Termite assemblage structure and function: a study of the importance of termites in lowland equatorial forests

By

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Abstract

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DPhil thesis written by Cecilia Dahlsjö, St Cross College, Submitted in Trinity term, 2014.

Termites are important ecosystem engineers in tropical and sub-tropical terrestrial regions where they influence ecosystem processes by altering the physical and chemical structure of the habitat. Termites affect nutrient availability by decomposition and comminution (shredding) of organic matter and act as agents of bioturbation as they re-work substrates during the construction of nests, tunnels and runways. At present we have a relatively good understanding of termite diversity patterns in the tropics through the extensive use of the standardised transect sampling protocol by Eggleton et al. (1995). These diversity data suggest that there is a functional difference in termite assemblage structure, and potentially in termite abundance and biomass, among comparable habitats across continents. However due to the lack of comparable abundance and biomass data from South America this has not previously been confirmed. In this thesis I, therefore, collected extensive data on termite taxonomic and functional assemblage structure in a South American site in Peru. The data were used to compare termite abundance and biomass from two comparable sites in Africa (Cameroon) and south east Asia (Malaysia) in order to gain better understanding of the role termites play in ecosystem processes. I found that there was an intercontinental difference in the abundance and biomass of termite feeding-groups mainly due to the dominance of soil-feeding termites in Cameroon and the absence of fungus-growing termites from Peru. The impact of certain lineages on the intercontinental differences suggests that the differences may be due to biogeographical evolution. Moreover, Eggleton et al. (1998) show that larger-bodied soil-feeding termites in Cameroon process more energy per unit area than predicted

by their body size. Due to the need for an examination of the allometric relationships in termite assemblages outside Africa and the development of a more sophisticated feeding-group classification I explore the findings in Eggleton et al. (1998) further using population density - body mass relationships in three termite feeding-groups among the three continental sites in Cameroon, Peru and Malaysia. I found that large-bodied soil-feeding termites in Cameroon and large-bodied wood-feeding termites in Peru had higher population densities than expected by their body masses. As the population density - body mass relationship is inverse to that of the energy - body mass relationship the results suggest that the two feeding-groups also use more energy than expected by their body masses. Further, we have a relatively good understanding of the role termites play as ecosystem engineers e.g. in nutrient cycling and distribution, however, compared with our understanding of wood and litter decomposition in tropical forests quantitative data on the impact of termites in soil processes is poorly understood. In this thesis I conducted, to our knowledge, the first *in situ* soil macrofauna exclusion experiment using translocated soil in Peru to examine the impact of termites on soil C and N loss. I found that termites promote soil C and N loss which may be linked to the increase in microbial activity due to the passage of soil through the termite gut as well as the affect termites have on bioturbation and nutrient distribution. To conclude, in this thesis I present the first intercontinental comparison of abundance and biomass as well as the first *in situ* soil macrofauna exclusion experiment to date. The link between termite ecology, biogeography and evolution is discussed as well as the contribution of this thesis to the field of termite ecology.

Declaration

The work in this thesis is my own except where otherwise acknowledged. The four results chapters have been submitted to relevant journals and subsequently edited to suit the journal guidelines. Care has been taken to ensure a consistent outline although due to specific journal requirements this may not always have been possible. This thesis contains no material that has been awarded any other degree or diploma in any university or other institution.

Cecilia A. L. Dahlsjö

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CHAPTER I

INTRODUCTION AND AIMS

1.1 Introduction

Tropical rain forests have high conservation status and play an important role in the biosphere, also promoting a growing tourism industry (Prance 1997) and increasing interest in bioprospecting. However, rain forests are being disturbed and eroded at an alarming rate and according to the latest figures in Hansen et al. (2013) deforestation rates are constantly increasing (210,100 ha each year).

