Soil Org. litter Decompos. Trop. 103–112.

Franzluebbers, a. J., 2002. Soil organic matter stratification ratio as an indicator of soil quality. Soil Tillage Res. 95–106 66, 2002. doi:10.1016/S0167-1987(02)00018-1

Gascon, C., Lovejoy, T.E., Jr, R.O.B., Malcolm, J.R., Stou, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., 1999. Matrix habitat and species richness in tropical forest remnants 91, 223–229.

Gonçalves-Alvim, S.J., Fernandes, G.W., 2001. Biodiversity of galling insects: Historical, community and habitat effects in four neotropical savannas. Biodivers. Conserv. 10, 79–98. doi:10.1023/A:1016602213305

Gotelli, N.J., Ellison, A.M., 2002. Assembly rules for New England ant assemblages 3, 591–599.

Grace, J.B., Anderson, T.M., Smith, M.D., Seabloom, E., Andelman, S.J., Meche, G., Weiher, E., Allain, L.K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M., Willig, M.R., 2007. Does species diversity limit productivity in natural grassland communities? Ecol. Lett. 10, 680–689. doi:10.1111/j.1461-0248.2007.01058.x

Gullan, J., Cranston, P.S., 2014. The Insects: An Outline of Entomology. Wiley-Blackwell.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Belknap Press.

Holway, D. a., Lach, L., Suarez, A. V., Tsutsui, N.D., Case, T.J., 2002. the Causes and Consequences of Ant Invasions. Annu. Rev. Ecol. Syst 33, 181–233. doi:10.1146/annurev.ecolsys.33.010802.150444

Hubert, B., Rosegrant, M., van Boekel, M.A.J.S., Ortiz, R.., 2010. The Future of Food: Scenarios for 2050. Crop Sci. 50, S33–S50.

IGAG, 2004. Mapa de suelos de la Altillanura de los Llanos Orientales de Colombia.

J, D., Levey, B., Margaret M, 1993. Complex Ant-Plant Interactions : Rain-Forest Ants as Secondary Dispersers and Post- Dispersal Seed Predators. Ecology 74, 1802–1812.

Jones CG, Lawton JH, S.M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., Bignell, D., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. 47, 215–222. doi:10.1016/j.ejsobi.2011.05.005

Kaspari, M., 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76, 443–454.

Kaspari, M., Pickering, J., Longino, J., Windsor, D., 2001. The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. Behav. Ecol. Sociobiol. 50, 382–390. doi:10.1007/s002650100378

Lach, L., Parr, C.L., Abbott, K.L., 2010. Ant Ecology.

Lal, R., 1993. Tillage effects on soil degradation, soil resilience, soil quality, soil quality and sustainability. Soil Tillage Res. 27, 1–8.

Lal, R., 1988. Effects of Macrofauna on Soil Properties in Tropical Ecosystems. Agric. Ecosyst. Environ. 24, 101–116.

Laossi, K.-R., Barot, S., Carvalho, D., Desjardins, T., Lavelle, P., Martins, M., Mitja, D., Carolina Rendeiro, A., Rousseau, G., Sarrazin, M., Velasquez, E., Grimaldi, M., 2008. Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures. Pedobiologia (Jena). 51, 397–407. doi:10.1016/j.pedobi.2007.11.001

Lascano, C.L., Estrada, J., 1989. Long-term productivity of legume based and pure grass pastures in the Eastern Plains of Colombia., in: Proceedings of the XVI International Grassland Congress. pp. 1179–1180.

Laurance, W.F., Vasconcelos, H.L., 2009. Consequências ecológicas da fragmentação florestal na amazônia. Oecologia Bras. 13, 434–451. doi:10.4257/oeco.2009.1303.03

Lavelle, P., Bignell, D., Lepage, M., Wolters, W., Roger, P., Ineson, P., Heal, O.W., Dhillion, S., 1997. Soil function in a changing world : the role of invertebrate ecosystem engineers. Eur. J. Soil Biol. 33, 159–193.

Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M.D.P., Loaiza, S., Pullido, S.X., Rodríguez, E., Sanabria, C., Velásquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. Agric. Ecosyst. Environ. 185, 106–117. doi:10.1016/j.agee.2013.12.020

Lavelle, P., Spain, A. V., 2001. Soil ecology.

Lobry de Bruyn, L.A., 1999. Ants as bioindicators of soil function in rural environments. Agric. Ecosyst. Environ. 74, 425–441. doi:10.1016/S0167-8809(99)00047-X

Majer, J.D., Delabie, J.H.C., McKenzie, N.L., 1997. Ant litter fauna of forest, forest edges and adjacent grassland in the Atlantic rain forest region of Bahia, Brazil. Insectes Soc. 44, 255–266. doi:10.1007/s000400050046

Marichal, R., Grimaldi, M., Feijoo M., A., Oszwald, J., Praxedes, C., Ruiz Cobo, D.H., del Pilar Hurtado, M., Desjardins, T., Silva Junior, M.L. Da, Silva Costa, L.G. Da, Miranda, I.S., Delgado Oliveira, M.N., Brown, G.G., Tsélouiko, S., Martins, M.B., Decaëns, T., Velasquez, E., Lavelle, P., 2014. Soil macroinvertebrate communities and ecosystem services in deforested landscapes of Amazonia. Appl. Soil Ecol. 83, 177–185. doi:10.1016/j.apsoil.2014.05.006

Marinho, C.G.S., Zanetti, R., Delabie, J.H.C., Schlindwein, M.N., Ramos, L.S., 2002. Diversidade de Formigas (Hymenoptera : Formicidae) da Serapilheira em Eucaliptais (Myrtaceae) e Área de Cerrado de Minas Gerais. Neotrop. Entomol. 31, 187–195. doi:10.1590/S1519-566X2002000200004

Marques, T., Schoereder, J.H., 2014. Ant diversity partitioning across spatial scales: Ecological processes and implications for conserving Tropical Dry Forests. Austral Ecol. 39, 72–82. doi:10.1111/aec.12046

MEA, 2005. Millenium Ecosystem Assessment) Ecosystems and Human Well- being: Synthesis. Island Press, Washington, DC. Naidoo.

Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. Trends Ecol. Evol. 28, 461–468. doi:10.1016/j.tree.2013.01.001

Osorio-Pérez, M.F., Barberena-Arias, Aide, T.M., 2007. Changes in Ant Species Richness and Composition During Plant Secondary Succession in Puerto Rico. Caribb. J. Sci. 43, 244–253.

Pagliai, M., Vignozzi, N., Pellegrini, S., 2004. Soil structure and the effect of management practices. Soil Tillage Res. 79, 131–143. doi:10.1016/j.still.2004.07.002

Philpott, S.M., Foster, P.F., 2009. Nest-Site Limitation in Coffee Agroecosystems : Artificial Nests Maintain Diversity of Arboreal Ants Published by : Ecological Society of America NEST-SITE LIMITATION IN COFFEE AGROECOSYSTEMS : 15, 1478–1485.

Philpott, S.M., Greenberg, R., Bichier, P., 2005. The Influence of Ants on the Foraging Behavior of Birds in an Agroforest 1 37, 468–471.

Philpott, S.M., Perfecto, I., Armbrecht, I., Parr, C.L., 2000. Ant Diversity and Function in Disturbed and Changing Habitats, in: Ant Ecology. pp. 137–156.

Philpott, S.M., Perfecto, I., Vandermeer, J., 2006. Effects of Management Intensity and Season on Arboreal Ant Diversity and Abundance in Coffee Agroecosystems. Biodivers. Conserv. 15, 139–155. doi:10.1007/s10531-004-4247-2

Pinto, R., Jonge, V.N. De, Carlos, J., 2014. Linking biodiversity indicators , ecosystem functioning , provision of services and human well-being in estuarine systems : Application of a conceptual framework. Ecol. Indic. 36, 644–655. doi:10.1016/j.ecolind.2013.09.015

Ribas, C.R., Schoereder, J.H., Pic, M., Soares, S.M., 2003. Tree heterogeneity , resource availability , and larger scale processes regulating arboreal ant species richness 305–314.

Rico-Gray, V., Oliveira, P.S., 2007. The Ecology and Evolution of Ant-Plant Interactions. University of Chicago Press.

Rippstein, G., Escobar, G., Motta, F., 2001. Agroecologia y Biodiversidad de las Sabanas en los Llanos Orientales de COlobia. Publicacion CIAT, Cali-Colombia.

Rodriguez, A.F., 2011. Metodología para detectar cambios en el uso de la tierra utilizando los principios de la clasificación orientada a objetos , estudio de caso piedemonte de Villavicencio , Meta. Universida Nac. Colomb.

Romero, M.H., Maldonado-Ocampo, J.A., Usma, J.S., Umaña-Villaveces, A.M., Murillo, J.I., Restrepo-Calle, S., Alvarez, M., Palacios-Lozano, M.T., Valvuena, M.S., Mejia, S.L., Aldana-Dominguez, J., Payan, E., 2009. Informe sobre el estado de la biodiversidad en Colombia 2007-2008: Piedemonte orinoquense, sabanas y bosques asociados al norte del río Guaviare. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Romero-Ruiz, M.H., Flantua, S.G.A., Tansey, K., Berrio, J.C., 2012. Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. Appl. Geogr. 32, 766–776. doi:10.1016/j.apgeog.2011.08.010

Rousseau, L., Fonte, S.J., Téllez, O., van der Hoek, R., Lavelle, P., 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. Ecol. Indic. 27, 71–82. doi:10.1016/j.ecolind.2012.11.020

Sanabria, C., Dubs, F., Lavelle, P., Fonte, S.J., Barot, S., 2016. Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. Eur. J. Soil Biol. 74, 81–92. doi:10.1016/j.ejsobi.2016.03.008

Sanabria, C., Lavelle, P., Fonte, S.J., 2014. Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos. Appl. Soil Ecol. 84, 24–30. doi:10.1016/j.apsoil.2014.07.001

Schmidt, F., Diehl, E., 2008. What is the Effect of Soil Use on Ant Communities? Neotrop. Entomol. 381–388.

Schmidt, F.A.., Ribas, C.R., Schoereder, J.H., 2013. How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. Ecol. Indic. 24, 158–166. doi:10.1016/j.ecolind.2012.05.031

Schoonover, J.E., Crim, J.F., 2015. An Introduction to Soil Concepts and the Role of Soils in Watershed Management. J. Contemp. Water Res. Educ. 154, 21–47. doi:10.1111/j.1936-704X.2015.03186.x

Silva, J.M., Bates, J., 2002. Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot. Bioscience 52, 225–234.

Silva, R., Brandao, C.R., 2010. Morphological patterns and community organization in leaf-litter ant assemblages. Ecol. Monograpohs 80, 107–124.

Torres, J. a, Snelling, R.R., 1997. Biogeography of Puerto Rican ants: a non-equilibrium case? Biodivers. Conserv. 6, 1103–1121. doi:10.1023/a:1018332117719

Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia.

Vasconcelos, H.L., Leite, M.F., Vilhena, J.M.S., Lima, A.P., Magnusson, W.E., 2008. Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecol. 33, 221–231. doi:10.1111/j.1442-9993.2007.01811.x

Wallace, K.J., 2007. Classification of ecosystem services: Problems and solutions. Biol. Conserv. 139, 235–246. doi:10.1016/j.biocon.2007.07.015

Chapter 2: Ants as indicators of soil-based Ecosystem Services

Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos

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2.1 Introduction

Tropical savannas cover approximately 15% of the total land area in South America (Rippstein et al, 2001) and are of critical importance for agricultural production and a range of other ecosystems services in the region. In Colombia, these savannas occupy much of the eastern plains (locally referred to as the Llanos Orientales), a rapidly developing part of the Orinoco River Basin that has been traditionally managed under extensive livestock and low-input agriculture. Recent investment in the region has focused on large-scale agricultural intensification involving the conversion of semi-natural savanna to annual crops of rice, maize and soy bean, perennial crops such as oil palm and rubber, and improved pastures (typically sown with Brachiaria species and fertilized every few years). This conversion usually involves high inputs of fertilizer and lime combined with deep and rather intensive tillage. Such intensification has generated much concern, as soils and ecosystems of the region are generally fragile and comprise a patchwork of agricultural land uses mixed with semi-natural savanna and riparian forests, both critical landscape components in regulating regional water quality and biodiversity (Goosen, 1971; Correa et al., 2005; Lavelle et al., 2014).

Soils are involved in the provision of many ecosystem services that are of great importance for the maintenance of ecosystem functioning and human societies, with farmers primarily

responsible for the management of this resource (Millenium Ecosytem Assessment, 2005; Wall et al., 2012). Soils are also considered a large reservoir of biodiversity that has received less attention relative to above ground communities (Brussaard et al., 1997). Deforestation and the conversion of natural systems to intensified agriculture can have devastating impacts on both above- and below ground biodiversity (Lawton et al., 1998; Lavelle and Lapied, 2003). This biodiversity is highly vulnerable to management changes, but also critical to maintaining key ecosystem functions and contributing to the long-term sustainability of agroecosystems (Wall et al., 2012).

Soil macrofauna, in particular, represent an important part of agroecosystem biodiversity and some groups have received considerable attention as ecosystem engineers that fundamentally influence the nature and functioning of soils they inhabit (Lavelle et al., 2006). Past research indicates that the loss of soil macroinvertebrate diversity degrades soil structure and dismisshes nutrient cycling (Blanchart et al., 1997; Velasquez et al., 2012). Ants, in particular, fulfill key roles in the maintenance of energy and material flow in soils. Among the many functions performed by ants is a constant rearrangement of soil particles, favoring the movement of organic matter and more rapid mineralization of litter and organic residues (Folgarait, 1998; Wagner et al., 2004). Ants also contribute to improving soil aggregation and aeration by creating macropores and subterranean galleries constructed with a mixture of organic matter and mineral soil, formed into biogenic structures. Ants have also been shown to modify soil chemical processes via modifications of pH (Hölldobler and Wilson, 1990; Lafleur et al., 2005; Frouz and Jilková, 2008) and enhancement of microbial activity (Dauber et al., 2001). In addition to their fundamental role as ecosystem engineers, ants have been proposed as valuable indicators of soil quality (Lobry de Bruyn, 1999; Paoletti, 1999), since they are involved in many belowground functions, are highly sensitive to changes in management, and respond quickly and consistently to environmental alterations (Philpott et al., 2010).

The aim of this study was to identify indicator species for key soil-based ecosystem services and evaluate the impact of land use on soil-dwelling ant communities in the Llanos region of Colombia. This represents a strategic objective since farmers have little access to many of the costly and complex scientific techniques for measuring ecosystem services, nevertheless generally possess considerable knowledge of plants and invertebrates that occur in their fields (Rousseau et al., 2013). Indicator species identified by scientists and validated by farmers (with support from trained technicians) could thus be used to evaluate the provision of ecosystem services on farms, and allow farmers to be more active participants in land management decision-making.

2.2 Materials and Methods

2.2.1 Study region and design

This research was carried out in the Meta Department of eastern Colombia. At roughly 200 m in elevation, the region experiences a humid tropical climate, with an average annual temperature of 26 °C, rainfall averaging 2500 mm yr^{-1}, and a marked dry season between December and March (Decaëns et al., 2001). Sampling was conducted along a 200 km transect extending from Puerto Lopez to Carimagua (to the Northeast) and bounded to the North by the Meta River (Figure 1). Soil-based ecosystem services and biodiversity were assessed within five representative production systems in the region: 1) annual crops (rice, maize and soybeans), 2) rubber plantations, 3) oil palm, 4) improved pastures, and 5) semi-natural savannas. Fifteen fields for each production system were distributed regularly along the transect, such that all systems sampled were equally present in each of three municipalities studied (Puerto Lopez, Puerto Gaitan and Carimagua), yielding a total of 75 sampled fields (Figure 1).
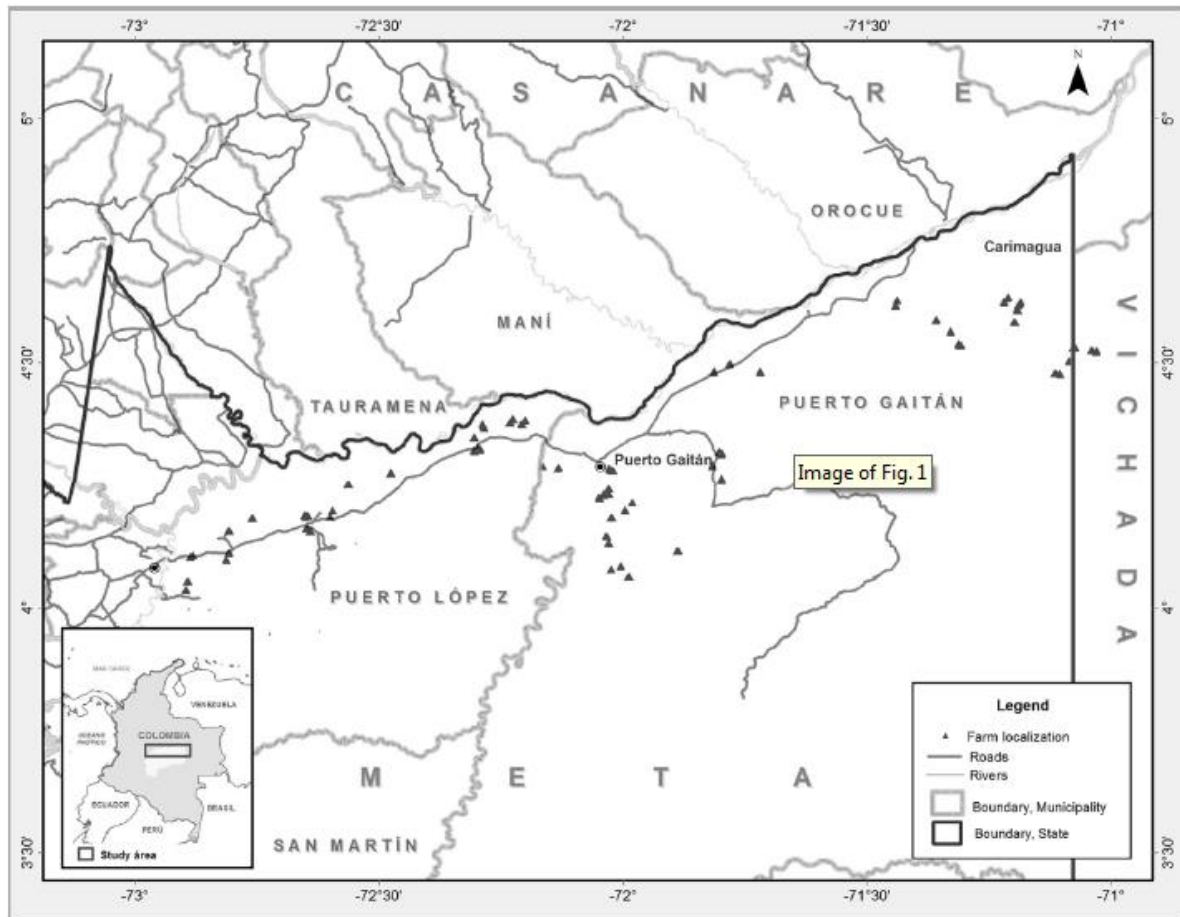
Figure 1. Location of the 75 plots and associated land use sampled between June and July 2011, in the Meta Department, Colombia.

2.2.2 Ecosystem service evaluation and development of synthetic indicators

Within each field, three equally-spaced sampling points (200 m apart) were located along a 400 m transect, starting at least 50 m from the field edge. Ant communities and soil-based ecosystem services were sampled at each of these points between June and August 2011. Methodologies and results for the assessment of soil-based ecosystem services have already been detailed by Lavelle et al. (2014), and will thus not be described in full. Briefly, a suite of soil physical, chemical and biological parameters were measured to evaluate key ecosystems services

including: nutrient provision, water regulation, maintenance of soil structure, biodiversity, and climate regulation. Nutrient provision services were assessed by measuring soil chemical fertility parameters (pH, SOM, total N, available P, Al saturation, cation exchange capacity, and macronutrient concentrations) at the 0-10 cm and 10-20 cm depths. Soil hydrological services (water regulation) were assessed by soil physical characteristics including volumetric and gravimetric moisture content, porosity, plant available water (based on water retention curves), aggregate stability, bulk density, penetration resistance and shear strength resistance. The maintenance of soil structure (particularly relevant for these easily compacted soils) was assessed by visual inspection of soil macroaggregates (> 4 mm) to determine the origins of soil structure (i.e., fauna vs. root vs. microbial or physical aggregation processes vs. non-macroaggregated soils). This method, outlined by Velasquez et al. (2007), provides an integrative measure of recent soil biological activity and offers an important proxy measurement for C stabilization, crop rooting potential, water infiltration and aeration. Soil biodiversity and biological activity was assessed via the collection and sorting of soil macrofauna (including ants) into 16 taxonomic groups (e.g., Oligochaeta, Isoptera, Coleoptera) largely separated by order (see details below for sampling of ant communities). Finally, climate regulation was evaluated by measuring aboveground C in living biomass, soil C in the surface layer (0-20 cm), and greenhouse gas (GHG) emissions of CO_2, CH_4, and N_2O at monthly intervals between June and November of 2011.

The data sets generated for nutrient provision, soil hydrological services, maintenance of soil structure, and biodiversity were summarized into a set of four synthetic indicators of ecosystem services (as well as a more direct indicator for climate regulation mentioned below) according to methods adapted from Velasquez et al. (2007). Principal components analysis (PCA) was used to determine the parameters that best capture the variance within each dataset across the five land uses sampled. This was done by selecting those with a significant contribution (>50%

of the variance explained by the most influential variable) to either of the first two principal axes. The selected variables were then combined into a single value and scaled to a number ranging from 0.1 to 1.0 using a homothetic transformation. Since widely accepted standard conventions already exist for climate regulation services, GHG fluxes were converted into global warming potential based on CO_2 equivalents, while ecosystem C storage was calculated as the sum of aboveground biomass and soil C in the surface (0-20 cm) layer. The resulting numbers for all services were then scaled to between 0.1 and 1.0 (using the inverse value for GHG emissions, since high emissions imply a negative service and low emissions a positive service) and then averaged to generate a single indicator of climate regulation.

2.2.3 Ant diversity sampling and calculations

At the sampling points described above, ants were collected along with other groups of soil macrofauna by employing a modified TSBF collection method (Anderson and Ingram, 1993). Sampling involved the excavation and hand-sorting of litter and soil from a central monolith (25 x 25cm x 20 cm deep) and two adjacent monoliths (25cm x 25cm x 10 cm deep) located 10 m to the North and South of each central monolith. Standing plant biomass was cut 2-3 cm above the soil surface and removed prior to sampling. With three sampling points per transect, a total of nine soil monoliths were collected for each field. In the laboratory, ants were separated from other macrofauna and the samples were cleaned and preserved in 96% alcohol. Identification of ants to the genus level was performed following keys of Palacio and Fernandez (2003) and Bolton (1994); updated keys that are specific for each gender were used for finer level identifications according to AntWeb (http://www.antweb.org) and Longino (2003).

We performed a descriptive analysis of the percentage of collection by the different subfamilies, genera and species, based on morphological assessment of the number of ant species for each sampling point and land use. Effectiveness of sampling was estimated with species accumulation curves using the program EstimatesS v.8.2.0 (Colwell 2013).

Two indices were calculated to compare the five soil uses: a) species richness (density) per sampling point, and b) diversity using the exponential of the Shannon index ($e^{H'}$) calculated as:

$$e^{H'} = \exp\left(-\sum_{i=1}^{s} p_i \, \text{Log } p_i\right)$$

Where p_i is the proportion of workers of the species i and s the total number of species. The value $e^{H'}$ can be interpreted as the 'effective number of species', and provides a more intuitive comparison of species diversity than the traditional Shannon index (Jost 2006).

2.2.4 Comparison of land uses

One-way ANOVA was used to compare abundance and species richness between the different land uses using JMP 10.0 statistical software (SAS Institute 2012). Analyses were conducted at the field level, using the average value for the three sampling points (nine soil monoliths) in each field. Tukey's honestly significant difference was used to examine specific differences between the five land use systems. Natural log transformations were applied to meet the assumptions of ANOVA when necessary.

2.2.5 Identification of ant indicators using the IndVal method

Indicator ant species for ecosystem services were identified using the IndVal method developed by Dufrêne and Legendre (1997), based on the degree of specificity (occurrence of a species in a particular category, but not in others) and fidelity (frequency of a species in samples from a category) of a species to a particular habitat or soil condition (i.e., level of ecosystem service provision). The association of species with ecosystem service provision was accomplished by defining three categories of performance (irrespective of land use) based on the synthetic indicators described above. Each of the sampled fields was considered to have low (0.1-0.4), medium (0.4-0.7), or high performance (0.7-1.0) for each of the five consolidated ecosystem services, based on a similar methodology applied by Rousseau et al.

(2013). An ant species (or morphospecies) is thus considered a bioindicator of ecosystem services if it is commonly found in samples of a particular category (but not in other categories) and is present in most samples from this category. The IndVal value for each species is calculated as follows:

$$A_{ij} = \text{N.ind }(ij) \text{ / N.ind }(i)$$

$$B_{ij} = \text{N.samples }(ij) \text{ / N.samples }(j)$$

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$$

where: A_{ij} represents specificity, N.ind (ij) is the average number of individuals of the species (i) within samples of a particular category (j) and N.ind (i) is the sum of the average number of individuals of species (i) across all categories examined. The fidelity is represented by B_{ij}, where N.samples (ij) is the number of samples in category (j) where species (i) is present and N.samples (j) is the total number of samples in this category. A_{ij} yields a maximum value when a species is present in only one category and B_{ij} is maximum when the species is present in all samples of this category. The IndVal index was obtained by multiplying these two terms together, thus yielding a value which ranges from 0 to 100, such that 100 represents a perfect indicator species (Dufrêne and Legendre, 1997). Finally, Monte Carlo simulations were performed using 1000 simulation runs with PC-ORD v.4.34 (McCune and Grace, 2002). This test results in a p-value based on the proportion of randomized runs with an indicator value greater than or equal to the observed indicator value.

2.3 Results

2.3.1 Composition of ant communities

In total, 5154 ant individuals were collected, comprised of 91 ant species, 33 genera, and 9 subfamilies (Table S1). This corresponds to roughly 10 % of the species, 37 % of genera and

64% of the known subfamilies in Colombia (Fernández and Sendoya, 2004). Of all the taxonomic groups collected, 64 were identified to the species level and the remaining 28 are mainly morphospecies belonging to diverse genera with poorly known taxonomy. Among these genera, two of them, *Pheidole* and *Solenopsis*, contained 10 and 7 morphospecies, respectively, representing 18.6 % of total species richness. The most diverse subfamily was Myrmicinae, with 43 % of the species collected, followed by Ponerinae, with 14 % of the species observed. The genus with the highest number of species was *Pheidole* (11), and the most abundant species were: *Brachymyrmex* sp. 1 (1511 individuals), *Acromyrmex* sp. 1 (853) and *Pheidole subarmata* (551; Table 1). Assessment of the species accumulation curve suggests that the average sampling efficiency was 75.5%, with 29 species singletons and 18 species doubletons (data not shown). Although the sampling method used in this work is not specifically designed for the capture of ants, the effectiveness appears acceptable.

Table 1. Number of individuals encountered for the five most common ant species (or morphospecies) in each of five land uses sampled in the Llanos region of Colombia. Values represent the total from 15 replicate plots distributed across the region, each with nine TSBF samples (0.25 m x0.25 m) taken along a 400 m transect and collected between June and July of 2011.

Species	Rubber	Annual Crops	Palm	Improved Pasture	Savanna
Acanthostichus sanchezorum	--	--	54	--	--
Acromyrmex sp. 1	--	--	--	--	846
Acropyga palaga	--	--	--	284	--
Brachymyrmex longiocornis	--	--	--	--	242
Brachymyrmex sp. 1	139	207	235	549	381
Crematogaster nigropilosa	33	--	--	--	283
Ectatomma confine	--	17	--	--	--
Hypoponera creola	--	12	--	--	--
Hypoponera opacior	--	--	60	--	--
Nylanderia fulva	79	--	26	75	--
Pheidole scalaris	49	--	--	--	--
Pheidole subarmata	40	40	173	136	162
Solenopsis geminata	--	29	--	--	--
Tranopelta gilva	--	--	--	56	--

2.3.2 Indicators for ecosystem services

Fourteen ant species were identified as significant ($P < 0.05$) bioindicators for soil-based ecosystem services, with at least one species identified for each ecosystem service evaluated (Table 2). For example, the presence of *Hypoponera punctaticeps* indicates a soil with high capacity to supply nutrients to crops, while *Crematogaster curvispinosa* indicates a system with low greenhouse gas emissions and/or high C storage.

Table 2: Indicator ant species for soil-based ecosystem services in the Llanos region of Colombia. The displayed values range from 0 (no indication) to 100 (perfect indicator) and indicate either an indicator of low (-) or high (+) ecosystem service provision. P-value based on Monte Carlo significance test.

Ecosystem service indicator	Species	Indval value		Monte Carlo test	Grup or category
		Observed	Expected		
Biodiversity	*Brachymyrmex* sp. 2	22.2	6.8	0.005	+
	Hypoponera sp. 2	15.4	5.0	0.020	+
	Monomorium pharaonis	13.8	5.7	0.030	+
	Pheidole inversa	24.7	11.1	0.010	+
	Pseudomyrmex gracilis	20.7	6.3	0.008	+
Aggregate Morphology	*Acromyrmex sp. 1*	23.0	8.8	0.005	+
	Pheidole inversa	22.7	10.7	0.010	+
	Nylanderia fulva	28.0	15.5	0.017	+
	Solenopsis sp. 1	11.5	5.1	0.050	+
	Pseudomyrmex pallens sp.1	17.6	7.2	0.010	+
Water Regulation	*Hypoponera creola*	27.9	15.7	0.050	-
Nutrient Provision	*Crematogaster nigropilosa*	21.0	13.3	0.07	-
	Ectatomma ruidum	26.0	13.5	0.02	-
	Hypoponera creola	22.3	14.6	0.05	+
	Hypoponera punctaticeps	14.3	4.9	0.03	+
Climate Regulation	*Crematogaster curvispinosa*	44.5	11.8	0.05	+

a) Indicator value index with observed and expected values, based on Monte Carlo simulations with 1000 runs.

2.3.3 Comparison of ant communities between land use systems

When considering the total number of species encountered across the fifteen replicates of each treatment, the land use with the highest species richness (gamma diversity) was improved pasture (52 species), followed by semi-natural savanna (45), rubber plantations (39), oil palm (38) and annual crops (20) (Table 3). Management systems with the highest number of unique species (i.e., those not found in other soil use systems) encountered were improved pasture (11), rubber (10) and semi-natural savanna (9) (Table S1).

According to the exponential of Shannon, $e^{H'}$, improved pasture continued to be the most

diverse system and suggested an effective community diversity of 33 species (Table 3). In comparing the effective number of species across systems, rubber and savanna were found to possess 94.4% and 92.9%, respectively, of the effective species diversity observed in improved pasture. At the same time oil palm contains only 72.2%, and transitory crops have less than 50% of the species occurring in the three most diverse management systems.

Table 3. Number of ant species (or morphospecies), genera, and sub-families observed in each of five land uses in the Llanos region of Colombia, as well as effective number of species (Shannon exponential) for each land use. Values represent the total from 15 replicate plots distributed across the region, each with nine TSBF samples (0.25 m*0.25 m) taken along a 400 m transect and collected between June and July of 2011.

Diversity measures	Annual crops	Rubber	Oil palm	Improved pasture	Savanna
Species	20	39	38	52	45
Genera	8	24	17	22	8
Sub-families	5	9	8	7	6
Effective number of species $e^{H'}$	15.3	30.7	23.8	32.9	31.1

Comparison of ant abundance and species richness between management systems by ANOVA revealed significant differences. For total ant abundance, the semi-natural savanna was significantly higher than annual crops, rubber and oil palm ($P < 0.001$), while improved pastures demonstrated intermediate values (Figure 2a). Meanwhile, improved pasture demonstrated the highest richness, and both this system and savanna were significantly higher than annual crops ($P = 0.003$; Figure 2b).
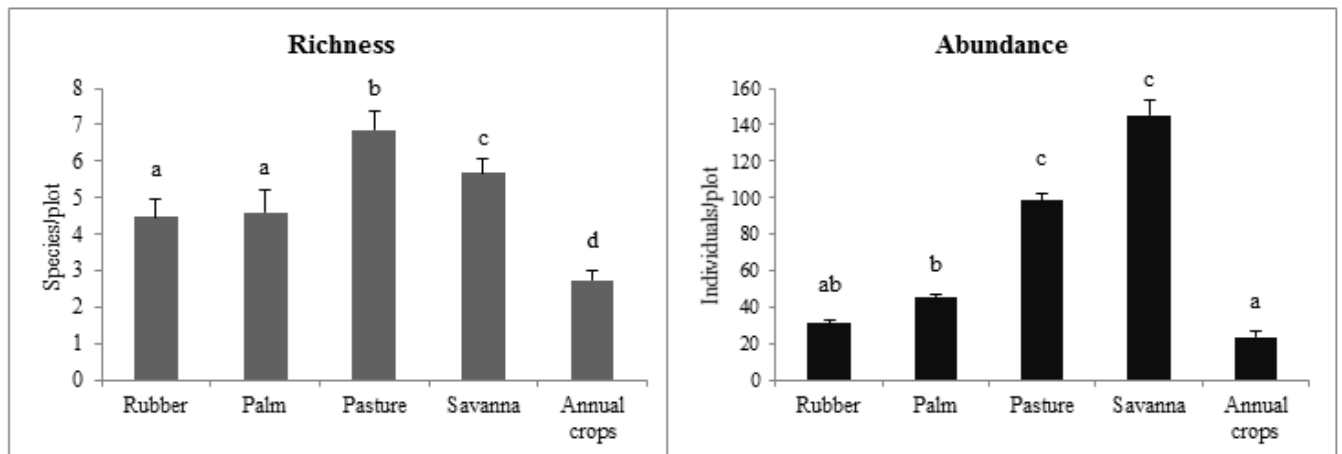
Figure 2. Average ant species richness (a) and abundance (b) in five land uses in the Llanos region of Colombia (15 replicate fields per land use). Each sampled field comprised nine TSBF samples (0.25 m * 0.25 m) taken along a 400 m transect and collected between June and July of 2011. Different letters above each bar indicate statistically significant differences between land uses according to Tukey's test.

