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**Impact of Cocoa Agroforests on Termite
Diversity in Peruvian Amazon**

Master Thesis

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Declaration

I, Matěj Zídek, declare that I have written the following M.Sc. thesis entitled “Impact of Cocoa Agroforests on Termite Diversity in Peruvian Amazon” independently and cited only quotations listed in the references.

In Prague, 2017

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Signature

.....

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Abstract

In Amazon Basin agroforestry systems are promising alternative agricultural farming, that should preserve the structural diversity that simulate the native tropical forests better than do conventional agriculture. This study investigated how cacao agroforestry management in the lowlands of Peruvian Amazon support and change termite species composition, diversity and functions and if it's in term of relative biodiversity composition closer to primary and secondary forest or if it's more close to slash and burn farming. We decided to monitor termites (*Isoptera: Termitoidae*) as bioindicators for their quick reaction to environmental changes and human disturbance.

We hypothesized that termite species diversity level will decrease along with increasing level of disturbance in four monitored areas. Including primary forest (PF), secondary forest (SF), cocoa agroforestry system (AF) and annual maize field crop (AC). Highest species diversity will be in forest habitats and lowest in annual maize field due to the high disturbance connected with burning. Termite species density was calculated by averaging the number of species that was found in each transect section among feeding-groups and sites while relative abundance was calculated by averaging the number of encounters of species in each transect section among feeding-groups and sites. In total, eighteen termite species from five subfamilies were recorded in this study area, including three feeding-groups. The most abundant PF and SF had the same species richness, with nine species gathered in each sites, followed by four species in AC and three species in AF. We have showed that agroforestry does not necessarily always provide protection for termite population. This result surprisingly unconfirmed our hypotheses which was state on various studies where agroforestry outcome more positive in biodiversity conservation than slash and burn farming. This may be linked to the level and frequency of weeding in AF, while fallow in AC, even when it's highly disturbed habitat, may allow for rapid termite re-colonization. In this context our study forms a good scientific background for the further monitoring of ecological changes in human modified landscape in the Amazon region.

Key words: Cacao agroforestry, Peru, species richness, *Isoptera*, *Termitoidae*, disturbance, bioindicator, land-use gradient

Abstrakt

V Amazonii se zdají být agrolesnické systémy alternativního zemědělství nadějí pro zachování diverzity, protože simulují přirozené tropické lesy lépe, než konvenční zemědělství. Tato studie se zabývá tím, jak management kakaovníkového agrolesnictví v nížinách Peruánské Amazonie podporuje a mění druhovou rozmanitost a funkci termitů, ve vazbě na složení a biologickou rozmanitost primárních a sekundárních lesů. Jako bioindikátor jsme se rozhodli využít řád termitů (*Isoptera: Termitoidae*) pro jejich rychlou reakci na změnu prostředí a rušení lidskými vlivy.

Naší hypotézou bylo, že úroveň druhové rozmanitosti termitů se sníží spolu se zvyšující se úrovní narušení ve čtyřech sledovaných oblastech. Oblasti zahrnují primární les (PF), sekundární les (SF), kakaový agrolesnický systém (AF) a jednoletou polní plodinu kukuřici (AC). Nejvyšší druhová rozmanitost se předpokládá v lesních stanovištích a nejnižší na kukuřičném poli, z důvodů vysokého narušení ekosystému vypalováním. Hustota výskytu jednotlivých druhů termitů byla vypočtena zprůměrováním počtu druhů, které byly nalezeny v každé sekci transektů mezi skupinami a jednotlivými typy ekosystémů. Zatímco abundance byla vypočtena zprůměrováním počtu výskytu druhů v každé transektové části mezi skupinami a ekosystémy. Celkem bylo v této oblasti studie zaznamenáno osmnáct druhů termitů z pěti podčeledí včetně tří potravních skupin. Nejhojnější PF a SF měly stejnou druhovou bohatost, na každé této lokalitě bylo nalezeno devět druhů, následovaly čtyři druhy v AC a tři druhy v AF. Tento výsledek překvapivě nepotvrdil naši hypotézu. Prokázali jsme, že agrolesnictví nemusí nutně vždy zajišťovat ochranu populací termitů.. Hypotéza byla stanovena na základě jiných studií, jejichž výsledkem z pravidla bylo, že agrolesnické systémy mají pozitivní vliv na ochranu biologické rozmanitosti oproti žďárovému zemědělství. Tento náš výsledek může vyplývat z vyššího počtu agrotechnických zásahů v AF, zatímco úhor, i ve vysoce narušených stanovištích, jako je AC, může umožnit rychlou rekolonizaci některých druhů termitů. V této souvislosti pro nás tato práce tvoří dobrý vědecký základ pro další sledování ekologických změn v lidmi pozměněné krajině v Amazonské oblasti.

Klíčová slova: kakaovníkové agrolesnictví, Peru, druhová rozmanitost, *Isoptera*, *Termitoidae*, narušení ekosystému, bioindikátor, stupeň využití půdy

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1. Introduction

Agricultural practices are a leading because of biodiversity loss and land degradation (Bai *et al.* 2008). One approach to develop more sustainable agriculture is to harness ecosystem services of naturally occurring organisms (Evans *et al.* 2011).

Deforestation in the tropics is increasing at an annual rate of 2,101 km² which is faster than in any other habitat domain. Rain forests make up 32% of the deforested area globally, half of which is represented by forest ecosystems in South America (Hansen *et al.* 2013). The predominant driving force of tropical habitat loss is population growth and demand for agricultural products (Defries *et al.* 2010). In order to compensate the increasing demands farmers use intensification methods to reduce natural crop variability and increase crop stability (Darnhofer *et al.* 2011). However, while intensification can bring short term benefits, in the long-term view the sustainability of the farms, both economic and ecological may be endangered. (Asare *et al.* 2014,). One approach seem to be a good alternative land use system that can decrease deforestation and is called agroforestry. (Brookfield & Padoch 1994)

Agroforestry systems is a summary term for practices that involve the integration of trees and other large woody perennials into farming systems through the conservation of existing trees, their active planting and tending, or the tolerance of spontaneous tree regrowth (Schroth *et al.*, 2004). Agroforestry becoming more and more important land use system because traditional shifting cultivation ceases to be unsustainable due to increasing population density and increasing worldwide demand for the agricultural products from tropical regions. Therefore is crucial to know all the aspects which can agroforestry provide. (Alvarez & Naughton-Treves, 2003)

One of the most common agroforestry systems in the tropics are cocoa agroforests, where cocoa (*Theobroma cacao*) is grown under the canopy of various shade trees. The areas in Peru which are covered with cocoa production annually increase. In 2011 cacao cultivation covered around 84,000 ha whereas in 2013 it was already more than 97,000 ha and also with increasing average yield of cacao beans which is over 730 kg/ha. (FAO, 2013), most of them are usually cultivated in

agroforestry scheme under the complex vegetation of shade trees. About 30,000 Peruvian families are dependent on cocoa cultivation (Anduaga, 2009).

Most authors present that it is not simple to choose single group of organisms which can be sufficient for adequate measurements of general richness or diversity values (Landres *et al.*, 1988), since each group subtends its own patterns for extrapolation from species-time accumulation curves or genetic diversity (Soberón and Llorente, 1993). Monitored insect group should be common, biologically and taxonomically well understood, easily observed and identified in any site or season, widespread and comparable across sites, seasons, habitats and human use regimes, sensitive to given physical and biological factors and processes in their habitat, closely associated with other taxa, resources, and ecosystem characters, and show a predictable early reaction to any unsustainable resource use which could lead to local habitat degradation (Pearson and Cassola, 1992; Pearson, 1994).

Termites (*Isoptera: Termitoidae*) fulfil most of mentioned important features and from this reason we used them as a bioindicators. Bioindicator specify biological processes, species, or communities that are used to assess the quality of the environment and how it changes over time. Changes in the environment are often attributed to anthropogenic disturbances (e.g., pollution, land use changes) or natural stressors (e.g., drought, late spring freeze), although anthropogenic stressors form the primary focus of bioindicator research (Holt & Miller, 2010).

Termites are very important example for soil-dwelling ‘ecosystem service providers’ (Jouquet *et al.*, 2007), that affect the functioning of ecosystems by physically changing their biotic and abiotic environment (Jones *et al.*, 1997).

While we have a relatively good understanding of how termite populations respond to disturbance, studies from South America are sparse. Additionally, little is known about the drivers of species composition among different land-use regimes (Krishna *et al.*, 2013).

This is why we chose Peruvian Amazon to closer research. Moreover about 72% of the neotropical species occur in South America (Constantino, 2014) and the sites with good termite surveys are between the parallels 0° S and 20° S, which include the Amazon and Atlantic Forests, Cerrado and Caatinga (Constantino & Acioli, 2006).

Important fact for farmers is that termite taxa include species that may become a pest in agricultural systems; nevertheless, they are much more often beneficial for the ecosystem (Evans *et al.*, 2011).

2. Literature review

2.1 Diversity of insects in tropics

It is widely speculated that isolation and fragmentation induced changes in forest structure may cause the disruption of those biological processes that maintain biodiversity and ecosystem functioning, such as pollination, seed dispersal and nutrient recycling. To a large degree these processes are mediated by insects. What is known, at least in general terms, is that forest fragmentation not only influences the abundance and diversity of insects, but also modifies higher order interactions between insects and other organisms, both directly and indirectly. While the ecological roles of insects are occasionally well documented, the effects of forest fragmentation on insect populations are poorly understood and the empirical data diffuse and contrasting. (Didham *et al.*, 1996)

Godfray *et al.* (1999) state that understanding insect diversity in the humid tropics is one of the major challenges in modern ecology. Some information sources estimate that tropical forest in the Amazon basin is a living site for over 30% of insect species worldwide; however, insects also play a significant role in agro-ecosystems found in the Amazon which have not yet been thoroughly studied. Crops grown in conventional monoculture systems often suffer from severe pest problems. This is usually because of applying wrong cropping system. Monoculture reduces a complex natural plant system to a single-species community. This may lead to reduction in insect diversity and can promote rapid population growth of a single, or very few, insect species (Stamps & Linit, 1997). Agroforestry induces a different proportion of insect species, even herbivores, and this is supposed to lower the occurrence of pest. There was conducted study on 287 species of herbivorous insects. Where researcher records a lower density of herbivore pests in polyculture systems than in monoculture cropping in approximately 52% of the species studied. Only 15% had higher densities. Monocultures in the Peruvian Amazon contain mainly beetles (most commonly Chrysomelids), Hymenopterans represented by the family *Vespidae*, Homopterans, and others. The variety of species is normally low, but with a large number of individuals for each species (Andow, 1991). In agroforestry systems,

another view into insect diversity, equilibrium and conservation could be offered. (Perry *et al.*, 2016)

Each of insects groups has its position and the role in the ecosystem and representatives are well adapted to the environment. Under the special conditions, there is created a strong interaction between insects and rainforest. Closely related species are more sensitive to forest disturbance and often undergo changes or even extinction. (Lojka *et al.*, 2010).