Tropical rain forests, particularly undisturbed and remote parts, are incompletely characterised biologically, due to many factors which can include remote location and associated logistical challenges, taxonomic intractability, an absence of comprehensive sampling methods and the sheer scale of the species richness they contain. Many studies today are devoted to understanding the intricate relationships within these forest ecosystems from species assemblage structure (Eggleton et al. 1996, 1999, Bourguignon et al. 2011) and species interactions (Ingham et al. 2010, Buitenwerf et al. 2011) to carbon (C) storage (Reay et al. 2008, Malhi et al. 2009), nutrient cycling (López-Hernández 2001, Brossard et al. 2007, Craine et al. 2007) and the role of decomposer organisms (Donovan et al. 2001b, McGuire & Treseder 2010, Jouquet et al. 2011). However, the yearly increase in newly described species of both flora and fauna suggests that we do not have a full understanding of these complex ecosystems (Grieneisen et al. 2014). Better understanding of ecosystem processes and functioning, both at the local and global scales, may provide insights into how to conserve tropical rain forests and find sustainable ways of living alongside them. Understanding of ecosystem processes may also provide insights into how ecosystems respond to climate change which is an additional threat to the future of these biodiverse habitats.

Termites are important ecosystem engineers (Jouquet et al. 2011) and one of the most dominant invertebrate decomposers in lowland tropical rain forests where their abundance

and biomass are the highest (Eggleton et al. 1996, 1999, Bignell & Eggleton 2000). They play a vital role in transforming dead organic matter into forms which are available to plants through decomposition and comminution (shredding). Termites have been shown to contribute to 20% of carbon mineralisation in a semi-arid Australian ecosystem (Holt 1987) while 2.9% of the total annual wood production has been shown to be consumed by *Nasutitermes* in Brazil (Vasconcellos & Moura 2010) and in Malaysia approximately 30% of the daily litter fall was removed by *Macrotermitinae* (Matsumoto & Abe 1979).

The range of termite functional groups enable breakdown of an array of dead organic matter from sound wood to highly mineralised soil organic matter (SOM) (Donovan et al. 2001a, Inward et al. 2007). The termites may be divided into five groups depending on where along the humification (decomposition) gradient they feed (Donovan et al. 2001a). The decay process in all functional groups is made possible due to the presence of symbiotic microorganisms in the termite gut and in fungus-growing termites with the addition of external symbiotic fungi (*Termitomyces*) (Hongoh 2010, Nobre et al. 2011).

As ecosystem engineers termites change the chemical and physical structure of the habitat which makes them highly influential in the functioning of the ecosystem as a whole (Jouquet et al. 2011). Tunnels and runways contribute to bioturbation which is important for the distribution of nutrients and infiltration of water (Jouquet et al. 2006, 2011). Nesting structures also play an important role in nutrient distribution as the surrounding area contains a higher nutrient content due to erosion of the structures (Rückamp et al. 2010). Despite their clear importance, however, we do not have a full understanding the role termites play in tropical forest ecosystems either at local or global scales.

Termites exist in sub-tropical and tropical regions (Bignell & Eggleton 2000) where termite assemblages differ in their taxonomic and functional composition across regions and

continents (Davies et al. 2003). While some regional differences in species and functional composition and abundance may be due to local effects, such as rainfall (Dibog et al. 1998, Gathorne-Hardy et al. 2001), disturbance (Eggleton et al. 1995, 2002, Vasconcellos et al. 2010) or elevation (Gathorne-Hardy et al. 2001, Palin et al. 2010), intercontinental differences of termite species diversity may be affected by long term effects such as evolution or termite dispersal (Davies et al. 2003). Although, termite assemblage structure are well studied (e.g. Eggleton et al. 1996, 1999, Schuurman 2005, Vaessen et al. 2011, Dosso et al. 2013) data from South America are sparse (Vasconcellos et al. 2010) and while a global comparison of termite diversity has been conducted (Davies et al. 2003) no global comparison of abundance and biomass data exists due to the lack of comparable datasets. A comparison of termite abundance and biomass data is important in order to quantify the role termites play in ecosystem processes such as decomposition of organic matter, bioturbation and nutrient cycling. Comparable abundance and biomass data exist for one site in Cameroon (Eggleton et al. 1996) and one site in Malaysia (Eggleton et al. 1999) with data from South America are missing from the three main equatorial forest blocks.

1.2 Aims and objectives

I explore the role of termites in lowland tropical forests in further detail in four results chapters with aims and objectives described below.