2.4. Discussion

2.4.1 Developing indicators of soil-based ecosystem services

The principal objective of this research was to identify ant species that could serve as bioindicators for the provision of ecosystem services in the Llanos region. In total, we identified fourteen species that were deemed significant indicators of soil-based ecosystem services. Twelve were associated with the high provision of soil-based ecosystem services, while two were associated with the poor provision of ecosystem services (Table 2). For example, species (or morphospecies) such as *Acromyrmex* sp. 1, *Pheidole inversa*, *Solenopsis* sp. 1, were associated with the maintenance of soil structure (i.e., the presence of biogenic aggregates and overall soil aggregation). These species are likely to be indicators, since they are actively involved in relevant ecosystem processes related to soil aggregation. For example, large colonies typically associated with the genus *Acromyrmex* can greatly modify the structure of

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the soil though nest building activities, which alter the chemical and physical properties of soil, accelerate nutrient turnover and promote plant growth (Moutinho et al., 2003). More specifically, enhanced soil porosity associated with ant mounds has been suggested to enhance organic matter turnover by creating more favorable conditions for microbial growth (Petal and Kusinska, 1994). Similarly, species of the genera *Pheidole* and *Solenopsis*, often build their mounds from excavated soil and incorporate different organic materials, such as seeds and leaf fragments (*pers. comm.*). In the case of climate regulation, the indicator species *C. curvispinosa* is known to nest in woody stems and occupy habitats with perennial vegetation (www.AntWeb.org). Such systems are generally associated with reduced disturbance and lower fertility inputs (at least relative to annual crops), both attributes that favor C storage and lower GHG emissions (Lavelle et al., 2014). For many of the bioindicators of ecosystem services identified in this study, their life strategies and impacts on soil functioning are still not well understood and it is difficult to know if these species contribute to the regulation of the ecosystem service to which they are associated or if their presence is simply governed by the same soil properties that drive the ecosystem services they indicate.

While the underlying mechanisms linking ants to certain soil processes may not always be clear, the identification of bioindicators of ecosystem services offers an important tool for a more integrated management of agroecosystems that considers multiple functions and the conservation of the soil capital as a key objective, in addition to crop yield and profitability. Such indicators could be monitored by field technicians and farmers, leading to better understanding and management of ecosystem services in agricultural soils. For example, the presence of species such as *Acromyrmex sp. 1* and *Pheidole inversa* indicated the maintenance of good soil structure, while the presence of *Ectatomma ruidum* was associated with poor nutrient provision capacity (or soil fertility). Armed with such knowledge farmers (aided by trained technicians) could implement preventive or corrective actions (e.g., avoidance of tillage,

nutrient and/or pesticide additions). Similarly, practitioners may be able to determine, based on the presence of *C. curvispinosa* or *Pseudomyrmex gracilis,* that particular fields or management practices better mitigate climate change or better conserve soil biodiversity. We note that sampling of ant species is faster and cheaper than measurement of greenhouse emissions and C storage, or assessing entire soil macroinvertebrate communities. While direct measurements can be very powerful, indicator species have the advantage of being region-specific.

2.4.2 Response of ant communities to manangement

While the sampling method employed in this study was not ideal for evaluating entire ant communities, but was instead designed for a broader group of soil invertebrates, our findings provide valuable information regarding the relative impacts of management on soil-dwelling ant species. We note that different management systems yielded clear responses in ant abundance and community structure characteristic of each regime (Table 1; Figure 2). For example, annual crops experience the most intensive disturbance regime, with frequent tillage and relatively high inputs of agrochemicals, and this land use corresponded to the lowest abundance, richness and diversity of ants compared to the other, relatively less-disturbed agroecosystems studied here. This corroborates past findings suggesting that the structure of ground dwelling ant communities is at least partially determined by soil disturbance and vegetation type (Vasconcelos, 1999; Silva et al., 2007; Hoffmann, 2009).

Despite being relatively young in age (< 5 yr), the tree-based systems (oil palm and rubber) appeared to promote the establishment of arboreal ant species (e.g., *Crematogaster* and *Pseudomyrmex spp.*). More specifically, these systems supported species that are sensitive to high temperatures, such as the legionary ant *Labidus*, found mainly within the Neotropical forest floor (Longino, 2003). The finding suggests that tree cover and multiple vegetative strata may be important for promoting these key taxonomic groups, and that perennial agroecosystems may play an important role in the conservation of ant species from forested

areas across the broader region (e.g., riparian forests). Others have suggested that tree-based cropping systems can play an important role in biodiversity conservation in tropical landscapes, as they commonly occupy zones of transition between highly disturbed land uses and natural ecosystems and can contribute to the conservation of native plant and animal biodiversity (Schroth et al., 2004; Perfecto and Snelling, 1995; Perfecto and Vandermeer, 2008). Given the relatively young ages of the plantation systems studied here, we might expect ant community assemblages to become more complex as these systems mature, such that they could host ant communities even more similar to those found in the forested areas of the Llanos. This may be of particular importance for rubber plantations, as these systems were found to possess some of the rarest species encountered in this study.

Improved pastures demonstrated the greatest overall diversity in terms of both species richness and the Shannon Index. This finding is in agreement with several studies in the Llanos region that found semi-natural and improved pastures to favor the presence of ants and other macroinvertebrates (Decaëns et al., 2001; Lavelle et al., 2014). The high diversity observed in the improved pastures may be related to the fact that the pastures studied were implemented several years earlier than the other production systems, so they have been relatively free of disturbance (e.g., chemical fertilizers, pesticides, tillage) for longer than the other production systems. Higher levels of soil organic matter in this system (Lavelle et al., 2014) also suggest a greater resource base to support decomposer-based food webs. While semi-natural savanna was not the most diverse system, overall diversity, in terms of species richness, was generally high. We suspect that this is related to the low levels of disturbance as well as some level of increased habitat complexity associated with the lack of tillage and the presence of scattered trees. We note that some of these grassland systems are lightly grazed and occasionally burned, but that such interventions apparently do not yield long-lasting impacts on ant communities or other

soil invertebrates. This idea is supported by the findings of Decaëns et al. (2001), who reported high soil macrofauna abundance and diversity in both protected savannas as well as those with regular burning and grazing.

2.5 Conclusion

Throughout the tropics the conversion of natural areas to pasture for livestock and large-scale agriculture represents threats to ecological stability, resilience and biodiversity conservation. Despite this concern, the overall impacts of land use conversion remain poorly understood and are likely to differ from region to region. In this study we evaluated soil-dwelling ant communities across a rapidly changing agricultural landscape and used this information to develop bioindicators of soil-based ecosystem services. These indicators offer a valuable tool to better understand the impacts of land use change and allow farmers to better manage the provision of ecosystem services on their land. Additionally, policy makers could apply such indicators as a monitoring tool to help guide the decision making process and potentially support mechanisms for allocation of subsidies aimed at protecting natural capital. Our findings also suggest that land use greatly impacts ant abundance and community diversity, and that an improved understanding of these effects could greatly contribute to biodiversity conservation and ecosystem functions at the regional scale.

2.7 References

Anderson, J.P.E., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility. A Handbook of methods. CAB International, Wallingford, UK.

Blanchart, E., Lavelle, P., Braudeau, E., Le Bissonnais, Y., Valentin, C., 1997. Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. Soil Biol. Biochem. 29, 431–439.

Bolton, B., 1994. Identification Guide to the Ant Genera of the World. Harvard University Press, Cambridge. MA, USA.

Brussaard L., Behan-Pelletier V.M., Bignell D.E., Brown V.K., Didden W., Folgarait P., C. Fragoso C., Wall Freckman D., Gupta V.V.S.R., Hattori T., Hawksworth D.L., Klopatek C., Lavelle P., Malloch D.W., Rusek J., Soderstrom B., Tiedje J.M., Virginia R.A., Biodiversity and ecosystem functioning in soil. Ambio 26, 1997, 563-570.

Correa, H. D., Ruiz, S. L., Arévalo, L. M. (Eds.) 2005. Plan de acción en biodiversidad de la cuenca del Orinoco Colombia 2005-2015. Propuesta Técnica. Bogotá, Colombia.

Colwell, R.K., 2013 EstimateS: Statistical estimation of species richness and share species from samples. Version 9 and earlier. User Guide and Application. http://purl.oclc.org/estimates

Dauber, J., Schroeter, D., Wolters, V. 2001. Species specific effects of ants on microbial activity and N-availability in the soil of an old-field. Eur. J. Soil Biol. 37, 259-261.

Decaëns, T., Lavelle, P., Jimenez, J.J., Escobar, G., Rippstein, G., Schneidmadl, J., Sanz, J.I., Hoyos, P., Thomas, R.J., 2001. Impacto del uso de la tierra en la macrofauna del suelo de los Llanos Orientales de Colombia, in: Jimenez, J., Thomas, R. (Eds.) El Arardo Natural: Las Comunidades de Macroinvertebrados del Suelo en las Sabanas Neotropicales de Colombia. Publicacion CIAT, Cali, Colombia.

Dufrêne, M. and P.Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monog. 67, 345-366.

Fernández F., Sendoya, S., 2004. List of neotropical ants. Biota Colombiana. 5, 3-88.

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodivers. Conserv. 7, 1221-1244.

Frouz, J., Jilková, V., 2008, The effect of ants on soil properties and processes (Hymenoptera: Formicidae) Myrmecol. News 11: 191-199

Goosen, N, D. 1971. Physiography and Soils of the Llanos Orientales, Colombia. Publications of the International Institute for Aerial Survey and Earth Sciences (ITC), Amsterdam, Netherlands.

Hoffmann, B.D., 2009. Using ants for rangeland monitoring: global patterns in the responses of ant assemblages to grazing. Ecol. Indic. 10, 105–111.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press. Cambridge, MA, USA.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–374.

Lafleur, B., Hooper-Bui, L.M., Mumma, E.P. Geaghan, J.P., 2005. Soil fertility and plant growth in soils from pine forests and plantations: effect of invasive red imported fire ants Solenopsis invicta (Buren). Pedobiologia 49, 5 415–423.

Lavelle P., Lapied, E., 2003. Endangered earthworms of Amazonia: an homage to Gilberto Righi. Pedobiologia. 47, 419-427.Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.-P., 2006. Soil invertebrates and ecosystem services. Eur. J. Soil Biol. 42, S3–S15.

Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M.P., Loaiza, S., Pulido, S.X. Rodríguez, E., Sanabria, C., Velásquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. Agric. Ecosyst. Environ. 185, 106-117.

Lawton, J. H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsenk, T.B., Mawdsley, N.A., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72-75.

Lobry de Bruyn, L.A., 1999. Ants as bioindicators of soil function in rural environments. Agric. Ecosyst. Environ. 74, 425-441.

Longino, J.T., 2003. (Review: December 2013). Ants of Costa Rica. http://www.evergreen.edu/ants/AntsofCostaRica.html

Millennium Ecosystem Assessment, 2005. Maweb.org.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities.PC-ORD V. 4.34. MjM Software design. Gleneden Beach, OR, USA.

Moutinho, P., Nepstad, D.C., Davidson, E.A., 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. Ecology. 84,1265–1276.

Palacio, E.E., Fernández, F. 2003. Clave para las subfamilias y géneros, in: F. Fernández (Ed.), Introducción a las Hormigas de la Región Neotropical. Instituto de Investigación de recursos Biológicos Alexander von Humboldt. Bogotá, Colombia.

Paoletti, M.G., 1999. Using bioindicators based on biodiversity to assess landscape sustainability. Agric. Ecosyst. Environ. 74, 1–18.

Perfecto, I., Snelling, R., 1995. Biodiversity and transformation of a tropical agroecosystems: Ants in coffee plantation. Ecol. Appl. 5, 1084-1097.

Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agrosystems: a new conservation paradigm. Annals New York Acad. Sci. 1134, 173–200.

Petal, J., Kusinska, A., 1994. Fractional composition of organic matter in the soil of anthhills and of the environment of meadows. Pedobiologia 38, 493-501.

Philpott, S.M., Perfecto, I., Armbrecht, I., Parr, C.L., 2010. Ant diversity and function in disturbed and changing habitats, in: L. Lach, C.L. Parr and K.L. Abbott (Eds.), Ant Ecology. Oxford University Press. Oxford, UK.

Rippstein G., Escobar G., F. Motta (Eds.), 2001. Agroecología y Biodiversidad de la Sabana en los Llanos Orientales de Colombia. Publicaciones Ciat. Cali, Colombia.

Rousseau, L., Fonte, S.J., Téllez, O., Hoek R., Lavelle, P., 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. Ecol. Indic. 27, 71–82.

SAS Institute, 2012. JMP 10.0, Cary, NC, USA.

Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, L.H. and Izac, A.M.N., 2004. The role of Agroforestry in biodiversity conservation in tropical landscapes, in: Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, L.H. and Izac, A.M.N. (Eds.). Agroforesty and Biodiversity Conservation in Tropical Landscapes. Island Press. Washington DC, USA.

Silva, R.R., Feitosa, R.S.M., Eberhardt, F., 2007. Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest. Forest Ecol. Manag. 240, 61–69.

Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiv. Conserv. 8, 409–420.

Velásquez, E., Fonte, S.J., Barot, S., Grimaldi, M., Desjardins, T., Lavelle, P., 2012. Soil macrofauna-mediated impacts of plant species composition on soil functioning in Amazonian pastures. Appl. Soil Ecol. 56, 43-50.

Velasquez, E., Lavelle, P., Andrade, M., 2007. GISQ, a multifunctional indicator of soil quality. Soil Biol. Biochem. 39, 3066–3080.

Wagner, D., Jones, J.B., Gordon, D.M., 2004. Development of harvester ant colonies alters soil chemistry. Soil Biol. Biochem. 36, 797–804.

Wall, D.H.E. (Ed.), 2012. Soil Ecology and Ecosystem Services. Oxford UniversityPress, Oxford, U.K.

2.8 Anexes

Table S1: Ant species abundance for five common land uses, sampled in the Llanos region of Colombia between June and July of 2011. Values represent the total from 15 replicate plots distributed across the region, each with nine TSBF samples (0.25 m x 0.25 m) taken along a 400 m transect and collected between June and July of 2011.

Species	Annual Crops	Rubber	Oil Palm	Improved Pasture	Savanna	Total
Acanthostichus sanchezorum		1	54			55
Acanthostichus sp. 1			2			2
Acromyrmex sp. 1				7	846	853
Acropyga exsaguis				2		2
Acropyga palaga				284	1	285
Acropyga sp. 1				13	40	53
Brachymyrmex longiocornis					242	242
Brachymyrmex sp. 1	207	139	235	549	381	1511
Brachymyrmex sp. 2	6		1	1		8
Brachymyrmex sp. 3					8	8
Camponotus mucronatus					1	1
Camponotus novogranadensis					1	1
Camponotus sp. 1			4	30		34
Camponotus sp. 2		2				2
Camponotus sp. 3		3		1	1	5
Camponotus sp. 4			2			2
Camponotus sp. 5		1				1
Camponotus sp. 6			1			1
Carebara brevipilosa					1	1
Centomyrmex sp. 1				1		1
Centromyrmex alfaroi			1			1
Centromyrmex brachicola		1	2		1	4
Cephalotes atratus				1		1
Cephalotes minutus				1		1
Crematogaster (cf) snellingi		2				2
Crematogaster curvispinosa			6	3	2	11
Crematogaster foliocrypta			1	5		6
Crematogaster limata					1	1
Crematogaster longispina		32	9	23	2	66
Crematogaster nigropilosa		33	6	56	283	378
Crematogaster obscurata		1		2		3
Crematogaster rochai		2		5	3	10
Crematogaster sotobosque				1		1
Cyphomyrmex rimosus				4		4
Dolichoderus bispinosus			1	1	1	3
Dolichoderus sp. 1					1	1
Dorymyrmex goeldii		1		1		2
Ectatomma brunneum	3		3		2	8
Ectatomma confine	17					17
Ectatomma ruidum		8	7	9	11	35
Ectatomma tuberculatum		1			1	2
Hypopnera punctatisima	2	1	1			4
Hypoponera creola	12	17	12	6	13	60
Hypoponera opacior	9	8	60	8	6	91

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Hypoponera punctatisima	9					9
Hypoponera sp. 1	1					1
Hypoponera sp. 2			8	10		18
Labidus praedator		3	6			9
Leptanilloides sculpturata		1				1
Linepithema neotropicum		1				1
Monomorium pharaonis				4		4
Mycocepurus smithii		1				1
Neivamyrmex punctaticeps		12		1		13
Nylanderia fulva		79	26	75	20	200
Odontomachus yucatecus		1	5			6
Pachycondyla arhuaca			7			7
Pachycondyla harpax					1	1
Pachycondyla sp. 1		3	1			4
Paratechina longicornis	1	1	2			4
Pheidole cocciphaga	1			6		7
Pheidole inversa	1	2		17	3	23
Pheidole radowskoski				4		4
Pheidole scalaris		49	11	4	2	66
Pheidole sp. 1	5	1	1	13	2	22
Pheidole sp. 2				21	1	22
Pheidole sp. 3				4	1	5
Pheidole sp. 4	1		1		1	3
Pheidole subarmata	40	40	173	136	162	551
Pheidole vallifica		2		46	1	49
Pseudomyrmex flavicornis				1		1
Pseudomyrmex gracilis sp. 1				1	1	2
Pseudomyrmex gracilis sp. 2		1			1	2
Pseudomyrmex gracilis sp. 3					1	1
Pseudomyrmex gracilis sp. 5		1		1		2
Pseudomyrmex oculatus sp. 1			1	1		2
Pseudomyrmex pallidus			1	1	1	3
Pseudomyrmex sp. 1	2	2	4	2	6	16
Psudomyrmex gracilis sp. 4	3					3
Rogeria curvipubens		8				8
Solenopsis geminata	29		12	31	111	183
Solenopsis picea			2	9	1	12
Solenopsis sp. 1		2		1		3
Solenopsis sp. 2			1	2	1	4
Solenopsis sp. 3	4		1			5
Solenopsis sp. 4				3	1	4
Strumigenys louisianae		1				1
Tapinoma melanocephalum				2		2
Tranopelta gilva		3		58	6	67
Typhlomyrmex sp. 1				2	3	5
Wasmannia auropunctata	2	1	5		1	9
Wasmannia sigmoidea				8		8
Total	355	468	676	1478	2177	5154

Chapter 3: Influence of Landscape and Soil properties on Soil engineers communities

Original article

Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos

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3.1 Introduction

Colombian savannas are part of the second largest savanna system in South America (Olson et al. 2001). In these savannas the intensification of land use and high population growth has turned the region into one of the most threatened ecosystems in Colombia (Romero et al. 2012). Savannas are rapidly being converted from semi-natural systems, dedicated largely to extensive cattle ranching and low-input traditional agriculture, to highly intensified commercial production of annual crops (rice, soybean, maize), biofuels (sugar cane and oil palm) and tree crops such as rubber. It is estimated that over 50,000 ha have been converted over the last two decades and recent trends show this agricultural expansion to be rapidly accelerating (Romero et al. 2012).

Soil is considered to be one of the most diverse and least understood reservoirs of biodiversity in the biosphere (Lavelle and Spain 2001). Threats to this biodiversity are a source of concern for the intrinsic value of biodiversity, but also because soil fauna provide many ecosystem services (Lavelle et al. 2006). The functions performed by soil biota have large, direct and indirect effects on crop growth and quality, soil and residue-borne pests, disease incidence, nutrient cycling and water transfer and the overall sustainability of agroecosystems. They also

influence the resistance and resilience of agroecosystems to abiotic disturbance and stress (Lavelle et al. 1997). This study focuses on termites and ants, recognized as important soil engineers. Ecosystem engineers directly or indirectly modulate the availability of resources to other species, by causing physical, biological and chemical changes in the properties of their environment (Jones et al. 1994), which potentially influences all organisms sharing the same environment. Typically, soil ecosystem engineers modify and in some instances may determine the major physical, chemical and microbiological properties of the soil (Decaëns et al. 1994; Rocha et al. 2012, Barros et al. 2003; Decaëns et al. 2012, Jouquet et al. 2011) especially those associated with soil aggregate stability and fertility (Decaëns et al. 2004, Jouquet et al. 2011). As social insects with high abundance and biomass (Luke et al. 2014), and active in nest building and tunneling, termites and ants are hypothesized to deliver a number of services including contribution to organic matter decomposition, nutrient recycling, bioturbation, tilth, porosity and cation exchange capacity (Lav 2014elle et al. 1997, Marichal et al. 2014, Heininger et al. 2014, Sanabria et al. 2014). In addition, their consumption or manipulation of organic materials creates biogenic structures (Lavelle and Spain 2001) that can be significant components of the soil profile, and as they usually comprise mixtures of clay and organic materials, they exist as microsites for biological transformations (Lavelle et al. 1997). Termites (as prey) (Lavelle and Spain 2001) and ants (as predators) (Höllodobler and Wilson 1990) may also regulate the abundance of other soil organisms, including pests, at several ecological levels (Lavelle and Spain, 2001; Marichal et al. 2014, Sanabria et al. 2014)

Direct evidence of the beneficial role of termites and ants in tropical soils is scarce (Lavelle et al. 1997), since definitive experiments would necessitate their exclusion, which is difficult or impossible to achieve in the field except by methods that simultaneously destroy ecological structure (Lavelle et al. 2014). However, land use changes such as deforestation and agricultural intensification (including mono-cropping) along with associated habitat fragmentation, are

known to have negative impacts on soil macrofauna (Decaëns et al. 1994; Barros et al. 2003; Marichal et al. 2014; Heininger et al. 2014; Lavelle et al. 2014). Because many of these changes lead to a rapid decline in fertility or erosion (Luke et al. 2014) comparison of the fauna across mosaic landscapes and between different land uses and regions provides both an indirect test of the validity of the soil engineer concept and guidance for future management of cropping systems (Lavelle et al. 2014, Sanabria et al. 2014)

Depletion of soil macrofauna is partly explained by their physical vulnerability to disturbance, but may also result from changes to soil properties, especially soil chemistry, and/or from the removal or reduction of niche heterogeneity and from severe modifications of microclimates (Decaëns et al. 1994; Barros et l. 2003, Decaëns et al. 2004; Laossi et al. 2008). Examples of impacts on soil fauna are known for tillage, soil properties, microclimate, food availability and pesticide application, both in Colombia and elsewhere (Barros et al. 2003, Lavelle et al. 2014). In the present study land uses sampled are well-defined representing different levels and types of disturbance in regions of the Orinoco river basin, using a standard monolith method. This enabled termites and ants to be co-collected at each sampling point together with soil from the immediately adjacent wall of the monolith pit. The analysis attempted to elucidate the influence of land use on soil properties and on termite and ant communities, and in turn the influence of soil properties on these faunal groups. These analyses are complementary to the results of Lavelle et al. (2014) and Sanabria et al. (2014) that respectively focus on the impact of land use on some soil ecosystem services, and the possibility to use ant as indicators of ecosystem services.

3.2 Materials and methods

3.2.1 Study region and sampling design

The study sites are located in the Altillanura Plana within the Meta Department of eastern Colombia (between 3°55'21"N–71°01'43"W and 4°38'07"N–72°53'55"W). This region is at about 200 m in elevation, has a humid tropical climate with an average annual temperature of 26 °C and rainfall averaging 2500 mm yr-1, and have a marked dry season between December and March (Decaëns et al. 2004). Sampling was conducted between June and August 2011 along a 200 km transect extending from Puerto López (PL), Puerto Gaitán (PG) and Carimagua (C) (to the Northeast) and bounded to the North by the Meta River. In total, five land uses were sampled: 1) annual crops (AC) (include together rice, maize and soybeans), 2) rubber plantations (R), 3) oil palm plantations (OP), 4) improved pastures (IP), and 5) semi-natural savannas (S). In each region, 5 replicates of each land use were sampled, this results in a total of 75 sampled fields (5 land uses x 5 replicates x 3 regions) and because each sampled field contains three sampled points a total of 225 sub-samples were done.

3.2.2 Physical and Chemical Soil analyses

A set of ten soil physical properties were documented (Table 1): volumetric (VM) and gravimetric or soil moisture (SM) content, micro (<0.03 μm; MIC), meso (0.03–3 μm; MES) and macro (>3 μm; MAC) porosity, available water storage capacity (AWC), bulk density (BD), texture: sand (Sa), silt (Si) and clay (Cl). Only two of the three texture variables were kept in the multivariate analyses (Sa and Si). In addition, sixteen soil chemical properties (Table 1) were measured including, pH, total soil carbon (C) and nitrogen (N) concentrations, cation exchange capacity (CEC), Al saturation (SAl), macro and micronutrient concentrations (Ca, K, Mg, P, Al, S, B, Fe, Mn, Cu and Zn). At each sampling point soil for physical analyses was taken from the vertical walls of the central monolith pit, while soil for chemical analyses was taken from soil excavated from the pit after sorting out macrofauna.

Table 1. List of chemical and physical variables used in the study, with their description and unit.

Chemical Variables	Description	Unit	Technique
pH	Hydrogen potential	--	Potentiometric
N	Nitrogen Total	$g\,kg^{-1}$	UV-VIS
C	Carbon Total	$g\,kg^{-1}$	UV-VIS
P	Available Phosphorus Total	$mg\,kg^{-1}$	UV-VIS
K	Potassium Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Ca	Calcium Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Mg	Magnesium Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Al	Aluminum Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
CEC	Cation Exchange Capacity	$cmol\,kg^{-1}$	Potentiometric
SAl	Aluminum Saturation	%	Potentiometric
S	Sulfur Total	$mg\,kg^{-1}$	UV-VIS
B	Boron Total	$mg\,kg^{-1}$	UV-VIS
Fe	Iron Total	$mg\,kg^{-1}$	UV-VIS
Mn	Manganese Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Cu	Copper Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Zn	Zinc Total	$mg\,kg^{-1}$	Atomic absorption spectroscopy
Physical Variables	**Description**	**Unit**	**Technique**
SM	Soil Moisture	$g\,100\,g^{-1}$	
VM	Volumetric Moisture	$cm\,100\,cm^{-1}$	
BD	Bulk density	$g\,cm^{-3}$	Rings and clod
AWC	Available Water Capacity	%	
MAC	Macropores ($>3\mu m$)	%	Yolder
MES	Mesopores ($0.03–3\mu m$)	%	Yolder
MIC	Micropores ($<0.03\mu m$)	%	Yolder
Sa	Sand	%	Bouyoucos
Si	Silt	%	Bouyoucos
Cl	Clay	%	Bouyoucos

3.2.3 Ants and termites biodiversity

In each sampled field three sampling points were located equidistant along a 400 m transect. At each sampling point, ants and termites were collected along with other groups of soil macrofauna (only ant and termite results are considered in the present paper) by employing a modified TSBF collection method (Anderson and Ingran 1993). Sampling consisted in the

excavation, at each sampling point, of a central monolith (25 x 25cm x 20 cm deep) and two adjacent monoliths (25cm x 25cm x 10 cm deep) located 10 m to the North and South of each central monolith and hand-sorting of all macrofauna from the litter and soil of these three monoliths. Hence, a total of nine soil monoliths were collected for each sampled field. Standing plant biomass was cut 2-3 cm above the soil surface and removed prior to sampling. In the laboratory, ants and termites were separated from other macrofauna organisms and were cleaned and preserved in 96% alcohol. Identification of ants to the genus level was performed following keys of Palacio and Fernandez (2003) and Bolton (1994); keys that are specific for each gender were used for finer level identifications according to AntWeb and Longino (2004). The identification of termites was carried out with keys of Constantino (2002) and Rocha and Cancello (2012). In general, the specimens were identified to species level whenever possible, or alternatively, individuals were separated into morphospecies based on differences of physical characteristics.

3.2.4 Statistical analysis

From the records of the different species and morphospecies of ants and termites collected in each field (75), a data set was built in which species abundance were replaced by species occurrence (i.e. number of monoliths per field in which the species was found) as is commonly done for ants and termites. Given that they are social insects, a single sample may contain an extreme abundance of a rare species (Longino 2004). Thus occurrence data provides reliable information on species presence and relative abundance within a community and can be analyzed using general linear models. The multivariate statistical analyses were run removing species occurring in less than two samples, but this did not change the structure of the data set or the main conclusions. Based on these criteria, 13 out of a total of 60 ant species and 10 termite species were selected for multivariate analysis.

3.2.4.1. Between-group analysis

To analyze the effect of the different regions and land use on soil chemical or physical properties, a between-group multivariate analysis was performed for each factor (region and land use), which provides the best linear combination of variables maximizing between-group variance (Baty et al. 2006). These analyses were performed on an initial Principal Component Analysis (PCA) to identify the best linear combination of sub-variables describing the regions (Puerto López (PL), Puerto Gaitán (PG), Carimagua (CAR)) or land uses (annual crops (AC), rubber plantations (R), oil palm plantations (OP), improved pastures (IP), semi-natural savannas (S)) quantifying their respective effect on soil physical or chemical properties. The significance of each explanatory variable (region or land use) was tested using a Monte-Carlo permutation test. A between-group analysis was also performed in order to assess the respective effect of region or land use on ant or termite occurrences using Correspondence Analysis (CA) (Baty et al. 2006).

3.2.4.2 Co-inertia analysis

Co-inertia analyses, a two-table ordination method, were used to analyze the impact of soil properties (physics and chemistry) on ant and termite species occurrence. This involves a simultaneous projection, at the same scale, of the PCA conducted on soil properties and the CA conducted on ant and termite occurrences onto the same co-inertia factorial plane (Crawley 2012, Baty et al. 2006). Permutation tests were conducted to assess the statistical significance of the co-variation between physical or chemical soil properties and termites or ants communities.

3.2.4.3 General linear model

The occurrence of each ant and termite species was then analyzed using a Generalized Linear Model (GLM) testing for the effect of the region, land use and physical and chemical variables on occurrences. The GLM is based on a flexible generalization of ordinary linear models that allows for response variables to follow other distributions than the normal distribution

(Thioulouse et al. 2012, R-Core Team 2010). Poisson distributions were used on species present in 5 or more samples to avoid the issue of zero-inflated Poisson regression. GLM were run on 20 ant species and 6 termite species. An automatic step-wise selection procedure was implemented starting with a model without any effect to determine the variables to be kept in the model. All analyses were conducted in the R environment and for the multivariate analyses was used the ade4 library (Lobry de Bruyn and Conacher 1990, Amezquita et al. 2004).

3.3 Results

3.3.1 Soil engineers diversity

A total of 5154 ant individuals representing 33 genera, 9 subfamilies and 91 ant species were found, 64 of those were identified to the species level and the remaining 28 are identified as morphospecies because they belong to diverse genera with poorly known taxonomy or mega diverse groups (see complete list in Appendix 1). Termite comprised 8052 individuals belonging to 4 families, 5 subfamilies, 10 genera and 16 species were identified (see complete list in Appendix 2).

3.3.2 Effect of region or land use on soil properties

3.3.2.1 Physical soil properties.

Between-group analyses performed on soil physical properties with land use as the explanatory variable extracted 17.42% of the total variance (Figure 1a). Axes 1 and 2 accounted for 76.82% and 16.69% of the variance extracted, respectively. Three physical variables contributed to the formation of axis 1, three on the negative side (mesoporosity, sand concentration and available water capacity) and on in the positive side (microporosity). Axis 1 discriminated soil physical aspects, along with soil water availability for plant. Annual crops and improved pastures are on the positive side and rubber plantations, oil palm plantations and savannas on the negative side. Three variables contributed to the formation of axis 2, one on the positive side (macroporosity) and two on the negative side (silt concentration and bulk density). Axis 2 discriminated soil

physical structure, along a soil compaction gradient, with rubber plantations and annual crops on the positive side and improved pastures and savannas on the negative side. A Monte-Carlo permutation test showed that land use is significantly related to soil physical properties (p= 0.001).