2.2 Introduction to termites

Termites are easily recognizable from all other groups of insect, because they have very significant morphology in all castes.. However, the phylogenetic position of termites has been discussed for long time. The majority opinion is that termites are part of the order *Dictyoptera* (along with cockroaches and mantids), and that they are phylogenetically placed within the cockroaches. They are close to the *Blattidae*, and their sister group is the wood roach, *Cryptocercus*. (Legendre *et al.* 2008; Ware *et al.* 2010).

There are approximately 2,750 described species of termites with perhaps 400–900 species still left to describe (Bignell *et.al.*, 2011)

The most recent higher classification splits termite species into nine extant families and proposes two fossil ones, with one “family” of uncertain status. Generally, the basal families are more cockroach-like and the apical ones more specialised: this can be particularly seen in the *Mastotermitidae* and the “*Termopsidae*”. All groups are fully eusocial, although some dry-wood-nesting termites (*Kalotermitidae*) may not have functionally active workers. The *Mastotermitidae*, with just a single extant species restricted to northern Australia, are acknowledged to be the oldest family, with many cockroach-like features (e.g. wing venation, retention of an ootheca, presence of the endosymbiont *Blattabacterium*). However, they have true workers and nest away from their food. Two slightly more recent groups, the ‘*Termopsidae*’ and the *Kalotermitidae* both nest and feed in single pieces of dead wood: the termopsids in wet logs in temperate rain forests, and the kalotermitids in dry wood in tropical rainforest tree canopies, isolated islands and semi-deserts. These groups do not have true workers, although they always have soldiers (Engel *et al.* 2009).

A specialised group within or close to the termopsids, the *Hodotermitidae*, are grass-feeders across semi-arid regions of the Old World, and have well developed nests built away from their food. The *Rhinotermitidae* are widespread, being the only family that extends significantly into subtropical and warm temperate regions, for example in North America and Europe (Weesner, 1965).

The ranks between family and generic levels are generally poorly worked out. The *Mastotermitinae* has only one species. The *Termopsidae* have three fairly

disparate subfamilies (*Termopsinae*, *Stolotermitinae*, *Porotermitinae*). The *Kalotermitidae* have no accepted subfamily classification. The *Rhinotermitidae* have subfamilies that mostly contain a single or two genera, with the exception of the *Rhinotermitinae*. Within the *Termitidae* seven subfamilies were most recently recognised by Engel *et al.* (2009): *Macrotermitinae*, *Sphaerotermitinae*, *Foraminitermitinae*, *Apicotermitinae*, *Syntermitinae*, *Termitinae*, and *Nasutitermitinae*.

Termites have the abilities to forage over long distances (metres to tens of metres) and to partially control their own living environments through the creation of nest structures where the humidity and temperature remain constant throughout all seasons. This gives them a striking ability to remain active in harsh environments, or during severe seasons, where most other soil macroinvertebrates are diminished or eliminated. (Jacquet *et al.*, 2011)

Termite diversity and abundance are highest in tropical forests (Bignell and Eggleton, 2000). However, in arid and semi-arid regions where diversity and abundance are usually lower, the functional importance of termites may be higher than in humid forests. In some semi-arid savannas, termites are responsible for more than 20% of carbon mineralisation (Holt, 1987).

Only workers forage. Termites feed on dead plant material at all stages of decomposition. This includes, in order of humification: microepiphytes, living stems and roots, dry grass, dead leaves, dead wood, very decayed dead wood plastered with soil, humus and (apparently mineral) soil (Donovan *et al.* 2000; Hyodo *et al.* 2008).

The ecological importance of termites is based on several aspects, which have been observed in ecosystems. They participate in the decomposition and flow of carbon and nutrients moving particles at different depths (Jouquet *et al.*, 2011), increasing soil porosity and consequently increasing water retention, which directly affects the vegetation structure and the local primary productivity (Nash & Whitford, 1995). For these reasons, they are considered to be key organisms to maintain the structure and functional integrity of ecosystems and have been considered for ecological monitoring analysis (Brown Jr, 1997)

2.2.1 Symbiosis with microorganisms

The diet of termites is diverse. But cellulose is the main food resource of wide range termite species which is usually found in dead plant material such as wood, bark and straw (Bignell *et al*, 2011). However, termites are deficient in enzymes that breaks cellulose and lignin molecules, which provides them extra carbohydrates (Williams, 1965). Therefore termites require the support of symbiotic microorganisms associated with the intestine in its supply channel to the digestion of these compounds (Breznak and Brune, 1994; Ni & Tokuda, 2013).

Termites depend upon the microbes in their gut (see **Fig. 1**) or digestive tract to digest the complex sugars in wood into more simple molecules that they can use for food. Cellulose is broken down in the hindgut of the termite by flagellates into molecules short-chain fatty acids. Acetic acid for example. The termite's cells use these acids as nourishment, same as human cells do. The microbes in human guts break down the food into these short-chain fatty acids to feed its tissues. The termite's microbes also produce gasses during this breakdown process. Methane gas is a major product and termites are a large source of methane in our atmosphere. Methane is a more potent greenhouse gas than carbon dioxide (Noll, 2015).

No single type of microbes in the termite gut can mediate complete complex sugars digestion. A whole community of microorganisms is necessary. These microbes belong to three groups, bacteria, archaea and protozoans (see **Fig 1**). Organisms that live with one another for long periods of time are said to live in symbiosis. The symbioses in the termite gut are often beneficial to both partners and so are called a mutualistic relationship. Sometimes neither partner can live without the other, so the relationship is called an obligate symbiosis. The protozoans and the bacteria and archaea that live inside them often depend upon one another and cannot live without each other, so they are an example of an obligate symbiosis. The bacteria and archaea that live inside their partner are also called endosymbionts, "endo-" meaning "within." (Noll, 2015)

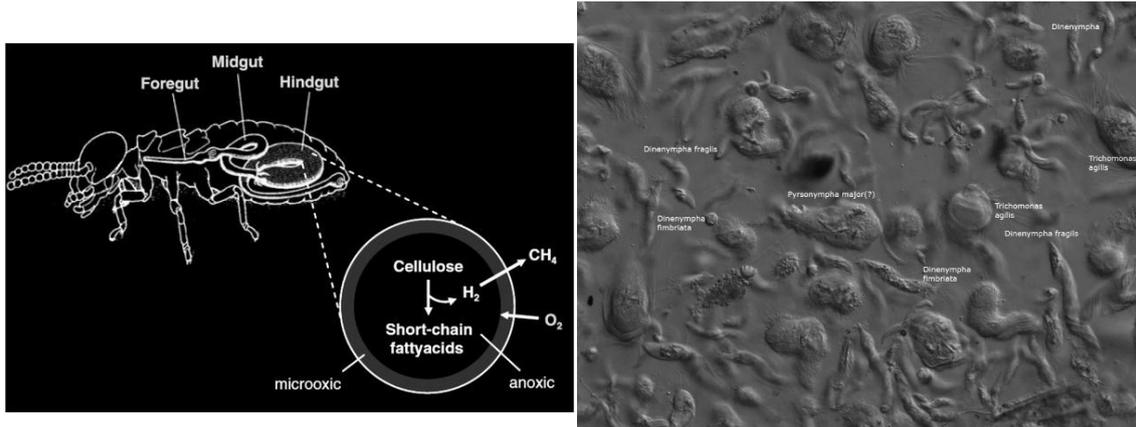


Figure 1: The gut of wood feeding termite
 Schematic image (left), termite's gut microbes (right)
 Source: Kennet Noll (<http://www.kennethnoll.uconn.edu>)

2.2.2 Ecosystem engineers

High biodiversity contributes to a wide range of ecosystem processes (e.g. seed dispersion, pollination, bioturbation, nutrient cycling and decomposition) due to the presence of organisms from different functional groups and trophic levels. The decrease of biodiversity, as a consequence of intensive land-use, may therefore have a negative impact on ecosystem functioning (Palm et al. 2005, Kagezi et al. 2011). Termites contain a number of functional groups that decompose a number of dead organic compounds (e.g. wood, fungus, leaf-litter, humus and mineralised soil (Donovan et al. 2001, Inward et al. 2007)) and nest both above and below-ground. Termites are therefore vital ecosystem engineers that contribute to a series of ecosystem processes (Jouquet et al. 2011, Jones et al. 1994); nevertheless, termites are highly sensitive to land-use change (Jones et al. 2003, Vaessen et al. 2011). Kagezi et al. (2011) showed that agricultural land holdings consistently show a lower rate of removal of cellulose by termites than forest stands or pastures. Reducing decomposition mediated by termites and intensification of agriculture may therefore reduce the prosperity farmland compared to more economically and ecologically sustainable agroforestry with higher biodiversity (Asare et al. 2014).

One of the major effects of termites in ecosystems is their role in soil loosening (reduction of bulk density) and both vertical and horizontal transport through bioturbation, and subsequent erosions of their constructions. A large amount of soil moves from various depths of the profile to the surface of the soil during mound-, gallery- and sheeting constructions. This is especially true with termites of the subfamily *Macrotermitinae* (Holt & Lepage, 2000) although it was also evaluated and documented in the genus *Trinervitermes* (Brossard et al., 2007). Use of rare earths and trace elements concentrations, Sako et al. (2009) confirmed that the nests of *Macrotermes* sp. are produced through the accumulation of highly weathered soil originating from deeper layers. The size and route of soil translocation resulting from termite activity is directly related to their specific dietary habits and the properties of the soil they use (Ackerman et al., 2007, Brossard et al., 2007, Jouquet et al. 2002a]. The mounds of humivorous termites are constructed from materials coming mainly from the surface horizon and recycled at this level by erosion. In contrast, the fungus-growing *Macrotermitinae* can get their material (wet soil particles) very deep in the profile, even down to the water table (which may be in places like the Sahel region of Senegal as low as 50 m) (Holt & Lepage, 2000). Over time these effects of termites on soil translocation will have strong consequences on the profile, thus rendering termite factors a pedogenic as well as responsible for the distribution of resources in the ecosystem (Jouquet et al., 2007).

2.2.3 Physical changes to the ecosystem

Soil-transferred termites usually contain a higher proportion of finer particles and therefore typically exhibit different clay mineral compositions than those that predominate on the original surface (Abe & Wakatsuki, 2010; Donovan et al., 2001; Jouquet et al., 2005)

Termite nests and biomass were characterized as "sinks" because they carry large amounts of waste and soil organic matter from "normal" decomposition routes (Whitford et al, 1992). The use of organic matter by termites is used in the production of termite biomass and in the construction of nesting structures. Re-entry of organic substances and mineral nutrients into the soil environment is manifested

by feces, salivary secretions, corpses and predators. Mortality, particularly from ant predation and massive erosion contributes significantly to the turnover and redistribution of the organic matter and mineral nutrients in the ecosystem (Jouquet et al., 2011).