1.2.1. Describing termite assemblage structure in a Peruvian lowland tropical rain forest: a comparison of two alternative methods

First I examine the diversity and compositional patterns of termites within a Neotropical lowland tropical rain forest using two methods: (a) a transect method (TM) and, (b) a quadrat method (QM). I explore the degree to which the two methods reveal similar patterns, and examine the strengths and weaknesses of each method. I also investigate the environmental

and spatial drivers of the observed compositional patterns. These data will provide important insight into the suitability and efficiency of the two methods for different types of data.

1.2.2. First comparison of quantitative estimates of termite biomass and abundance reveal strong intercontinental differences

After having established and explored methodologies in the context of a single site, I next explore termite biomass and abundance in three comparable sites across the tropics. The aims for this study are to (a) compare species density data for functional groups from the three study sites to confirm the existence of the functional diversity anomaly across our study areas, (b) compare biomass and abundance data for termite functional groups across the three sites, (c) explore the potential causes (termite evolutionary history or present day climate) of the differences uncovered, and (d) discuss the implications of these differences for ecosystem processes across the main tropical forest blocks.

1.2.3. Density - body mass relationships: inconsistent intercontinental patterns among termite feeding-groups

Having established differences in termite communities and body mass across the three tropical sites, I next investigate (a) population density - body mass relationships in three feeding-group categories (soil, humus and wood-feeding termites) across old-growth tropical rain forest sites in Africa, south east Asia and South America and (b) discuss the causes of the observed patterns (biogeography and evolution) and the potential implications for ecosystem processes.

1.2.4. Termites promote soil carbon and nitrogen depletion: results from an *in situ* macrofauna exclusion experiment, Peru

In the final results chapter, I explore the affect of termites on soil carbon and nutrient status. I translocated humus-rich organic soil from a Peruvian montane forest to a lowland forest site and conducted a decomposition experiment using two different containment mesh sizes, with the smaller mesh size excluding macrofauna. Specifically, I investigated a) an *in situ* microcosm of translocated soil initially lacking termites but with assumed access for all biota and b) an identical microcosm lacking access for termites and other macrofauna of equivalent size. In the second case, abundance and biomass of macrofauna were estimated during colonisation.

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CHAPTER II

LITERATURE REVIEW

Overview

I will start off by giving a short introduction to termites with the aim of setting the scene for the following sections. In section 2.2 I discuss the literature concerning termite assemblage structure and some of its potential drivers. This section is linked to the first data chapter (chapter IV) in which I investigate the drivers of the assemblage structure in a Peruvian lowland tropical forest using two alternative sampling methods. Section 2.3 looks at termite biogeography and evolution which is linked to chapter V where I examine the intercontinental differences of termite biomass and abundance in Peru, Cameroon and Malaysia, and discuss the results in an evolutionary context. Section 2.4 is relevant to most of the data chapters as it touches on termite symbiotic relationships and gut function which provides an indication of the differences between termite functional groups. This is relevant to the thesis as a whole. In section 2.5 I discuss energy flow and nutrient acquisition in termites which is linked to chapter VI in which I examine the allometric body size relationships in termites. Section 2.6, in which I look at termites as ecosystem engineers, is also relevant to the thesis as a whole as I link all the results chapters to ecosystem processes.

2.1. Introduction to termites

Termites (Termitoidae) are eusocial insects and the sister group of the wood-feeding cockroaches in the genus *Cryptcercus* within the order Blattodea (Inward et al. 2007a). Termites comprise seven (present day) families of which the Termitidae and Rhinotermitidae families are the most recently evolved (Davies et al. 2003a) (Figure 2.1). Termitidae contains 75% of all described termite species and four of the five recognised termite functional groups (Bignell & Eggleton 2000, Donovan et al. 2001a). Termites have three castes: the reproductives (alates, which have the potential to turn into queens and kings), soldiers, and workers. All three castes are found in most groups, with the exception of some early diverging clades that do not have a true worker caste (e.g. the Termopsidae and Kalotermitidae) (Eggleton 2011) and some soil dwelling genera (e.g. Apicotermitinae) that do not have soldiers (Eggleton 2011).