Between-group analyses performed on physical soil properties taking region as the explanatory variable extracted 8.04% of the total variance (Figure 1b). Axes 1 and 2 accounted for 78.48% and 21.24% of the variance extracted, respectively. Four physical variables contributed to the formation of axis 1, three for the positive side (macro and mesoporosity and silt concentration) and one on the negative side (bulk density). The Carimagua region is on the positive side and Puerto López and Puerto Gaitán regions on the negative side. Three variables contributed to the formation of axis 2, one on the positive side (soil moisture) and two on the negative side (silt concentration and bulk density). The Puerto López region is on the positive side and Puerto Gaitán region on the negative side. A Monte-Carlo permutation test showed that region significantly determines soil physical aspects (p= 0.01).
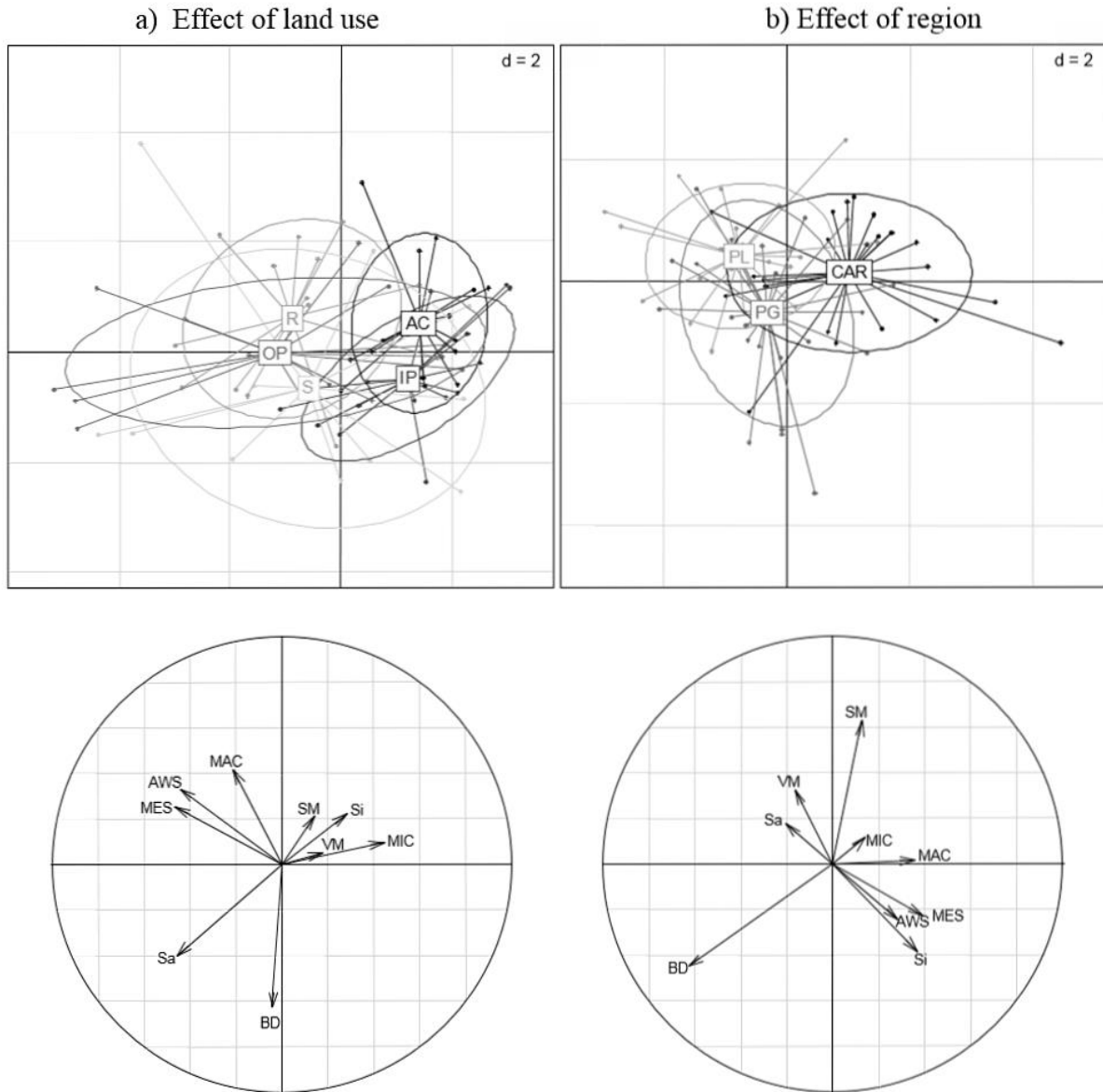
Figure 1. Between-group analysis on the physical soil properties with land use (a) or region (b). Top: projection of data set variability plotted on a factorial map of the first two discriminating axis according to respective factor. Labels on the gravity center correspond to sub-factor of respective factor. Bottom: correlation circles plot with variable vectors (for codes, see Table 1) for each respective factor. (a) Land uses: IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation. Eigen values 76.82%, 16.69% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.001. Explained variance: 17.42%. (b) Regions: PL: Puerto López, PG: Puerto Gaitán, CAR: Carimagua. Eigen values 78.48%, 21.24% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.01. Explained variance: 8.04%.

3.3.2.2 Chemical soil properties.

Between-group analyses performed on soil chemical properties taking land use as the explanatory variable extracted 27.87% of the total variance (Figure 2a). Axes 1 and 2 accounted for 84.90% and 11.39% of the variance extracted, respectively. Two chemical variables contributed to the formation of axis 1, all on the positive side (Al total concentration and Al saturation). Annual crops are on the positive side and all other land uses on the negative side. Three variables contributed to the formation of axis 2, all on the positive side (C and N concentration and Cu presence). Improved pastures are on the positive side while other land uses are on the negative side. A Monte-Carlo permutation test showed that land use is significantly related to chemical aspects of the soil ($p= 0.001$).

Between-group analyses performed on chemical soil properties taking region as the explanatory variable extracted 5.42% of the total variance (Figure 2b). Axes 1 and 2 accounted for 69.81% and 30.19% of the variance extracted, respectively. Three chemical variables contributed to the formation of axis 1, two for the positive side (pH and available P) and one on the negative side (N concentration). The Carimagua and Puerto Gaitán regions are on the positive side and Puerto López region is on the negative side. Three variables contributed to the axis 2, one on the positive side (Fe concentration) and two on the negative side (Zn and K concentrations). The Carimagua and Puerto Gaitán regions are on the positive side and Puerto López region is on the negative side. A Monte-Carlo permutation test showed that region has a significant impact on soil chemical properties ($p= 0.034$).
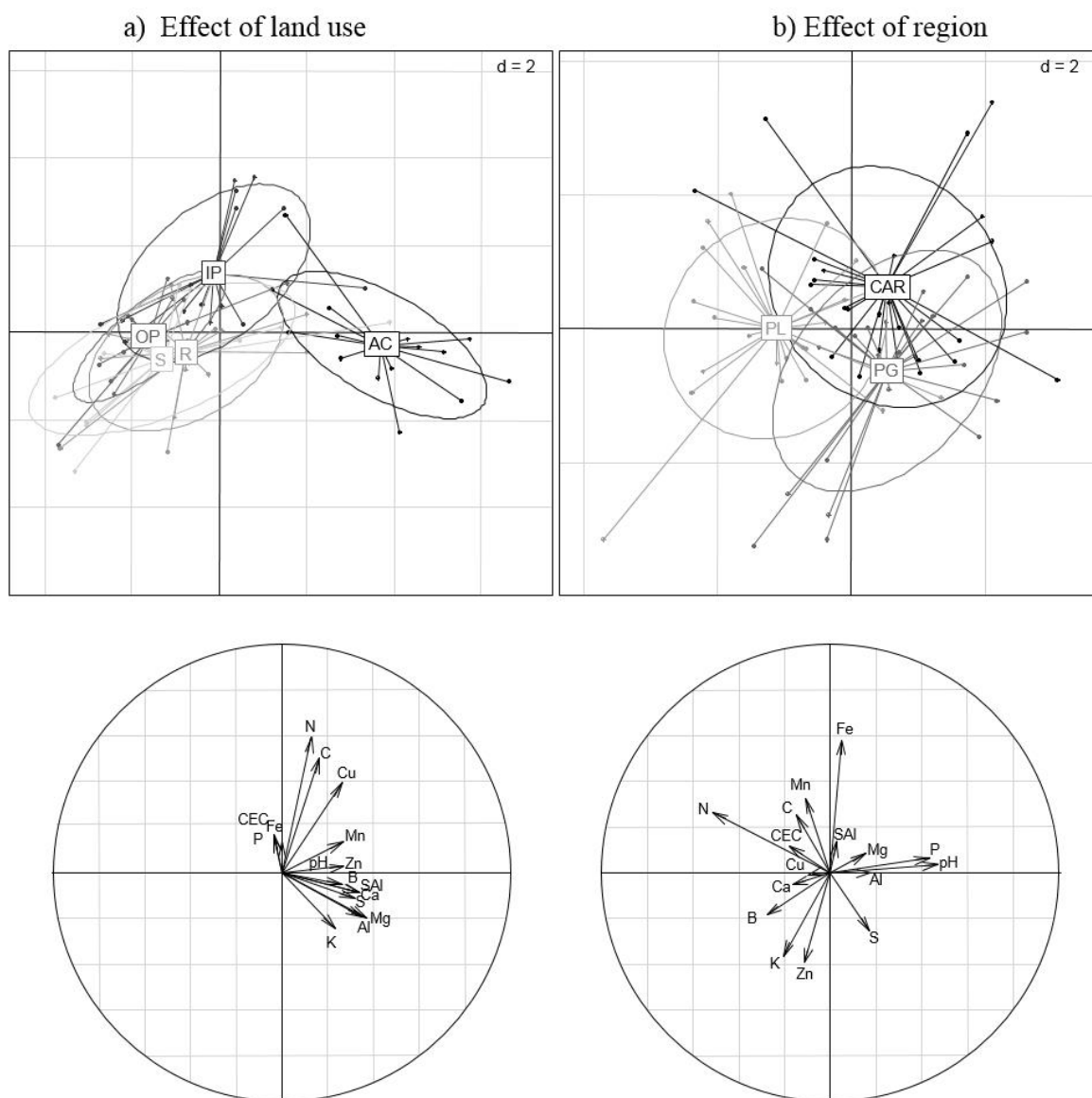
Figure 2. Between-group analysis on the chemical soil properties with land use (a) or region (b) factor. Top: projection of data set variability plotted on a factorial map of the first two discriminating axis according to respective factor. Labels on the gravity center correspond to sub-factor of respective factor. Bottom: correlation circles plot with variable vectors (for codes, see Table 1) for each respective factor. (a) Land uses: IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation. Eigen values 84.90%, 11.38% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.001. Explained variance: 27.87%. (b) Regions: PL: Puerto López, PG: Puerto Gaitán,

CAR: Carimagua. Eigen values 69.81%, 30.19% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.034. Explained variance: 5.49%.

3.3.3 Effect of region or land use on community structure

3.3.3.1 Termites.

Between-group analyses performed on the termite community data set with land use as the explanatory variable extracted 10.32% of the total variance (Figure 3). Axes 1 and 2 accounted for 58.44% and 11.38% of the variance extracted, respectively. Six termite species contributed to the formation of axis 1, three on the positive side (*Neocapritermes talpoides*, *Nasutitermes* sp.2 and *Termes* sp.1) and three on the negative side (*Anoplotermes* sp.1 and sp.4 and *Neocapritermes talpa*). Axis 1 discriminated termite communities according to land uses, with savannas on the positive side and all other land uses on the negative side. Three termite species contributed to the formation of axis 2, two on the positive side (*Neocapritermes talpoides, Nasutitermes* sp.2) and one on the negative side (*Neocapritermes talpa*). Axis 2 discriminated termite communities with annual crops and oil palm plantations on the positive side and savannas on the negative side. A Monte-Carlo permutation test showed that land use is significantly associated with termite communities (p= 0.028). No effect of region on termite communities was observed.

a) Effect of land use
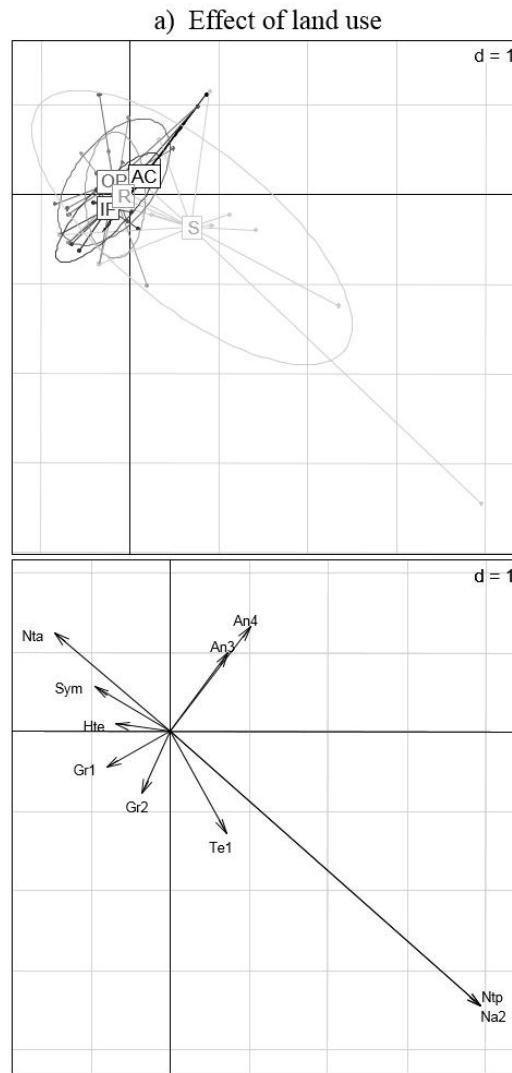
Figure 3. Between-group analysis on the termite communities with land use factor (no effect were found for the region factor). Top: projection of data set variability plotted on a factorial map of the first two discriminating axis according to land use factor. Labels on the gravity center correspond to sub-factor of land use. Bottom: correlation circles plot with variable vectors (for codes, see Appendix 2). Land uses: IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation. Eigen values 58.44%, 11.38% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.028. Explained variance: 10.32.

3.3.3.2 Ants.

Between-group analyses performed on the ant community data set taking land use as the explanatory variable extracted 6.93% of the total variance (Figure 4a). Axes 1 and 2 accounted

for 34.88% and 29.76% of the variance extracted, respectively. Eight ant species contributed to the formation of axis 1, all on the positive side (*Hypoponera punctatissima* sp.1, *Solenopsis* sp.3, *Ectatomma brunneum*, *Pachycondyla arhuaca*, *Pheidole* sp.4, *Brachymyrmex* sp.2, *Paratrechina longicornis* and *Hypoponera punctatissima* sp.2). Axis 1 discriminated ant communities according to land uses, with annual crops and oil palm plantations on the positive side and improved pastures on the negative side. Twenty ant species contributed to the formation of axis 2, ten on the positive side (*Monomorium pharaonis, Cyphomyrmex rimosus*, *Acropyga palaga*, *Typhlomyrmex* sp.1, *Solenopsis* sp.4, *Pseudomyrmex gracilis* sp.1, *Pheidole* sp.2 and sp.3, *Acromyrmex* sp.1, *Acropyga* sp.1) and ten on the negative side (*Camponotus* sp.2, *Crematogaster negripliosa, Pachycondyla* sp.1, *Neivamyrmex punctaticeps, Odontomacus yucatecus, Labidus praedator, Solenopsis* sp.1, *Camponotus* sp.3, *Pseudomyrmex gracilis* sp.2, *Ectatomma tuberculatum*). Axis 2 discriminated ant communities with improved pastures and savannas on the positive side and rubber plantations on the negative side. A Monte-Carlo permutation test showed that land use is significantly associated with the ant communities present (p= 0.032).

Between-group analyses performed on the ant community data set with region as the explanatory variable extracted 4.46% of the total variance (Figure 4b). Axes 1 and 2 accounted for 56.41% and 43.59% of the variance extracted, respectively. Ten ant species contributed to the formation of axis 1, all on the positive side (*Typhlomyrmex* sp.1, *Pseudomyrmex gracilis* sp.2, *Odontomacus yucatecus*, *Hypoponera punctaticeps*, *E. tuberculatum, Acropyga palaga, Acropyga* sp.1, *Camponotus* sp.1, *Crematogaster nigropilosa*, *C. obscurata*). Axis 1 discriminated ant communities according to region, with Carimagua on the positive side and Puerto Gaitán and Puerto López on the negative side. Seventeen ant species contributed to the formation of axis 2, ten on the positive side (*Pachycondyla arhuaca, Hypoponera* sp.2, *Pheidole* sp.2 and sp.3, *Pseudomyrmex gracilis* sp.5, *Solenopsis* sp.4, *Crematogaster*

curvispinosa, *C. foliocrypta*, *Solenopsis* sp.1 and B*rachymyrmex* sp.2) and seven on the negative side (*Pheidole* sp.4, *B. longicornis*, *Dolichoderus bispinosus*, *C. rochai, Acanthostichus sanchezorum, Pseudomyrmex pallens* and *Solenopsis* sp.2). Axis 2 discriminated ant communities with the Puerto López region on the positive side and Puerto Gaitán on the negative side. A Monte-Carlo permutation test showed that region significantly affects ant communities (p= 0.001).

a) Effect of land use   b) Effect of region
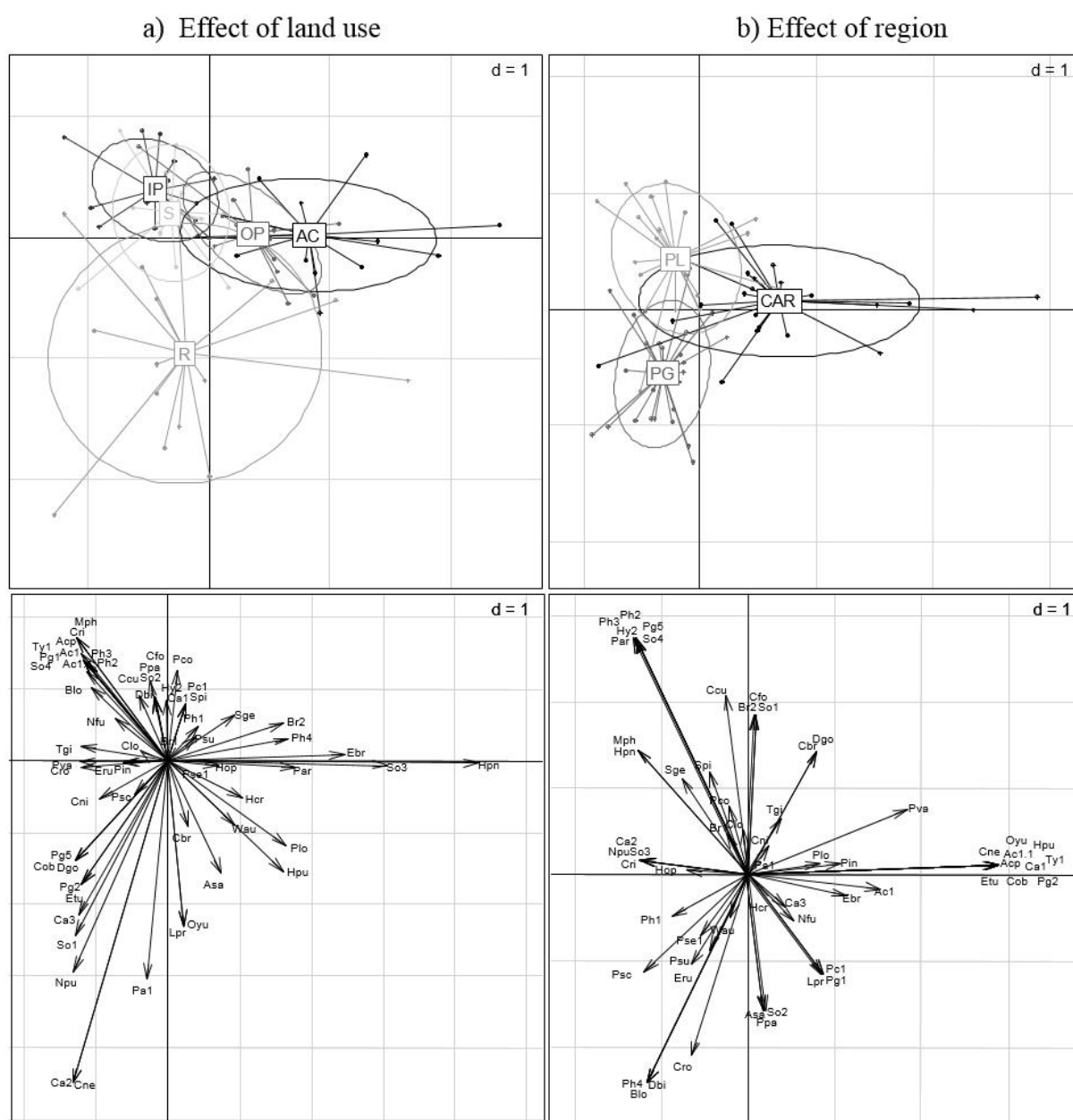
Figure 4. Between-group analysis on ant communities with land use (a) or region (b) factor. Top: projection of data set variability plotted on a factorial map of the first two discriminating axis according to respective factor. Labels on the gravity center correspond to sub-factor of respective factor. Bottom: correlation circles plot with variable vectors (for codes, see Appendix 1) for each respective factor. (a) Land uses: IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation. Eigen values 34.81%, 29.76% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.032. Explained variance: 6.93%. (b) Regions: PL: Puerto López, PG: Puerto Gaitán, CAR: Carimagua. Eigen values 56.41%, 43.59% for axes 1 to 2 respectively. Randtest: simulated p-value: 0.001. Explained variance: 4.46%.

Co-inertia analysis, to analyze covariation with soil physical and chemical properties, was also used on ant or termite species occurrences. However, no significant co-variation was found between physical or chemical soil properties and termite or ant community data sets.

3.3.4 Effect of environmental factors on soil engineer species occurrence

General linear models (GLM) testing the effect of environmental factors (region, land use, physical and chemical soil properties) on soil engineer species occurrence allowed for examination of the association between soil properties, regional differences and land use and each ant (Table 2) and termite (Table 3) species taken separately. This work only considered the species present in five or more sampled fields. Nineteen soil physical and chemical properties, in addition to land use and region, are significantly associated with the occurrences of 15 ant species (Table 2). Two species of ants were influenced by the region (*Crematogaster rochai* and *Pheidole subarmata*) and 5 by land use *Acromyrmex* sp.1, *C. nigropilosa, Ectatomma brunneum, Nylanderia fulva*, *Ph. subarmata*). The species significantly affected by the highest number of factors, *Solenopsis geminata* was positively related to CEC and Cu concentration and negatively associated with Mn concentration, mesoporosity and silt. Five species were significantly associated with four different combinations of environmental

variables: *C. rochai* (pH, Ca and B concentrations and region), *E. brunneum* (cation exchange capacity, Fe concentration, total porosity and land use), *N. fulva* (B concentration, macroporosity, silt concentration and land use) and finally, *Ph. subarmata* (CEC, B concentration, land use and region); (see Table 2). Interestingly, CEC is the factor that was associated with the highest number of ant species, two positively and three negatively. This was followed by B concentration which was associated with four ant species, two positively and two negatively. In addition, land use was related to five ant species: *Acromyrmex* sp.1 (higher occurrence in improved pastures than in oil palm plantations), *C. nigropilosa* (higher occurrence in annual crops than in savannas), *E. brunneum* (higher occurrence in rubber than in oil palm plantations), *N. fulva* (higher occurrence in annual crops than in improved pastures) and *Ph. subarmata* (higher occurrence in in annual crops than in oil palm plantations) (Table2).

Eleven soil physical and chemical variables, in addition to land use and region, are significantly associated with six termite species (Table 3), five of those variables have a positive association and eight a negative association. The observed occurrences of two termite species were significantly influenced by silt concentration: *Grigiotermes* sp.1 negatively and *Syntermes modestus* positively. *Grigiotermes* sp.1 and *Grigiotermes* sp.2 were significantly associated with land use (high occurrence in annual crops than in improved pasture). *Anoplotermes* sp.4 was affected by the region (highest occurrence in Puerto López and lowest in Carimagua). Additionally, this species was associated with the three soil characteristics: negatively by pH and Cu concentration, and positively by volumetric moisture.

Table 2. Effect of environmental descriptors (physical and chemical soil properties (for codes, see Table1), land uses and regions on the occurrence of ant species. The results come from an automatic step-wise procedure. Only variables with a significant effect and species present in 5 or more samples were kept. % sp with significant effect: Total number of species with effect of physical and chemical features; % sp with positive effect: Percentage of species with positive effect. % sp with negative effect: Percentage of number of species with negative effect; P-value: *** = 0.001, ** = 0.01, * = 0.05, ° = 0.10.

	pH	N	C	Ca	Mg	CEC	S	B	F	Mn	Cu	VM	BD	MAC	MES	MIC	POR	Si	Cl	Land Use	Region	Occurrence
Acromyrmex sp. 1			°(-)			*(+)														** (OP< R< AC< S< IP)		8
Brachycmyrmex sp. 1										*(-)					**(-)							37
Camponotus sp. 3						*(-)			*(-)													5
Crematogaster longispina		°(+)													°(+)							5
Crematogaster nigropilosa				°(+)								°(-)								*(AC< OP< IP< R < S)		12
Crematogaster rochai	°(+)		***(-)					**(+)													*(PL < C< PG)	7
Ectatomma brunneum						°(-)		°(+)									°(+)			° (R< IP < AC < S < OP)		7
Ectatomma ruidum	*(+)				°(-)								**(+)									14
Hypoponera creola																		°(+)				18
Hypoponera opacior			°(-)			**(-)										***(-)			**(+)			16
Nylanderia fulva								*(-)							°(+)			°(+)		** (AC< R< OP< S< IP)		19
Pheidole inversa										**(+)		°(+)										9
Pheidole sp. 1										*(-)	*(+)											10
Pheidole subarmata						*(-)		**(+)												** (AC< R< S< IP< OP)	** (PL<C < PG)	20
Solenopsis geminata						°(+)				*(-)	°(+)				*(-)			*(-)				7
% sp with significant effect	13.3	6.6	13.3	13.3	6.6	33.3	6.6	26.6	13.3	20	13.3	13.3	6.6	13.3	13.3	6.6	6.6	13.3	13.3	33.3	13.3	0
% sp with positive effect	13	6.6	0	6.65	0	20	0	20	6.65	0	13.3	6.65	6.6	13.3	0	0	6.6	6.65	13.3	--	--	--
% sp with negative effect	0	0	13.3	6.65	6.6	13.3	6.6	6.6	6.65	20	0	6.65	0	0	13.3	6.6	0	6.65	0	--	--	--

Land uses (IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation) and regions (PL: Puerto López, PG: Puerto Gaitán, CAR: Carimagua)

Table 3. Effect of environmental descriptors (physical and chemical soil properties (for codes, see Table1), land uses and regions on the occurrence of termite species. The results come from an automatic step-wise procedure. Only variables with a significant effect and species present in 5 or more samples were kept. % sp with significant effect: Total number al of species with effect of physical and chemical features; %sp with positive effect: Percentage of species with positive effect % sp with negative effect: Percentage of number of species with negative effect. P-value: *** = 0.001, ** = 0.01, * = 0.05, ° = 0.10.

	pH	S	B	Mn	Cu	SM	VM	BD	MAC	POR	Si	Land use	Region	Occurrence
Anoplotermes **sp. 3**	°(-)	** (-)								°(-)				34
Anoplotermes **sp. 4**	* (-)				** (-)		* (+)						°(PL< PG< C)	14
Grigiotermes sp. **1**												***(AC< S< R< OP< IP)		33
Grigiotermes **sp. 2**						° (+)		**(+)			*(-)	** (AC< S< R< OP< IP)		27
Heterotermes tenius									* (+)					6
Syntermes modestus			° (-)	* (-)							** (+)			10
% sp with significant effect	33.3	16.6	16.6	16.6	16.6	16.6	16.6	16.6	16.6	16.6	33.3	33.3	16.6	
% sp with positive effect	0	0	0	0	0	16.6	16.6	16.6	16.6	0	16.65	--	--	--
% sp with negative effect	33.3	16.6	16.6	16.6	16.6	0	0	0	0	16.6	16.65	--	--	--

Land uses (IP. Improved Pasture, S. Savanna, OP: Oil Palm plantation, AC. Annual Crop, R: Rubber plantation) and regions (PL: Puerto López, PG: Puerto Gaitán, CAR: Carimagua)

3.4 Discussion

Two groups of land use can be distinguished according to their ant communities: (1) savannas and (2) oil palm plantations, annual crops, rubber plantations and improved pastures (Figure 4). Similarly, three groups of land use can be distinguished according to their termite communities: (1) rubber plantations, (2) improved pastures and savannas and (3) annual crops and oil palm plantations (Figure 3). Co-inertia analyses suggest that there is no general relation between ants or termites and soil properties. However, this does not preclude the observance of significant relations between certain soil properties and species when the data are analyzed at the species level. Indeed, co-inertia tests for general patterns between groups of soil properties and groups of species and the fact that such patterns are not encountered does not exclude the possibility

of significant relationships between single soil properties and species. Indeed, the GLM analyses show positive and negative relationships of soil properties with ant and termite species occurrence. Ants are positively associated with high soil porosity and negatively related with CEC (Table 2). Termites appear to be positively affected by physical factors such as the volumetric moisture, bulk density and macroporosity. Termites are also negatively associated with high soil chemical fertility (associated to high pH and high N, C, Mn and Cu concentrations, Table 3).

3.4.1 Effect of the regions or land uses on soil properties

This study was carried out along transect through the 'eastern Colombian plains'. In this region, there exists a gradient in precipitation between Puerto López and Carimagua as well as a subtle gradient in soil texture, with a higher sand concentration, in Puerto López than in Carimagua, and also a marked local variability (Lavelle et al. 2014). This may cause slight differences in the physical and chemical properties of their soils. However, differences in soil chemical and physical properties between land uses appear to exert a much stronger influence on soils than regional trends.

Human activities such as the conversion of natural land into cropland can significantly affect and modify soil chemical and physical properties, often resulting in land degradation (Lobry de Bruyn and Conacher 1990). Due to the high bulk densities encountered in this region, establishment of annual crops requires improving soil physical properties via tillage (Amezquita et al. 2004), which serves to increase soil porosity. It was indeed found that the microporosity increases in annual crops, but mesoporosity decreases. In improved pastures, compaction by cattle might be expected to increase bulk density and to decrease pore space (Decaëns et al. 2001). However, we found relatively low bulk densities in improved pastures (Lavelle et al. 2014), and this might be explained by high earthworm densities and/or root growth in this land use (Decaëns et al. 1994). In fact, the high microporosity under annual crops

and improved pastures might be linked to their lower sand concentration and slightly higher silt concentration. Such concentrations are difficult to explain, but it can be argued that farmers may select finer textured and probably more fertile soils for annual crops and improved pastures. Savannas and oil palm plantations have high bulk density and clay concentration, this was unexpected for the oil palm plantations and may be related to farmers choosing heavier textured soils for these plantations. Rubber plantations have a high macro and mesoporosity, which could be explained by the high amounts of biogenic soil aggregates in these plantations or the high density of perennial roots. Alternatively, farmers may choose savanna soils that exhibit among other features a higher porosity, a deeper profile and high available water storage capacity to implement these plantations (Lavelle et al. 2014). Annual crops are characterized by a high chemical fertility, with elevated values of base cations. This is probably due to the creation of an arable layer when savannas are converted into cropland (Amezquita et al. 2004), which involves substantial inputs of lime, fertilizers and deep tillage (Lavelle et al. 2014; Amezquita et al. 2004). In contrast, rubber, oil palm plantations and savannas have relatively low chemical fertility, reflecting both the low intrinsic nutrient status of the parent soil in the Altillanura Lavelle et al. 2014) and reduced fertilization.

3.4.2 Effect of the regions or land uses and ant or termite communities.

In the Colombian Altillanura, termites represent over 45% of the total biomass of macroinvertebrates (Black et al. 1997). In general, termites are prolific and are very important for the ecology of savannas. Termites recycle mineral nutrients through their feeding activities, they modify soil texture and create heterogeneity in soil properties through the building of termite mounds. This study confirms that termite communities in savannas differ from the other land uses (Figure 3), mainly due to the presence of two species: *Nasutitermes* sp.2 and *N. talpoides*. Their ecology is poorly known, but they are subterranean and this type of nesting behavior is likely more susceptible to tillage or intensive grazing. In this sense, savanna is the

only system where tillage has not been carried out, highlighting that this practice may be quite important in determining termite assemblage in this region. In the other land uses, the dominance of a particular group of termites is not evident, but the genus *Heterotermes* was present in almost all of them, suggesting a greater plasticity. Annual crops were negatively associated with all termite species. Indeed, this system does not provide the ideal conditions for the establishment of termite colonies due to tillage or the application of pesticides (Costa-Milanez et al. 2014; Vasconcelos et al. 2008) and the absence of permanent vegetation cover. This result is contrary to Barros et al. (2003) who found the highest termite densities in annual crops within the Brazilian Amazonia. However, the authors mention that they collected macrofauna immediately after harvest, when there are crop residues on the soil, which could favor some termite groups. In our case, the sampling of soil fauna was carried out during the middle of the cropping season.