In purely metabolic terms and in a global context, the decomposition of plant material is carried out primarily by free-living fungi and bacteria, but in many tropical habitats termites also contribute to the consumption and mineralisation of a significant part of litter by processing large quantities of plant material (Bignell & Eggleton, 2000; Yamada *et al.*, 2005).

Through soil replacement (tunnelling and sheeting production) in their mass and nesting activities, termites and ants further aerate the soil, increase absorption and storage of water in the soils, and facilitate carbon fluxes and storage (Lobry de Bruyn & Conacher 1990; Sileshi et al. 2010)

2.2.4 Chemical changes to the ecosystem

Termites have also been considered to be substances caused by weather conditions due to their ability to chemically transform minerals (Jouquet et al. 2002a, Sako et al, 2009). This process can be indirect, due to the exposure of clays from deeper soil layers to the atmosphere and the effects of rain water against weathering or direct soil reprocessing by termites. Using laboratory experiments, Jouquet et al. 2002a showed that this reuse can lead to an increase of the expandable layers of the silicate clay minerals. However, the effect depends on the required (or available) control intensity of the individual structures (Jouquet et al, 2002b, Jouquet et al, 2007). The precise mechanisms by which termites affect the mineralogical properties of clays are unknown, but it may be assumed that the grinding of soil particles by termite mandibles in the saliva-rich environment of the buccal cavity increases the surface area exposed to the surrounding solution, and then a release of interlayer K and the adsorption of hydrated or polar ions between the layers. If it has proven to be practicing in large areas of the world's savannah, this cumulative action for decades and centuries could be the ultimate determinant of soil fertility in environments where low-activity countries, such as kaolinite, predominate. This role can be expected in *Macrotermitinae* (Jouquet et al, 2011).

2.3 Termite diversity

Termite diversity generally declines with increased elevation, unlike that of most other tropical invertebrates studied (Akhtar et al. 1992). This is usually explained by reducing the temperature associated with metabolic rate (Gathorne-Hardy et al. 2001). Termites have also been observed to have a smaller altitudinal range on smaller mountains relative to large ones. This is attributed to the Massenerhebung effect, a phenomenon in which cloud formation occurs at lower altitudes on smaller mountains that reflect sunlight and reduce daytime temperatures at lower altitudes (Gathorne-Hardy et al. 2001). Although temperature is an important factor for termites (because they are ectothermic), different termite functional groups react differently to temperature due to their different feeding habits (see **Fig. 14**). Soil feeders, for example, are generally more negatively affected. This is likely because it depends on substrates with lower energy nutrition than wood feeders, which gives them energy with fewer colonies to overcome the physiological costs of living at lower temperatures (Jones 2000, Davies et al. 2003). Wherever the mean peak peaks in termite diversity were documented (Donovan et al. 2000), these have been attributed to factors such as anthropogenic disorder and limited height of the study (Inoue et al. 2006).

Besides the altitude and so connected temperature there are other non-mutually exclusive factors that may explain changes in termite diversity which include rainfall and the size of the regional species pool. Rainfall can have a negative effect on termite species richness and abundance in tropical rain forest systems, as very high levels can lead to flooding of the microorganism and the death of colonies (Dibog et al. 1998, Bignell & Eggleton 2000).

2.3.1 Feeding group classification

Termites show different ecological responses according to their (generally known) feeding habit, for example with respect to habitat disturbance, and in natural and human induced successions (Eggleton *et al.* 1996, 1997). Additionally, at least in African forests, more energy appears to flow through soil-feeders than through wood-feeders (Eggleton *et al.*, 1999) so it is important to recognise termite feeding

groups in order to understand the ecological processes that they mediate. This is especially true for the relatively poorly known soil-feeders. (Donovan *et al.*, 2001)

Feeding preferences vary between species and higher taxa and can be classified according to their position on the humification gradient (Donovan *et al.* 2001).

Termite worker imago mandibles are very diverse in the number of their marginal teeth, but functionally they appear to fit into two groups: (a) grinding (milling), and (b) pounding (pestle and mortar) (Donovan *et al.*, 2001).

Termite guts are very complicated structures. Early branching families are very similar to those closely related cockroaches but later branching families are heavily modified. The general formula for the cockroach-like guts is to have a generalist detritivore type structure, while the more derived guts switch to a more complex hindgut fermentation structure. Insect guts are split into three distinct parts: *foregut* (stomatodeum), *midgut* (mesenteron) and *hindgut* (proctodeum). The food is ingested and passes into the foregut, which contains the *crop* (stomach) and then the *proventriculus* (gizzard), a grinding organ. From the proventriculus the food enters the midgut, which is the primary source of enzymes in most insects.

The partly digested food then passes into the hindgut, which is of variable length and structure, but usually contains a rectum and an anus. The hindgut is often short in insects that have no significant microbial symbioses.

In all of the termite families except the *Termitidae*, the paunch is packed with flagellates. This form of gut represents a combination of a generalist detritivore-type (as in cockroaches, e.g. *Periplaneta*) and a hindgut fermentation system, where the flagellates ferment the partly digested food under anaerobic conditions. Most textbooks have generally attributed the digestion of dead wood to the hindgut flagellates. However, we now know that all studied wood and grass feeding termites produce their own celluloses, and in addition that many wood-feeding termites in the *Termitidae* digest wood efficiently without any flagellates (Bignell *et al.*, 2011)

Nearly all the important variations from this basic intestinal model are found in the *Termitidae*. The absence of flagellates appears to have accelerated the evolution of physiological and anatomical innovations. These new innovations provide feeding either more efficiently on evolutionally typical food (wood, grass) but also on relatively new feeding substrates (humus, soil). In both cases selection

seems to have produced hindgut fermentation systems of greater sophistication. (Bignell, 2011)

The most elaborated guts in termites are those of the *Cubitermes*-group termitids that feed on soil with no discernible plant material in it. The whole gut allows highly refractory organic material in soils to be digested, probably, in part, by releasing proteins, peptides and amino acids immobilised as soil organic matter. (Ji and Brune, 2005).

Between the two extremes of gut structure there are numerous forms, which generally fall in an intermediate position on the termite phylogenetic tree. The fungus growing termites (*Macrotermitinae*) have retained a rather phylogenetically basal gut structure, probably because much of their forage is digested by the mutualistic fungus (Donovan *et al.*, 2001).

Termite feeding groups classification is highly discussed topic and many researchers state their ideal classification. None of them could perfectly describe all the classification aspect, therefore we chose two feeding group table variants which makes together more complex view on specifying of termite feeding habits. See (**Table 1**) (Eggleton *et al.*, 1997) and (**Table 2**) (Donovan *et al.*, 2001).

Table 1. Definition of termite feeding groups

| Feeding group | Description |
|---------------|--|
| Soil | Termites distributed in the soil profile, surface litter (leaves and twigs), and/or epigeal mounds, feeding on mineral soil. |
| Soil/wood | Termites feeding only or predominantly within soil under or plastered within logs, or feeding within highly decayed wood that has become friable and soil-like. |
| Wood | Termites feeding on wood and excavating galleries in larger items of woody litter, which in some cases become colony centers. This group also includes termites having arboreal nests and others having subterranean or epigeal nests in which fungus gardens are cultivated (<i>Macrotermitinae</i>). |
| Litter | Termites that forage for leaf litter and small woody litter. This includes some subterranean and other mound-building <i>Macrotermitinae</i> with fungal associates, as well as certain <i>Nasutitermitinae</i> that forage on the surface of the litter layer. |
| Lichen | Termites that forage for lichens, mosses and algae on the bark of trees. |

Table 2. Feeding groups according to Donovan *et al.*, 2001

| Feeding groups | Description |
|----------------|--|
| FGI | Wood feeders, termites have simple guts and feed on high humification gradient. |
| FGII | Wood and leaf litter feeders, termites have more complex gut, feeding on wood and excavating galleries in larger items of woody litter, epiphytes or leaf litter |
| FGIII | Wood and leaf litter collectors on which fungi are grown and harvested (Macrotermitinae only) |
| FGIV | Organic material-rich soil and humus feeders, with visible plant parts, have a complex gut |
| FGV | Mineral soil feeders, have a highly complex gut, they are true soil-feeders, feeding on soil organic matter with a high mineral content and little recognizable plant material |

2.3.2 Studied termite species

In the view of (Table 3) were chosen following termite families and genera to be more closely described.

SYNTERMITINAE

The termite genus *Syntermes* consists of comparatively large number of species, which live in subterranean or epigeal nests and feed on leaf and grass litter. This genus, of which 23 species are known, occurs only in South America (Constantino, 1995). *Syntermes* species are the most dominant members of the guild of leaf-feeding termites in South America, and they are very abundant in rainforests (Bandeira 1991). The nests of *Syntermes* species can be totally subterranean (see Fig. 2), the only visible trace being the nest entrances on the soil surface. Those nests can extend to at least 3 meters depth into the soil, which makes the evaluation of their populations very difficult (Constantino, 1995; Martius, 1994)



Figure 2. *Syntermes* sp. soldiers (left), *Syntermes* workers (right)

Source: Jean Brodeur (jeanbrodeur.smugmug.com)

RHINOTERMITIDAE

Heterotermes and *Reticulitermes* (see **Fig. 3**) are currently the only genera placed in *Heterotermitinae*. *Reticulitermes* is restricted to the northern temperate zone, while *Heterotermes* is essentially tropical. Both *Heterotermes* and *Reticulitermes* are economically important, including some of the major pest termites in many regions. The genus *Heterotermes* has about 50 described species from all major tropical and subtropical regions of the World. There are 9 described species of *Heterotermes* in the New World, 5 of them occurring in South America (Constantino 1998).

Species of *Heterotermes* are among the most widespread termites in South America, being abundant both in natural and urban environments. Several South American species, especially *H. tenuis*, have been reported to be important both as agricultural and structural pests. Despite their economic importance, and contrasting with the vast amount of literature on *Reticulitermes*, the biology and geographic distribution of *Heterotermes* species remains poorly known. (Constantino, 2001)

According to Szalanski *et al.* (2004) presumably the existence of additional undescribed species is possible, although *Heterotermes* does not seem to be highly diverse in the South America.



Figure 3: *Heterotermes* soldiers and workers (left), soldier *Reticulitermes* (right)

Source: Rudolf Scheffrahn (www.boldsystems.org)

NASUTITERMITINAE

Nasutitermes spp. are multi-site nesters characterised by soldiers with nasute heads tapering to a long snout. Soldiers are smaller and more fragile than workers. In contrast, workers are arched and more heavily built in the front section. They also have two dark areas on the top of the head. Colonies contain a queen, king, soldiers, workers, and reproductives.