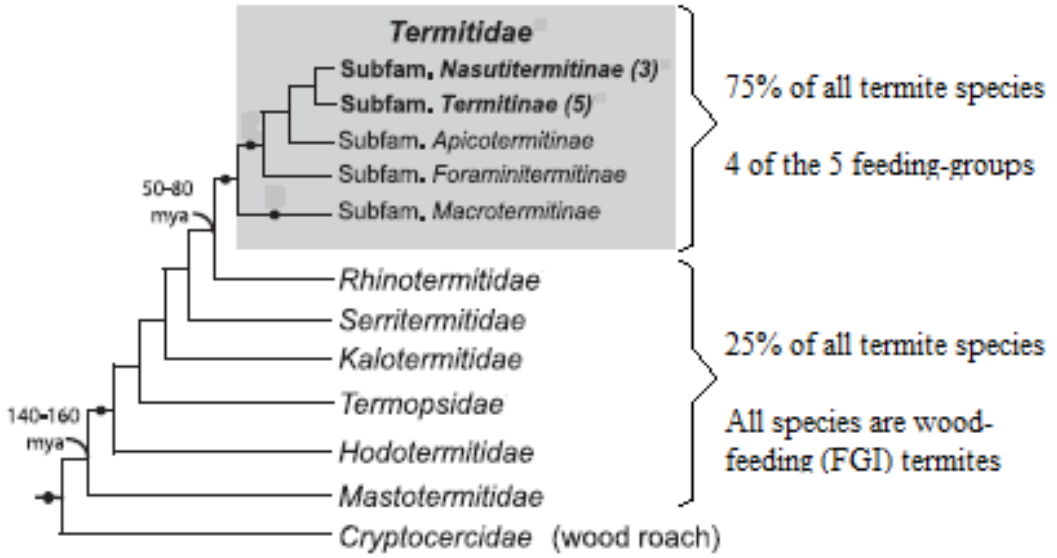

Figure 2.1. Cladogram of major termite families edited slightly from Zhang & Leadbetter (2012). 75% of all described termite species may be found within the Termitidae, where they can be allocated to four functional groups, based on feeding habits: wood-feeders (FGII), fungus-growers (FGIIF), humus-feeders (FGIII), true soil-feeders (FGIV). Other termites are allocated to the single-piece wood-feeders (FGI) (Donovan et al. 2001a, Inward et al. 2007b).

Out of the social insects termites are probably one of the least well known, perhaps because of their limited distribution compared with e.g. bees and ants, and because they are mostly subterranean which makes them hard to study (Bignell & Eggleton 2000). Termites are also pests of timber and crops (Nobre et al. 2011b), however, only 10% of all described termite species are recognised as pests (Nobre et al. 2011b).

Termites are ecologically important as they act as ecosystem engineers through decomposition of organic matter and by influencing bioturbation and affecting nutrient turnover and distribution (Jouquet et al. 2006, 2011, Ackerman et al. 2007). Additionally, they affect vegetation structure in savannahs (Moe et al. 2009) and are important sources of food for predators (Redford & Dorea 1984). Termites are particularly abundant in lowland tropical forests where they are thought to play an important role in ecosystem functioning

(Bignell & Eggleton 2000). However, we do not fully understand the role termites play in ecosystem processes at local and global scales.

2.2. Drivers of termite assemblage structure

Data on termite assemblage structure and their response to local drivers are relatively abundant (Eggleton et al. 1996, 1999, Jones 2000, Davies et al. 2003a, 2003b, Schuurman 2005, Palin et al. 2010, Vasconcellos et al. 2010, Vaessen et al. 2011, Souza et al. 2012, Olugbemi 2013). However, data from tropical rain forests are patchy (Eggleton et al. 1996, 1999, Bourguignon et al. 2011) and studies tend to include plots across different regions and land use gradients with little spatial replication (Jones 2000, Davies et al. 2003a, Palin et al. 2010).