Ant communities are strongly influenced by habitat type (Costa-Milanez et al. 2014) vegetation structure and land management (Sanabria et al. 2014) especially in South American savannas (Vasconcelos et al. 2008). This is because vegetation is a major regulator of microclimatic conditions, which influences ant activity. In the present case, this is clearly supported by the difference between savanna and improved pastures on the one side, and rubber plantations and oil palm plantations on the other. Past research suggests that ecosystems with trees are more complex and offer a higher diversity of micro-habitats and niches, which could allow them to host a higher ant diversity (Cabra-Garcia et al. 2012). However, in this study improved pastures showed the highest numbers of species followed by savannas, and they share 31 species in total (Sanabria et al. 2014). This finding contrasts with Dëcaens et al. (1994), who found lower abundances of ants in pastures of the same region. This result is likely due to the fact that their pastures were overgrazed, which reduces herbaceous cover. In this study, the similarity between ant communities in savanna and improved pastures can be explained by: (1) the majority of

savanna soils have been impoverished by decades of extensive grazing and dry season fires (Lavelle et al. 2014; Dray et al. 2003) which could reduce soil biodiversity; (2) soil invertebrate communities tend to be better preserved during a land use change when the new system has a vegetative cover similar to the original (Gomes et al. 2009) and savannas and improved pastures are the most similar land uses studied because they are both dominated by a permanent herbaceous layer. We expected ant communities to be similar in both oil palm plantations and rubber plantations, as they are both comprised of trees. However, ant communities are more similar between annual crops and oil palm plantation (they share about the 70% of their species). We suppose that this may partially be attributed to the presence of predatory ants, such as *Hypoponera punctatissima* sp.1 and *Ectatomma brunneum*, in both land uses. In these land uses they are likely to encounter abundant prey, such as immature Lepidotera or mites, which are very common in annual crops and young oil palm plantations. Moreover, predatory ants have been shown in some cases to greatly influence the structure of ant communities (Arcila et al. 2002).

3.4.3 Effect of soil properties, regions and land uses on ant or termite species

Overall, termite and ant communities are not linked to soil properties, as was indicated by co-inertia analyses. However, general lineal models applied separately to each species document many cases of significant positive or negative associations of soil characteristics on ant and termite species. Co-inertia is a multivariate method to assess the similarity between the overall structures of two data sets (Gomes et al. 2009). The GLM generalizes linear regression by allowing for the association of response variables, here the occurrence of termite and ant species to explanatory variables (Crawley 2012). Thus, the apparent contradiction between the results of co-inertia and GLM analyses would be due to the fact that environmental variables and land uses do not affect ant and termite communities in a consistent way across all species or due to

these species could have a mosaic distribution along the terrain, which cannot be evaluated by the employed method.

Acromyrmex sp.1 and *Solenopsis geminata*, (that construct their nest with, on and within soil) were positively associated with high values of CEC, which is related to clay concentation, organic matter and overall soil fertility. Such characteristics correspond well to improved pastures, the land use where these species were frequently encountered. Alternatively, the observed association between these species and CEC, could be due to the impact of ants (or termites) on soil properties, and not only to their habitat preference. We also found that total N to be positively associated with *Crematogaster longispina*. This could be explained by the fact that ants tend to increase C and mineral nutrient concentration in soils especially in and around their nests (Decaëns et al. 1994). The same authors mention that soil bulk density tends to decrease with the presence of ants due to their burrowing activities. This is in line with the fact that nine ant species are associated with bulk density, and that seven of them are negatively linked to bulk density.

E. brunneum, is encountered less often in rubber plantations and improved pastures, but more often in oil palm plantations and annual crops. Gomes et al. (2009) described this species as a solitary predatory with well-developed stingers. They build their nest on the ground and their abundance is remarkable in open fields or degraded areas, such as grasslands, plantations and roads, among others. It can be hypothesized that this predatory species is more common in oil palm plantations and annuals crops that are more suitable for its foraging and may host suitable prey (Hölldobler and Wilson 1990).

In Colombia, *Nylanderia fulva* is an introduced species and is considered a serious pest that often displaces native fauna (Arcila et al. 2002). This species was mainly associated with annual crops. This land use leads the highest level of disturbance (tillage and pesticides), which might

allow *N.fulva* to displace native termites. Soils of annual crops tend to have a high chemical fertility, and this may explain why termites tend to be associated with low chemical fertility in this study. This finding is consistent with Barros et al. (2003) who suggested that termite diversity decreases with land use intensification because of the negative impact of tillage, pesticides and the absence of perennial vegetation. Some termite species are associated with soil physical characteristics (Lavelle and Spain 2001). For example, *Heterotermes tenius* is positively associated with mesoporosity and available water capacity. This is a subterranean termite that is considered as an agricultural pest because they feed on wood or other cellulosic materials (Constantino 2002). It can be hypothesize that this species prefers more porous soil for nesting, and we have shown that soil porosity is higher in rubber plantations. This is consistent with the fact that *H. tenius* likely finds ideal conditions for feeding and nesting in rubber plantations (Constantino 2002). Many species (e.g. *Syntermes modestus* and *Neocapritermes talpa*) are associated to low microporosity, silt and clay values. This contradicts Barros et al. (2003), who say that high soil clay concentrations are favorable to termites because clay is important for all of the structures they build. This also contradicts Bruyn and Conacher (1990) who consider that termites increase water infiltration and aeration by incorporating organic matter into the soil and constructing galleries within the soil. Also, one of the major effects of termites in ecosystems is their role in loosening of soils (i.e., reduction of bulk density) (Jouquet et al. 2011). In this sense, if the termite need for clay and their impact on porosity can be generalized, the association of termites with low clay and microporosity values requires a supplementary mechanism. We can hypothesize that this association would thus be due to the effect of land use on termite communities and not to the direct effect of the associated soil properties on termites.

3.5 Conclusion

Here, land use and soil characteristics explain only a small part of the overall variability in ant and termite communities. The remaining unexplained variability could be attributed to the influence of factors that have not been taken into account: (1) interactions with other organisms such as predators and prey and (2) the history of each cultivated plot, (3) the precise structure of the landscape. However, this study showed that ant and termite communities depend on land use (type of vegetation cover), which is linked to management practices (inputs of fertilizer, tillage, etc). Annual crops are the most detrimental land use for ants and termites and tillage is probably the most important negative management driver associated with this effect (Schmidt et al. 2013, Sharma et al. 2001). Because ants and termites are important soil organisms that contribute to the maintenance of soil structure (Lavelle and Spain 2001), maintaining a high diversity of these soil engineers could increase the long-term provisioning of the ecosystem services they help regulate. Grimaldi et al. (2014), showed that landscape structure drives soil ecosystem services of regulation and support in Amazonian landscape. Some of them depend partially on soil ecosystem engineers (Lavelle et al. 2006), which suggests that these services and soil biodiversity should be managed at the scale of the land use mosaic. In order to maintain the benefits that soil ecosystem engineers provide, two types of recommendations may be suggested: 1) adapt practices within the more intensively managed land uses, especially annual crops, to be less detrimental. In this sense practices such as tillage and pesticide use could be reduced; and 2) decrease the proportion of annual crops in the landscape and keep and/or restore semi-natural systems such as savannas and improved pastures, which should facilitate the maintenance of heterogeneous mosaics of land uses that are favorable to soil organisms (Lavelle et al. 2014).

3.6 References

Amézquita, E., R.J. Thomas, I.M. Rao, D.L. Molina, P. Hoyos, Use of deep-rooted tropical pastures to build-up an arable layer through improved soil properties of an Oxisol in the Eastern Plains (Llanos Orientales) of Colombia, Agric. Ecosyst. Environ. 103 (2004) 269–277.

Anderson, J.M., J.S.I. Ingram, Tropical Soil Biology and Fertility. A Handbook of Methods, Second Ed, CAB International, Wallingford U.K., Wallingford U.K., 1993.

AntWeb, (2014). www.antweb.org (accessed January 20, 2014).

Arcila, A.M., L.A. Gómez, P. Ulloa-Chacón, lmmature Development and Colony Growth of Crazy ant Paratrechina fulva Under Laboratory Conditions (Hymenoptera: Formicidae), Sociobiology. 39 (2002) 307–321.

Barros, E., A. Neves, E. Blanchart, E.C.M. Fernandes, E. Wandelli, P. Lavelle, Development of the soil macrofauna community under silvopastoral and agrosilvicultural systems in Amazonia, Pedobiologia. 47 (2003) 273–280.

Baty, F., M. Facompré, J. Wiegand, J. Schwager, M.H. Brutsche, Analysis with respect to instrumental variables for the exploration of microarray data structures., BMC Bioinformatics. 7: 422 (2006) 1-8.

Black, H.I.J., M.J.N. Okwakol, Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites, Appl. Soil Ecol. 6 (1997) 37–53.

Bolton, B. Identification Guide to the Ant Genera of the World, Harvard University Press, Cambridge, 1994.

Cabra-Garcia, J., C. Bermudez-Rivas, A.M. Osorio, P. Chacon, Cross-taxon congruence of a and b diversity among five leaf litter arthropod groups in Colombia, Biodivers. Conserv. 21 (2012) 1493–1508.

Constantino, R. The pest termites of South America : taxonomy, distribution and status, J. Appl. Ent. 126 (2002) 355–365.

Costa-Milanez, C.B., G. Lourenço-Silva, P.T.A. Castro, J.D. Majer, S.P. Ribeiro, Are ant assemblages of Brazilian veredas characterized by location or habitat type?, Brazilian J. Biol. 74 (2014) 89–99.

Crawley, M. The R Book, 2nd edition, London U.K., 2012.

Decaëns, T., J.J. Jiménez, E. Barros, A. Chauvel, E. Blanchart, C. Fragoso, P. Lavelle, Soil macrofaunal communities in permanent pastures derived from tropical forest or savanna, Agric. Ecosyst. Environ. 103 (2004) 301–312.

Decaëns, T., P. Lavelle, J.J. Jimenez, G. Escobar, G. Rippstein, Impact of land management on soil macrofauna in the Oriental Llanos of Colombia, Eur. J. Soil Biol. 30 (1994) 157–168.

Decaëns, T., P. Lavelle, J.J. Jiménez, G. Escobar, G. Rippstein, J. Schneidmadl, J. I. Sanz, P. Hoyos, R. J. Thomas, Impact of land management on soil macrofauna in the Eastern plains of Colombia, in: J.J. Jiménez, R.J., Thomas (Eds.), Soil Macroinvertebrate Communities Neotropical Savannas of Colombia, CIAT publication 324, 2001, Pp 19-41.

Dray, S., D. Chessel, J. Thioulouse, Co-inertia analysis and the linking of data tables, Ecology. 84 (2003) 3078–3089.

Fernández, F., Introducción a las hormigas de la región Neotropical, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2003.

Gomes, L., I.C. Desuó, G. Gomes, Behavior of Ectatomma brunneum (Formicidae: Ectatomminae) Preying on Dipterans in Field Conditions, Sociobiology. 53 (2009) 913–926.

Grimaldi, M., J. Oszwald, S. Dolédec, M.P. Hurtado, I. de Souza Miranda, X. A. de Sartre, W. Santos De Assis, E. Castaneda, T. Desjardins, F. Dubs, E. Guevara, V. Gond, T.T. Santana Lima, R. Marichal, F. Michelotti, D. Mitja, N. Cornejo Noronha, M.N Delgado Oliveira, B. Ramirez, G. Rodriguez, M. Sarrazin, Jr. M. Lopes Da Silva L. Gonzaga Silva Costa, S. Lindoso de Souza, I. Veiga, E. Velasquez, P. Lavelle, Ecosystem services of regulation and support in Amazonian pioneer fronts: Searching for landscape drivers, Landsc. Ecol. 29 (2014) 311–328.

Heiniger, C., S. Barot, J.-F. Ponge, S. Salmon, L. Botton-Divet, D. Carmignac, F. Dubs, Effect of habitat spatiotemporal structure on collembolan diversity, Pedobiologia. 57 (2014) 103–117.

Hölldobler, B., E.O. Wilson, The Ants, Springer-Verlag, Berlin/Heidelberg, 1990.

Jones, C. G., J. H. Lawton, M. Shachak, Organisms as ecosystem engineers. Oikos. 69 (1994) 373-386.

Jouquet, P., S. Traoré, C. Choosai, C. Hartmann, D. Bignell, Influence of termites on ecosystem functioning. Ecosystem services provided by termites, Eur. J. Soil Biol. 47 (2011) 215–222.

Laossi, K.R., S. Barot, D. Carvalho, T. Desjardins, P. Lavelle, M. Martins, D. Mitja, A. C. Rendeiro, G. Rousseau, M. Sarrazin, E. Velásquez, M. Grimaldi, Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures, Pedobiologia. 51 (2008) 397–407.

Lavelle, P., A. V. Spain, Soil ecology, Kluger Academic Publishers, Netherlands, 2001.

Lavelle, P., D. Bignell, M. Lepage, W. Wolters, P. Roger, P. Ineson, O.W. Heal, S. Dhillon, Soil function in a changing world : the role of invertebrate ecosystem engineers, Eur. J. Soil Biol. 33 (1997) 159–193.

Lavelle, P., N. Rodríguez, O. Arguello, J. Bernal, C. Botero, P. Chaparro, Y. Gómez, A. Gutiérrez, M.P. Hurtado, S. Loaiza, S. X. Pulido, E. Rodríguez, C. Sanabria, E. Velásquez, S. J. Fonte, Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia, Agric. Ecosyst. Environ. 185 (2014) 106–117.

Lavelle, P., T. Decaëns, M. Aubert, S. Barot, M. Blouin, F. Bureau,P. Margerie, P. Mora, J.P Rossi, Soil invertebrates and ecosystem services, Eur. J. Soil Biol. 42 (2006) S3–S15.

Lobry de Bruyn, L.A., A. J. Conacher. The role of termite and ants in soil modification: A review, Aust. J. Soil. Res. 28 (1990) 55-93

Longino, J.T. Ants of Costa Rica, (2004). www.evergreen.edu/ants/AntsofCostaRica (accessed January 20, 2015).

Luke, S.H., T.M. Fayle, P. Eggleton, E.C. Turner, R.G. Davies, Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo, Biodivers. Conserv. 23 (2014) 2817–2832.

Marichal, R., M. Grimaldi, A. Feijoo M., J. Oszwald, C. Praxedes, D.H. Ruiz Cobo, M.P. Hurtado, T. Desjardins, M. Lopes da Silva, L. G. da Silva Costa, I. Souza Miranda, M. N. Delgado Oliveira, G. G. Brown, S. Tsélouiko, M. Bonifacio Martins, T. Decaëns, E. Velásquez, P. Lavelle, Soil macroinvertebrate communities and ecosystem services in deforested landscapes of Amazonia, Appl. Soil Ecol. 83 (2014) 177–185.

Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, I. Itoua, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, T.H. Ricketts, Y. Kura, J.F. Lamoreux, W.W. Wettengel, P. Hedao, K.R. Kassem, Terrestrial Ecoregions of the World: A New Map of Life on Earth, Bioscience. 51 (2001) 933-938.

Palacio, E.E., F. Fernández, Clave para las subfamilias y géneros, in: F. Fernández (Ed.), Introducción a Las Hormigas La Región Neotropical, 1st edition., Instituto de Investigación de Recursos Biológicos Alexander von Humboldt., Bogotá D.C., 2003: pp. 233–260.

R Foundation for Statistical Computing, R Development Core Team. R: A Language and Environment for Statistical Computing, Vienna, Austria. 2010.

Rocha, M.M., E.M. Cancello, T.F. Carrijo, Neotropical termites: Revision of Armitermes Wasmann (Isoptera, Termitidae, Syntermitinae) and phylogeny of the Syntermitinae, Syst. Entomol. 37 (2012) 793–827.

Romero-Ruiz, M.H., S.G.A. Flantua, K. Tansey, J.C. Berrio, Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia, Appl. Geogr. 32 (2012) 766–776.

Sanabria, C., P. Lavelle, S.J. Fonte, Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos, Appl. Soil Ecol. 84 (2014) 24–30.

Schmidt, F.A., C.R. Ribas, J.H. Schoereder, How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators, Ecol. Indic. 24 (2013) 158–166.

Sharma, R.K., K. Srinivasa Babu, R.S. Chhokar, A. K. Sharma, Effect of tillage on termites, weed incidence and productivity of spring wheat in rice–wheat system of North Western Indian plains, Crop Prot. 23 (2004) 1049–1054.

Thioulouse, J., Y. Prin, R. Duponnois, Multivariate analyses in soil microbial ecology: a new paradigm, Environ. Ecol. Stat. 19 (2012) 499–520.

Vasconcelos, H.L., M.F. Leite, J.M.S. Vilhena, A.P. Lima, W.E. Magnusson, Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants, Austral Ecol. 33 (2008) 221–231.

3.7 Annexes

Appendix 1: List of ant species used in the analysis. Only species that appeared in 2 or more samples were kept. The last column (#samples) gives the number of samples in which each ant specie appeared from a total of 75 samples.

Species Code	Specie	# samples (x/75)
Asa	*Acanthostichus sanchezorum*	3
Am1	*Acromyrmex sp.1*	8
App	*Acropyga palaga*	3
Ap1	*Acropyga sp.1*	3
Blo	*Brachymyrmex longicornis*	2
Br1	*Brachymyrmex sp.1*	37
Br2	*Brachymyrmex sp.2*	3
Ca1	*Camponotus sp.1*	2
Ca2	*Camponotus sp.2*	2
Ca3	*Caponotus sp.3*	5
Cbr	*Centromymex brachycola*	4
Cne	*Crematogaster negripliosa*	2
Ccu	*Crematogaster curvispinosa*	4
Cfo	*Crematogaster foliocrypta*	2
Clo	*Crematogaster longispina*	5
Cni	*Crematogaster nigropilosa*	12
Cob	*Crematogaster obscurata*	2
Cro	*Crematogaster rochai*	7
Cri	*Cyphomyrmex rimosus*	3
Dbi	*Dolichoderus bispinosus*	3
Dgo	*Dorymyrmex goeldii*	2
Ebr	*Ectatomma brunneum*	7
Eru	*Ectatomma ruidum*	14
Etu	*Ectatomma tuberculatum*	2
Hpu	*Hypoponera punctatissima*	3
Hcr	*Hypoponera creola*	18
Hop	*Hypoponera opacior*	16
Hpn	*Hypoponera punctatisima*	2
Hy2	*Hypoponera sp.2*	2
Lpr	*Labidus praedator*	2
Mph	*Monomorium pharaonis*	3
Npu	*Neivamyrmex punctaticeps*	3
Nfu	*Nylanderia fulva*	19
Oyu	*Odontomacus yucatecus*	2
Par	*Pachycondyla arhuaca*	1
Pa1	*Pachycondyla sp.1*	3
Plo	*Paratrechina longicornis*	4
Pco	*Pheidole cocciphaga*	4
Pin	*Pheidole inversa*	9

Psc	*Pheidole scalaris*	4
Ph1	*Pheidole sp.1*	10
Ph2	*Pheidole sp.2*	2
Ph3	*Pheidole sp.3*	2
Ph4	*Pheidole sp.4*	3
Psu	*Pheidole subarmata*	20
Pva	*Pheidole vallifica*	4
Pg1	*Pseudomyrmex gracilis sp.1*	2
Pg2	*Pseudomyrmex gracilis sp.2*	2
Pg5	*Pseudomyrmex gracilis sp.5*	2
Pc1	*Pseudomyrmex occulatus sp.1*	2
Ppa	*Pseudomyrmex pallens*	3
Pse1	*Pseudomyrmex sp.1*	11
Sge	*Solenopsis geminata*	7
Spi	*Solenopsis picea*	4
So1	*Solenopsis sp.1*	3
So2	*Solenopsis sp.2*	3
So3	*Solenopsis sp.3*	2
So4	*Solenopsis sp.4*	2
Tgi	*Tranopelta gilva*	4
Ty1	*Typhlomyrmex sp.1*	2
Wau	*Wasmannia auropunctata*	4

Appendix 2. List of termite species used in the analysis. Only species that appeared in 2 or more samples were kept. The last column (#samples) gives the number of samples in which each termite specie appeared from a total of 75 samples.

Specie code	Specie	# samples (x/75)
An3	*Anoplotermes sp.1*	34
An4	*Anoplotermes sp.4*	14
Gr1	*Grigiotermes sp.1*	33
Gr2	*Grigiotermes sp.2*	27
Hte	*Heterotermes tenius*	6
Na2	*Nasutitermes sp.2*	3
Nta	*Neocapritermes talpa*	2
Ntp	*Neocapritermes talpoides*	2
Sym	*Syntermes molestus*	10
Te1	*Termes sp.1*	5

Chapter 4: Response of ant traits to agricultural changes

Do biological traits respond to agricultural changes? The case of ground dwelling ants in Colombian Llanos

4.1 Introduction

Agriculture is one of the most influential drivers of change for biodiversity and habitat fragmentation (Chapin et al. 2000). The need for energy resources and food production increases the pressure to expand agricultural lands such that "agricultural frontiers" have reached the last unprotected natural areas in many regions of the world (Hubert et al. 2010). In the Colombian Eastern Plains (Llanos) diverse agricultural activities have pressured natural ecosystems during the last 50 years (Romero-Ruiz et al. 2012). The intensive conversion of natural ecosystems to intensive agriculture results in habitat loss and fragmentation as well as changes in the structure of biological communities (from weeds, and large mammals and birds to small soil-dwelling animals) and impacts their integrity and functioning (Altieri and Nicholls 2003, Fischer et al. 2006). Understanding how land use and land use changes impact these communities remains difficult to predict and new approaches are needed to better quantify and predict the effects of agricultural expansion.

Many methods to predict the impacts of agricultural activities on biodiversity have been developed (Schmidt and Diehl 2008). The most obvious option is to describe taxonomic diversity and to try to predict the impact of land uses on each species, however this restricts predictions to species that have been identified and thoroughly studied (Vandewalle et al. 2010, Moretti et al. 2013). Instead, the trait composition of communities for different types of trait (*e.g.* morphological, eco-physiological and life history characteristics) could be used to better analyze the impact of land use changes and agriculture on communities (Bello et al. 2008) and find general patterns that could allow for improved prediction and mitigation of these impacts (Webb et al. 2010, Pey et al. 2014). In this sense, a combination of morphological, physiological, behavioral, and ecological and life history traits can be used to predict species

distribution and community composition (Sarty et al. 2006, Gibb and Parr 2013). Moreover, trait frequencies are relatively easy to estimate once they have been defined and standard methodologies have been established to assess them (Ribera et al. 2001, Vandewalle et al. 2010, Pey et al. 2014). Of course, all this requires developing a sound knowledge on the links between traits and the ecology of the considered species.

Ant communities constitute a good model to examine the relationship between characteristics of the environment and communities and how these relationships vary along environmental gradients (Gotelli and Ellison 2002). They constitute a diverse and abundant group in most terrestrial communities of ground-dwelling organisms (Hölldobler and Wilson 1990) and perform a range of important ecological functions such as the modification of the physical and chemical environment and affects plants, microorganisms, and other soil organisms (Folgarait 1998). They nest in different substrates and have very diverse diets (scavengers, predaceous, granivorous, herbivorous, etc.) (Hölldobler and Wilson 1990, Retana et al. 2015). Moreover, several studies have pointed out that some ant species have specific traits that are correlated with environmental characteristics in which they live, which can be explained by the ecology or behavior of the species (Hölldobler and Wilson 1990, Kaspari 1993, Schilman et al. 2007). For example, leg length has been shown to be negatively correlated with vegetation cover, and allows increasing ant foraging surface (Wiescher et al. 2012). Recent studies have demonstrated strong relationships between ant morphological traits (*i.e.* pilosity presence of spines, leg length) with habitat complexity and disturbance (Ribera et al. 2001, Bihn et al. 2010, Chown and Gaston 2010, Silva and Brandao 2010, Yates et al. 2014) and confirm that ants are a particularly suitable model to study the factors framing trait covariation in animals (Retana et al. 2015). However, the relation between a set of traits and a set of environmental characteristics in a tropical context has been very rarely tested in ants. This is the goal of our study.

In agricultural landscapes of the Colombian Llanos, we tested the relationship between morphological (*e.g.* Weber's length, head size) and ecological traits (*e.g.* nest size, nest material, type of colony) of ant communities, soil properties and land uses. Indeed, ecological traits are likely to be directly linked to ant habitats and key features of these habitats, while these linkages are likely more indirect and fuzzier for morphological traits. Ecological characteristics such as ant colony features have likely directly evolved as adaptation to environmental features and often have a clear ecological meaning. Morphological traits are also evolving in response to environmental features and may reveal evolutionary pressures (Ricklefs 1987, Ricklefs and Miles 1994). However, the ecological meaning of these characteristics is not always clear. For example, small, mobile colonies are likely to allow for colonization and survival in disturbed environments, while large body size or legs could support either a higher mobility (for example as an adaptation to perturbed open environments) (Silva and Brandao 2010, Retana et al. 2015) or enhance predation success. We also expect significant association between morphological and ecological traits because the two types of traits evolve jointly as responses to the same environmental constraints and because each type of trait evolves according to the evolution of the other type. For example, large body parts such as legs and small mobile colonies might have evolved in response to disturbed environments, but large body size may have evolved in response to the evolution of predatory behaviors on large insects (Carroll and Janzen1973, Hölldobler and Wilson 1990).

Land use clearly influences the distribution of ant species in the agricultural landscape of the Llanos (Sanabria et al. 2016). The dominant land uses have distinct vegetation types that influence ants through different factors: (1) micro-climates, (2) resource availability, (3) abundances of predators, (4) environmental features favoring certain types of nests, (5) the intensity and frequency of disturbance (Hölldobler and Wilson 1990, Folgarait 1998, Díaz et al. 2007, Schmidt and Diehl 2008, Bihn et al. 2010, Wiescher et al. 2012, Toro et al. 2013,

Schmidt et al. 2013, Yates et al. 2014). Soil characteristics are components of ant environment and also influence their distribution (de Bruyn and Conacher 1990, Sanabria et al. 2016). For example, soil texture can influence soil nesting activities, while soil fertility affects the availability and quality of nutritional resources (prey or plants) (Lavelle and Spain 2001). However, the impact of land use on ants should be more profound and pervasive than the impact of soil features, at least at the scale of an agricultural landscape. As stated above, ants might depend on the general soil condition and, for example, soil texture likely influences ant capacity to build their nests within the soil. However, the type of land use determines the microclimate, the type of food ants can encounter, the level of disturbance that ants have to bear, the type vegetal material they can use for their nests. Taken together we have tested the following hypotheses: H1: There is an association between both morphological and ecological traits and land use, such that traits associated with a higher adaptability to extreme conditions and perturbations, are more frequent in land uses such as annual crops and improved pastures. H2: Both morphological and ecological traits are also associated with soil properties, but this relation is less clear than that observed for land use. H3: There is a relation between morphological and ecological traits.

4.2 Materials and Methods

4.2.1 Study area

Fieldwork was carried out in three municipalities (Puerto López (PL), Puerto Gaitán (PG) and Carimagua (CAR)), in the eastern plains of Colombia (between 3°55'21"N–71°01'43"W and 4°38'07"N–72°53'55"W), between June and August 2011. The Llanos region extends to the northeast from the Meta Department to Venezuelan border and is bounded to the north-west by the Andean Eastern Cordillera. At roughly 200 m in elevation, the region has a humid tropical

climate, with an average annual temperature of 26°C, rainfall totaling 2500 mm per year and a marked dry season between December and March (Decaëns et al. 2001, Sanabria et al. 2014).

4.2.2 Sampling scheme

Five representative land uses were sampled in the region: 1) annual crops (AC; including rice, maize and soybeans), 2) rubber plantations (R), 3) oil palm plantations (OP), 4) improved pastures (IP), and 5) semi-natural savannas (S). For each land use, fifteen replicates were sampled leading to a total of 75 fields sampled. In each sampled field a transect of three sampling points was implemented leading a total number of 225 sampling points (5 land uses x 15 field replicates x 3 sampling points). At each sampling point, a modified Tropical Soil Biology and Fertility (TSBF) protocol (Anderson and Ingram 1993) was used to collect soil fauna. Each sampling point consisted in the excavation of a central monolith (25 x 25cm x 20 cm deep) and two adjacent monoliths (25cm x 25cm x 10 cm deep) located 10 m to the North and South of each central monolith leading to a total of 675 fauna samples (225 sampling points x 3 monoliths). All the macro-fauna from the litter and soil of each monolith was hand-sorted. Standing plant biomass was cut 2-3 cm above the soil surface and removed prior to sampling.

4.2.3 Ant identification.

At each sampling point, ants were collected along with other groups of soil macrofauna (only ant data is used here). In the laboratory, ants were separated from other macrofauna organisms and were preserved in 96% alcohol. Identification of ants to the genus level was performed following keys of Palacio and Fernández (2003) and Bolton (1994). For the identification to the species, the "AntWeb" (2016) and Longino (2004) were used. In total, 92 ant species, belonging to 35 genera and nine subfamilies were identified, 70.3% to the species level (64 species) and the remaining 29.7% to the morphospecies level (28 morphospecies) (mainly due to the lack of precise taxonomic knowledge) (see Annex 1 for ants names).

4.2.4 Soil characteristics

A total of eleven soil physical properties were used in this study (Lavelle et al. 2014): volumetric (VM) and gravimetric moisture (GM) content, microporosity (<0.03 μm; MIC), mesoporosity (0.03–3 μm; MES) and macroporosity (>3 μm; MAC), available water storage capacity (AWC), bulk density (BD), resistance to vertical penetration (POR), sand (Sand), silt (Silt) and clay (Clay). Sixteen soil chemical properties were measured including total soil C and N content, cation exchange capacity (CEC), Al saturation (AlS), macro and micronutrient concentrations (Ca, K, Mg, P Bray II (PBr), Al, B, Fe, Mn, Cu and Zn) (Table 1). All measurements were taken at 0-20 cm depth from soil excavated from the pit after sorting out macrofauna except for the bulk density samples which were removed from the vertical walls of the central monolith excavated for soil macrofauna sampling (Table 1).

Table 1. Description of the physic-chemical soil parameters (Lavelle et al. 2014)

	Variables	Names	Units	Analysis techniques
	pH	Hydrogen potential	--	Potentiometric
Chemical	N	Nitrogen Total	g kg-1	UV-VIS
	C	Carbon Total	g kg-1	
		Available Phosphorus	mg kg-1	
	PBry	Total		
	K	Potassium Total	mg kg-1	Atomic absorption spectroscopy
	Ca	Calcium Total	mg kg-1	
	Mg	Magnesium Total	mg kg-1	
	Al	Aluminum Total	mg kg-1	
	CEC	Cation Exchange Capacity	cmol kg-1	Potentiometric
	SAl	Aluminum Saturation	%	
	S	Sulfur Total	mg kg-1	UV-VIS
	B	Boron Total	mg kg-1	
	Fe	Iron Total	mg kg-1	
	Mn	Manganese Total	mg kg-1	Atomic absorption spectroscopy
	Cu	Copper Total	mg kg-1	
	Zn	Zinc Total	mg kg-1	
Physical	SM	Soil Moisture	g 100 g-1	Rings and clod
	VM	Volumetric Moisture	cm 100 cm-1	
	BD	Bulk density	g cm-3	
	AWC	Available Water Capacity	%	
	MAC	Macropores (>3μm)	%	Yolder
	MES	Mesopores (0.03–3μm)	%	
	MIC	Micropores (<0.03μm)	%	
	Sa	Sand,	%	Bouyoucos
	Si	Silt	%	

4.2.5 Trait description

Fifteen ant traits were used in this study, nine are morphological and the remaining six are ecological or behavioral traits (Table 2). Morphological traits are based on features of ant bodies such as the size of different body parts (*i.e.* body size, head size, ocular length, scape length). The ecological traits used are features of ant colonies that depend on ant behavior (*e.g.* size of the nest, nest material, polymorphism, nest localization). While morphological traits are

relatively easy to measure on ant individuals, assessing ecological traits requires time consuming field observations and an extensive literature search.

Morphological traits are measures of the size of different parts of ant bodies or indices calculated from these measures (see Table 2). The measurements were taken using an ocular micrometer mounted on a microscopy stereoscope (Nikon SMZ 500). The morphological traits are Weber's length (WL), head width (HW), scape length (SL), eye length (EL), head length (HL), cephalic index (CI), ocular index (OI) and scape index (SI). Each of those traits was measured on five randomly selected workers of each species. In the cases of morphological dimorphism (*i.e. Pheidole*) or polymorphism (*i.e. Camponotus*) only minors were measured. Pigmentation (P) was informed from literature sources and was coded with 0 for absence of pigmentation (white or very light yellow) and 1 for pigmented species (black, red, brown, etc). Ecological traits were obtained from information available in different literature sources (Fernández 2003, Longino 2004, Lozano-Zambrano et al. 2008, AntWeb 2014). They are linked to ant behavior and describe colony and nest type (Table 2). In a few cases, when the information was not available for a species, the mean trait value from the genera or taxonomically close species was used. The ecological traits are colony type (CT), nest localization (NL), nest material (NM), nest size (NS), crypsis (CR) and castes (CA). Ecological traits are coded in two different ways. Caste and colony type were numerical coded because their categories can be ordered while others traits were considered as purely qualitative because they cannot be ordered (Table 2). For caste we have assigned 1 to monomorphic (workers with not clear difference in size), 2 to polymorphic species (workers in a gradient of sizes) and 3 to dimorphic species (minors and majors workers). In colony type we have assigned 1 to polygenic species (>1 queen per colony) and 0 to monogenic species (=1 queen per colony).