The genus *Nasutitermes* (*Termitidae: Nasutitermitinae*) comprises 243 currently described species, including approximately 71 Neotropical species in which the soldier caste possesses a frontal projection (nasus) and vestigial mandibles (see **Fig. 4**). Most species build arboreal nests and are wood-feeders. They occur in a variety of habitats, including primary and secondary forests, cropland and urban areas. Some *Nasutitermes* species play a major role in soil ecological processes, consuming up to 3% of the annual production of wood litter in Brazilian forests (Vasconcellos & Moura 2010). However, several species of *Nasutitermes* are important pests in South America (Constantino, 2002), causing significant damage in agriculture (e.g. on coffee, maize, cotton, eucalyptus, fruit trees, rice and sugar cane) and to wood and other cellulosic materials. For example, *Nasutitermes nigriceps*, *N. ephratae* and *N. surinamensis* are well known to ravage timber wood, and *N. corniger* is a major urban pest in Brazil and Argentina (Constantino, 2002). In French Guiana, three pest species of timber wood, *N. nigriceps*, *N. ephratae* and *N. surinamensis*, have been reported among the twenty species of *Nasutitermes* recorded from this region (Ensaf & Eggleton 2004).



Figure 4: *Nasutitermes* soldiers – wood galleries
Source: Alex Wild (blogs.scientificamerican.com)

APICOTERMITINAE

The *Anoplotermes*-group is one of the most diversified termite taxa in South American rainforests. Because of this reason, this termite family is still not so well described and further survey is needed.

The members are known to feed on soil, or more exclusively at the wood-soil interface (Bourguignon *et al.*, 2015) they are characterised by the loss of the soldier caste, which is a trait they share with the unrelated genera *Invasitermes*, *Orientotermes* (Miller, 1984). Soldier morphology provides the most commonly used characters in current termite taxonomy, but the systematics of the *Anoplotermes*-group must be served by characters of the workers (**Fig. 5**) the most useful identification features are provided by parts of gut: the digestive tube and in particular the enteric valve and the mixed segment (Grassé and Noirot, 1954)



Figure 5. Detail of *Anoplotermes* sp. worker
Source: CBG Photography Group (www.boldsystems.org)

TERMITINAE

The only presented genus, in our study, from *Termitinae* subfamily was *Microcerotermes*. This is genus of termite that often builds distinctive arboreal nests made of carton material (**Fig. 6**), although there are subterranean and mound building species as well.

Like other termites, *Macrotermitinae* are soil engineers, mixing their salivary secretions with soil particles to make their strong, hard mounds and galleries. Their mounds are some of the largest built by any species of termite, with volumes of thousands of litres and lasting for many decades. They are probably the most complex mound colonies of any insect group. There are 11 accepted genera in the *Macrotermitinae* and about 330 species, with the greatest diversity being in Africa. (www.wikiwand.com, 2016)

Their nests can be a common sight in coconut plantations, and seen attached to tree trunks in rural areas. They are small termites usually 0.5-0.7 cm long, and the soldiers are distinctive in having a rectangular head and relatively long, curved, mandibles with tiny serrated teeth on the inside half of the mandibles. (see **Fig. 6**)

They usually feed on dead, fallen wood, and are not considered a threat to urban houses, while being a minor pest in some rural housing. A few species are considered pests in tree plantations and forestry, due to their ability to cause damage to living trees (and high numbers). Fallen and abandoned *Microcerotermes* nests are a common sight in certain localities; these serving as convenient refuge for many other life forms (like ants, beetles, and cockroaches) to take over. (www.termiteweb.com, 2010)



Figure 6: Representative soldier and workers of *Microcerotermes* family (left), *Microcerotermes* nest (right)

Source: www.termiteweb.com/microcerotermes

2.4 Land use systems

2.4.1 Secondary forest

With past and continued destruction of primary forests worldwide, there is increasing interest in secondary forests, their role, structure, and function (Bormann and Likens, 1979). Secondary forests now constitute large areas in many countries and are becoming an increasing component of forest cover in many tropical countries as regrowth following deforestation (Brown and Lugo, 1990; Dubois, 1990; Emrich *et al.*, 2000; de Jong *et al.*, 2001). This large and growing renewable resource can provide a wide range of valuable goods and services important at the local, national, and international levels. In order to establish clear policies with regard to secondary forests, integrate them into land use plans, and guide their management and development along sustainable pathways, it is essential to first clearly identify the true nature of the resource and the different types that it encompasses. (Chokkalingam & de Jong, 2001)

There is considerable ambiguity and confusion in current use of the term “secondary forest” both in the literature and in people’s perceptions (TCA 1997, Emrich *et al.* 2000). Numerous types of forests with varying characteristics and arising from many different processes are considered to be “secondary” (Corlett 1995) given regional differences in patterns of disturbance and land and resource use. Need exists to both arrive at a common broad working definition of secondary forests and to identify and elucidate the relevant forest types that would fall under such a definition. This will help to build up data, knowledge, and management expertise on secondary forests; to focus and compare research in different regions; and to develop harmonious statistics (Sist *et al.* 1999, Emrich *et al.* 2000). Further, a coherent working definition and typology based on ecological and management considerations will enable national and other institutions to better identify and categorise forests and develop appropriate policies for the different categories. Definitions and classifications most often involve compromises and may not satisfy all needs, but it helps to have clear and useful criteria that can be applied objectively (FAO 1998).

The term *primary forest* is commonly perceived to be the “climax forest type” for a given region and environment, which is thought to be relatively stable. The

term *secondary forest* then relates to successional forests that develop after clearing of the original forest, and secondary succession is complete when they develop again into climax communities or primary forests. However, ecological thinking has evolved further from these early concepts that emphasised predictable deterministic succession in plant communities developing into relatively stable climax communities (Chokkalingam & de Jong, 2001). Plant succession is seen today as a non-equilibrium spatial process that is the outcome of disturbance and population processes under changing environmental conditions (Glenn-Lewin *et al.* 1992). Disturbance and response to disturbance are now recognised as natural processes that lie at the core of forest ecosystem dynamics (Chokkalingam & de Jong, 2001).

2.4.2 Cacao agroforestry

Agroforestry systems are generally characterized by a canopy cover of shade trees below which a wide range of crop plants can be grown. In human-dominated, deforested landscapes, agroforestry systems provide the only remaining habitat type with a substantial tree cover (Schroth *et al.* 2004). Agroforestry supports some of the most important tropical cash: crops oil palm (*Elaeis spp*), rubber tree (*Hevea braziliensis*), coffee (*Coffea spp.*) and also for our study the most important cacao (*Theobroma cacao*). Additionally, various kinds of timber, local fruit trees and annual crops are grown in agroforestry systems, thereby providing building material, firewood and food for local communities (Rice and Greenberg, 2000).

Very important factor is that, agroforestry do not require any sophisticated technology or sophisticated technical know-how: their establishment and management call on very simple techniques which all shifting cultivators in humid tropical countries have at their disposal (de Foresta and Michon, 1993). That's why agroforestry systems range widely in land-use intensity from extensively managed, patchy and densely shaded plantations owned by large numbers of smallholders to large scale, almost non-shaded and monotonous plantations owned by few farmers (Jones *et al.* 2003, Foley *et al.* 2005).

Cocoa (*Theobroma cacao*) is evergreen understory plant/tree, native to tropical South America. The genus *Theobroma* belongs to family *Malvaceae* (Alverson *et al.* 1999). The fruit is a drupe, ovoid in shape, 15-30 cm long and 8-10 cm wide with

fleshy pericarp. The flowers are produced in clusters directly on the trunk and older branches; they are white to pink (**Fig. 7**) (Wood, 1975). In Peru, most of the cocoa trees are grown among the eastern slopes of the Andes and Amazonian region between 200 and 1,300 m above sea level (**Fig. 8**). Cocoa trees grow mainly just on nutrient rich alluvial soils (Wood & Lass, 2008). The seeds of cocoa have commercial utilization as cocoa powder, cocoa butter and chocolate. Cocoa is a tropical commodity, grown on plantations but also by many small-scale farmers (Rice & Greenberg, 2000).



Figure 7. Sequentially shown *Theobroma cacao*,
flowers of cacao tree and cacao pods

Historically, cocoa has been an important source of tropical deforestation. Most traditional cocoa farms were established by removing the forest understorey and thinning the forest canopy so that cocoa seedlings can grow into productive trees by utilising the forest rent of the newly cleared area and the shade provided by the remaining trees (Schroth *et al.*, 2004; Rice & Greenberg, 2000). For plantations of cocoa it is quite usual that they are grown in combination with shading trees and perennial crops (Somarriba, 2003). At the beginning of growth shading of seedlings

and young trees is very important. Optimal density of shade in these months is around 25-50% (Wood, 1975). Cocoa trees have quite superficial root system in comparison with shade trees which can reach up 2 m root depth (Moser *et al.*, 2010). Right timing of pruning can have positive impact on root competition on soil nutrients between cocoa and shade trees. The negative aspects of unshaded cocoa are that the trees are more vulnerable and can rapidly degrade (Schroth *et al.*, 2000). Cocoa trees should suffer physiologically by reduction of shade because of their natural understory way of life (Wood & Lass, 2008). Shade loss also support growth of weeds, which can be reservoirs of pests and diseases (Schroth *et al.*, 2000).



Figure 8: Cocoa growing regions in Peru

Source: MINAG

The majority of the trees in cocoa agroforests are native tree species, and also occur in surrounding forest fragments. The use of native trees in cocoa agroforestry systems is not common elsewhere. Exotic leguminous trees and/or marketable timber trees are preferred. For cocoa trees, suitable shading trees are usually from the family *Fabaceae*, because of nitrogen important for growth of cocoa trees

(Hartemink, 2005). This connection is quite useful for many reasons. Shading trees alter conditions in plantation like the light regime, humidity, temperature and affecting on photosynthesis (de Almeida & Valle, 2007). The other positive aspect is maintaining of nutrients in soil thanks leguminous tree species and support of natural fertility (Hartemink, 2005). Plantation grown in combination with trees provides additional services and many timber (firewood) and non-timber goods (fruit, medicinal plants) (Bentley *et al.*, 2004). According to Padoch and de Jong (1995) medicinal plants accounted for about 27% of total plant species in the cocoa agroforestry in Amazon. Use of this pruned firewood reduces the pressure on rainforest wood. Beer *et al.* (1998) state that in Central America there is marketable timber production from shade trees species (i.e. *Cordia alliodora*), which are grown commercially, in the range of 4-6 m³ ha/year. For sustainable agroforestry management, it is important to ensure various layers of shade trees which will be pruned (Tschardt *et al.*, 2011). From trees serving as shading trees for cocoa is important to mention genus *Inga*. *Inga edulis* is one of the most widely distributed and economically useful tree species in the whole Amazon region and it is often integrated in the local agroforestry systems (Pennington, 1997). Genus *Inga* is acid soil tolerant tree, which improves soil fertility through nitrogen fixation and is traditionally used to shade perennial crops such as coffee and cocoa, provide firewood and charcoal, and produce a sweet pulp suitable for human consumption (Pennington & Fernandes, 1998). Other species used in cocoa agroforestry plantations in Peru are *Ficus sp.*, *Cedrela odorata*, *Retrophyllum Rospigliosi*, *Gliricidia sp.*, *Erythrina sp.*, *Leucaena sp.* (Rice & Greenberg, 2000). The shade trees provide benefit of security for farmers' families. There are many aspects which can involve prices for cocoa and their falling (economic, environmental). From fruit trees (in Peru mainly *Persea americana*, *Mangifera indica* and *Musa sp.*), shrubs and vegetable farmers have income and should be self-sufficient (Sonwa *et al.*, 2007).