2.2.1. Disturbance

Habitat disturbance is one of the most studied effects on termite assemblage structure (Eggleton et al. 1995, 1996, 1999, 2002, Dibog et al. 1999, Vasconcellos et al. 2010, Vaessen et al. 2011, Kagezi et al. 2011, Dosso & Yéo 2012, Olugbemi 2013, Dosso et al. 2013) and may include anything from a tree fall to clear cut areas or farmed land. These disturbances may all affect ecosystems from microhabitats to landscapes, and therefore termite assemblage structure, with regional or even global consequences. Generally, termite species diversity, abundance and biomass decrease along a disturbance gradient (Eggleton et al. 1995, 1996, 2002, Jones et al. 2003, Kagezi et al. 2011, Olugbemi 2013) with highest diversity in old growth forests and lowest diversity in clear cut areas.

Wood-feeding termites tend to be more resilient to disturbance than soil-feeding termites (Eggleton et al. 1996, 2002, Jones et al. 2003); e.g. wood (FGI) feeding termites nest within the wood that they feed on which provides a protective environment (Eggleton &

Tayasu 2001). Additionally, foraging wood (FGII, FGIIF) feeding termites depend on the ability to move between dead wood and so have a thicker exoskeleton that makes them more resilient to desiccation outside the nesting structure (Jones et al. 2003). Some studies have even showed an increase of wood-feeding termite abundance in disturbed areas due to the increase of dead wood (Jones et al. 2003, Olugbemi 2013). In contrast, soil (FGIII, FGIV) feeding termites depend on the climatic buffer that the canopy provides and are therefore very sensitive to aridity (Dibog et al. 1999, Davies et al. 2003a). While these patterns represent a broad overview of the literature Olugbemi (2013) showed that fungus-growing termites (Macrotermitinae) increased in farmland areas. The type of disturbance (clear cut, fragmentation, farmland) may therefore play an important role in the effect the disturbance has on species diversity and abundance. Moreover, a higher proportion of studies have been conducted in Africa or south east Asia while the representation of data from South America is poor. Due to biogeographical differences in species and functional group composition (Davies et al. 2003a) disturbance may therefore affect species assemblages differently depending on where, and under what conditions, the study has been conducted.

2.2.2 Rainfall seasonality

There is a scattered literature showing the effects of seasonal flooding on termites in the Amazonian basin, which has to some extent shaped our view of the South American termite fauna and its structure. Accurate data on humid forests which are not inundated to the point of flooding seem rare and have therefore been needed before true comparisons can be made with Africa and SE Asia, where inundation has more limited effects. In tropical forests termites are sensitive to extreme climatic conditions (e.g. high rainfall) that may disturb termite colonies by interrupting foraging and the flooding of tunnels, runways and nesting structures (Jones & Gathorne-Hardy 1995, Dibog et al. 1998). For these, and perhaps other reasons, termite activity is higher in the dry season than in the wet season in tropical forest

ecosystems (Dibog et al. 1998). Seasonality has been shown to affect termite abundance and biomass rather than species diversity and composition with more drastic changes in the short-term (days) (Dibog et al. 1998) suggesting that the increase in rainfall in the wet season has a 'disturbance effect' on the termite assemblage. However, these findings are based on a single study from Cameroon and so further data on the effect of rainfall on termite activity must be obtained before a general conclusion can be made.

2.2.3. Temperature

Termite species density decreases with latitude and altitude which may be related, in part, to the reduction in temperature along these gradients (Bignell & Eggleton 2000, Palin et al. 2010). As a reduction in temperature slows metabolism termites that feed on high energy substrates, such as wood, may be more resilient to reduced temperatures than species feeding on soil (Figure 2.1), which is nutrient poor (Gathorne-Hardy et al. 2001). Additionally, wood-feeding single-piece nesting termites (FGI), i.e. termites that feed and nest in the same piece of wood (Abe 1987), may be more resilient than foraging wood-feeding termites (FGII) as the wood provides a protective environment. Similar patterns may be observed along an altitudinal gradient where soil-feeding termites reach zero abundance at lower altitudes than wood-feeding termites (Gathorne-Hardy et al. 2001, Donovan et al. 2002, Palin et al. 2010).