All morphological and ecological traits we have documented have been used previously for ants. The literature provides insight on the ecological significance of most morphological traits

and their links with the occupation of a heterogeneous agricultural landscape (Table 2) (Ribera et al. 2001). For example, Weber's length and nest localization could be associated to habitat complexity, scape length and ocular index could be related to mobility. By definition, ecological traits are directly linked to the demography (Webb et al. 2010) and behaviour of ant colonies (Carroll and Janzen 1973). For example, colony type indicates the ability of species to expand their colony (Hee et al. 2000). Nest localisation and nest material are linked to the tree cover complexity. Note however, that none of the morphological or ecological traits can so far be unambiguously linked to a unique land use.

Trait name	Code.	Measure	Trait functional significance
MORPHOLOGICAL TRAITS			
Weber's length	**WL**	Viewing mesosoma in lateral profile, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck, to posteroventral propodeal lobes	Indicative of worker body size (Weber, 1938), correlates with metabolic function and habitat complexity.
Head width	**HW[a]**	Maximum width of head in face view, including eyes if they project beyond the sides of the head	Size of gaps through which worker can pass (Sarty et al. 2006); mandibular musculature (Kaspari, 1993).
Scape length	**SL[a]**	Length of scape shaft from apex to basal flange, not including basal condyle and neck	Mechano and chemoreception (Schneider, 1964). Sensory abilities, longer scapes facilitate following of pheromone trails (Weiser and Kaspari, 2006).
Eye length	**EL[a]**	Measured along maximum diameter	Eye size indicates feeding behavior, predatory ants have smaller eyes, and activity times (Weiser and Kaspari, 2006).
Head length	**HL[b]**	Perpendicular distance from line tangent to rearmost points of vertex margin to line tangent to anterior most projections of clypeus, in full face view	May be indicative of diet; longer length may indicate herbivory.
Cephalic index	**CI**	100*HW/HL	Those index are frequently used as index of overall size and to construct ant community morphospace (Wesiner and Kaspary 2006)
Ocular index	**OI**	100*EL/HL	Give an idea of how much of the head are occupied by eyes. Species with big eyes are in general good predators or have more ability to the displacement (Longino 2004).
Scape index	**SI**	100*SL/HL	
Pigmentation	**P**	Presence or absence of pigmentation in workers	Stronger cuticle and ability to withstand sunlight
ECOLOGICAL TRAITS			
Colony type	**CT**	It refers to the presence of one or more queens in each colony: 1 = Poligeny (>1 queen) and 0 = Monogeny (one queen per colony).	Poligeny may indicate a better capacity to establish and expand the colony (Hölldobler and Wilson, 1991)
Nest localization	**NL**	Place where ants build their nest: canopy (**NL.cn**), cavities (**NL.cv**), litter (**NL.l**), subterranean or under soil (**NL.s**), substratum or on soil (**NL.st**)	Is associated with the mobility of workers thought the environment. Species with nest in canopy are more mobile than those who nest in soil or substratum.
Nest material	**NM**	Material used by the workers to build the nest: carton (**NM.cn**), soil (**NM.s**), deadwood (**NM.dw**), litter (**NM.l**) and varied (**NM.v**)	Associated with the availability of use different kinds of resources for nesting
Nest size	**NS**	The physical size of the nest: big (**NS.b**), medium (**NS.m**), small (**NS.s**) and very small (**NS.vs**)	
Crypsis	**CR**	Ability of an organism to avoid observation or detection by other organisms: cryptic (**CR.cr**), conspicuous (**CR.co**), tramp ants (**CR.ta**)	Capacity of detection of workers: associated to the ability to not be seen (cryptic) or very conspicuous (tramp ant).
Castes	**CA**	Type of colonial organization: monomorphic = 1, type of size workers (minor); polymorphic = 2, diverse range of size in workers; dimorphic = 3, discrete minor and major (soldier) castes.	Polymorphism: different worker castes perform different tasks within the colony, allowing higher specialization (Hölldobler and Wilson, 1991).

[a]: As many size related characteristics are correlated, in the statistical analysis these features were considered as residuals based on the regression with Weber's length.

[b]: Because HL is used in the morphological index computations, we don't included it in the statistical analysis.

4.2.6 Data analysis

Abundance tables allow building tables of species occurrence (number of monoliths per field in which the species was found). This is a common procedure for ants, due to the social nature of these insects allowing a single sample to contain an extremely high abundance of a rare species (Hölldobler and Wilson 1990).This procedure provides consistent information on species presence and relative abundance inside the community. Only species that occurred in more than five sampled fields were included in the analysis.

The morphological trait values of HW, SL and EL were log-transformed to reduce the effect of extreme values and regressed against $\log_e$ (WL). We used as traits the residuals of these regressions that are thus independent of body size (Gibb et al. 2015). Additionally, to avoid correlations between head length and indices (Ocular, Cephalic and Scape Index) that depend on head length, head length was not taken in account in the analyses.

To describe the relationships between traits and environmental variables we performed a RLQ analyzing the link between table R (environmental variables) and table Q (species traits) through the table L (species occurrence) (see Figure 1). The RLQ analysis has been previously explained by Dolédec et al. (1996) and consists of analyzing the joint structure of these tables in order to decompose the eigenvalue of the cross-matrix and provides the common ordination axes onto which traits and environmental variables are projected.

We used four data tables: the environmental characteristic table (R for physic-chemical parameters and land use types), the species table (L for species occurrence) and two trait tables (Qm and Qe for morphological and ecological traits, respectively). First, each table was analyzed by specific multivariate analysis separately, which allows for determination of how much of the total variance of each table is represented in the RLQ. The species table (table L) was analyzed by a correspondence analysis (CA). A principal component analysis (PCA) was applied to quantitative morphological traits (table Qm) and a Hill-Smith ordination to

ecological traits (table Qe) that are both quantitative and qualitative data. A Hill-Smith ordination was also applied to environmental site characteristics (table R) as we included the land use in it (Figure 1).

After analyzing a RLQ with both ecological and morphological traits, two RLQ were performed separately, the first one with morphological traits (table Qm) and the second one with ecological traits (table Qe). The significance of the relationship between the environmental attributes and traits was tested using random permutations. Here values of sites and traits were permuted (*i.e.* permutes entire rows of tables R and Q) (Dray and Legendre 2008, Ter Braak et al. 2012). Finally, a Ward's hierarchical classification based on Euclidian distance between species along the first two RLQ axes allowed defining species response groups. Each of them was described by its trait distribution.
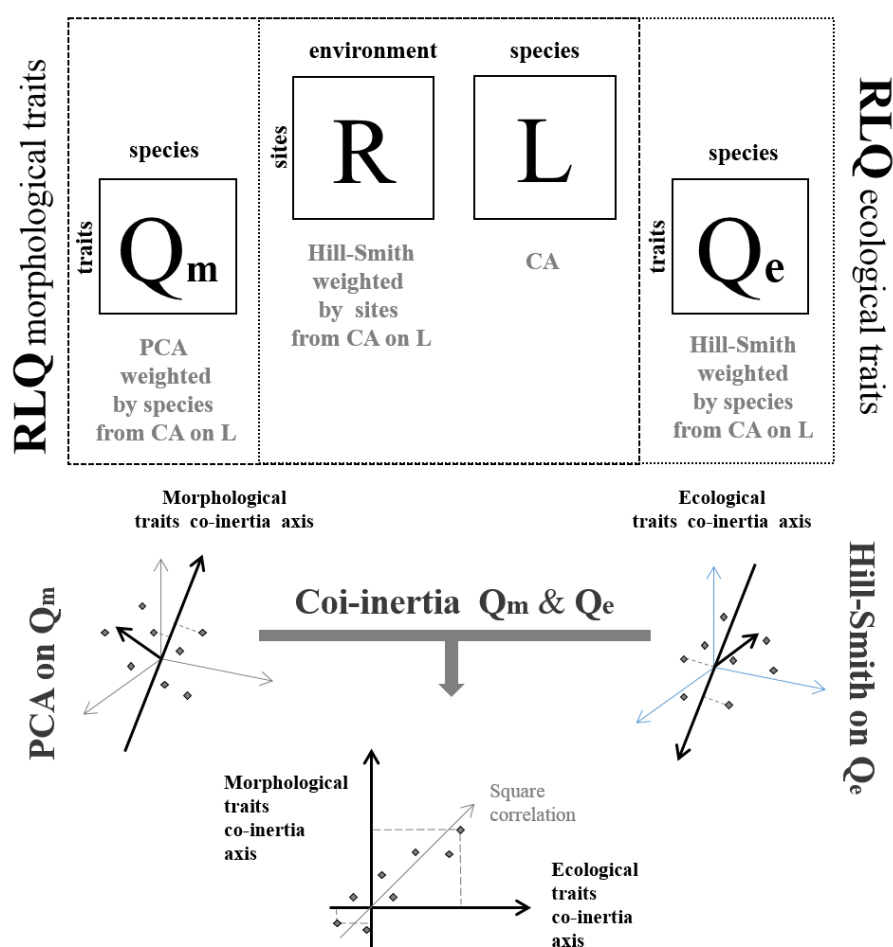

Figure 1. Flow diagram of the different steps to do statistical analyses

In order to understand relationships between morphological traits (table Qm) and ecological traits (table Qe), a co-inertia analysis, a two-table ordination method, was performed (Figure 1) (Doledec and Chessel 1994). This co-inertia analysis was done using the same trait tables, weighted in the same way, as for the RLQ analyses. All analyses where conducted using the ADE-4 package (Thioulouse et al. 1997) for the R software, version 3.3.1 (R Foundation for Statistical Computing 2010).

4.3 Results

4.3.1 Joint analisys of ecological traits, environmental variables and ant community

A first RLQ analyzing jointly ecological and morphological traits was not significant (p-value = 0.0576). We then analyzed the two types of traits separately The RLQ on morphological traits (RLQm) was not significant (p-value = 0.3975). However, the RLQ on ecological traits (RLQe) was significant (p-value = 0.0194), the first two axes of the RLQe analysis extracted 74.5% of the total variance (63.42% and 11.08% repectively). The proportion of variance attributed to each RLQe axis and the proportion of variance that they take into account from the separate analysis (environment characteristics of sites, traits or species distribution) was evaluated (Annex 2). In this sense, the first axis of the RLQe represented well the environmental characteristics and accounted for 81% of the eigenvalue of the first axis of the separate analysis for environmental characteristics. The first axis of the RLQe represents also 92% of the variability of the first axis of the Hill-Smith ordination on ecological traits. This is evidence of a good representation of the environmental characteristics and the ecological traits in the first RLQe axis. When considering the two first ecological axes of RLQe, the representation is still very good as they accounted for 80% of the eigenvalue of the first two axes of the separate analysis for environmental characteristics and for 71% of the variability of the first two axes of the Hill-Smith ordination on ecological traits. The intensity of the relationship between

environmental characteristics and ecological traits was not very strong and the first RLQe axis represents the major costructure between the three tables R, L and Qe (see Annex 2 for details). The first RLQe axis is built by the first axis of the Hill-Smith on R and by the first axis of the Hill-Smith on Qm. In adittion, the second RLQe axis is build only by the second axis of the Hill-Smith on R, so that the correlation between the ecological traits and the environment is mostly expressed on the first RLQe axis.

The first axis of the RLQe (RLQe1) was positively associated with annual crops (LU.AC), and copper (Cu), and negatively associated with rubber plantations (LU.R), mesoporosity (MES), avalaible water capacity (AWC) and sand (Sa) (see Annex 3). This axis separates systems with some tree cover and perennial crops from annual crops that are characterized by an intense use of chemical inputs and tillage. The factorial plan of the RLQe (Figure 2a) showed that annual crops and rubber plantations are the most influential environmental factors on RLQe1 (explained by both the length and angle between the axes and vectors). The distribution of land uses along RLQe1 shows that savanna (S), rubber plantations (R) were on the negative side, while annual crops (AC) and improved pasture (IP) were on the positive side (Figure 3). RLQe1 shows an opposition between land uses with some tree cover (such as savannas, and rubber plantations) and land uses without tree cover such as annual crops and improved pastures. Oil palm plantations remain in the middle of the gradient. Considering ecological traits, the first axis of the RLQe was positively associated with colony type (CT), nest localization in substratum (NL.st) and tramp ants (CR.ta), and negatively associated with nest built in dead wood (NM.dw) or in cavities (NL.cv), in litter (NM.l) or in carton (NM.cn) and medium nest (NS.m) (see Annex 4). This first RLQe axis opposes smaller species with a better capacity to exploit the available resources (such tramp ants) to those with larger body size and that build their nests in cavities or dead wood.
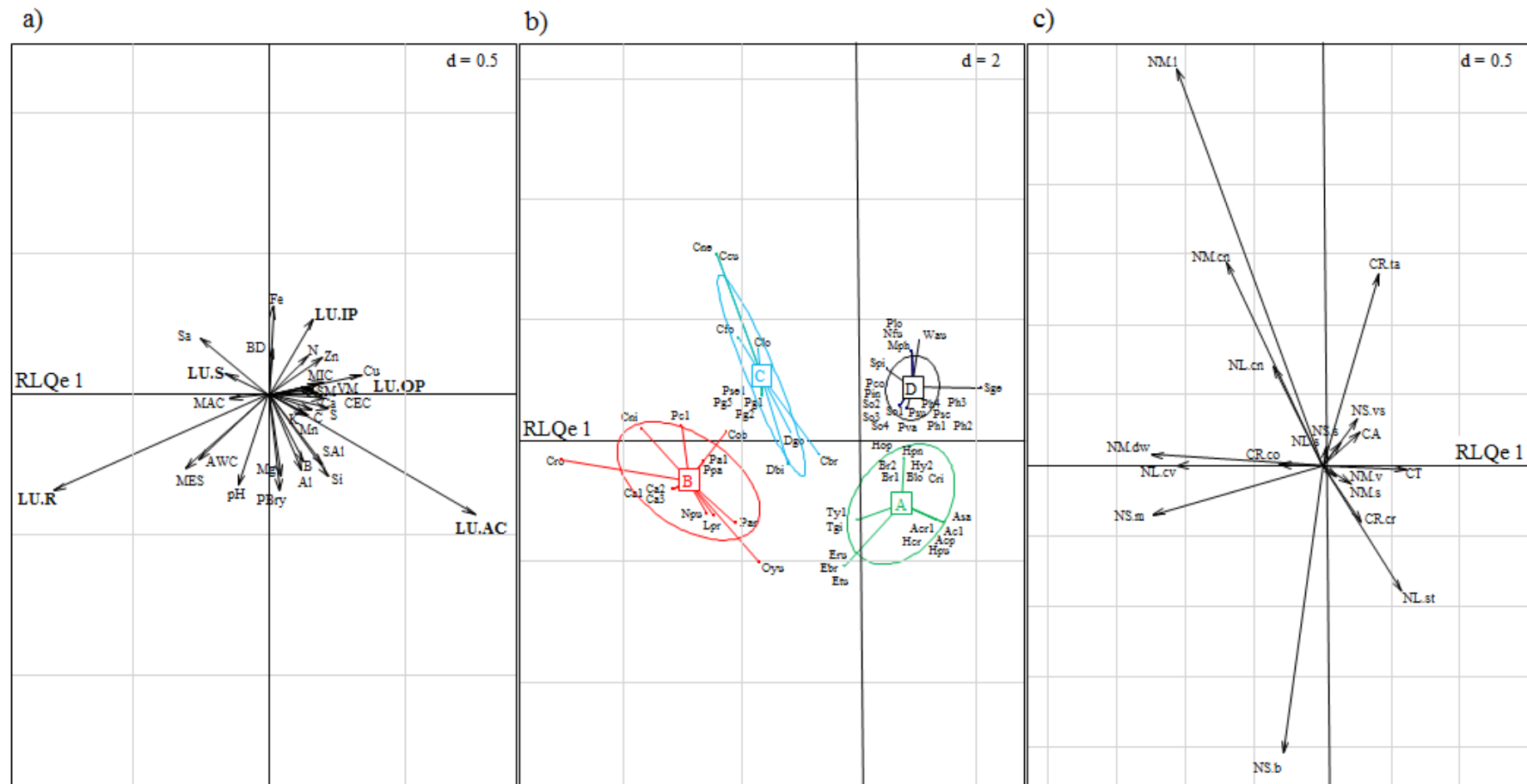
Figure 2. Multiple representation of the RLQe ordination on the first two axes: a) environmental variables, b) mean position of species and species response groups, c) ecological traits (see Tables 1 and 2 for full names of traits and variables and Annex 1 for the full names of the species). Eigenvalues 63.42%, 11.08% for axes 1 to 2 respectively. The values of a d gives the grill size.

The second axis of the RLQe (RLQe2) opposed improved pastures (LU.IP) where soils have relatively high iron (Fe) contents to annual crops (LU.AC) and rubber (LU.R) plantations that have high contents of P, Mg and Al, elevated pH, high mesoporosity, and silt contents (See Annex 3). The second RLQe axis shows a more complex association, based mainly on chemical inputs and soil acidity (explained by high percentages of Al). This axis is also positively associated with nest built in the litter (NM.l), in canopy (NM.cn and NL.cn) and with tramp ants (CR.ta), and negatively associated with big nest (NS.b) and nest built in the substratum (NL.st) (see Annex 4). The second RLQe axis represents a species gradient from those who build bigger nests in soil to those who can better exploit different nesting resources such tramp ants.

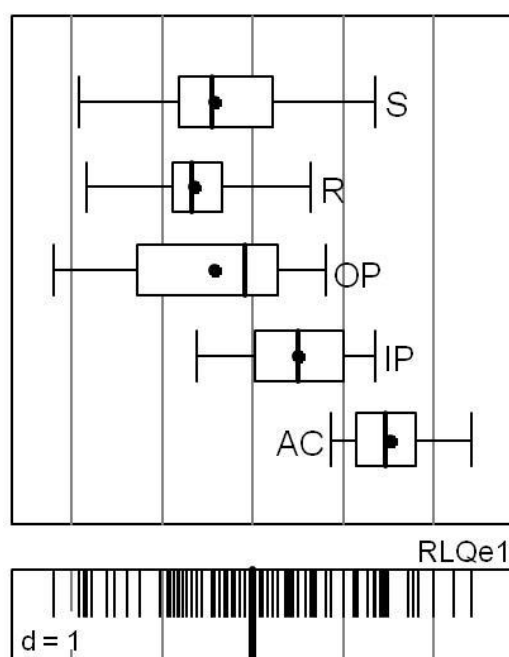**Figure 3**. Boxplot representation of land uses on the first axis of the RLQe. S: Savanna, R: Rubber plantations, OP: Oil palm plantations, IP: Improved Pasture and AC: Annual crops. Vertical lines inside boxes represent medians, while the dots represent means. Minimums, maximums, and second and fourth quartiles are also displayed. Small vertical lines at the bottom of the panel correspond to the position of sites along the axis.

The results of the RLQe analysis were best summarized by representing the scores of the environment, the species and the trait variables on the RLQe axes (Figure 2).

RLQe axis 1 – Colony type (CT), nest localized into cavities (NL.cv), in dead wood (NM.dw), of medium size (NS.m) were the most powerful explanatory attributes for this RLQe axis (explained by both the length and the angle between the axes and the vectors); they are strongly related to the arboreal cover in land uses (Figure 2). Species with negative position on this axis tended to be conspicuous (CR.co), to have large and medium nest size (SN.b, SN.m), built carton nest, or in deadwood or in litter (NM.cn, NM.dw, NM.l) and localized in canopy and cavities (NL.cn, NL.cv); while species with a positive position on this axis tended to be tramp species (CR.ta) and polygenic species (CT) (Figure 4).

RLQe axis 2 – Nest built in the litter (NM.l), in carton (NM.cn), localized in canopy (NL.cn), tramp species (CR.ta), big nest (NS.b) localized in the substratum or soil (NL.st) were the main attributes related to RLQe2 axis (Figure 3). Species with negative position on this axis tended to be cryptic (CR.cr), to build big nest (NS.b) and use deadwood to nest (NM.dw), in the substratum or in cavities (NL.st, NL.cv). On the positive side of RLQe2 axis, species tended to be tramps (CR.ta), to build nest in carton (NM.cn) and in the canopy (NL.cn) (Figure 4).
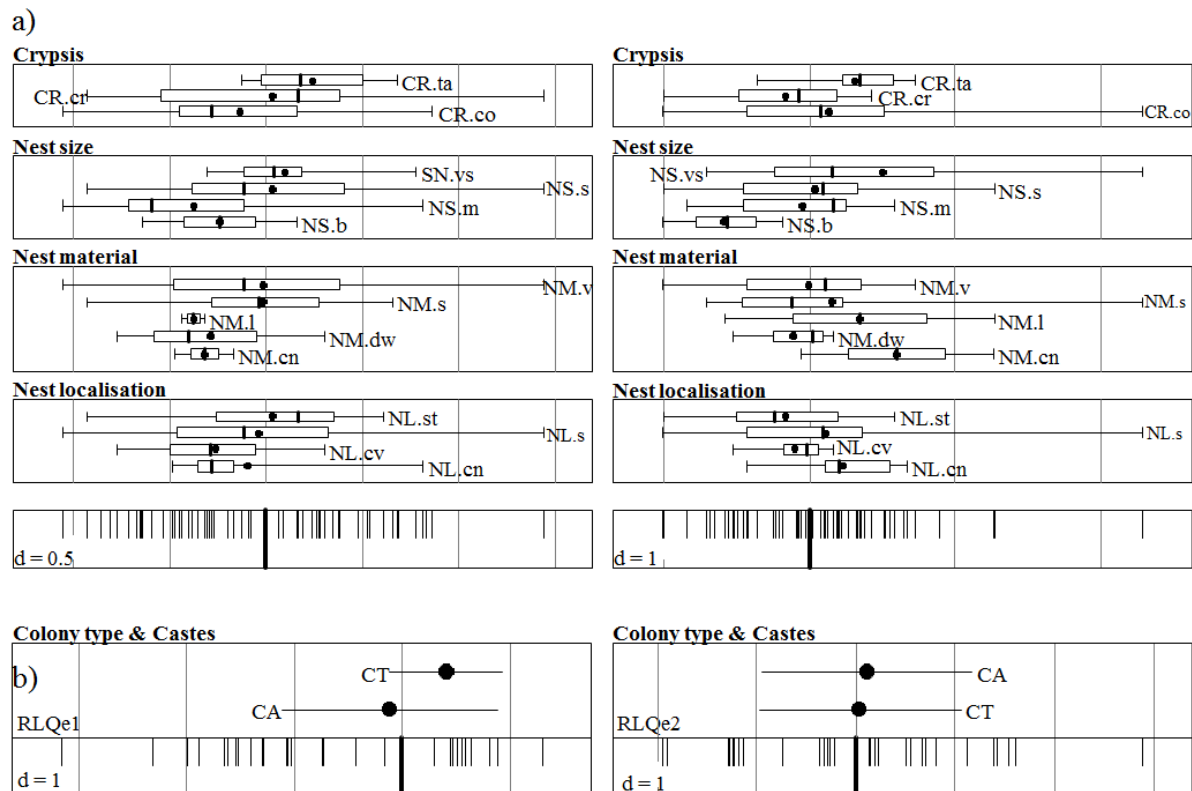
Figure 4. Boxplot of representation of the a) qualitative and b) quantitative traits, on the first two RLQe axes (RLQe1 on the left, RLQe2 on the right). Vertical lines inside boxes represent medians, while the dots represent means. Minimums, maximums, and second and fourth quartiles are also displayed. Small vertical lines at the bottom of the panel correspond to the position of sites along the axis. The full names of traits and their modalities are given in Table 2.

4.3.2 Classification of species based on environmental variables and species ecological traits

The Ward's hierarchical classification separated four clusters based on the mean position of every species on the first two RLQe axes (Figure 2b; see Annex 5 for a dendrogram of the clustering). Each cluster was then described based on the distribution of ecological attribute traits (see Annex 6) and represented in the species distribution on the first RLQe axis (mean position and amplitude distribution of the species, Figure 5).
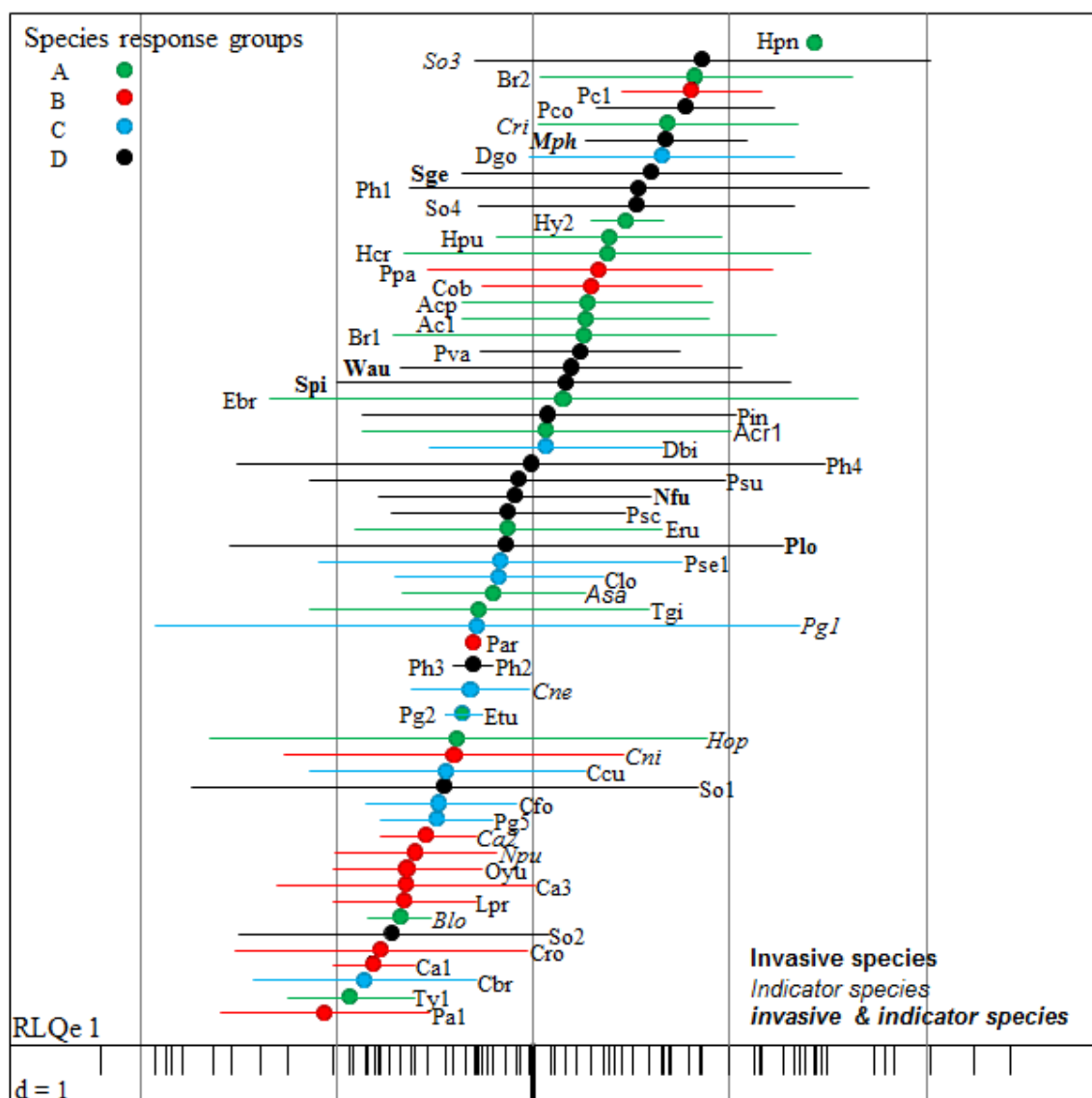
Figure 5. Mean position and amplitude distribution of the species on the first axis of the RLQe analysis (see Annex 1 to the name of species). The dots represent the average score of the sites in which species occur and the length of lines represents the standard deviation of these scores. The species in bold are known to have an invasive behaviour (*i.e.* invasive species), species in italic was reported as indicator species for land use in Sanabria *et al*. (2014) and the species in italic and bold are both. Species response groups: A (green), B (red), C (blue) and D (black). Short vertical lines at the bottom correspond to the position of sites along the axis. Full names of species are given in the Annex 1.

Species response group A – It is formed by 18 species (*Acanthostichus sanchezorum, Brachymyrmex longicornis, Hypoponera punctatissima, Ectatomma brunneum, E. tuberculatum, E. ruidum*, etc). This group of species build small nest (NS.s) in soil and in substratum (NL.s, NL.st), with soil or various materials (NM.s, NM.v). They are mainly cryptic species (CR.cr), polymorphic (CA= 2) and polygenic (CT= 1) (Figure 2, Annex 6).

Species response group B - It contains 13 species (*Camponotus* (sp1, sp.2 sp.3), *Crematogaster rochai, C. nigropilosa, C, obscurata, Odontomacus yucatecus,* etc.) which localize their medium size nest (NS.m) mainly in soil (Nl.s), build them mainly with soil (NM.s). They are conspicuous (CR.co), mono- or polymorphic and monogenic (Figure 2, Annex 6).

Species response group C - –This group is formed by 18 species (*Crematogaster curvispinosa, C. foliocrypta, Dolichoderus bispinosus, Centromyrmex brachicola*, etc.). They have small nests (NS.s) that are mainly located in the soil (NL.s), but also in canopy (NL.cn), and constructed from varied materials (NM.v), as well as carton and litter (NM.cn, NM.l). These species are conspicuous (CR.co), polymorphic and monogenic (Figure 2, Annex 6).

Species response group D - This group is formed by 19 species (*Solenopsis geminata, Wasmannia auropunctata, Paratrechina longicornis, Nylanderia fulva, Solenopsis picea,* ect.). They build small and very small nest (NS.s, NS.vs), with various materials and with soil (NM.v, NM.s) and localize them in soil (NL.s). They are conspicuous but also tramp species (CR.co, CR.ta), mainly dimorphic and polygenic (Figure 2, Annex 6).

Species response groups A and D are on the positive side of the first RLQe axis 1 while species response groups B and C are on the negative side (Figures 2b and 5). Under land uses with tree cover (negative side of RLQe1), species response groups are more specialized, and composed of conspicuous species, while under land uses without tree cover (positive side of RLQe1) species response groups are more generalist, with an increased ability to expand their colony and to exploit resources. This suggests that RLQe1 represents a gradient of species

specialization and colonization ability and according to the presence/absence of tree cover. Stenotopic species are on the negative side and more eurytopic species on the positive side of the RLQe1 axis (Figure 5). This is indicating that some species could be considered as stenotopic, such as *Rasopone arhuaca, Crematogaster negripliosa*, *C. rochai, Pseudomyrmex gracilis* sp.2, *Pseudomyrmex gracilis* sp.5, *E. tuberculatum, Camponotus* sp.2, *Labidus praedator, Brachymyrmex longicornis, Camponotus* sp. 1, *Typhlomyrmex sp 1., Odontomacus yucatecus* (even if some are on the positive side like *H. puntatissima, Pseudomyrmex occulatus* sp.1, *Hypoponera* sp.2), are more present under land uses with tree cover (negative size of RLQe1). This indicates that more specialized species have a narrow ecological distribution. Meanwhile, species that could be considered as eurytopic are more dominant under land uses without tree cover (positive side of RLQe1), for example *Solenopsis* sp.3, *Pheidole* sp.1 *Solenopsis picea, Solenopsis geminata, Paratrechina longicornis* (but see also *Hypoponera opacior, Solenopsis* sp.1, *Pheidole* sp.4 on the negative side). Finally, all the species that are reported as tramp ants or have invasive behaviours (in black, Figure 5) belong to the species response group D.