Vegetation structure in shaded cocoa plantations is forest-like, often with multiple strata and diverse tree species, and high insect, bird and mammal species diversity. Cocoa farms with diverse shade have the potential to support greater local diversity and act as a more effective refuge for some tropical forest organisms than alternative lowland tropical crops, particularly annual crops and cattle pasture (Rice

& Greenberg, 2000). Management strategies should include the selection and reintroduction of original forest species into plantations of cocoa trees (Zapfack *et al.*, 2002). The retention of forest trees and the introduction of native and exotic plants determine the composition and structure of the cocoa agroforests. The result is generally a multi-strata and multi-species agroforest whose species composition reflects the needs of the local people (Sonwa *et al.*, 2007). The study of cocoa-based agroforestry systems is of high priority due to its global cultivation and its integral foundation to small-holder farmer livelihood in many regions of the world (Duguma *et al.*, 2001).

2.4.3 Slash and burn

Shifting cultivation is land use system which is widespread throughout the Amazonia and in the tropics generally and it is practiced by millions of farmers (Lojka *et al.*, 2011a). Shifting cultivation or swidden-fallow or slash-and-burn agriculture is the oldest agroforestry system (Mertz *et al.* 2008), which has rotational concept—after cropping period is fallow period with soil and vegetation restoration. The estimation of some researchers is that shifting cultivation is practiced almost at 30% of the world's exploitable soils. Shifting cultivation is the most widespread type of tropical soil management technique (Warner, 1991). About one third of deforestation in the Amazon is caused by shifting cultivation and at least one half of forest retreat is caused by cattle ranching (Serrao, 1996).

Slash-and-burn agriculture can only be sustainable when population densities are low enough to allow re-establishment of the forest within slash-and-burn fields (Lojka *et al.*, 2011a). The slash-and-burn agriculture employed by farmers in the Pucallpa area is similar to other small-scale colonist areas in the lowland semi-humid areas of the Amazon Basin (Riesco 1995). For rural peasants shifting cultivation provides economic benefits such as source of food, timber and firewood (Szott & Palm, 1996). The rural population in the Peruvian Amazon consists primarily of small-scale, migrant crop farmers who practice slash-and-burn agriculture and use method of migratory agriculture. They leave cultivated areas and they establish new plots after slashing and burning the forest, where cultivate some annual crops (maize / *Zea mays*, rice / *Oryza sativa*, cassava / *Manihot esculenta*

etc.) generally in monoculture. After one or three years established plots losing their fertility. Peasants come back usually after several years. Population pressure causes higher food demands and therefore shifting cultivators are coming back earlier on the previous cultivated areas where the secondary vegetation doesn't have enough time to renew. The vegetation is degraded and soil fertility is lost more rapidly (Krausová, 2007). Shifting cultivation associated with short fallow-rotation is often connected with *Imperata* grasslands expansion. *Imperata* spp. is a noxious weed of significant importance in tropical and subtropical zones, as well as in some warm parts of the world's temperate regions and is an indicator of land degradation (Garrity *et al.* 1996). Left grasslands are under-utilized resource, and contributing to the deforestation process (Lojka, 2012).

2.5 Study area

Physical characteristics of the Amazon region are diverse, as well as its famous plant communities and animal populations. Topography and land varies across the region, from fertile alluvial soils along rivers on nutrient-poor, acidic soils in mountain areas (Denevan 1984). Therefore broad generalizations regarding sources of funding or suitability of agriculture cannot be made. (Galarza & La Serna, 2005)

The study was conducted in Peruvian region Ucayali. The Ucayali region in the Central Peruvian Amazon is one of the four lowland Amazon states of the country and represents approximately 8% of Peru's national territory. The population in Ucayali has grown from about 16,000 people in 1940 to more than 430,000 in 2007 (INEI, 2014).

Peru, which is host to 84 of the planet's 117 life zones, is one of the world's 17 megadiverse countries. Comprising 66 million hectares, the Peruvian Amazon accounts for 60% of Peru's land mass and 90% of its forests. It represents the second-largest forest in South America, after Brazil. (Miranda *et al.*, 2015)

The climate is typically that of the humid tropical lowlands, with little day-to-day temperature variation and two well defined periods, the rainy and the dry season respectively. Depending upon the location, mean temperature ranges between 25 and 28°C, rainfall varies between 1 500 and 3 000 or more mm per year distributed over

a period of 9-11 months. Relative humidity is almost always in the high 80s or more. (FAO, 2006)

Main agricultural activities are logging, and to a much smaller extent, some cropping (rice, maize, cassava, beans) particularly along the river borders and on river islands that surface during the dry season. Cattle are of very limited and localized importance. In some areas, cattle populations fell significantly in the early 90s as result of guerrilla activities. Plantations of tropical fruits and various other products are developing. (Miranda *et al.*, 2015)

Pucallpa, capital city of Region Ucayali, has 432,195 inhabitants and lies on the River Ucayali, 860 km from Lima. Pucallpa is Peru's fastest growing jungle town and logging centre of Ucayali region (Riesco, 1995). Pucallpa was established in the 1840s by missionaries. In 1945 there was finished road from Pucallpa to Lima through Tingo María, it was very important event for Pucallpa economic. The Pucallpa urban population uses the road Federico Basadre and river for trade connection with Lima and other districts. The population living on the margins of the city and their surrounding subsist by agriculture activities mainly. The original, natural vegetation is a tropical semi-evergreen seasonal forest, now mixed with palm forest, dominated by *Mauritia* spp. palms (Lojka et al., 2011b). The area is characterized by a constant humid climate without high changes in temperature throughout the year. Annual precipitation in Pucallpa are within range from 1,500 to 2,100 mm, (a mean of 1 546 mm/year, with rainfall increasing towards west of Pucallpa). The rural inhabitants practice agriculture (slash-and-burn farming with cultivation of cash crops such as cocoa), livestock husbandry, forestry, and other land-based production (Gonzales 2008). Farmers cultivate their traditional staple crops as rice (*Oryza sativa*), maize (*Zea mayz*), cassava (*Manihot esculenta*) and fruit like citrus (*Citrus* spp.), papaya (*Carica papaya*) and banana (*Musa* spp.) (Vebrová, 2012)

3. Objectives

The aims of this thesis were to: (1) evaluate termite species diversity and abundance in different land use systems and natural habitats in comparison with cocoa agroforestry at the study area around San Alejandro, region of Ucayali, Peruvian Amazon; (2) identify the environmental variables that affect the termite diversity patterns; (3) assess the importance of cocoa agroforestry for biodiversity conserving and examine the overall influence on local ecosystems using termites as a bioindicators, while they quickly react to environmental changes.

According to various scientific studies which support, and most of the time proved, basic hypotheses that biodiversity of fauna and flora decrease along with rising disturbance level, we hypothesize that termite species diversity level will decrease along with increasing level of disturbance in four monitored areas. Including primary forest (PF), secondary forest (SF), cocoa agroforestry system (AF) and annual maize field crop (AC). Highest species diversity will be in forest habitats and lowest in annual maize field due to the high disturbance connected with burning. Then we expect that cocoa agroforestry will share considerable number of termite species with secondary forest than with any other site. We also expect change in presence of different termite feeding groups among the different ecosystems.

4. Materials and Methods

4.1 Study site

Studied four habitat types we situated on following coordinates: primary forest – 8°52'49.7"S 75°00'23.6"W, secondary forest – 8°48'45.2"S 75°14'00.9"W, cacao agroforestry system – 8°48'39.2"S 75°13'43.4"W and traditional annual maize field – 8°53'23.6"S 75°08'03.1"W. (see **Fig. 9**) Study area, surrounding of the San Alejandro town, is one of a major cacao growing areas in Peruvian Amazon. Climatic characteristics include high temperatures throughout the year (in the days and nights), heavy rains from November to March, and little rain during the rest of the year. In Irazola district there is 16,248 ha of land covered by agriculture, 15,858 ha by pastures and 15,145 ha by forest (Gonzales, 2008). This area is originally covered by high and lowland very humid tropical forest, altitude 250-350 m.a.s.l. with mean annual temperature 26.2°C and air humidity 85%. The average rainfall is 2,719 mm.

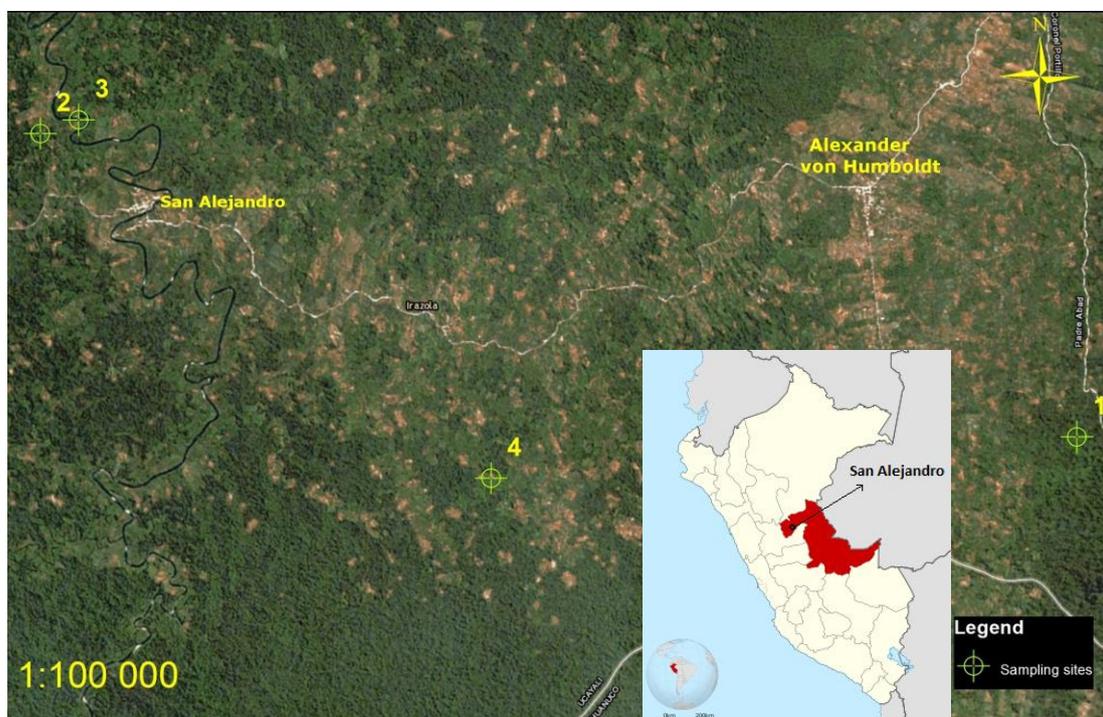


Figure 9: Map with study sites, Ucayali region:

1.= Primary forest; 2.= Secondary forest; 3.= Cocoa agroforestry; 4.= Annual maize field

Source: GIS (Geographic information system)

Sampling took place between July and August 2015 in four sites situated along a land-use gradient outside Pucallpa in lowland Amazonia. Pucallpa is one of the fastest growing cities in Peru and is dominated by slash-and-burn agriculture with a growing cocoa industry (Angelsen & Kaimowitz 2004). Neither fertilisers, pesticides nor insecticides were used in any of the sites previous to, or during, the sampling.

- **PF** (primary forest, -8.87S, -75.01W) a 2,469 ha forest area at 230 m asl that is owned and managed by Universidad Nacional de Ucayali, Pucallpa and it was situated about 50 km from the San Alejandro. The forest has been selectively logged in recent history but has not been subjected to clear cutting or burning. The average canopy cover was 98.4% while the mean volumetric moisture, soil and ambient temperature during the sampling were 40.1%, 25.3°C and 24.8°C, respectively. The primary forest area had the highest tree diversity (*Ceiba sp.*, *Diospyros sp.*, *Chrysophyllum sp.*, etc.).

- **SF** (secondary forest, -8.81S, -75.23W) a 10 ha secondary forest (>30 years old) at 234 m with a history of clear-cutting and burning for the purpose of farming. The average canopy cover was 98.5% while the mean volumetric moisture, soil and ambient temperature during the sampling were 35.1%, 24.8°C and 25.0°C, respectively.

- **AF** (cocoa agroforestry, -8.81S, -75.23W) a 5 ha managed (constant weeding and cocoa harvesting at regular intervals) plantation at 210 m a.s.l. with mature cocoa trees of approximately 15 years of age, combined with various shade trees (e.g. *Inga edulis*, *Calycophyllum spruceanum*, *Guazuma crinita*, *Croton draconoides*, *Cecropia polystachya* and *Musa ssp.*). The average canopy cover was 91.5% while the mean volumetric moisture, soil and ambient temperature during the sampling were 29.2%, 26.2°C and 26.8°C, respectively.

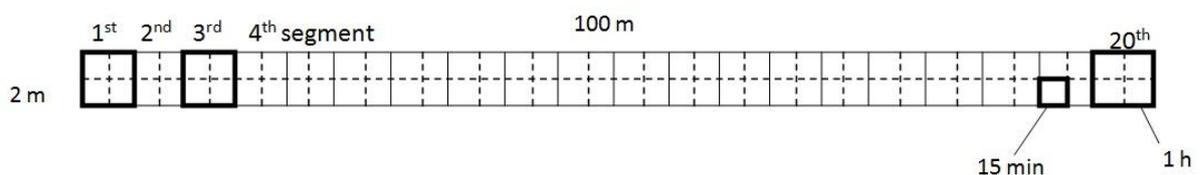
- **AC** (slash and burn annual maize field crop, -8.90S, -75.13W) a 6 ha maize field at 265 m a.s.l. in a 24 ha mixed farmland along with cocoa, banana and fallow land. The maize field was burned in August 2014 after which maize was planted and harvested in March 2015. During sampling the plantation had been fallow for one to two months. The average vegetation cover was 69.6% while the mean volumetric

moisture, soil and ambient temperature during the sampling were 31.6%, 26.1°C and 25.7°C, respectively.

4.2 Data collection

Collecting of study material was conducted from June to September 2015. The transects were 100m long and 2m wide, and divided into 20 continuous segments (each 5x2m) with four sections and numbered sequentially, which is visible in the **Fig. 10**. In each section one researcher actively searched for 15min (a total of 1h of collecting per segment). In order to unify sampling effort, work must be done steadily and continuously during each collecting period. In each section was searched in following microhabitats, which are common for termites occurrence: accumulations of litter and humus at the base of trees and between buttress roots; inside of dead logs, if the dead wood is very large it was took three subsamples of the wood, tree stumps, branches and twigs; all subterranean nests, mounds, carton sheeting, in three set upped soil pits 10cm x 10cm x 10cm and on vegetation up to a height of 2m above ground level. (Jones & Eggleton, 2000)

Figure 10: Dividing of used transect



For more accurate and usefull data and better determination of environmental variables we decided to measure also canopy cover. Canopy cover has been shown to be a multipurpose ecological indicator, which is useful for distinguishing different plant and animal habitats, assessing forest floor microclimate and light conditions. (Korhonen *et al.*, 2006). Estimation of canopy cover was done by using a spherical crown densiometer, convex model A. The canopy cover was estimated above each of transect segment. At each sampling point four reading was estimated facing each points of the compass: south, north, east and west. 30 readings were taken per site which was 120 readings in total.

4.3 Data evaluation

4.3.1 Identification of material

Termites were identified by Dr. C.A.L. Dahlsjö (**Table 3**-detailed list of species). Soldiered termites were identified to genus using Constantino's (2002) key to Neotropical genera. Species were identified using keys for specific genera (e.g. Bourguignon & Roisin 2011) or the reference collection at the Natural History Museum (NHM) in London. When soldiers were not available, gut morphology and enteric valve structures were used to identify the worker caste. Soldierless termites were identified to species by their gut morphology and enteric valve structures described in Bourguignon *et al.* (2010 and 2015) and in the unpublished key to *Apicotermitinae* species of the Guiana Shield (Hernandez L. M. unpubl. data). Species that were unavailable in the published literature were classified as morpho-species in accordance with Dahlsjö *et al.* (2014).

4.3.2 Data analysis

Species rarefaction curves were scaled using section data for each transect. Classic Chao 95% unconditional confidence intervals were calculated in EstimateS (version 9.1.0) and significant differences were estimated using the *prop.test* command in R (version 3.2.3). Rarefaction curves were visualised using *errbar()* command in the [sciplot] package in R. Bray Curtis termite species dissimilarity indices were calculated using the *vegdist* command and *bray* method in the [vegan] package in R.

The calculation of Classic Chao is based on following equations:

$$Schao1 = Sobs + \frac{f_1^2}{2f_2}$$

where Schao1 = classic Chao for abundance data

Sobs = is the total number of species observed in a sample

f_1 = the number of singleton species

f_2 = the number of doubleton species

Termite species density was calculated by averaging the number of species that was found in each transect section among feeding-groups and sites while relative abundance was calculated by averaging the number of encounters of species in each transect section among feeding-groups and sites. ANOVA was used to examine the variance of termite species density and relative abundance data among feeding-groups and sites using the *aov()* command in R. Both species density and relative abundance data were visualised using the *errbar()* command in R. Unique and shared species within and among sites were visualised in a Venn diagram using an online database hosted by Bioinformatics and Evolutionary Genomics (<http://bioinformatics.psb.ugent.be/webtools/Venn/>). Constrained unimodal Canonical Correspondence Analysis (CCA) with log transformation species abundance data and linear transect permutation was used to examine the impact of environmental and spatial variables on termite species assemblage structure separately for soil and wood. The environmental variables that were shown to have a significant or near significant conditional effect on termite assemblage structure were used to conduct a CCA Variation Partitioning analysis to examine the proportion of the environmental and spatial variables that contributed to the variation in termite species composition among the sites. Only significant parameters were used to visualize the results in biplots. Species response plots with fitted Generalized Linear Models (GLM) were used to test the significant impact of the environmental variables on individual species. Analyses were conducted in CANOCO 5.

5. Results

In total, eighteen termite species from five subfamilies were recorded (see **Table 3**) in this study including three feeding-groups (wood-feeders (FGI), wood- and litter-feeders (FGII) and humus-feeders (FGIV) (Donovan *et al.* 2001)). The most abundant PF and SF had the same species richness, with nine species gathered in each of the sites, followed by four species in AC and three species in AF. (**Fig. 11**)

Table 3: Detailed list of termite species collected in the study, including feeding-group classifications and the total number of 4 species encounters per site.

| Taxonomy (Family/Subfamily/Species) | Feeding group | Relative abundance | | | |
|--|---------------|--------------------|----|----|----|
| | | PF | SF | CA | AM |
| <i>RHINOTERMITIDAE</i> | | | | | |
| <i>Heterotermes sp. I</i> | I | 14 | 11 | - | 33 |
| <i>Rhinotermes sp. I</i> | I | - | 2 | - | - |
| <i>TERMITIDAE</i> | | | | | |
| <i>APICOTERMITINAE</i> | | | | | |
| <i>Anoplotermes pacificus</i> | III | - | - | - | 1 |
| <i>Anoplotermes banksi</i> | III | - | 2 | - | - |
| <i>Anoplotermes sp. F</i> | III | 2 | - | - | 7 |
| <i>Anoplotermes sp. K</i> | III | 1 | - | - | - |
| <i>Anoplotermes grp. GL</i> | III | 1 | - | - | - |
| <i>Anoplotermes grp. sp. XY</i> | III | - | 4 | - | - |
| <i>Anoplotermes sp. new</i> | III | 3 | 1 | - | - |
| <i>NASUTITERMITINAE</i> | | | | | |
| <i>Nasutitermes sp. I</i> | II | 9 | - | - | - |
| <i>Nasutitermes sp. II</i> | II | 1 | - | 4 | 44 |
| <i>Nasutitermes sp. III</i> | II | - | 34 | 45 | - |
| <i>Nasutitermes sp. IV</i> | II | - | 4 | - | - |
| <i>Nasutitermes sp. V</i> | II | - | - | 7 | - |
| <i>Velocitermes sp. I</i> | III | - | 1 | - | - |
| <i>SYNTERMITINAE</i> | | | | | |
| <i>Syntermes grp. sp. I</i> | II | - | 6 | - | - |
| <i>TERMITINAE</i> | | | | | |
| <i>Microcerotermes sp. I</i> | II | 5 | - | - | - |
| <i>Microcerotermes sp. II</i> | II | 8 | - | - | - |

Although, PF and SF had the same species richness the two sites only shared two species, *Heterotermes sp. I* and *Anoplotermes sp. new* (**Fig. 12**), resulting in a dissimilarity index of 0.8, where 1 is complete dissimilarity and 0 is complete similarity. PF and AC shared the highest number of species (three) which resulted in the lowest dissimilarity index among sites of 0.5 (**Fig. 12**) while all other sites shared one species per paired sites and had a dissimilarity index of 0.8, or 0.7 in the case of AF-AC (**Fig. 12**).