4.3.3 Co-inertia analysis between morphologic and ecological traits

The co-inertia between morphological (Qm) and ecological (Qe) traits was significant (RV: 0.37; p-value = 0.016). The first three axes accounting for 86.26% of the variance extracted (45.07, 29.57 and 11.62% respectively). For morphological traits (Figure 6a), the first co-inertia axis (CO1) was negatively correlated to ocular index (OI), eye length (EL residuals) and Weber's length (WL) while the second co-inertia axis (CO2) was positively correlated to head width (HW residuals) and cephalic index (CI) and negatively correlated to pigmentation (P). For ecological traits (Figure 6b), the first co-inertia axis was mainly linked, on the negative side, to nest localization in canopy (NL.cn) and the second co-inertia axis was correlated to smaller nest size (NS.vs) and nest built with soil (NM.s) in the positive side in opposition to

larger nest sizes (NS.b) in the negative side. The first co-inertia axis represents a gradient of decreasing species size and eyes size and a gradient of nest localization from canopy to the ground. Species with larger eyes (*i.e.* high values of ocular index and eye length) and larger bodies (*i.e.* high values Weber's length) have a tendency to build their nest in the canopy more than in the soil. The second co-inertia axis represents a gradient of depigmentation and a gradient of nest size. Species non pigmented (generally cryptic species) have smaller nests that are mainly built in the soil with various materials; they also have smaller heads (low values of head width and cephalic index). Pigmented species tend to build larger nests. Finally, species response groups were discriminated by ecological traits except for species response groups B and C that were superimposed on the co-inertia factorial plan (Figure 6c), while morphological traits cannot allowed to distinguish the species response groups (Figure 6d).
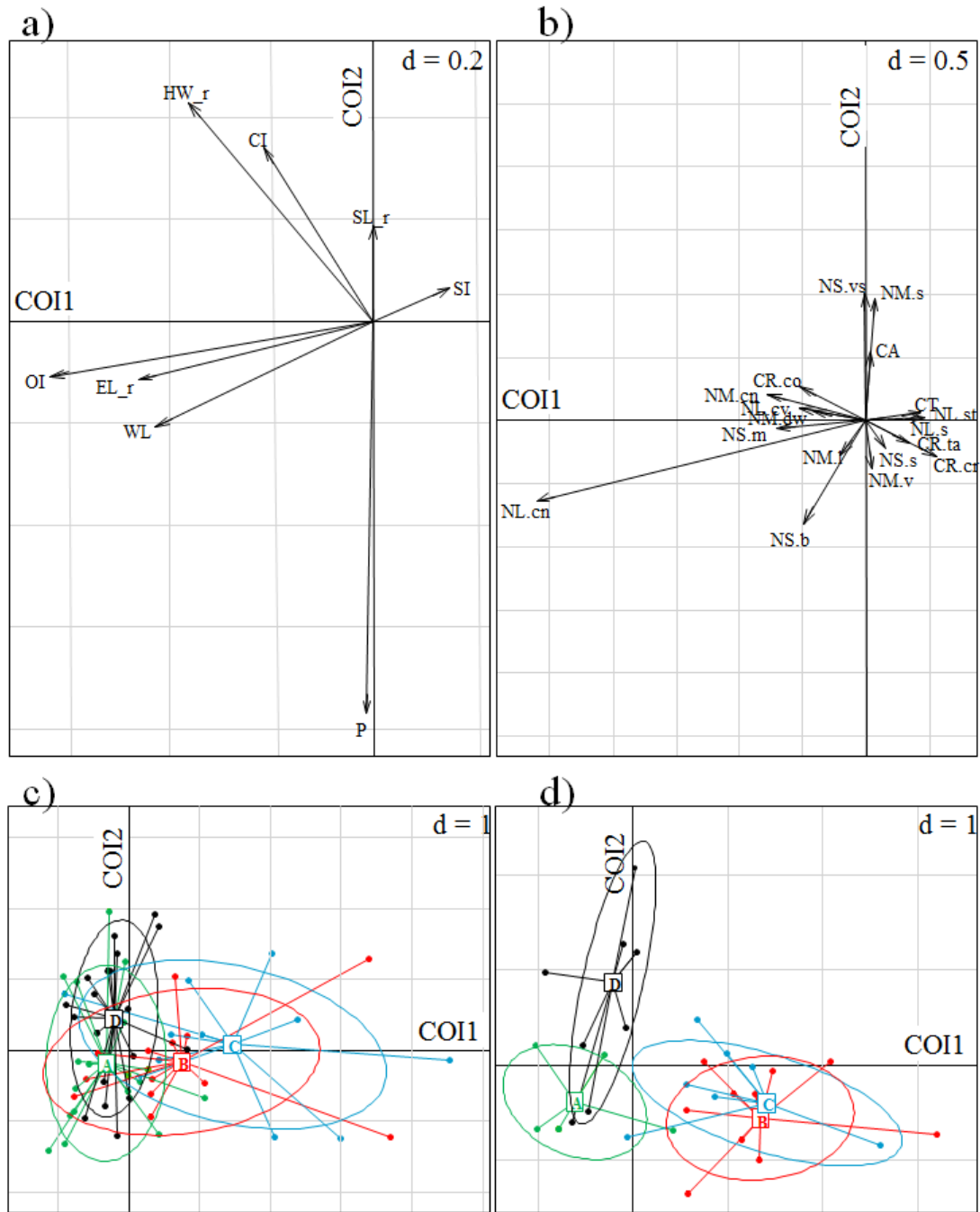
Figure 6. Multiple representation of the co-inertia between weighted values of a) ant morphological traits (Qm), b) ant ecological traits (Qe), c) mean position of species response groups view by morphological traits, and d) mean position of species response groups view by ecological traits.. Eigen values 45.07%, 29.57% for axes 1 to 2 respectively. RV: 0.37; p-value = 0.016. The values of a *d* denotes the scale of the graphic. (see Table 2 for full names of traits).

4.4 Discussion

4.4.1 Joint structure between ant species distribution, environment and species traits.

The RLQ analyses showed that the joint structure between species distribution, environmental factors and species trait was significant for ecological traits. However, no relationship was found for morphological traits or when morphological and ecological traits were considered together. The principal advantage of RLQ analysis is its capacity to detect and analyze the relationship between an optimized measure of environmental variability and an optimized measure of trait variability. In the RLQe analysis, the first axis explained a large proportion of the total variance of the environmental and species ecological traits data sets, suggesting a strong gradient structuring both the site characteristics and the species traits distribution. The ordination of the sites along the first RLQe axis opposed sites with tree cover (*i.e.* land uses with a highest tree cover such rubber, savanna) to sites without tree cover (*i.e.* such annual crops and improved pastures). From the ant species point of view, when trees are present, the community tended to include species with more specialized diets and dependent to nest localization (i.e. cavity-dwelling species) and in some cases bigger nests. The land uses with less tree cover such as annual crops and improved pastures are also more disturbed by human activity. In these land uses, ant species show better adaptability to habitat destruction by tillage or high fertilizer inputs or livestock settlement (Holway and Case 2001). This was evidenced by the presence of species with a better capacity to find resources, as well as to defend and expand their colonies. Thus, a direct link exists between the presence of polygenic species and tree cover. This corroborates partially our first hypothesis as a strong relationship was established only between ecological traits and land uses. The second hypothesis, of a relationship between traits and physic-chemical soil properties, was also at least partially verified: along the RLQe1 axis, ants with larger and medium nests are present in soil with a better availability of water and higher macroposity. This could be due to the fact that these ants

are soil engineers (Lavelle and Spain 2001) and have important impacts on soil structure. For example, the galley systems affects pore space and ants can drive the flow of water through their channels (especially vertical ones) (de Bruyn and Conacher 1990). The magnitude of the impact is based on the longevity and size of the nest.

The case of oil palm plantations is particular, because this land use has a tree cover but also share characteristics of land uses without tree cover: oil palm plantations are managed with tillage and pesticides. Moreover, the studied plantations are relatively young (2 years at most). The specificity of oil palm plantations is supported by studies showing that they host much fewer species than natural systems and often fewer than other tree plantations, and that their ant assemblages tend to be dominated by generalists and pests (Fitzherbert et al. 2008, Fayle et al. 2010).

4.4.2 What explains the ant species distribution?

Land uses with tree cover are associated with some ant traits linked to the presence of trees such as nest located in canopy and built with litter or dead wood. These land uses are associated with (1) species of the genera *Crematogaster*, mainly *C. curvispinosa,* an inconspicuous species that is very common in brushy habitats and young secondary forests (Longino 2004), (2) *C. foliocryopta* and *C. longispina* that are known to form small carton nests in leaves (Longino 2004). Land uses with tree cover are also associated with medium and large nests and species such as: (1) *Crematogaster rochai*, that has medium nests and is distributed in a wide variety of plant cavities (Longino 2004), (2) different species of *Camponotus*, considered as generalist foragers, with big colonies, often polydomous, with numerous separate "nests" (Longino 2004) and a well-marked polymorphism (major workers and minor workers). On the contrary, land uses without tree cover are associated with species that can be considered as tramp ants (among which stand out species): *Solenopsis geminata, Nylanderia fulva, Solenopsis picea, Monomorum pharaonis, Paratrechina longicornis*, *Wasmannia auropuctata,* etc). "Tramp

species" are ants known as pests that have been transported worldwide through human activities. They tend to displace local ant species when introduced; move out when disturbed; show an absence of intraspecific, but a high rate of interspecific aggressiveness; are polygynous; and reproduce by colony fission (Holway et al. 2002, Holway and Suarez 2006). *Wasmannia auropunctata*, a neotropical species has been recognized as a tramp ant, is ubiquitous in the leaf-litter in South American forests. Its populations sometimes explode in cultivated areas, so that its presence usually indicates human-related perturbation (Achury et al. 2012, Delabie et al. 2009). Even in its original range of distribution (as in Colombia) disturbances increase the probability of dominance of this species and they are recognized as indicator of low diversity ant communities (Achury et al. 2012). *Monomorium pharaonis* is an indicator of improved pastures (Sanabria et al. 2014) and is considered as a tramp ant. Despite invasive ants are usually not specialised, this species shows specificity and fidelity to this land use. This can be explained because both (the ant species and improved pastures) are introduced in neotropical regions. It is known that ecological synergies may exist among introduced species and that exotic ants can be more abundant in edges or areas dominated by exotic vegetation (Suarez et al. 1998).

In general, land uses with tree cover are associated to a decrease in polymorphic species. However, exceptions have been found. For instance, some species belonging to the tribe genera *Camponotini*, recognized as medium size polymorphic species were present in latter successional habitats with open ground and low shrub cover (Gibb and Cunningham 2013) such as rubber plantations. For these species, moist conditions and the presence of deadwood are important for nesting (Longino 2004). Besides, in land uses without tree cover, the more prevalent species were relatively small dimorphic species such as *Pheidole* or *Solenopsis* (with some species recognized as tramp ants). This could be attributed to their higher competitive

ability and their higher ability to exploit food sources in open habitats (Arnan et al. 2013), which could increase their foraging time and enhance colony success (Cerda et al. 1997, Achury et al. 2012).

Species respond in different ways to different habitats and this may have resulted in differences in trait-environment relationships between studies based on microhabitat and macrohabitat (Gibb et al. 2015). Some studies on ant assemblages have revealed a strong trait-environment relationship at the microhabitat scales (Silva and Brandao 2010, Gibb and Parr 2013) and considered microhabitat as an important factor in driving assemblages (Suggitt et al. 2011). Indeed, it is hypothesized that morphology and ecology provides alternative, but mutually consistent expression of the outcome of ecological and evolutionary adjustment between phenotype and environment (Ricklefs and Donald 1994). However, this study shows no strong relation between soil variables and ecological traits (and no relation at all between morphological traits and the environment characteristics). This type of result was also reported by Yates et al. (2014) who explained this by the absence of measures of soil characteristics known to influence ants such as soil clay content, soil texture and bulk density. However, though we documented many soil characteristics, we did not find any significant relationship with morphological traits and between ecological traits and soil characteristics. Our results can thus be explained by three non-exclusive hypotheses. (1) For this ant assemblage and their traits what really matters is the combination of soil factors (better represented by the land use) and not each particular physical or chemical soil characteristic. (2) Traits chosen in this study are not the most appropriate to evaluate the relationships between ant traits and soil characteristics. For example, it could be relevant to include traits such as jaw size, legs size or pilosity that can be linked to micro-habitat specialization (Arnan et al. 2013) or traits such as dispersal ability, competitive ability or trophic position that have been proven to be relevant predictors of species sensitivity to fragmentation and land use (Henle et al. 2004, Schweiger et al. 2005, Didham et

al. 2007) depending on scale and interactions with other traits (Davies et al. 2000). (3) It might be important to include other environmental characteristics that better describe ant habitat, *e.g.* percentage of bare ground, canopy cover, the depth of leaf litter, soil and litter temperatures. These characteristics could be better linked to ant ecology and could therefore be more strongly associated to ant traits.

4.4.3 Relation between morphological and ecological traits.

The covariation between ecological and morphological traits shows that species tend to be smaller, have smaller eyes and less pigmented cuticle when they localize their nest on or in the soil. Those results corroborate the third hypothesis of this study that there is a relation between morphological and ecological traits. Morphological traits are known to represent important aspects of the relation between organisms and their environment, because they are selected thought environmental filters (Ricklefs and Miles 1994). In the present study, ants with larger eyes and larger bodies are more frequent in canopy; contrary to smaller and non-pigmented ants that localize their nest in the soil or use wood, rock cavities, or leaf litter to build their nest. This study focused on ground dwelling ants meaning that ants from canopy were also sampled as they forage on the ground mainly in systems with tree cover as savannas or rubber plantations such as species from the genera *Pseudomyrmex.* They have large eyes and they built their nests in the stems of woody plants ("AntWeb" 2016). This could indicate that larger eyes provide a better adaptation to arboreal life and a better perception of environment because of a good motion detection, pattern recognition and visual orientation compare to dwelling species which forage only in leaf litter layer (Fischer 1999).

Though we found a relationship between ecological and morphological traits, there was not a common structure between morphological traits and environmental characteristics (RLQ analysis). This is linked to the fact that the species response groups identified by the RLQe were not discriminated by morphological traits. It is well known that morphological traits are linked

to environmental characteristics (Gibb et al. 2015), and it was surprising not to find such a relationship in this study. This result can partially be explained by the morphological traits used. For example, head length and head width are not associated with environmental characteristics and may have similar values along different habitats (Wiescher et al. 2012). Other traits that have been shown to be linked to environmental characteristics could be included in the future, for example leg length, that decreases with the complexity of the cover (*i.e.* Forest) (Sarty et al. 2006, Schofield et al. 2016).

4.5 Conclusion

As far as we know, few studies have studied the factors shaping the structure of ant assemblages at the landscape scale in the Colombian Llanos (see Sanabria *et al*. 2016). Indeed, in the Colombian Llanos the study of ant assemblages may be problematic because many species that we found are new records and their ecology is poorly known. Nevertheless, we have identified some ant traits that can be used to analyze and predict how ant species respond to tree cover in this landscape. This supports results of others works that showing how the traits of invertebrate communities respond to land uses and environmental gradients (Ribera et al. 2001, Martins da Silva et al. 2016, Schofield et al. 2016). In the future, using complementary characteristics of the environment (*e.g.* percentage of bear soil, depth of the leaf litter or canopy cover) and complementary morphological ant traits, it should be possible to extend our results to better understand the impact of each land use on ant traits (and not only the response to tree cover), detect other key environmental characteristics that affects ant communities and better understand the ecology of their communities. Traits are often viewed as a systematic way to make predictions on responses of communities to their environment even when the ecology of the species is poorly known, but our results conversely suggest that studies based on traits can also help understanding the ecology of the studied organisms.

4.6 References

Achury, R., Chacon de Ulloa, P. and Arcila, A.M. 2012. Effects of the Heterogeneity of the Landscape and the Abundance of Wasmannia auropunctata on Ground Ant Assemblages in a Colombian Tropical Dry Forest. -Psyque. 1-12

Altieri, M. A. and Nicholls, C. I. 2003. Soil fertility management and insect pests: Harmonizing soil and plant health in agroecosystems. - Soil Tillage Res. 72: 203–211.

Anderson, J. M. and Ingram, J. S. I. 1993. Tropical Soil Biology and Fertility: A Handbook of methods. - CAB International, Wallingford U.K.

AntWeb. 2014. www.antweb.org

Arnan, X., Cerda, X., Anselm, R. and Retana, J. 2013. Response of ant functional composition to fire. - Ecography (Cop.). 36: 1182–1192.

de Bello, F., Lavore, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M. Cipriotti, P.Cornelissen, H.,Feld, C., Hering, D. Martins da Silva, P., Potts, S., Sandin, L., Sousa, J.P., Storkey, J. and Wardle, D. The Project Rationalising Biodiversity Conservation in across different trophic levels.: 1–21.

Bihn, J. H., Gebauer, R., Brandl, R. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. - Ecology 91(3):782–792.

Bolton, B. 1994. Identification Guide to the Ant Genera of the World. - Harvard University Press.

Carroll C. R. and Janzen D. H. 1973. Ecology of Foraging by Ants. - Annu. Rev. 4: 231–257.

Cerda, X., Retana, J. and Cros, S. 1997. Thermal Disruption of Transitive Hierarchies in Mediterranean Ant Communities. - J. Anim. Ecol. 66: 363–374.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. and Díaz, S. 2000. Consequences of changing biodiversity. - Nature 405: 234–42.
Chown, S. L. and Gaston, K. J. 2010. Body size variation in insects: A macroecological perspective. - Biol. Rev. 85: 139–169.

Davies, N., Norris, R. and Martin, C.T. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics . - Freshw. Biol. 45: 343–369.

De Bruyn, L. L. A. and Conacher, A. J. 1990. The role of termites and ants in soil modification - a review. - Soil Res. 28: 55–93.

Decaëns, T., Lavelle, P., Jiménez, J. J., Escobar, G., Rippstein, G., Schneidmadl, J., Sanz, J. I. Hoyos, P. and Thomas, R. J. 2001. Impact of land management on soil macrofauna in the Eastern savannas of Colombia. - In: Jiménez, J.J., Thomas, R. J. (Eds.), Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia. Publicaciones Ciat.

Delabie, J.H.C., Régis, C., Groc, S., Dejean, A., Gibernau, M., Corbara, B. and Dejean, A. 2009. Ants as biological indicators of Wayana Amerindian land use in French Guiana. - C. R. Biol. 332: 673–84.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, M. 2007. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. - Freshw. Biol.: 104(52): 20684-20689

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T. and Ewers, R.M. 2007. Interactive effects of habitat modification and species invasion on native species decline. - Trends Ecol. Evol. 22: 489–96.

Doledec, S. and Chessel, D. 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biology 31:277-294. - Freshw. Biol. 31: 277–294.

Dolédec, S., Chessel, D., ter Braak, C. J. F. and Champely, S. 1996. Matching species traits to environmental variables: a new three-table ordination method. - Environ. Ecol. Stat. 3: 143–166.

Dray, S. and Legendre, P. 2008. Testing the Species Traits-Environment relationships: The Fourth-Corner problem revisited. - Ecology 89: 3400–3412.
Fayle, T.M., Turner, E.C., Snaddon, J.L.,Chey, V.K., Chung, A.Y.C., Eggleton, P. and Foster, W. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. - Basic Appl. Ecol. 11: 337–345.

Fernández, F. (Ed.). 2003. Introducción a las hormigas de la región Neotropical. - Instituto de Investigacion de Recursos Biologicos Alexander von Humboldt.

Fischer, J., Lindenmayer, D.B. and Manning, A.D.2006. Ten guiding principles for commodity production landscapes. - Front. Ecol. Environ. 4: 80–86.

Fischer B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. - Ecol. Appl. 9: 714–731.

Fitzherbert, E.B., Struebig, M.J. Morel, A., Danielsen, F., Donald, P.F. and Phalan, B.2008. How will oil palm expansion affect biodiversity? - Trends Ecol Evol 23: 538–545

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning : a review. - Biodivers. Conserv. 1244: 1221–1244.

Gibb, H. and Parr, C. L. 2013. Does Structural Complexity Determine the Morphology of Assemblages? An Experimental Test on Three Continents. - PLoS One 8: 1–7.

Gibb, H. and Cunningham, S. A. 2013. Restoration of trophic structure in an assemblage of omnivores, Considering a revegetation chronosequence. - J. Appl. Ecol. 50: 449–458.

Gibb, H., Stoklosa, J., Warton, D. I., Brown, A. M., Andrew, N. R. and Cunningham, S. A. 2015.. Does morphology predict trophic position and habitat use of ant species and assemblages? - Oecologia 177(2): 519–31

Gotelli, N. J. and Ellison, A. M. 2002. Assembly rules for New England ant assemblages. 3: 591–599.

Hee, J., Holway, D. A., Suarez, A. V. and Case, T. J. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. - Conserv. Biol. 4: 559–563.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. and Settele, J. 2004. Predictors of species sensitivity to fragmentation - Biodivers. Conserv. 13: 207–251.

Hölldobler, B. and Wilson, E. O. 1990. The Ants. Harvard University Press/Springer.

Holway, D. and Case, T. J. 2001. Effects of colony-level variation on competitive ability in the invasive Argentine ant. - Anim. Behav. 61: 1181–1192.

Holway, D. and Suarez, A. V. 2006. Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion. - Biol. Conserv. 127: 319–326.

Holway, D., Lach, L., Suarez, A., Tsutsui, N.D., and Case, T.J. 2002. the Causes and Consequences of Ant Invasions. - Annu. Rev. Ecol. Syst 33: 181–233.

Hubert, B., Rosegrant, M., van Boekel, M.A.J.S. and Ortiz, R.A. 2010. The Future of Food: Scenarios for 2050. - Crop Sci. 50: S33–S50.

Kaspari, M. 1993. Body size and microcimate use in Neotropical granivourus ant. - Oecologia 96: 500–507.

Lavelle, P. and Spain, A. V. 2001. Soil ecology. Kluwer Academic Publishers. pp 654.

Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M.P., Loaiza, S., Pullido, S.X., Rodríguez, E., Sanabria, C., Velásquez, E. and Fonte, S.J.2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. - Agric. Ecosyst. Environ. 185: 106–117.

Longino, J. T. 2004. Ants of Costa Rica. www.antsofcostarica.org

Lozano-Zambrano, F., Fernández, F., Jiménez, E. and Arias, T. 2008. Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia. - Instituto de Investigacion de Recursos Biologicos Alexander von Humboldt.

Martins da Silva, P., Carvalho, F., Dirilgen, T., Stone, D., Creamer, R., Bolger, T. and Sousa, J.P. 2016. Traits of collembolan life-form indicate land use types and soil properties across an European transect. - Appl. Soil Ecol. 97: 69–77.

Moretti, M., de Bello, F.,Ibanez, S., Fontana, S., Pezzatti, G.B., Dziock, F., Rixen, C. and Lavorel, S. 2013. Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. - J. Veg. Sci. 24: 949–962.

Palacio, E. E. and Fernández, F. 2003. Clave para las subfamilias y géneros. - In: Fernandez, F. (ed), Introducción a las hormigas de la región neotropical. 1st ed.. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt., pp. 233–260.

Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Decaens, T., Deharveng, L., Dubs, F., Joimel, S. and Cluzeau, D. 2014. Current use of and future needs for soil invertebrate functional traits in community ecology - Basic Appl. Ecol. 15(3): 194–206.

R Foundation for Statistical Computing 2010. R Development Core Team. R: A Language and Environment for Statistical Computing.

Silva R. and Brandao, C.R. 2010. Morphological patterns and community organization in leaf-litter ant assemblages. - Ecol. Monograpohs 80: 107–124.

Retana, J., Arnan, X. and Cerdá, X. 2015. A multidimensional functional trait analysis of resource exploitation in European ants A multidimensional functional trait analysis of resource exploitation in European ants. - Ecology 96: 2781–2793.

Ribera, I., Doledec, S., Downie, I.S. and Foster, Garth. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages - Ecology 82: 1112–1129.

Ricklefs, R. E. 1987. Community Diversity: Relative Roles of Local and Regional Processes.Pdf. - Science: 167–171.

Ricklefs, R. E. and Miles, D. 1994. Ecological and Evolutionary Inferences from Morphology: An Ecological Perspective. - In: Ecological Morphology. University of Chicago Press, pp. 376.

Ricklefs, R. E. and Donald, M. 1994. Ecological and Evolutionary Inferences in Morphology: An Ecological perpestive. - In: Peter C. Wainwrigth and Stephen M. Reilly (eds), Ecological Morphology: Integrative Organismal Biology. 1st ed.n. The University of Chicago Press, pp. 367.

Romero-Ruiz, M.H., Flantua, S.G.A., Tansey, K. and Berrio, J.C. 2012. Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. - Appl. Geogr. 32: 766–776.

Sanabria, C., Lavelle, P and Fonte, S.J. 2014. Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos. - Appl. Soil Ecol. 84: 24–30.

Sanabria, C., Dubs, F., Lavelle, P., Fonte, S.J. and Barot, S. 2016. Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. - Eur. J. Soil Biol. 74: 81–92.

Sarty, M., Abbott, K. L. and Lester, P. J. 2006. Habitat complexity facilitates coexistence in a tropical ant community. - Oecologia 149: 465–473.

Schilman, P.E., Lighton, J.R.B. and Holway, D. A. 2007. Water balance in the Argentine ant (Linepithema humile) compared with fice common native ant species from southern California. - Physiol. Entomol. 37: 1–7.

Schmidt, F. and Diehl, E. 2008. What is the effect of soil use on ant communities? - Neotrop. Entomol. 37: 381–388.

Schmidt, F. Ribas, C.R. and Schoereder, J.H. 2013. How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. - Ecol. Indic. 24: 158–166.

Schofield, S., Bishop, T.R. and Parr, C.L. 2016. Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes. - Myrmecological News 23: 129–137.

Schweiger, O., Maelfait, J. P., Van Wingerden, W., Hendrickx, F., Billeter, R. and Speelmans, M. 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. - J. Appl. Ecol. 42: 1129–1139.

Suarez A. V., Bolger, D. T. and Case, T. J. 1998. Effects of fragmentation and invasion on native ant communities in Coastal Southern California. - Ecology 79: 2041–2056.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E. Roy, D.B. and Thomas, C.D. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. - Oikos 120: 1–8.
Ter Braak, C.J., Cormont, A. and Dray, S. 2012. Improved testing of species traits–environment relationships in the fourth-corner problem - Ecology 93: 1525–1526.

Thioulouse, J., Chessel, D., Doledec, S. and Olivier, J.M. ADE-4 a Multivariate Analysis and Graphical Display Software. - Stat. Comput. 7: 75–83.

Del Toro, I., Towle, K., Morrison, D.N. and Pelini, S.L.2013. Community Structure , Ecological and Behavioral Traits of Ants (Hymenoptera: Formicidae) in Massachusetts Open and Forested Habitats. - Northeastern Natur. 20: 1–12.

Vandewalle, M., de Bello, F., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P., Lavorel, S., da Silva, P.M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J. and Woodcock, B.A. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. - Biodivers. Conserv. 19: 2921–2947.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. and Poff N.L.2010. A structured and dynamic framework to avance trait-based theory and prediction in ecology. - Ecol. Lett. 13: 267–283.

Wiescher, P.T., Pearce-Duvet, J.M.C., Feener, D.H.2012. Assembling an ant community: Species functional traits reflect environmental filtering. - Oecologia 169(4): 1063–1074.
Yates, M.L., Andrew, N.R., Binns, M. and Gibb, H. 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. - PeerJ 2: 1-20

4.7 Annexes

Annex 1: List of Ants species used in the analysis. We only keep the species present in 2 or more samples (#sample (x/75) = number of samples in which each specie was appear from a total of 75 samples).

Species Code	Species names	# samples (x/75)	Species Code	Species names	# samples (x/75)
Asa	*Acanthostichus sanchezorum*	3	Npu	*Neivamyrmex punctaticeps*	3
Am1	*Acromyrmex sp.1*	8	Nfu	*Nylanderia fulva*	19
App	*Acropyga palaga*	3	Oyu	*Odontomacus yucatecus*	2
Ap1	*Acropyga sp.1*	3	Par	*Rasopone arhuaca*	1
Blo	*Brachymyrmex longicornis*	2	Pa1	*Pachycondyla sp.1*	3
Br1	*Brachymyrmex sp.1*	37	Plo	*Paratrechina longicornis*	4
Br2	*Brachymyrmex sp.2*	3	Pco	*Pheidole cocciphaga*	4
Ca1	*Camponotus sp.1*	2	Pin	*Pheidole inversa*	9
Ca2	*Camponotus sp.2*	2	Psc	*Pheidole scalaris*	4
Ca3	*Caponotus sp.3*	5	Ph1	*Pheidole sp.1*	10
Cbr	*Centromymex brachycola*	4	Ph2	*Pheidole sp.2*	2
Cne	*Crematogaster negripliosa*	2	Ph3	*Pheidole sp.3*	2
Ccu	*Crematogaster curvispinosa*	4	Ph4	*Pheidole sp.4*	3
Cfo	*Crematogaster foliocrypta*	2	Psu	*Pheidole subarmata*	20
Clo	*Crematogaster longispina*	5	Pva	*Pheidole vallifica*	4
Cni	*Crematogaster nigropilosa*	12	Pg1	*Pseudomyrmex gracilis sp.1*	2
Cob	*Crematogaster obscurata*	2	Pg2	*Pseudomyrmex gracilis sp.2*	2
Cro	*Crematogaster rochai*	7	Pg5	*Pseudomyrmex gracilis sp.5*	2
Cri	*Cyphomyrmex rimosus*	3	Pc1	*Pseudomyrmex occulatus sp.1*	2
Dbi	*Dolichoderus bispinosus*	3	Ppa	*Pseudomyrmex pallens*	3
Dgo	*Dorymyrmex goeldii*	2	Pse1	*Pseudomyrmex sp.1*	11
Ebr	*Ectatomma brunneum*	7	Sge	*Solenopsis geminata*	7
Eru	*Ectatomma ruidum*	14	Spi	*Solenopsis picea*	4
Etu	*Ectatomma tuberculatum*	2	So1	*Solenopsis sp.1*	3
Hpu	*Hypoponera punctatissima*	3	So2	*Solenopsis sp.2*	3
Hcr	*Hypoponera creola*	18	So3	*Solenopsis sp.3*	2
Hop	*Hypoponera opacior*	16	So4	*Solenopsis sp.4*	2
Hpn	*Hypoponera punctatisima*	2	Tgi	*Tranopelta gilva*	4
Hy2	*Hypoponera sp.2*	2	Ty1	*Typhlomyrmex sp.1*	2
Lpr	*Labidus praedator*	2	Wau	*Wasmannia auropunctata*	4
Mph	*Monomorium pharaonis*	3			

Annex 2. Results of the RLQ on ecological traits. Total inertia: 1.624. *Inertia %*: percentage of total variance accounted for by each RLQ axis. *Covariance*: covariance between the two new sets of factorial scores projected onto the first two RLQ axes (square root of eigenvalue). *Correlation*: correlation between the two new sets of factorial scores projected onto the first two RLQ axes.

Eigenvalues decomposition	Eigenvalues	Inertia %	Covariance
RLQe axis 1	1.03	63.42	1.01
RLQe axis 2	0.18	11.08	0.42
Inertia & coinertia R	**Inertia**	**max**	**ratio**
Axis 1	7.22	8.86	0.81
Axes 1 & 2	10.52	13.17	0.80
Inertia & coinertia Q	**Inertia**	**max**	**ratio**
Axis 1	2.58	2.80	0.92
Axes 1 & 2	3.71	5.19	0.71
Correlation L	*Correlation*	**max**	**ratio**
Axis 1	0.235	0.81	0.29
Axis 2	0.22	0.79	0.27

The set of species scores had a correlation of 0.235 along the first axis of RLQe which, compared to the highest possible correlation between sites and species given by the square root of the first eigevalue of the CA on table L (0.81), represents a ratio of 0.29. This ratio is 0.27 for the second axis of the RLQe. The covariance among the new set of scores for the sites and the species in the RLQe space is 1.01 (square root of 7.22 x square root of 2.58 x 0.235) for the first RLQe axis (RLQe1) and 0.42 for the second RLQe axis. The covaraince of the second RLQe axis is less than half of the first RLQe axis.

Annex 3. Scores of the environmental variables on the first two axes of the RLQe analysis performed on ecological traits. (see Table 1 for description of the variables). This shows the ordination of environmental variables on the first two axes of the RLQe (*i.e.* linear combination according to the weigth of the variables that provides the coordinates of the sites).

|	RLQe1	RLQe2
pH	-0.11	**-0.33**
N	0.14	0.14
C	0.15	-0.05
PBry	0.04	**-0.34**
K	0.13	-0.07
Ca	0.20	-0.01
Mg	0.04	**-0.29**
Al	0.12	**-0.27**
CEC	0.18	0.01
Sal	0.19	**-0.25**
S	0.22	-0.05
B	0.13	-0.24
Fe	0.02	**0.31**
Mn	0.14	-0.08
Cu	**0.34**	0.07
Zn	0.20	0.13
SM	0.16	0.02
VM	0.20	0.04
BD	0.01	0.17
AWC	**-0.26**	-0.23
MAC	-0.14	-0.01
MES	**-0.31**	**-0.27**
MIC	0.18	0.04
Sa	**-0.25**	0.20
Si	0.22	**-0.29**
LU.AC	**0.75**	**-0.43**
LU.IP	0.16	**0.27**
LU.OP	0.16	0.02
LU.R	**-0.79**	**-0.34**
LU.S	-0.16	0.07

Annex 4. Scores of the quantitative ecological traits on the first two axes of RLQe analysis (see Table 2 for description of the variables). This shows the ordination of quantitative ecological traits on the first two axes of the RLQe (*i.e*. linear combination according to the weigth of the variables that provides the coordinates of the species).