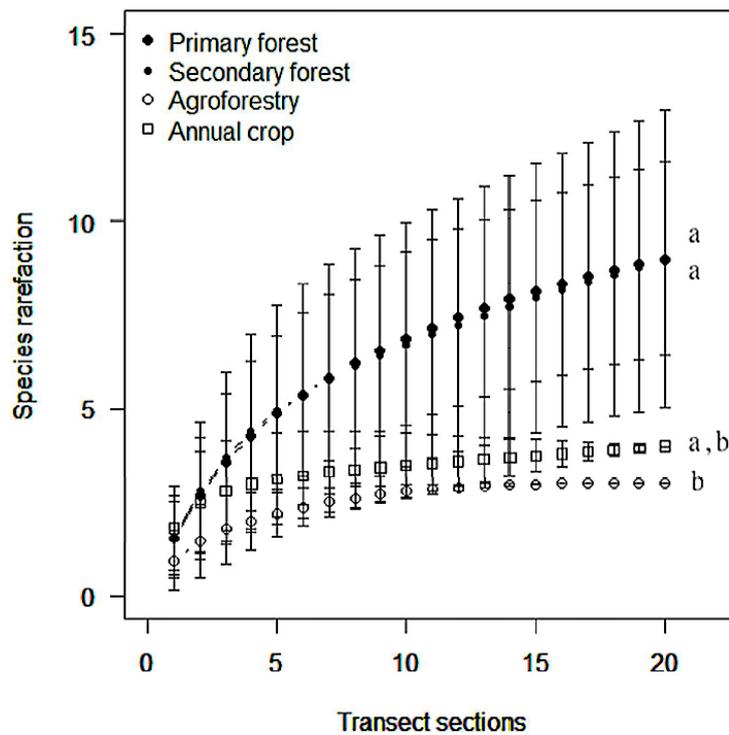


Figure 11. Species rarefaction curves of species accumulation among the land-use sites. Different letters represent significant differences and the error bars represent the 95% confidence intervals.

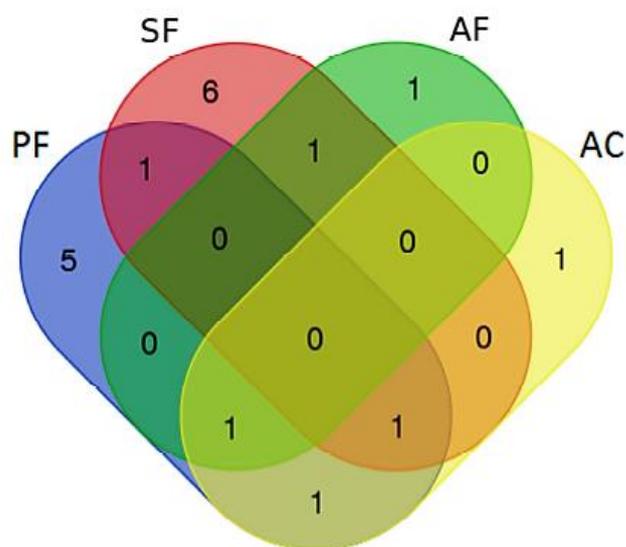


Figure 12: Venn diagram of unique and shared species within and among sites. The numbers indicate the number of species that are shared among the overlapping oblongs. PF = primary forest, SF = secondary forest, AF = cocoa agroforestry, AC = annual maize crop.

Total termite species density (number of species per section) was significantly higher in AC with 1.8 ± 0.2 species per section than in AF with 1.0 ± 0.09 species per section (Fig. 13). Among feeding-groups, species density of wood-feeding termites (FGI) was significantly different between AF and the remaining three sites (Fig. 13). Species density for wood- and litter feeders (FGII) was not significantly different among sites while species density for humus feeders (FGIV) was significantly different between SF and AF (**Fig.13**). Total termite species relative abundance was significantly different between PF and AC while no significant difference was observed among feeding-groups (**Fig. 13**).

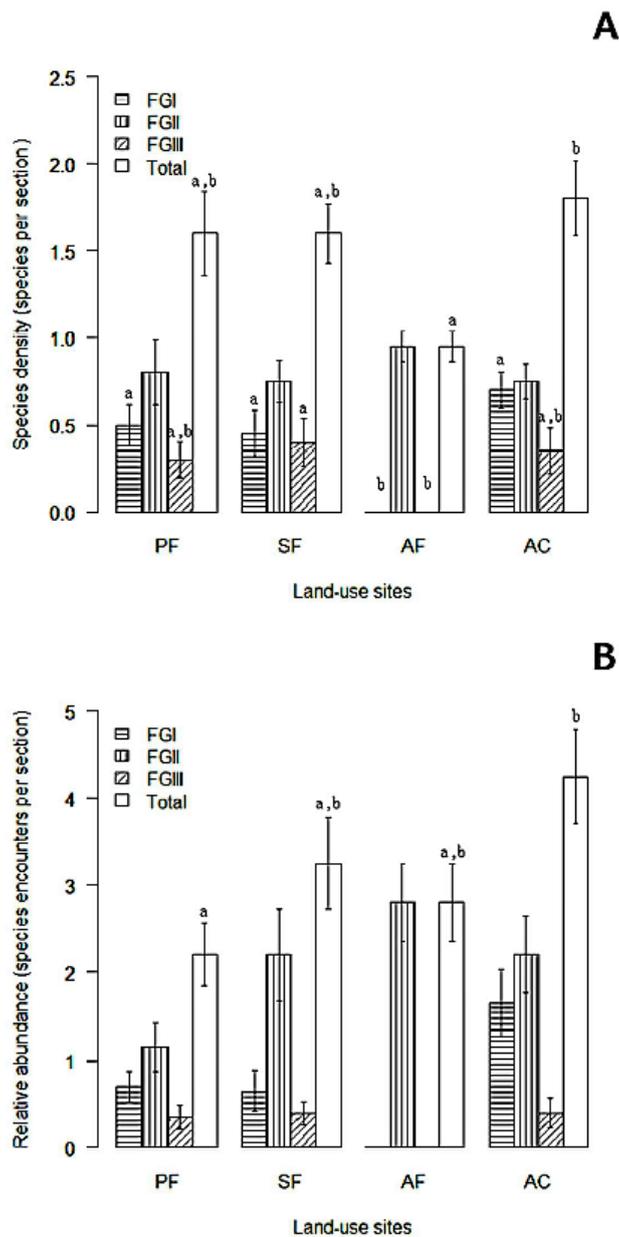


Figure 13: Termite species density (A) and relative abundance (B) for termite feeding-groups and total number of species in the land-use sites. FGI = wood-feeders (non-*Termitidae*), FGII = wood/litter-feeders (*Termitidae*), FGIV = humus-feeders. Different letters represent significant differences among sites. PF = primary forest, SF = secondary forest, AF = cocoa agroforestry, AC = annual maize crop.

Termite species composition in soil was significantly associated with soil temperature and the latitudinal position of the sites (**Table 4**).

The abundance of *Anoplotermes group sp XY* and *Syntermes group sp I* significantly decrease with increasing soil temperature while the abundance of

Nasutitermes sp II significantly increased with increasing soil temperature (GLM, $p < 0.05$). The abundance of *Anoplotermes sp F*, *Heterotermes sp I* and *Nasutitermes sp II* decreased with increasing latitude while the abundance of *Syntermes group sp I* and *Nasutitermes sp III* increased with increasing latitude (**Fig. 14**). Termites species composition in wood was significantly associated with the latitude and longitude of the sites. The abundance of *Nasutitermes sp II* and *Heterotermes sp I* decreased significantly and *Nasutitermes sp III* increased significantly with increasing latitudinal coordinates, while the abundance of *Microcerotermes sp I*, *Microcerotermes sp II*, *Heterotermes sp I*, *Anoplotermes new sp I* and *Nasutitermes sp I* significantly increased and *Nasutitermes sp III* significantly decreased with increasing longitudinal coordinates (**Fig. 14**).

Table 4: Canonical Correspondence Analysis (CCA) permutation test examining the association between termite species composition in soil (S) and wood (W) and environmental and spatial variables.

| Conditional effects | Explains % | | Pseudo-F | | P-Value | |
|---------------------------------------|------------|-----|----------|-----|--------------|--------------|
| | S | W | S | W | S | W |
| <i>Environmental variables</i> | | | | | | |
| Canopy | | 3.1 | | 2.4 | | 0.1 |
| pH | 6.8 | | 2.6 | | 0.08 | |
| Soil temperature | 10.6 | | 3.5 | | 0.02 | |
| <i>Spatial variables</i> | | | | | | |
| Latitude | 10.6 | 6.9 | 3.5 | 5.2 | 0.02 | 0.004 |
| Longitude | 2.2 | 9.6 | 1.9 | 6.8 | 0.001 | 0.008 |

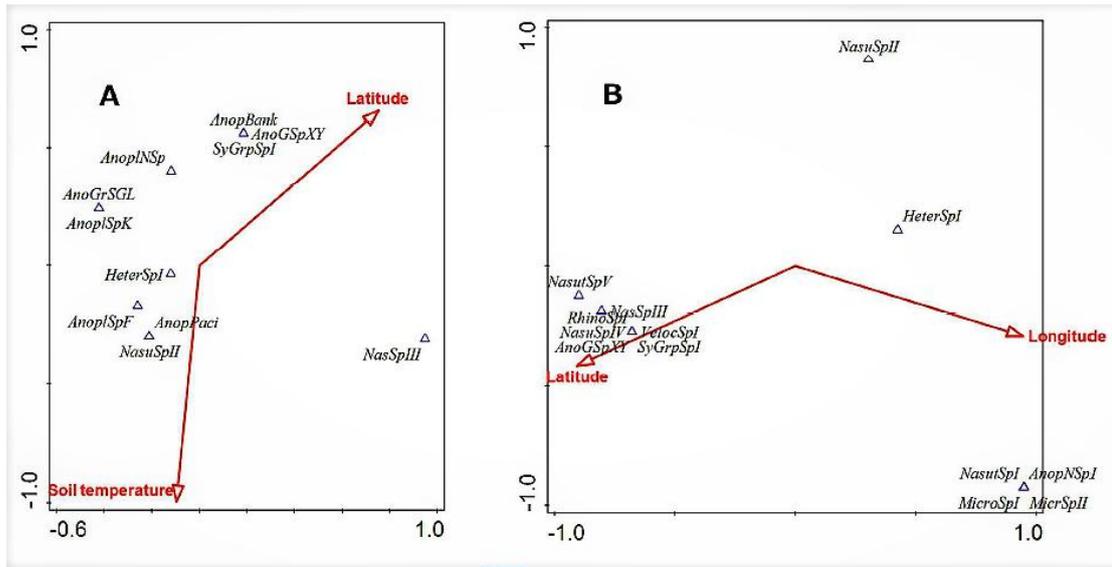


Figure 14: Canonical Correspondence Analysis (CCA)

variation partitioning with environmental and spatial variables in (A) soil and (B) wood.