	RLQe1	RLQe2
NL.cn	-0.35	**0.70**
NL.cv	**-1.06**	0.00
NL.s	0.02	0.14
NL.st	**0.57**	**-0.89**
NM.cn	**-0.69**	**1.44**
NM.dw	**-1.24**	0.08
NM.l	**-1.06**	**2.82**
NM.s	0.20	-0.13
NM.v	0.09	-0.08
NS.b	-0.29	**-2.04**
NS.m	**-1.23**	-0.35
NS.s	0.13	0.16
NS.vs	0.25	0.33
CR.co	-0.32	0.00
CR.cr	0.28	-0.4
CR.ta	**0.41**	**1.36**
CA	0.27	0.23
CT	**0.61**	-0.02

Annex 5. Dendrogram of the clustering of the Ward's hierarchical classification based on the mean position of every species on the first two RLQe axes. The four clusters represent the species response groups: A (green), B (red), C (blue) and D (black).
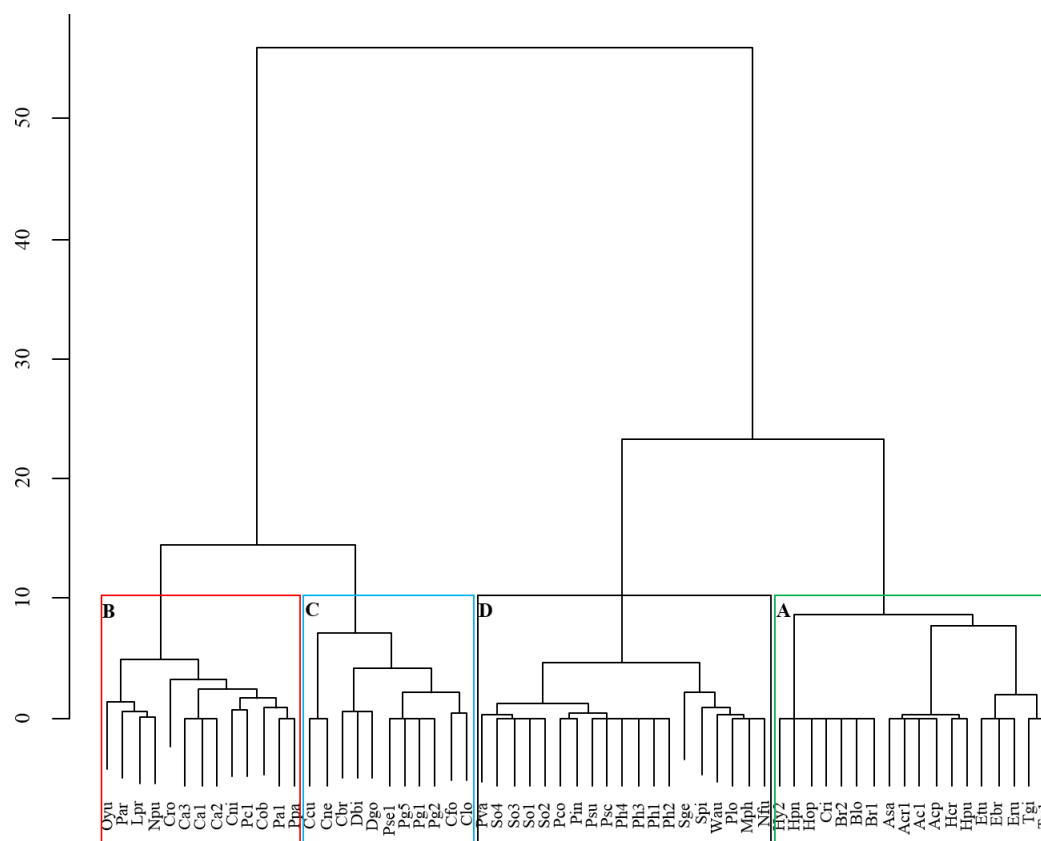
Annex 6. Ecological trait distribution in the four species response groups (A, B, C and D), (see Table 2 for full names of traits).
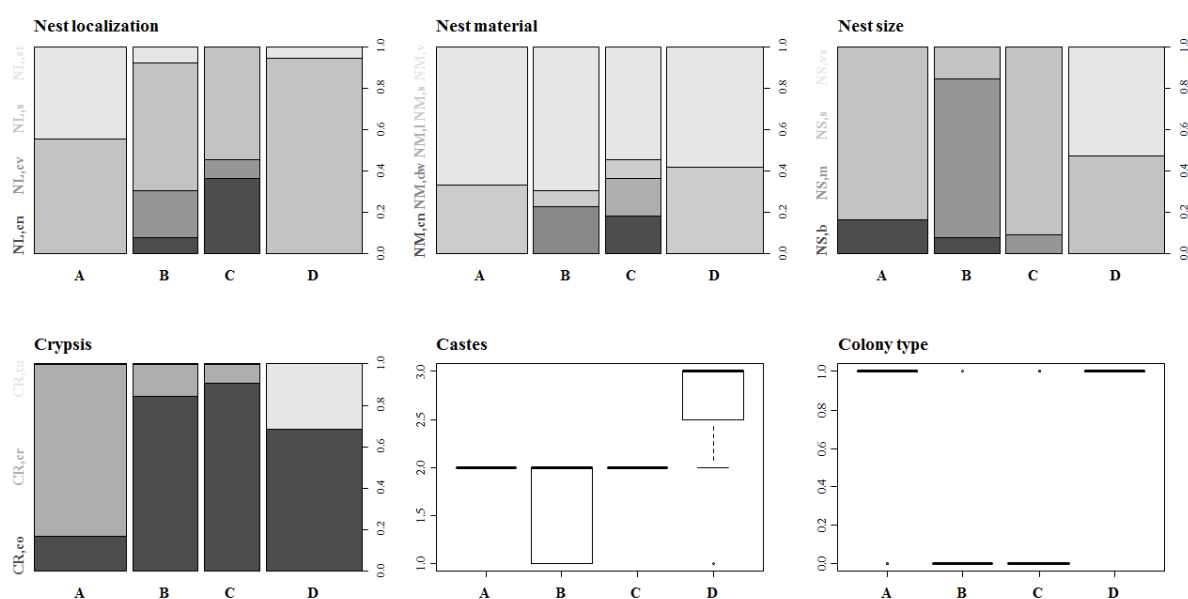
Chapter 5: Discussion, conclusions and perspectives

5.1 General Discussion

Currently, land-use change due to agricultural expansion and intensification is one of the highest global threats to biodiversity and is heavily associated to ecosystem functions and services. In particular, in tropical regions, the conversion of forest and agroforests into monocultures such as annual crops is happening at an extremely rapid rate, which leads to highly simplified landscapes and affects the physical and chemical characteristics of soil (Fahrig, 2003). However, conservation concepts are increasingly moving beyond the traditional, strict division between managing protected areas for biodiversity by excluding or minimizing human influence on one side (Terborgh, 1999) and managing lands to produce goods to support human development on the other (Schroth and McNeely, 2011). At the scale of agricultural landscapes land-sharing approach recognizes the contribution of conservation efforts to supporting agricultural production such as pollination and pest control services, and in securing the multiple benefit provided by these landscapes, clean water for example, The challenge for researchers is to demonstrate how managing biodiversity for these services to and from agriculture can contribute to increasing the productivity, value, and resilience of the farming system (Andersen et al., 2004; Edwards et al., 2014; Egan and Mortensen, 2012; Fischer et al., 2014; Grau et al., 2013).

Agricultural landscapes may contribute significantly to the conservation of threatened species and ecosystems (Schroth et al., 2004). A critical element in the approach of integrating conservation and livelihood improvement within landscapes is therefore to add the concept of "ecosystem services" to concerns about biodiversity and land productivity (MEA, 2005). Indeed, taking into account ecosystem services allows promoting alternative agricultural practices that might produce less food than standard practices but could provide other services, e.g. maintenance of soil fertility or the regulation of greenhouse gas emissions. Soil fauna can be used as an indicator to determine the impact of the transformation through the landscape,

because is recognized their role as soil engineers and in the provision of ecosystem services (Fonte and Six, 2010; Jouquet et al., 2006; Lavelle et al., 2006; Prather et al., 2013; Raphael et al., 2010). In this case, ants have been chosen because they are relatively easy to collect, their taxonomy is relatively well known, they have a wide range of distribution (Hölldobler and Wilson, 1990) and because they use soil as a main habitat. Termites are also considered as soil engineers. They play a key role in the functioning of many tropical systems, are amongst the main macroinvertebrate decomposers, and exert additional impacts through the creation of biostructures (mounds, galleries, sheetings, etc.) with different soil physical and chemical properties (Jouquet et al., 2006; Lavelle et al., 2006).

The present thesis has sought to respond to three main questions:

1) Can ants be used as bioindicators of soil based ecosystem services?

2) Can land uses and soil chemical and physical properties impacts directly ant and termite communities?

3) Do the morphological and ecological traits of ants respond to agricultural changes?

5.1.1 Overview and main results of the thesis

The second chapter of this thesis responds to the first question and the objective was to identify ant species that could serve as bioindicators for the provision of ecosystem services in the Llanos region. Fourteen indicator species were identified. Twelve were associated with the high provision of soil-based ecosystem services, while two were associated with the poor provision of ecosystem services.

As expected, species that build their nest mainly in soil as *Acromyrmex* sp. 1, *Pheidole inversa* and *Solenopsis* sp. 1, were associated with the maintenance of soil structure, because they could

be actively involved in relevant ecosystem processes related to soil aggregation and modification of soil structure (nest building activities), which alters the chemical and physical properties of soil and accelerates nutrient turnover (Moutinho et al., 2003). In the case of climate regulation, the indicator species was *C. curvispinosa* that nests in woody ecosystems and habitats with perennial vegetation (AntWeb, 2014). Indeed, these ecosystems better capture greenhouse gas emissions than others agroecosystems. *Ectatomma ruidum* was associated with a poor mineral nutrient provision capacity and a low soil fertility. This species is directly dependent on soil properties because its nests are belowground and because it forages in the leaf litter (AntWeb, 2014), but the mechanism whereby the species can be directly associated to poor soil fertility is not clear. The species associated to a better mitigation of climate change and conservation of soil biodiversity were *C. curvispinosa* and *Pseudomyrmex gracilis*. These two species are mainly associated to systems with tree cover.

Additionally, I found that different management systems yielded clear responses in ant abundance and community structure characteristic (Table 1; Figure 2, chapter 2). For example, annual crops experience the most intensive disturbance regime, with frequent tillage and relatively high inputs of agrochemicals, corresponded to the lowest abundance, richness and diversity of ants. The tree-based systems (oil palm and rubber) promote the establishment of arboreal ant species (e.g., *Crematogaster* and *Pseudomyrmex spp.*). More specifically, these systems supported species that are sensitive to high temperatures, such as the army ant of the genera *Labidus*. This suggests that tree cover and multiple vegetation strata may be important for promoting these key taxonomic groups, and that perennial agroecosystems may play an important role in the conservation of ant species from forested areas across the broader region and this may be of particular importance for rubber plantations, where some of the rarest species encountered in this study were found.

Semi-natural savanna was not the most diverse system for ants (contrary to my expectations).

However, these savannas have relatively high species richness due to low levels of disturbance (no tillage) as well to a relatively high habitat complexity (presence of scattered trees). Instead, improved pastures had the highest overall diversity, which may be related to the fact that the pastures studied were settled many years earlier than the other production systems. Consequently, these pastures had been relatively free of disturbance (e.g., chemical fertilizers, pesticides, tillage) for longer than the other production systems.

Overall, I found that the mechanisms linking ants to soil processes are not always clear. Throwing new lights on these relations would require more knowledge about the biology and ecology of the ant species. However, this would help developing the use of ants as bioindicators of ecosystem services, which could offer an important tool for a more integrated management of agroecosystems.

The second question was tackled in the third chapter of this thesis, where the aim was to evaluate the impact of land use on ant and termite communities in Colombian savanna landscapes, and to assess whether this impact is associated with the modification of soil physical and chemical properties.

The results of this part of the work showed that two groups of land use can be distinguished according to their impact on ant communities: one group is formed only by savannas and the other is composed by all the others land uses. Three groups of land uses were distinguished for their impact on termite communities: one composed by rubber plantations, the second composed by improved pastures and savannas and the third and final group composed by annual crops and oil palm plantations. Co-inertia analyses showed that there is no general relation between ants or termite communities and soil properties.

However, through a GLM analysis I found 19 significant associations between soil physical or chemical properties, land uses or regions with 15 ant species and 14 significant associations

with 6 termite species. In general ants are positively associated with high soil porosity and negatively with CEC and termites are positively affected by volumetric moisture, bulk density and macroporosity, but negatively affected by soil chemical fertility. I found that microporosity and chemical fertility are higher in annual crops. Besides savannas and oil palm plantations have high bulk density and clay concentrations, but low chemical fertility compared with annual crops.

The general conclusion of this part of the work, is that an association exists between land use and ant or termite communities and this influence is likely due to changes in ant and termite habitats resulting from agricultural practices such as tillage, fertilization, and lime addition. In that sense, the results suggest that annual crops are the most detrimental land use for termites and ants, because their communities are highly sensitive to vegetation cover and agricultural practices such as tillage. Land use and soil characteristics explain only a small part of the variability in ant and termites communities, for this reason maintaining a high diversity of soil engineers and the ecosystem services they provide likely depends on the maintenance of natural ecosystems in the landscape and the adoption of practices that reduce negative impacts on soil ecosystem engineers when native ecosystems have been transformed into agricultural systems.

In the fourth chapter the aim was to test the relationship between morphological (*e.g.* Weber's length, head size) and ecological traits (*e.g.* nest size, nest material, type of colony) of ant communities and whether those traits respond to soil properties and land uses. Through a RLQ analyses I found that there is not relationship when morphological traits were analyzed separately or when morphological and ecological traits were considered together. However, the joint structure between species distribution, environmental factors and species traits was significant only for data set of ecological traits analyze separately.

The ordination of sites showed an opposition between sites with tree cover (rubber and savanna) from those without tree cover (annual crops and improved pastures). In general land uses with tree cover are associated with a decrease in polymorphism, big nest. Meanwhile in land uses without tree cover the species more prevalent were those relatively small and dimorphic species who better exploit food resources, showing that species respond in different ways to different habitats and this may result differences in trait-environmental relationships.

Based on the distribution of the ecological attributes, four groups of species were distinguished. The first group was formed by 18 ant species that tend to build small nest and use soil to build them. These species are mainly cryptic, polymorphic and polygenic. The second group was formed by 13 species that localize their medium size nests in the soil and the majority of these species can be considered as conspicuous. The third group was formed by 18 species. These species tend to have small nest, located in soil but also in canopy. The nests are constructed with varied materials and the species tend to be conspicuous. The last group was formed by 19 species which have very small nest that are located in soils. The majority of the species are conspicuous or considered as tramp ants and are dimorphic.

For this assemblage of ants and the traits chosen for this study, the combination of soil factors (which is better summarized by the land use) is more important than particular soil characteristics. Finally, the conclusion of this chapter was that even if the trait approach can be used to analyze the impact of land use changes on ant communities and find general rules that could allow predicting these impacts, in the Llanos region this objective is not easy to accomplish because the ant fauna is poorly known. Nevertheless, we found some traits that can be used to analyze and predict how ant species respond to tree cover and we hypothesized what other traits can be useful for futures researches.

5.1.2 Species richness and composition

The savannas of South America support a relatively diverse ant fauna, with several unique species (Silva and Bates, 2002; Vasconcelos et al., 2008). In total, 5154 ant individuals were collected and belonged to 91 ant species, 33 genera, and 9 subfamilies. The genera *Pheidole* and *Solenopsis*, represented 18.6% of total species richness. The most diverse subfamily was Myrmicinae (43%) and Ponerinae (14% of the species observed). The genus with the highest number of species was *Pheidole* (11), and the most abundant species were: *Brachymyrmex sp*. 1 (1511 individuals). My sampling method is not the most recommended to collect ants (Agosti et al., 2000) because (1) the TSBF method is better able to describe quantitatively soil fauna than to describe it qualitatively (Ciat, 2002; Rippstein et al., 2001), (2) the method is not the best for social insects, especially when, as ants, they do to not only live within the soil. The ALL protocol would have been more suitable to collect ants (Agosti and Alonso, 2000). However, I reported roughly 10% of the species, 37% of genera and 64% of the known subfamilies in Colombia (Fernández and Sendoya, 2004), which shows that the region studied is quite diverse and that the method can be used as a tool to make a rapid sampling of ant communities.

Regarding termites, 8052 individual were found and belonged to 4 families, 5 subfamilies, 10 genera and 16 species were identified. The family with the highest number of species was the Termitidae with 13. Five genera, including *Anoplotermes, Grigriotermes, Heterotermes, Neocapritermes* and *Termes* had two representative species each one, while the remaining genera had only one species. The most abundant specie was *Grigiotermes* sp. 1 with 3086 individuals (38.32% of the total abundance of termites collected).

5.1.3 Effect of the agricultural landscape on soil communities

I have studied five of the most common land uses in the Colombian Llanos. As expected, savanna is the land use with the highest richness of termites (11 species), followed by tree plantations (oil palm plantations with 10 species and rubber with 9 species). Additionally, improved pastures had 8 species and annual crops had the lowest richness with only two species of termites: *Anoplotermes* sp. 1 and *Anoplotermes* sp. 2 that were the only species present in all land uses. *Anoplotermes* are also called soldierless termites and they are well represented in the Neotropics where they constitute about one-third of the total termite species richness. However, despite their substantial diversity, they have been neglected by most taxonomists because they lack soldiers (Bourguignon et al., 2010). Five species: *Grigriotermes* sp. 1, *Grigriotermes* sp. 2, *Heterotermes tenius, Syntermes molestus* and *Termes* sp. 1 were absent only in annual crops. The land use with the highest abundance of termites was improved pastures with 2710 individuals. It has been observed that in tree plantations the development of species such as the Rhinotermitidae, especially *Heterotermes convexinotatus* (present only in oil palm), is favored by abundant food resources and by favourable foraging conditions, since a closed canopy leads to less severe fluctuations in temperature and moisture in the topsoil due to less direct sun exposure. It has also been identified that systems such as savannas and rubber plantations that have an abundant litter and accumulate pieces of dead wood in the soil favour the density of some xylophaga species (Gonçalves et al., 2005).

For ants, contrary to my expectations, the most species-rich land use was improved pasture (52 spp), with seven species more than savanna (45). The poorest system was annual crops with less than 50% of the species occurring in the three most diverse systems evaluated in this study. However, improved pastures and annual crops appear to have similarities in physical characteristics but not in chemical characteristics (Figures 2 and 3, chapter 3). But when ant fauna is compared, savanna and improved pastures are closer (figure 4, chapter 3). Even if the

management or the origin of both systems are different they are compose in part by a similar type of vegetation (grasses). This could be the reason for which they share 28 ant species. This reinforces the idea that the type of vegetation is very important for ants (De la Mora et al., 2013; Schmidt and Diehl, 2008; Vasconcelos, 1999) as well as for soil communities in general that indeed are highly sensitive to land use changes and quickly respond to subtle changes in resource availability and habitat conditions (Barros et al., 2002; Decaëns et al., 2001; Grimaldi et al., 2014; Lavelle and Pashanasi, 1989; Lavelle and Spain, 2001; Lavelle et al., 2006; Rousseau et al., 2013). This also suggests that ants could be used as indicators of the whole community of macroinvertebrates.

When the ecological traits of ants were compared between lands uses the results showed a gradient of land uses defined by the presence or absence of trees and ordered as follows: (1) savanna and rubber plantations, (2) oil palm plantation, (3) improved pastures and annual crops (Figure 5, chapter 4). Particularly, the response of ant community showed that both oil palm plantations (38 spp) and rubber plantations (39 spp) appeared to have a high species richness and also promotes the establishment of arboreal ants. However, the results of the fourth chapter of this thesis showed that if traits composition is taken into account oil palm plantations are located in the middle of the RLQe1 and separated from rubber plantations, as a land use hosting generalist species and having an intermediate tree cover. The environmental impact of oil palm plantations has been addressed in a rather large number of publications (Comte et al., 2012; Lavelle et al., 2014; Sayer et al., 2012). In the study region the impact of this land use might need to be assessed in a larger number of sites to reach a definitive conclusion on the overall impact of these systems.

As a general overview, only few species (15) were affected positively or negatively by single physic-chemical variables, and my work suggests that ants and termites are mainly affected by combinations of soil variables (chemical and physical), differences in management (tillage and

chemical inputs), the complexity of the habitat (type of vegetation, presence of trees and land cover). Due to the complexity of the underlying relations it is easier to directly link ant communities with land uses.

All these results show that responses of species can be influenced by different factors such as soil quality and management. This leads to differences in ant assemblages. However, it is important better understand the mechanisms underlying these patterns (McGill et al., 2006; Wall et al., 2012). In that sense, identifying how traits are linked with environmental conditions is a step to assessing how ongoing environmental changes and ecosystem processes will alter ant assemblages (Folgarait, 1998). Trait-environment relations are important because may enhance the understanding of ecosystem functioning and enable predictions of how environmental changes can alter species assemblages (McGill et al., 2006; Webb et al., 2010; Wiescher et al., 2012) as a whole.

Although my results showed that ecological ant traits can be linked to some environmental filtering in ant communities, many of the morphological traits I used were not linked to any environmental characteristics. In the future, it would be useful to find other traits that respond more directly to modifications in the environment and pressures. Some of the morphological traits are used are probably not fully suitable (as shown by the non-significant RLQ based on morphological traits). I suggest including in the future morphological traits more directly linked to ant ecology. For instance, some traits are likely more directly linked to ant activities as: hide leg length (tibia length + femur length) associated with dispersal ability, the mandible length and width related with type of diet, the eye position related to hunting method, sculpturing and pilosity, related with tolerance to dehydration and sensorial capacity (Gibb and Cunningham, 2013; Gibb et al., 2015).

In order to obtain a more complete information about land uses and the response of ant to them, I would recommend to describe in a more comprehensive way the characteristics of the land uses. For example, such a description should involve variables describing the canopy cover percentage, the bare ground percentage, some variables associated with litter (abundance and/or diversity), if possible, plant diversity. This is important because the habitat structure influence the microclimate and because habitat complexity can be directly linked to a higher niche disponibility. This can promote the settlement of an ant community assemblage with more particular requirements for nest sites, food, refugees, etc. (De la Mora et al., 2013; Philpott et al., 2000). This is important because ant species are not all ground dwelling and highly depend on diverse resources that in turn depend on the vegetation

5.1.4 Ecosystem services and soil engineers

Functional traits have to be functional, meaning that they have to demonstrably effect or respond to ecosystems processes (Mlambo, 2014; Wood et al., 2015). This researchers highlights that demonstrating the crucial role that traits play in ecosystem processes requires a greater understanding of the ecology of organisms and their interactions with the environment.

At a finer scale and regarding the identity of the species, four ant groups were distinguished based on their traits. The groups B and C correspond to species that, some extent, are more related to tree cover and the heterogeneity of strata present in them. A gradient of land uses with tree cover goes from savanna as the system with more tree cover to annual crops recognize as the system without tree cover. The groups A and D correspond to species with a higher ability to exploit resources and perhaps more adaptations to respond to a lower quality of habitat. In that sense, of the fourteen species found as bioindicators of soil-based ecosystem services, seven belong to the response group A, four to group B, one specie to the group C and three to

the group D. All the indicators species of nutrient provision and water regulation belong to the group A, as well as some indicator of biodiversity and aggregate morphology as the case of *Acromyrmex* sp. 1. (Figure 5 and 8, chapter 4). Some of them also showed to have a positive or negative relation with single physic-chemical variables of soil such as: carbon content, cation exchange capacity, pH, Mg, bulk density (Table 2, chapter 3) these variables could be related to soil morphology and mineral nutrient availability.

Hypoponera creola, indicator of water regulation and nutrient provision, was associated positively with high clay contents, which reinforces the idea that it is common in soils with high moisture and with good capacity of water retention.

Crematogaster curvispinosa, indicator of climate regulation, was the single indicator species that belongs to the group C. This is a very common species in perturbed areas with tree cover such as secondary forests and perennial agrosystems. The species nests in cavities and hollows of trees (Longino, 2004). The species can thus be an indicator of climate regulation that was assessed through C storage in above- and belowground biomass and emissions of GHC that had their lowest values in annual crops and highest in oil palm plantations and savannas (Lavelle et al., 2014). The underlying mechanisms linking ants to certain soil processes may not always be clear. However, the indicators species presented offer a robust but preliminary set of taxa for evaluating the impacts of land management on soil quality. The methodology employed can be applicable across different agricultural landscapes, but the bioindicators developed here are useful only at the local scale in this study. Additionally, it is very important discuss and validate the indicators species by local farmers to better understand their potential value and applicability.

5.1.5 An approach to landscape ecology

As observed in this work, natural systems such as savannas are very important in different ways in agricultural landscapes of the Llanos. However, it is also important to determine the influence of other natural ecosystems. Gallery forests, also commonly termed riparian forest strips, are known to contribute to species richness mainly in regions characterized by human-dominated habitats (Seaman and Schulze, 2010) and represent one of the examples of naturally fragmented tropical forests. In fact, they are generally rich in woody plant species typical of continuous forests and are postulated to have provided refuge for tropical forest species in areas deforested (Kellman et al., 1996; Meave and Kellman, 1994). Tropical forest fragments occupy a variety of habitats, *e.g.* the steep slopes adjacent to streams and headwater basins. For these reasons, fragments of gallery forests are likely to provide useful models for the study of the impact of long-term forest habitat fragmentation on community composition and dynamics (Kellman et al., 1998)

Additionally, landscape ecology is largely founded on the notion that landscape pattern strongly influence ecological processes and biodiversity both at the local and landscape scales. A disruption of landscape pattern may compromise its functional integrity by interfering with critical ecological processes necessary for population persistence and the maintenance of biodiversity and ecosystem health. Human influence strongly modifies landscapes, and this significantly impacts biodiversity (Moser et al., 2002; Schmitzberger et al., 2005). Landscape metrics allow quantifying landscape patterns. The application of these metrics has been very wide despite several drawbacks such as scale dependence, interpretability, etc. (Li and Wu, 2004). Indeed, landscape metrics can serve as indicators for: land use changes, habitat functions (biodiversity, habitats), landscape regulating functions (fire control, microclimate control, etc.) (Uuemaa et al., 2013; Walz and Syrbe, 2013).

To increase the knowledge about the landscape and dynamics of the Colombian Llanos, a project I have been involved in has been implemented to determine how the agricultural matrix is affecting gallery forest and vice versa. For this, a field work campaign has been carried on between June and August 2012. A total of six farms were sampled: Merecure, Paujil and Carimagua belonging to Carimagua region and Andremoni, La Cocora and Santa Cruz in the region of Puestro Lopez. In each farm five linear transects (150 m between each of them) were sampled. Each transect consisted in five sampling points: one located next to the river (r_e), the second located in the middle of the forest (f_m), one located 5 m inside the edge forest (f_e_i), other 5 m outside the edge forest (f_e_e) and finished by a point 250 meters outside the forest edge in the agricultural matrix (crop). On each point a modified TSBF sampling method (Anderson and Ingram, 1993) similar to that used in the main sampling analysed in my thesis was carried out.

Land cover data for the study area were obtained from the land cover map made by Rodriguez (Rodriguez, 2011). He used a classification based on ALOS satellite images (2010 and 2011) and the digital image processing and analysis was made with program ENVI 4.6. The classification was based on the CORINE Land Cover methodology. A reclassification was made due to the former study include some land uses that were not present in transect. I reduced from 33 land uses categories to 10, based on the data the map source and also corroborated with the data collect in the field experience (Urban, forest degraded areas, swamp, cloud, pasture and crops, savanna, river and lakes, forestry crops, and rubber). The landscape pattern was describe around each sampled site on a buffer size of 250 m by using Fragstats 3.2 and ArcGIS 10.3 to calculate the landscape metrics (Schindler et al., 2013). A total of 10 landscape metrics have been calculated using the buffer around of each sampling point. Six metrics was related to each land use (leading to a total of 60) and 4 related to the landscape in general (see table 1).

Table 1: Landscape heterogeneity metrics used in this study

Land uses	
PLAND	Percentage of land use for a given land use
NP	Patch number for a given land use
ED	Edge density for a given land use
AREA_MN	Mean patch area for a given land use
PARA_MN	Mean perimeter-area ratio of patches for a given land use
ENN_MN	Mean nearest neighbor distance for a given land use
Mosaic land uses (*i.e.* Landscape)	
NP	Patch number
ED	Total density of edge
PR	Patch richness (i.e. number of land uses)
SHDI	Shannon index (Land use diversity)

As a first approach to describe the data set, I have described the pattern of the neighbouring landscape metrics using a PCA. In the PCA factorial plan of the metrics distribution. The first axis (F1) shows that all farms from Carimagua and Andremoni (from Puerto Lopez) were located in a landscape dominated by savannas, while the landscape of Puerto Lopez was dominated mainly by crops and pastures. In the same way the second axis (F2) shows that the variables from the negative side correspond to a more heterogeneous landscape dominated by fragmented forests and rubber plantations (see figure). This showed in transects, bectause the points located inside of forests (r_e and f_m) or in the edge (f_e_i and f_e_e) are clearly separated from those located in the agricultural matrix (crops). As expected the landscape is similar for the sampling points inside and at edge of the gallery forests (heterogeneous, dominated by the forest and rubber plantation) and they are different from points outside the forest where the landscape is dominated by savannas, crops and pasturages (Figure 1). The distribution of the farms shows that Andremoni, La Cocora and Santa Cruz (Puerto Lopez region) have a neighbouring landscape different from the farms of Carimagua region where the landscape was dominated mainly by crops and pastures. The farms of Carimagua region were located in the positive side of the first axis of the PCA1 and the landscape was mainly dominated

by savannas. Andremoni (belong to Puerto Lopez farms) showed to have a neighbouring landscape more similar to the farms from Carimagua to those of the two other farms of the Puerto Lopez, region to which it belongs (see Figure 1).
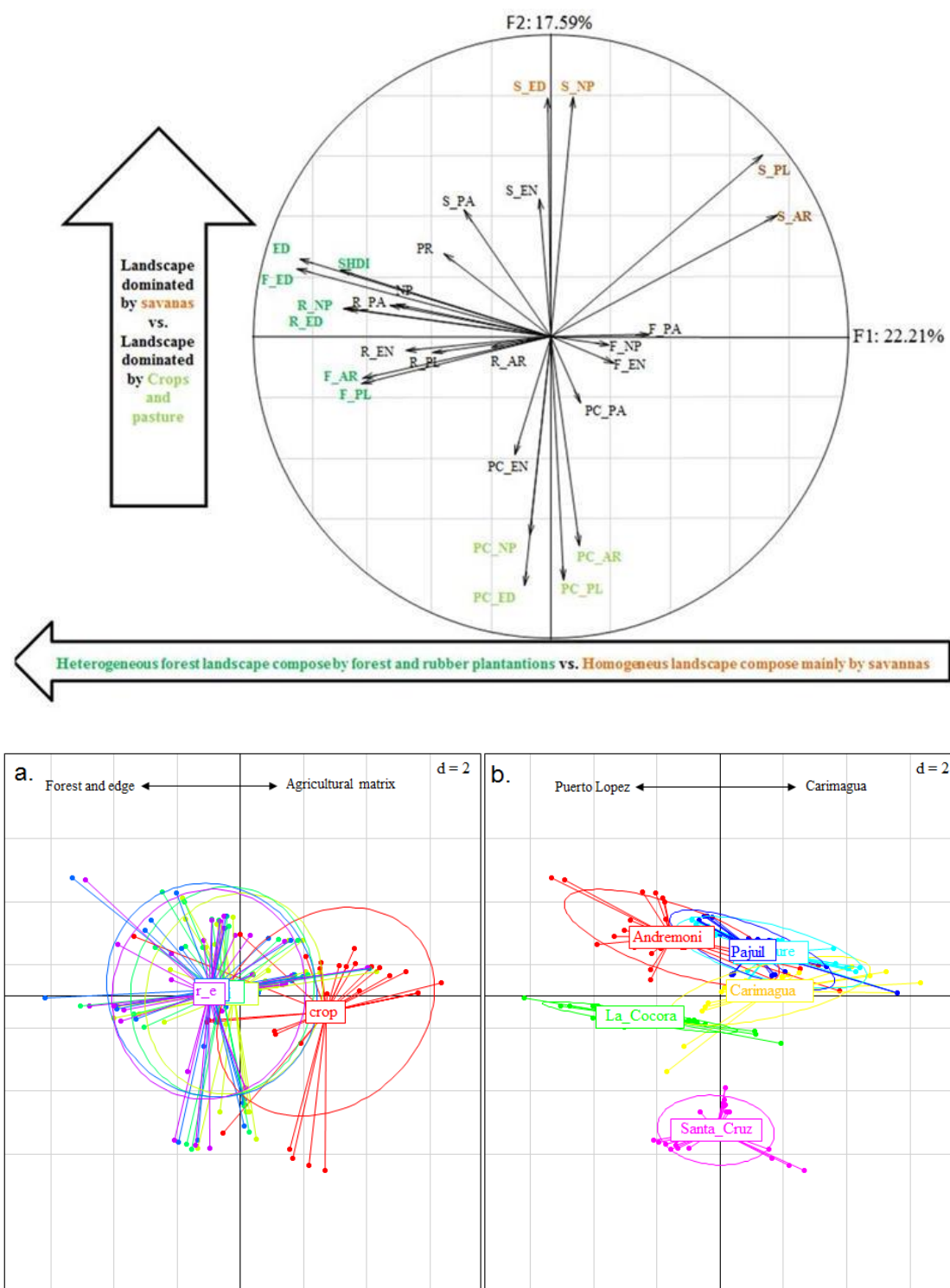

Figure 1: *above*: Projection of metrics in the plane formed by Factors 1 and 2 of a PCA analysis (see table to abbreviations names) and *down*: Projection of barycenter of near landscape in the

plane formed by Factors 1 and 2 of PCA analysis a) point of the transect (next to the river (r_e), middle of the forest (f_m), inside the edge of the forest (f_e_i), outside the edge of the forest (f_e_e) and in the agricultural matrix (crop), and b) Farms.

These results are preliminary and aim at preparing various analyses based on landscape metrics. Losses of biodiversity have occurred at an unprecedented scale and agricultural intensification has been a major driver of this global change (Matson et al., 1997). The conversion of complex natural ecosystems to simplified managed ecosystems and the intensification of resource use, including application of more agrochemicals, typical for open systems. In this sense, not only the biodiversity of pristine habitats and traditional, low-intensity agroecosystems, but also the biodiversity of intensively used agroecosystems has been greatly reduced. That is why a landscape perspective is needed to understand why agricultural land uses have well-known negative and less known positive effects on biodiversity and ecosystem services. Agricultural land uses and biodiversity conservation have been traditionally viewed as incompatible, but well-managed landscapes can also contribute to the conservation of high-diversity systems, which may provide important ecosystem services as pollination. Structurally complex landscapes enhance local diversity in agroecosystems, which may compensate for local high intensity management (Tscharntke et al., 2005).

In the future, I want to link the landscape metrics with the structure of the soil fauna communities, especially ants and termites, as well as with the traits of this fauna. The hypotheses to test can be: (1) The density and diversity of soil fauna are higher in gallery forests than in the agricultural matrix. (2) The structure of the landscape explains a significant part of the variability of communities because landscape heterogeneity and the presence of forest support a high biodiversity. (3) Species inside the forest are different inform those inside the

matrix (4) The edge of the forest hots particular assemblages, composed of bost species from the matric and the forest, and some species specialist of the edge.

An increasing number of publications show the value of landscape metrics to capture and review biological diversity at the highest level (ecosystems or landscapes) (Walz and Syrbe, 2013). Since many species depend strongly on specific habitat characteristics such as food, shelter, climate etc., it can be assumed that species diversity is determined by landscape structure. As I have mentioned, landscape heterogeneity is also a key to assess biodiversity (Turner, 2010) also indicates the spatial variability of the ecosystem properties. It is therefore considered essential for the occurrence and distribution of species from the local to the global level (Tscharntke et al., 2005).

5.2. Conclusion and perspectives

Land use and their management influence important ecosystem properties, processes and functions (Haines-Young, 2009; Lavelle et al., 2014) and, as a result, termite and ant communities and their traits are affected. A key to solve the problem of continued biodiversity loss is to (1) better manage agricultural landscapes, their heterogeneity and structure, (2) improve agricultural practices in each land use to favor biodiversity. The first point suggests that ecologically efficient agricultural landscapes could be designer through the maintenance of a sufficient proportion of land uses favorable to biodiversity (Landis, 2016). The second point suggests that some practices such as tillage or the use of pesticides could be reduced to locally favor biodiversity (Tscharntke et al., 2012). For example, soil chemical properties can be altered at very large time scales. For these reasons, some results observed in this thesis will need to be monitored over time to identify a long term trends and provide more conclusive information on the long-term impacts of agricultural landscapes on communities of soil engineers. In the particular case of the Llanos, the Colombian government has clearly the intention to ensure the

development of the region (Rippstein et al., 2001). However, resuming with the current management practices in agricultural systems will only lead to a worsening of the problem. I recommend paying particular attention to conserve natural ecosystems such as savannas, gallery forests or "morichales"(an neotropical ecosystem formed mainly by moriche palm (*Mauritia flexuosa*) (Lasso et al., 2013) known to be fundamental to preserve hydric resources and biodiversity). This systems conserve an important part of the biodiversity and promote Ecosystem services. Furthermore, it is important to promote the agriculture diversification and develop crops that do not require an intensive management that could be detrimental to the soil and their biodiversity. Hence, agricultural landscapes must be a mosaic of well-connected early and late successional habitats, to support a high biodiversity, and thereby, the capacity to recover from minor and major, small- and large-scale disturbances (Bengtsson et al., 2003). Many agricultural landscapes are dominated by arable crops and early successional fields such as fallows, and support only little non-crop area such as forest remnants and old grassland (Tscharntke et al., 2012, 2005).

The results of this thesis also confirm that ant communities are highly sensitive to changes and constitute good early indicators of change (Velasquez et al., 2012). More accurately, annual crops have shown to be detrimental to ant and termites communities and this is probably mainly associated to the application of chemical inputs to improve chemical fertility of this system, as well as to tillage and pesticide. Tillage causes a periodic disturbance of the soil that reduces the settlement of new colonies. During my thesis I have not directly tested the impact of such agricultural practices. In the future, comparing experimentally the impact of different agricultural practices within the same land use would be very important to increase our knowledge of the mechanisms at the origin of the links between biodiversity and land uses. This would also allow designing practices that are less detrimental to biodiversity.

Tree-based systems such as rubber plantations can play an important role in biodiversity conservation in tropical landscapes (Sanabria 2011; Sanabria-Blandón and Chacon de Ulloa, 2011), especially when compared with other types of agricultural land uses such as oil palm plantations or annual crops. These systems commonly occupy zones of transition between highly disturbed land uses and natural ecosystems, as was demonstrated with the evaluation of the response of ant traits to different soil conditions and land uses (Lavelle et al., 2014). For instance, rubber plantations preserve an assemblage of ants with traits somehow similar to those found in the semi-natural savannas because they have a significant tree cover. However, rubber plantations cannot be expected to have the same impact on biodiversity has savannas or forests because they only host a single tree species.

The improved pastures of the region maintain a constant vegetation due to the herbaceous cover that could be considered to some extent similar to the one of the native savannas due to the quality and quantity of organic matter they produce. Through this organic matter, they can favour an abundant and diverse soil fauna.

Although all land uses have a particular soil fauna (in this case termite and ant). Certain assemblages have species with more particular habitat requirements and others that are adapted to extreme environmental conditions. In this sense, the presence of all land uses contributes to a certain extent to the total diversity of the landscape (Turner et al., 2003; Turner, 2010). But land uses with tree cover could protect rare, some inconspicuous and perhaps fragile species. Due to the high ant diversity in the region some of this rare and endemic species could disappear without even being known. Thus, it is important to continue to study soil communities in the Llanos region, not only to evaluate the impact of the landscape transformation but also to enrich the knowledge of the soil fauna.

Despite the role of soil fauna (especially soil engineers) as mediators of soil function (Lavelle et al., 1997) and the delivery of ecosystem services is increasingly recognized (Folgarait, 1998; Jouquet et al., 2011; Lavelle et al., 2006; Rousseau et al., 2013), it is still important to continue to evaluate their response to changes in natural landscapes due to the agricultural transformation. However, this must be done not only from the point of view of species and species richness but also from the point of view of the ecological functions implemented by these species. In my thesis I have used ant traits, as response traits, to predict the impact of land uses and soil properties on ant communities. It should also be possible to use effect traits (i.e. rates of herbivory or predation, seed dispersal, etc.) to predict the impact of ant and other organisms on soil functioning and agro-ecosystems. For example, some ant species might improve soil fertility through the degradation and reincorporation of organic matter, some other might help in the biocontrol of crop pests (Armbrecht and Perfecto, 2003).

Furthermore, I recommend continue to perform similar studies at the landscape scale and overtime, in order to increase the understanding of determinants of ecosystem services and allow designing more efficient agricultural landscapes, which can assemble in a friendly way all the elements present in this landscape (MEA, 2005). Limits to large-scale land conversion should be set taking into consideration biodiversity conservation, ecosystem engineer promotion and waterway protection (Lavelle et al., 2014). This should protect landscape health on the long-term. In the organization of the agricultural territory at the landscape scale it is also important to consider gallery forests (dense network of forests covering over roughly 20% of the total area in the region). The conventional approach to landscape ecology assumes a poor ecological quality in the human-dominated matrix but this matrix likely has a large impact on the environment and soil communities and it is important to together this matrix and more natural land uses at the landscape scale. Indeed, biodiversity depends not only on the local properties of soil or the land use, it also depends on spatial interactions between multiple

ecosystems and land uses. Biodiversity, as ecosystem services, is influenced by the structure and geographical context of the landscape, such as the arrangement of landscape elements (Bastian et al., 2012; Benoît et al., 2012; Burkhard et al., 2012).

5.6 References

Agosti, D., Alonso, L., 2000. The ALL protocol, in: Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, p. 350.

Agosti, D., Majer, J., Alonso, E., Schultz, T.., 2000. Ants: Standard Methods for Measuring and Monitoring Biodiversity.

Andersen, A.N., Fisher, A., Hoffmann, B.D., Read, J.L., 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecol. 29, 87–92.

Anderson, J.M., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility. A Handbook of Methods, Second Ed. ed. CAB International, Wallingford U.K., Wallingford U.K.

AntWeb [WWW Document], 2014. URL www.antweb.org (accessed 1.20.14).

Armbrecht, I., Perfecto, I., 2003. Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agric. Ecosyst. Environ. 97, 107–115. doi:10.1016/S0167-8809(03)00128-2

Barros, E., Pashanasi, B., Constantino, Reginaldo; Lavelle, P., 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biol Fertil Soils 35, 338–347. doi:10.1007/s00374-002-0479-z

Bastian, O., Haase, D., Grunewald, K., 2012. Ecosystem properties, potentials and services - The EPPS conceptual framework and an urban application example. Ecol. Indic. 21, 7–16. doi:10.1016/j.ecolind.2011.03.014

Bengtsson, J., Angelstam, P., Elmqvist, T., Urban Emanuelsson, Folke, C., Ihse, M., Moberg, F., Nyström, M., 2003. Reserves, Resilience and Dynamic Landscapes. AMBIO A J. Hum. Environ. 32, 389–396.

Benoît, M., Rizzo, D., Marraccini, E., Moonen, A.C., Galli, M., Lardon, S., Rapey, H., Thenail, C., Bonari, E., 2012. Landscape agronomy: A new field for addressing agricultural landscape dynamics. Landsc. Ecol. 27, 1385–1394. doi:10.1007/s10980-012-9802-8

Bourguignon, T., Scheffrahn, R., Křeček, J., Nagy, Z.T., Sonet, G., Roisin, Y., 2010. Towards a revision of the Neotropical soldierless termites (Isoptera : Termitidae): redescription of the genus Anoplotermes and description of Longustitermes, gen. nov. Invertebr. Syst. 24, 357–370.

Burkhard, B., Kroll, F., Nedkov, S., Müller, F., 2012. Mapping ecosystem service supply, demand and budgets. Ecol. Indic. 21, 17–29. doi:10.1016/j.ecolind.2011.06.019

Ciat, 2002. Integrated Soil Fertility management in the tropics: TSBF-CIAT's achievements and reflections.

Comte, I., Colin, F., Whalen, J.K., Gruenberger, O., Caliman, J.P., 2012. Agriculturalpractices in oil palm plantations and their impact on hydrological changes, nutri-ent fluxes and water quality in Indonesia: a review., in: Advances in Agronomy. pp. 71–124.

De la Mora, a., Murnen, C.J., Philpott, S.M., 2013. Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. Biodivers. Conserv. 22, 871–888. doi:10.1007/s10531-013-0454-z

175

Decaëns, T., Lavelle, P., Jiménez, J.J., Escobar, G., Rippstein, G., Schneidmadl, J., Sanz, J.I., Hoyos, P., Thomas, R.J., 2001. Impact of land management on soil macrofauna in the Eastern savannas of Colombia, in: Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia. Ciat, Cali-Colombia, pp. 19–41.

Edwards, D.P., Gilroy, J.J., Woodcock, P., Edwards, F. a., Larsen, T.H., Andrews, D.J.R., Derhé, M. a., Docherty, T.D.S., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C., Wilcove, D.S., 2014. Land-sharing versus land-sparing logging: Reconciling timber extraction with biodiversity conservation. Glob. Chang. Biol. 20, 183–191. doi:10.1111/gcb.12353

Egan, J.F., Mortensen, D. a., 2012. A comparison of land-sharing and land-sparing strategies for plant richness conservation in agricultural landscapes. Ecol. Appl. 22, 459–471. doi:10.1890/11-0206.1

Fahrig, L., 2003. E Ffects of H Abitat F Ragmentation on B Iodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419

Fernández, F., Sendoya, S., 2004. Biota colombiana. Biota Colomb. 5, 3–93.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land sparing versus land sharing: Moving forward. Conserv. Lett. 7, 149–157. doi:10.1111/conl.12084

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning : a review. Biodivers. Conserv. 1244, 1221–1244.

Fonte, S.J., Six, J., 2010. Earthworms and litter management contributions to ecosystem services in a tropical agroforestry system. Ecol. Appl. 20, 1061–73.

Gibb, H., Cunningham, S.A., 2013. Restoration of trophic structure in an assemblage of omnivores, Considering a revegetation chronosequence. J. Appl. Ecol. 50, 449–458. doi:10.1111/1365-2664.12054

Gibb, H., Stoklosa, J., Warton, D.I., Brown, a M., Andrew, N.R., Cunningham, S. a, 2015. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177, 519–31. doi:10.1007/s00442-014-3101-9

Gonçalves, T.T., Reis Júnior, R., Souza, O.F.F. de, Ribeiro, S.P., 2005. Predation and interference competition between ants (Hymenoptera: Formicidae) and arboreal termites (Isoptera: Termitidae). Sociobiology 46, 409–419.

Grau, R., Kuemmerle, T., Macchi, L., 2013. Beyond "land sparing versus land sharing": Environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. Curr. Opin. Environ. Sustain. 5, 477–483. doi:10.1016/j.cosust.2013.06.001

Grimaldi, M., Oszwald, J., Dolédec, S., Hurtado, M.D.P., de Souza Miranda, I., Arnauld de Sartre, X., Assis, W.S. De, Castañeda, E., Desjardins, T., Dubs, F., Guevara, E., Gond, V., Lima, T.T.S., Marichal, R., Michelotti, F., Mitja, D., Noronha, N.C., Delgado Oliveira, M.N., Ramirez, B., Rodriguez, G., Sarrazin, M., Silva, M.L. Da, Costa, L.G.S., Souza, S.L. De, Veiga, I., Velasquez, E., Lavelle, P., 2014. Ecosystem services of regulation and support in Amazonian pioneer fronts: searching for landscape drivers. Landsc. Ecol. 29, 311–328. doi:10.1007/s10980-013-9981-y

Haines-Young, R., 2009. Land use and biodiversity relationships. Land use policy 26, S178–S186. doi:10.1016/j.landusepol.2009.08.009

Hölldobler, B., Wilson, E.O., 1990. The Ants. Belknap Press.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., Lepage, M., 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. Appl. Soil Ecol. 32, 153–164. doi:10.1016/j.apsoil.2005.07.004

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., Bignell, D., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. 47, 215–222. doi:10.1016/j.ejsobi.2011.05.005

Kellman, M., Tackaberry, R., Rigg, L., 1998. in two tropical forest Structure and function gallery in communities : implications for forest conservation fragmented systems 35, 195–206.

Kellman, M., York, N., Mjp, C., 1996. Redefining Roles : Plant Community Reorganization and Species Preservation in Fragmented Systems. Glob. Ecol. Biogeogr. Lett. 5, 111–116.

Landis, D. a, 2016. Title: Designing Agricultural Landscapes for Biodiversity-Based Ecosystem Services Designing Agricultural Landscapes for Biodiversity-Based Ecosystem Services. Basic Appl. Ecol. doi:10.1016/j.baae.2016.07.005

Lasso, C., Rial, A., Gonzales, V., 2013. Morichales y Cananguchales de la Orinoquia y Amazonia, in: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Ed.), Serie Editorial Recursos Hidrobiologicos Y Pesqueros Continentales de Colombia.

Lavelle, P., Bignell, D., Lepage, M., Wolters, W., Roger, P., Ineson, P., Heal, O.W., Dhillion, S., 1997. Soil function in a changing world : the role of invertebrate ecosystem engineers. Eur. J. Soil Biol. 33, 159–193. doi:35400007052344.0010

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.-P., 2006. Soil invertebrates and ecosystem services. Eur. J. Soil Biol. 42, S3–S15. doi:10.1016/j.ejsobi.2006.10.002

Lavelle, P., Pashanasi, B., 1989. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia (Jena). 33, 283–291.

Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M.D.P., Loaiza, S., Pullido, S.X., Rodríguez, E., Sanabria, C., Velásquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. Agric. Ecosyst. Environ. 185, 106–117. doi:10.1016/j.agee.2013.12.020

Lavelle, P., Spain, A. V., 2001. Soil ecology.

Li, H., Wu, J., 2004. Use and misuse of landscape Índices. Landsc. Ecol. 19, 389–399. doi:10.1023/B:LAND.0000030441.15628.d6

Longino, J.T., 2004. Ants of Costa Rica [WWW Document]. URL www.evergreen. edu/ants/AntsofCostaRica (accessed 1.20.15).

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural Intensification and Ecosystem Properties. Science (80-.). 277, 504–509.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. doi:10.1016/j.tree.2006.02.002

MEA, 2005. Millenium Ecosystem Assessment) Ecosystems and Human Well- being: Synthesis. Island Press, Washington, DC. Naidoo.

Meave, J., Kellman, M., 1994. Maintenance of Rain Forest Diversity in Riparian Forests of Tropical Savannas: Implications for Species Conservation During Pleistocene Drought. J. Biogeogr. 21, 121–135. doi:10.2307/2845467

Mlambo, M.C., 2014. Not all traits are "functional": insights from taxonomy and biodiversity-ecosystem functioning research. Biodivers. Conserv. 23, 781–790. doi:10.1007/s10531-014-0618-5

Moser, D., Zechmeister, H.G., Plutzar, C., Sauberer, N., Wrbka, T., Grabherr, G., 2002. Landscape space complexity as an effective measure for plant species richness in rural landscapes. Landsc. Ecol. 17, 657–669.

Moutinho, P., Nepstad, D.C., Davidson, E.A., May, N., 2003. Influence of Leaf-Cutting Ant Nests on Secondary Forest Growth and Soil Properties in Amazonia 84, 1265–1276.

Philpott, S.M., Perfecto, I., Armbrecht, I., Parr, C.L., 2000. Ant Diversity and Function in Disturbed and Changing Habitats, in: Ant Ecology. pp. 137–156.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T. a. S., Parsons, S., Joern, a., 2013. Invertebrates, ecosystem services and climate change. Biol. Rev. 88, 327–348. doi:10.1111/brv.12002

Raphael, M., Catarina, P., George, B., Edana, C., Valery, G., Michel, G., Edward, G., Johan, O., Max, S., Patrick, L., 2010. Earthworm biological traits , soil and landscape characteristics 2010.

Rippstein, G., Escobar, G., Motta, F., 2001. Agroecologia y Biodiversidad de las Sabanas en los Llanos Orientales de COlobia. Publicacion CIAT, Cali-Colombia.

Rodriguez, A.F., 2011. Metodología para detectar cambios en el uso de la tierra utilizando los principios de la clasificación orientada a objetos , estudio de caso piedemonte de Villavicencio , Meta. Universida Nac. Colomb.

Rousseau, L., Fonte, S.J., Téllez, O., van der Hoek, R., Lavelle, P., 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. Ecol. Indic. 27, 71–82. doi:10.1016/j.ecolind.2012.11.020

Sanabria, C., 2011. Ensamblaje de hormigas del suelo en ventanas productivas del piedemonte Amazonico Colombiano.

Sanabria-Blandón, M.C., Chacon de Ulloa, P.C., 2011. Hormigas cazadoras en sistemas productivos del piedemonte amazónico colombiano: Diversidad y especies indicadoras. Acta Amaz. 41, 503–512.

Sayer, J., Ghazoul, J., Nelson, P., Klintuni Boedhihartono, A., 2012. Oil palm expansion transforms tropical landscapes and livelihoods. Glob. Food Sec. 1, 114–119. doi:10.1016/j.gfs.2012.10.003

Schindler, S., Wehrden, H. Von, Poirazidis, K., Wrbka, T., Kati, V., 2013. Multiscale performance of landscape metrics as indicators of species richness of plants , insects and vertebrates. Ecol. Indic. 31, 41–48. doi:10.1016/j.ecolind.2012.04.012

Schmidt, F., Diehl, E., 2008. What is the Effect of Soil Use on Ant Communities ? Neotrop. Entomol. 381–388.

Schmitzberger, I., Wrbka, T., Steurer, B., Aschenbrenner, G., Peterseil, J., Zechmeister, H.G., 2005. How farming styles influence biodiversity maintenance in Austrian agricultural landscapes. Agric. Ecosyst. Environ. 108, 274–290. doi:10.1016/j.agee.2005.02.009

Schroth, G., McNeely, J. a., 2011. Biodiversity Conservation, Ecosystem Services and Livelihoods in Tropical Landscapes: Towards a Common Agenda. Environ. Manage. 48, 229–236. doi:10.1007/s00267-011-9708-2

Schroth, G., Moraes, V.H.F., da Mota, M.S.S., 2004. Increasing the profitability of traditional, planted rubber agroforests at the Tapajós river, Brazilian Amazon. Agric. Ecosyst. Environ. 102, 319–339. doi:10.1016/j.agee.2003.09.001

Seaman, B.S., Schulze, C.H., 2010. The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. Biol. Conserv. 143, 391–398. doi:10.1016/j.biocon.2009.11.002

Silva, J.M., Bates, J., 2002. Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot. Bioscience 52, 225–234.

Terborgh, J., 1999. Requiem for Nature.

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59. doi:10.1016/j.biocon.2012.01.068

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol. Lett. 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x

Turner, B.L., Matson, P., Mccarthy, J., Corell, R., Christensen, L., Eckley, N., Hovelsrud-broda, G.K., Kasperson, J.X., Kasperson, R.E., Luers, A., Martello, M.L., Mathiesen, S., Naylor, R., Polsky, C., Pulsipher, A., Schiller, A., Selin, H., Tyler, N., 2003. A framework for vulnerability analysis in sustainability science 100.

Turner, M., 2010. Disturbance and Landscape dynamics in a changing word. Ecology 91, 2833–2849.

Uuemaa, E., Mander, Ü., Marja, R., 2013. Trends in the use of landscape spatial metrics as landscape indicators : A review. Ecol. Indic. 28, 100–106. doi:10.1016/j.ecolind.2012.07.018

Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia.

Vasconcelos, H.L., Leite, M.F., Vilhena, J.M.S., Lima, A.P., Magnusson, W.E., 2008. Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecol. 33, 221–231. doi:10.1111/j.1442-9993.2007.01811.x

Velasquez, E., Fonte, S.J., Barot, S., Grimaldi, M., Desjardins, T., Lavelle, P., 2012. Soil macrofauna-mediated impacts of plant species composition on soil functioning in Amazonian pastures. Appl. Soil Ecol. 56, 43–50. doi:10.1016/j.apsoil.2012.01.008

Wall, D., Blackburn, T.H., Brussaard, L., Hutchings, P., Palmer, M.A., Snelgrove, P.V.R., 2012. Biodiversity Functioning of Soils Linking and and Ecosystem Sediments.

Walz, U., Syrbe, R., 2013. Linking landscape structure and biodiversity. Ecol. Indic. 31, 1–5. doi:10.1016/j.ecolind.2013.01.032

Webb, C.T., Hoeting, J.., Ames, G.M., Pyne, M.I., Poff N.L., 2010. A structured and dynamic framework to avance trait-based theory and prediction in ecology. Ecol. Lett. 13, 267–283.

Wiescher, P.T., Pearce-Duvet, J.M.C., Feener, D.H., 2012. Assembling an ant community: Species functional traits reflect environmental filtering. Oecologia 169, 1063–1074. doi:10.1007/s00442-012-2262-7

Wood, S., Karp, D., DeClerck, F., Kremen, C., Naeem, S., Palm, C., 2015. Functional traits in agriculture: Agrobiodiversity and ecosystem services. Trends Ecol. Evol. 30, 531–539. doi:10.1016/j.tree.2015.06.013

CrossMark

Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia

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ABSTRACT

In the Orinoco River Basin of eastern Colombia large scale and rapid conversion of natural savannas into commercial agriculture exists as a critical threat for the ecological integrity of this fragile region. The highly acidic and compacted soils inherent to this region require thorough physical and chemical conditioning in order for intensive cropping systems to be established. Assessing the impact of this dramatic soil perturbation on biodiversity, ecosystem services and other elements of the natural capital is an urgent task for designing sustainable management options in the region. To address this need, we evaluated soil macro invertebrate communities and soil-based ecosystem services (climate regulation, hydrologic functions, soil stability provided by macro aggregation and nutrient provision potential) in four major production systems: improved pastures, annual crops (rice, corn and soy bean), oil palm and rubber plantations, and compared them to the original savanna. Fifteen plots of each system were sampled along a 200 km natural gradient of soil and climatic conditions. In each plot, we assessed climate regulation by measuring green house gas emissions (N_2O, CH_4 and CO_2) and C storage in aboveground plant biomass and soil (0–20 cm). Soil biodiversity (macro invertebrate communities) and three other soil-based ecosystem services, were assessed using sets of 12–20 relevant variables associated with each service and synthesized via multivariate analyses into a single indicator for each ecosystem function, adjusted in a range of 0.1–1.0. Savannas yielded intermediate values for most indicators, while each production system appeared to improve at least one ecosystem service. For example, nutrient provision (chemical fertility) was highest in annual cropping systems (0.78 ± 0.03) due to relatively high concentrations of Ca, Mg, N, K, and available P and low Al saturation. Hydrological functions and climate regulation (C storage and GHG emissions) were generally improved by perennial crops (oil palm and rubber), while indicators for macro invertebrate biodiversity and activity (0.73 ± 0.05) and soil macro aggregation (0.76 ± 0.02) were highest within improved pastures. High variability within each system indicates the potential to make improvements in fields with lowest indicator values, while differences among systems suggest the potential to mitigate negative impacts by combining plots with contrasted functions in a strategically designed landscape mosaic.

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1. Introduction

The need to increase agricultural production for food and energy resources is driving agricultural frontiers into the last remaining arable lands (Hubert et al., 2010). In Colombia, the Eastern Plains (Llanos Orientales) are now being rapidly converted from semi-natural savanna, dedicated largely to extensive cattle ranching and low-input traditional agriculture, to highly intensified commercial production of food (rice, soy bean, maize), biofuels (sugar cane and oil palm) and rubber. It is estimated that over 50,000 ha has been

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Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos

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A B S T R A C T

Ants represent a widespread and functionally diverse taxonomic group that are both sensitive to land management and serve as important regulators of key soil processes. Building upon this idea, we sought to understand the impacts of agricultural management on ant communities in the Orinoco River Basin of eastern Colombia and to identify species that could be used as indicators of soil-based ecosystem services. Ants were collected and identified from the soil and litter layer within 75 fields (nine TSBF sub-samples along a transect in each field) divided among five common agricultural land uses in the region: 1) annual crops (maize, soy and rice), 2) rubber plantations, 3) oil palm plantations, 4) improved pastures (based on Brachiaria spp.), and 5) semi-natural savannas. As expected, land management was found to greatly influence ant communities. Improved pastures showed the highest species richness (6.9 species per transect) and semi-natural savanna the greatest abundance of ants (145 individuals per transect). Within each of these fields a suite of soil and agroecosystem characteristics were measured and combined into synthetic indicators of five soil-based ecosystem services: 1) nutrient provision, 2) water storage and regulation, 3) maintenance of soil structure, 4) climate regulation services and 5) soil biodiversity and biological activity. Ant species were then associated with these synthetic indicators using the IndVal method to identify indicator species for each of the five consolidated ecosystem services measured. In total, 14 indicator species were identified and found to be significantly associated with either the high or low provision of each of the five services. The development of such bioindicators offers a rapid and relatively inexpensive tool to facilitate land management and policy decisions in this biologically diverse and rapidly changing region of Colombia.

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1. Introduction

Tropical savannas cover approximately 15% of the total land area in South America (Rippstein et al., 2001) and are of critical importance for agricultural production and a range of other ecosystems services in the region. In Colombia, these savannas occupy much of the eastern plains (locally referred to as the Llanos Orientales), a rapidly developing part of the Orinoco River Basin that has been traditionally managed under extensive livestock and low-input agriculture. Recent investment in the region has focused on large-scale agricultural intensification involving the conversion of semi-natural savanna to annual crops of rice, maize and soybean, perennial crops such as oil palm and rubber, and improved pastures (typically sown with Brachiaria species and fertilized every few years). This conversion usually involves high inputs of fertilizer and lime combined with deep and rather intensive tillage. Such intensification has generated much concern, as soils and ecosystems of the region are generally fragile and comprise a patchwork of agricultural land uses mixed with semi-natural savanna and riparian forests, both critical landscape components in regulating regional water quality and biodiversity (Goosen, 1971; Correa et al., 2005; Lavelle et al., 2014).

Soils are involved in the provision of many ecosystem services that are of great importance for the maintenance of ecosystem functioning and human societies, with farmers primarily responsible for the management of this resource (Millennium Ecosystem Assessment, 2005; Wall et al., 2012). Soils are also considered a large reservoir of

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Original article

Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos

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ABSTRACT

Ants and termites, as soil engineers, provide many ecosystem services that can be important for the sustainability of agriculture. The aim of this study was to evaluate the impact of land use on ant and termite communities in Colombian savanna landscapes, and to assess whether this impact is associated with the modification of soil physical and chemical properties. Ants and termites were sampled in five different agricultural and semi-natural systems across three regions of the eastern Colombian Llanos: 1) annual crops (maize, soy and rice), 2) rubber plantations, 3) oil palm plantations, 4) improved pastures and 5) semi-natural savannas. A total of 91 ant and 16 termite species were collected. Multivariate analysis revealed that termite communities significantly differed among land uses, but not between regions. Ant communities differed between regions and land uses. Based on between group analyses of termite communities, three groups of land use can be distinguished: one formed by semi-natural savannas and improved pastures, the second by oil palm plantations and annual crops and the third by rubber plantations. General linear models applied separately to each species found 19 significant associations of soil physical or chemical properties, land uses or regions with 15 ant species and 14 significant associations with 6 termite species. Taken together, there is a strong association between land use and ant or termite communities and this influence is likely due to changes in ant and termite habitats resulting from agricultural practices such as tillage, fertilization, and lime addition. These results suggest that annual crops are the most detrimental land use for termites and ants, because their communities are highly sensitive to vegetation cover and agricultural practices such as tillage. Maintaining a high diversity of soil engineers and the ecosystem services they provide likely depends on the maintenance of natural ecosystems in the landscape and the adoption of practices that reduce impacts on soil ecosystem engineers when native ecosystems have been transformed into agricultural systems.

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1. Introduction

Colombian savannas are part of the second largest savanna system in South America [1]. In these savannas the intensification of land use and high population growth has turned the region into one of the most threatened ecosystems in Colombia [2]. Savannas are rapidly being converted from semi-natural systems, dedicated largely to extensive cattle ranching and low-input traditional agriculture, to highly intensified commercial production of annual crops (rice, soybean, maize), biofuels (sugar cane and oil palm) and tree crops such as rubber. It is estimated that over 50,000 ha have been converted over the last two decades and recent trends show this agricultural expansion to be rapidly accelerating [2].

Soil is considered to be one of the most diverse and least understood reservoirs of biodiversity in the biosphere [3]. Threats to this biodiversity are a source of concern for the intrinsic value of

Abstract

Tropical savannas are highly important for agricultural production and many other ecosystems services. In Colombia, these savannas have been traditionally managed through extensive livestock production and low-input agriculture. The current conversion of these natural systems to intensified agriculture can have devastating impacts on belowground and aboveground biodiversity. Soil macrofauna represents an important part of agroecosystem biodiversity and some groups have received considerable attention as ecosystem engineers. The general goal of the thesis is to evaluate and analyze the impacts of agricultural landscapes on soil engineer communities and soil ecosystem services in the Colombian Llanos. Three main questions were addressed: (1) What is the impact of agricultural management on ant communities and is it possible to identify ant species that could be used as indicators of soil-based ecosystem services? (2) What is the impact of land uses on ant and termite communities and is this impact associated with modifications of soil physical and chemical properties? (3) Do the ecological and morphological traits of ants respond to land uses and soil properties?

The results of this thesis confirm that ant communities are highly sensitive to land use changes and constitute good early indicators of soil-based ecosystem services. More accurately, annual crops have shown to be detrimental to ant and termites communities and this is probably due to the application of chemical inputs, as well as to tillage and pesticides. All land uses (Savannas, rubber or oil palm plantations, improved pastures and annual crops) have a particular soil fauna, but some species have particular habitat requirements for nest sites, food, refugees, etc. Some species are more generalist and are particularly adapted to disturbed environment. The presence of all land uses within a landscape contributes to a certain extent to the total diversity. It was found that sites with a tree cover protect rare, sometimes inconspicuous and perhaps fragile species.