The variables that were examined in this study the environmental variables explained 49.9% of the species composition in soil while spatial variables accounted for 64.0%. In wood, environmental variables explained 11.6%, although this trend was not significant ($p > 0.05$), while spatial variables explained 66.2% of the species composition (**Table 5**). The combined impact of both environmental and spatial variables accounted for -13.9% in soil and 22.2% in wood.

Table 5: Canonical Correspondence Analysis (CCA) variation partitioning of the explanatory environmental and spatial variables, and a combination of the two types, in association with species composition in soil (S) and wood (W).

| Fraction | Variation | | % of explained | | % of all | | Df | | Mean Square | | F-values | |
|---------------------------|-----------|-----|----------------|-------|----------|-------|----|----|-------------|------|----------|-----|
| | S | W | S | W | S | W | S | W | S | W | S | W |
| Environmental | 0.5 | 0.1 | 49.9 | 11.6 | 7.6 | 1.8 | 1 | 1 | 0.68 | 0.24 | 3.7 | 2.4 |
| Spatial | 0.7 | 0.1 | 64.0 | 66.2 | 9.7 | 10.4 | 1 | 2 | 0.82 | 0.50 | 4.4 | 5.0 |
| Environmental vs. Spatial | -0.1 | 0.3 | -13.9 | 22.2 | -2.1 | 3.5 | -- | -- | -- | -- | 3.8 | 5.0 |
| Total Explained | 1.0 | 1.2 | 100.0 | 100.0 | 15.1 | 15.7 | 2 | 3 | 0.7 | 0.51 | -- | -- |
| All Variation | 6.8 | 7.7 | -- | -- | 100.0 | 100.0 | 31 | 65 | -- | -- | -- | -- |

6. Discussion

Comparison of termite community patterns along the land-use gradient *Forest habitats (PF, SF)*

The sixteen termite species recorded in the Ucayali region represented a lower number than expected based on comparisons with other Peruvian studies (Palin *et al.* 2010, Dahlsjö *et al.* 2014). The low species richness in PF and SF may be due to the relative disturbance and fragmentation of the region as a whole including selective logging in PF and the isolation of SF, both of which have been shown to affect termite species richness and feeding-group composition (Davies 2002, Vasconcellos *et al.* 2010). The high dissimilarity among the forest habitats (PF and SF) may be due to the isolation and re-colonization of termite species to SF, while PF will have had a more stable environment for species populations to thrive. While termite species density and relative abundance were not significantly different among feeding-groups between the two sites, SF is likely to have been re colonized by termite species from the surrounding area including pastures and plantations. The re-colonization of termite species to SF is likely to only have affected termite species composition, rather than termite feeding-group composition, due to the relatively long forest regeneration that will have allowed for humus-feeding (FGIII) termites to re-colonize the site. Humus- and soil-feeding termites are sensitive to arid environments and depend on a closed canopy (Eggleton *et al.* 1999). The long regeneration of SF is therefore likely to have provided a suitable environment and enough time for humus-feeding termites to disperse across arid barriers (Davies *et al.* 2003).

Forest habitats and agroforestry (PF, SF, AF)

Agroforestry has long been discussed as a mechanism for biodiversity conservation in agro environments (Rice & Greenberg 2000, Schroth & Harvey 2007) and their termite populations have been compared to those of forest habitats (Ackerman *et al.* 2009). The agroforestry site in this study was categorised as *planted shade* as described in Rice and Greenberg (2000) with planted trees from a variety of species among the cocoa plants. AF contained the lowest species richness

of all sites in this study with significantly lower species richness than the forest habitats (PF and SF). Additionally, AF only shared one species with SF while no species were shared among AF and PF. Total termite species density and relative abundance in AF were not significantly different from PF and SF, however, individual feeding-groups showed significant differences due to the presence of only one genus in AF, the wood- and litter- feeding (FGII) *Nasutitermes* (**Table 5**). While the presence of a diverse canopy has been shown to support higher biodiversity than cocoa plantations with no shade component (Bos *et al.* 2007), the application of pesticides and weeding regimes also play an important role in biodiversity conservation (Gomiero *et al.* 2011). The cocoa agroforestry in this study contained a planted sparse canopy of a variety of tree species, however, the site was weeded at regular intervals so that the undergrowth was kept to a minimum. The constant disturbance to the undergrowth is likely to be the reason for the low termite species richness and the presence of only arboreal nesting *Nasutitermes* in AF. On the contrary, relative abundance was not significantly different between AF and the forest habitats, which suggests that the availability of dead wood and cocoa pods in AF may have provided a suitable environment for *Nasutitermes* to thrive.

Cocoa agroforestry vs. annual maize crop and the role of fallow land (AF, AC)

Species richness in AC was not significantly different from any of the land-use sites in this study and, although only four species of termites were encountered, the species included all feeding groups that were encountered in the forest habitats. The similarity between PF and AC was reflected in their high number of shared species (three) compared with the other sites. Termite species density was significantly higher in AC than in AF while relative species abundance in AC was significantly different from that in PF. The high relative abundance in AC was mainly made up of the abundance of wood (FGI) and wood- and litter-feeding (FGII) termites which may be due to the high density of dead wood (Eggleton *et al.* 1996) that did not fully burn during the fire regime. The observed termite community patterns in AC represent those that were expected for AF. While AC had been burned, planted and harvested, the land had been fallow for five months prior to sampling at which point the site contained dense undergrowth but no trees. The two sites, AF and AC,

therefore represent two different types of management regimes: AF, in which diverse shade is present but where the undergrowth is continuously cleared, and AC, in which the vegetation has been burned but where the land has been left as fallow. The results in this study suggest that the value of the planted shade is diminished by the weeding regime while termite communities are able to quickly re-colonise a burned area if it has been left undisturbed. Although, the re-colonization of termites to fallow land probably depends on the proximity to intact forest from which termite species can disperse (Dent & Wright 2009).

Environmental and spatial drivers of termite species composition patterns

Environmental variables explained half of the variation of species composition in soil while environmental variables did not show a significant impact on termite species composition in wood. In soil, species composition was partly driven by soil temperature which has been shown to have a significant impact on termite diversity (Palin *et al.* 2010, Gathorne-Hardy *et al.* 2001). Termites, particularly soil- and humus-feeders, are sensitive to weather extremes and generally decline with a reduction in temperatures, linked to metabolic rate (Gathorne-Hardy *et al.* 2001). The lower vegetation cover in AC and AF contributed to higher average temperatures than in the forested sites, an average difference of 1.4°C, which is likely to have caused a decline in the abundance of more sensitive species. The abundance of *Nasutitermes sp II*, on the other hand, increased with increasing temperatures. *Nasutitermes* species forage above-ground and therefore have a harder and thicker exoskeleton which enables them to colonise and thrive in arid environments (Nalepa 2011). The spatial variables explained the majority of the species composition in soil and wood. Latitude showed a significant effect on termite species composition in soil and wood while longitude had a significant effect on termite species composition in wood only. The spatial variables are likely to represent factors that were not sampled in this study and may be related to the geography and topography of the sites.

Implications of tropical degradation and conclusions

As mentioned above, the number of termite species found in this study was lower than expected based on data from other Peruvian studies (Dahlsjö *et al.* 2014, Palin *et al.* 2010). Only nine species of termites were found in the primary forest, which is a mere fraction of the number of species that one would expect to find in that habitat domain. It is therefore clear that forest fragmentation and degradation in the study region have had a noticeable impact on termite populations. While Pucallpa and vicinity are growing fast and agriculture is expanding rapidly, the presence of agroforestry is seen as a step in the right direction for biodiversity conservation (Asare *et al.* 2014). However, the fact that AC had higher termite species diversity than AF, with highest similarity with PF, suggests that the benefits of agroforestry are not clear-cut. The management regimes (e.g. weeding in AF and burning followed by fallow in AC) and the distance to nearby forest habitats, and environmental patterns such as soil temperature, are thought to have played a major role in the species composition patterns presented in this study.

Forest fragmentation has been shown to have a negative impact on specialist functional groups of both ants and termites (particularly specialist predators and climate specialist in ants and soil feeding termites that are sensitive to changing microclimatic conditions) (Leal *et al.* 2012, Davies 2002) suggesting that ecosystem processes and ecosystem dynamics (Jouquet *et al.* 2011) may be altered as a result of degradation.

7. Conclusion

In this study we have showed that agroforestry does not always provide protection for termite populations. According to *Table 2* we can see lowest species richness in AF - three species, followed by AC – four species and highest species number in PF and SF both with nine species. This result surprisingly unconfirmed our hypotheses which was state on various studies where agroforestry outcome more positive in biodiversity conservation than slash and burn farming. This may be linked to the level and frequency of weeding in AF, while fallow, even in highly disturbed habitats such as the AC, may allow for rapid re-colonization of termite species. Rapid termite re-colonization of AC could be also caused by situation of field surrounded by forest fragments as we can see in *Appendix D*. However, the low diversity of termites encountered in the primary and secondary forests suggests that termite diversity in the study region as a whole is in decline. It is therefore essential for regions with intact tropical forests, such as Petit Saut and Nouragues Nature Reserve in French Guiana (Bourguignon *et al.* 2011), Tambopata National Reserve in Peru (Dahlsjö *et al.* 2014), and Yasuní National Park in Ecuador (Bahder *et al.* 2009), to be carefully protected in order to preserve species that do not survive habitat fragmentation.

Therefore better understanding of community structure is needed in undisturbed and disturbed habitats in order to provide empirical data to promote the preservation of undisturbed tropical forests. Further, the implications of management regimes on biodiversity in agroforestry should be revised in order to improve the conservation value of agro-habitats. Also level of landscape fragmentation should be studied for its' implication to wild species distribution in forestry and agroforestry ecosystem. We can expect that mainly percentage of residues of primary forests could be important factor.

The continual research of these factors is therefore needed.

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Appendix

Appendix A. Primary forest - Transect



Appendix B. Secondary forest - Transect



Appendix C. Cocoa agroforestry – Transect preparation



Appendix D. Annual maize field – Habitat position



Appendix E. Annual maize field – Transect preparation