While feeding-group composition seems to be highly affected by temperature (latitude and altitude) termite lineages tend to show varying patterns across regions suggesting that no lineages are altitude specific (Donovan et al. 2002). Aside from temperature termite assemblage structure may therefore be dependent on site specific factors such as deforestation and fire history (Donovan et al. 2002). However, such hypotheses must be supported by comparable studies in a wider range of locations.

2.2.4. Soil quality

Soils are complex, heterogeneous and highly speciose environments which are vital components of most terrestrial habitats (Wolters 2001, Decaëns et al. 2006, Lavelle et al. 2006). Soil fauna play an important role in soils as they may alter both the chemical and physical structure of the substrate (Jouquet et al. 2011). *Cubitermes* species have been shown to mineralise 36% of soil protein, compared with 12.5% in soil without termites (Ji & Brune 2001), and mineralise approximately 3% of the total nitrogen content in their food substrate (Ngugi et al. 2011). Generally, as soil-feeding termites (FGIII and FGIV) feed on organic matter at different stages of humification (Donovan et al. 2001a) and as soil is a widely available substrate, that are rich in organic matter in closed canopy environments, resource availability in the soil is not likely to be an issue. However, as clay stabilises and adsorbs organic matter in soil the soil clay content may influence the availability of organic matter as well as being a good building material for nesting structures and soil galleries. Mound building wood-feeding termites (Termitidae only) may also be affected by the quality of the soil used in mound construction. A laboratory experiment showed that fungus-growing termites used higher quality soil for mound construction while lower quality top-soil was mainly used for temporary structures such as foraging galleries outside the nest and runways (Jouquet et al. 2002).

2.3. Termite biogeography and evolution

Present day termite assemblage structure differs conspicuously both taxonomically and functionally among continents (Davies et al. 2003a). While climate (such as rainfall and altitude) may affect local termite assemblage structure (Gathorne-Hardy et al. 2001, Palin et al. 2010) the difference in termite assemblage structure among continents seems to be influenced by evolutionary dispersal patterns. The intercontinental differences depend on the

presence or absence of certain lineages (Davies et al. 2003a, Jones & Eggleton 2011) whose dispersal is independent of recent climatic conditions.

The fossil record suggests that termites evolved on the super-continent Pangaea in the upper Jurassic (ca 170 Ma) (Engel et al. 2009, Eggleton 2011) along with the wood-feeding cockroaches *Cryptocercus* (Inward et al. 2007a, Engel et al. 2009). The Termitidae family, however, is thought to have diverged from the Rhinotermitidae family in the Early Paleocene (Engel et al. 2009) and diversification of this group is thought to have begun in the late Eocene (ca 40 Ma) (Davies et al. 2003a, Engel et al. 2009). Termitidae evolved from wood (FGI) feeding termites into fungus-growing termites (Macrotermitinae) through the development of symbiotic relationships with *Termitomyces* fungi (Aanen & Eggleton 2005). Although this represents a simplistic scenario of the evolution of Termitidae, due to the lack of data, it is thought that the employment of external symbiotic fungi for decomposition of organic matter may have led to the loss of the gut flagellates in the Termitidae (Inward et al. 2007b). Additionally the ingestion of soil, through construction of mounds, is thought to have conditioned the gut to decomposition of a more nutrient poor substrate which eventually led to the evolution of humus-feeding termites (FGIII) (Donovan et al. 2001a). A secondary evolution of wood-feeding termites (FGII) in Africa and South America is thought to have followed the evolution of humus-feeding termites (FGIII) (Donovan et al. 2001a). The reversion/s to wood-feeding termites have a large ecological importance as three genera (*Amitermes*, *Microcerotermes* and *Nasutitermes*) contain almost 500 species, about 18% of global termite diversity (Kambhampati & Eggleton 2000). Due to the dependence of true soil-feeding termites (FGIV; reduction of recognised plant tissue, predominance of silica particles and a more sophisticated gut morphology than the humus-feeding (FGIII) termites) (Donovan et al. 2001a) on highly buffered environments the evolution of these is thought to have

become widespread after the evolution of closed canopy tropical forests (Figure 2.2) (Donovan et al. 2001a, Davies et al. 2003a).

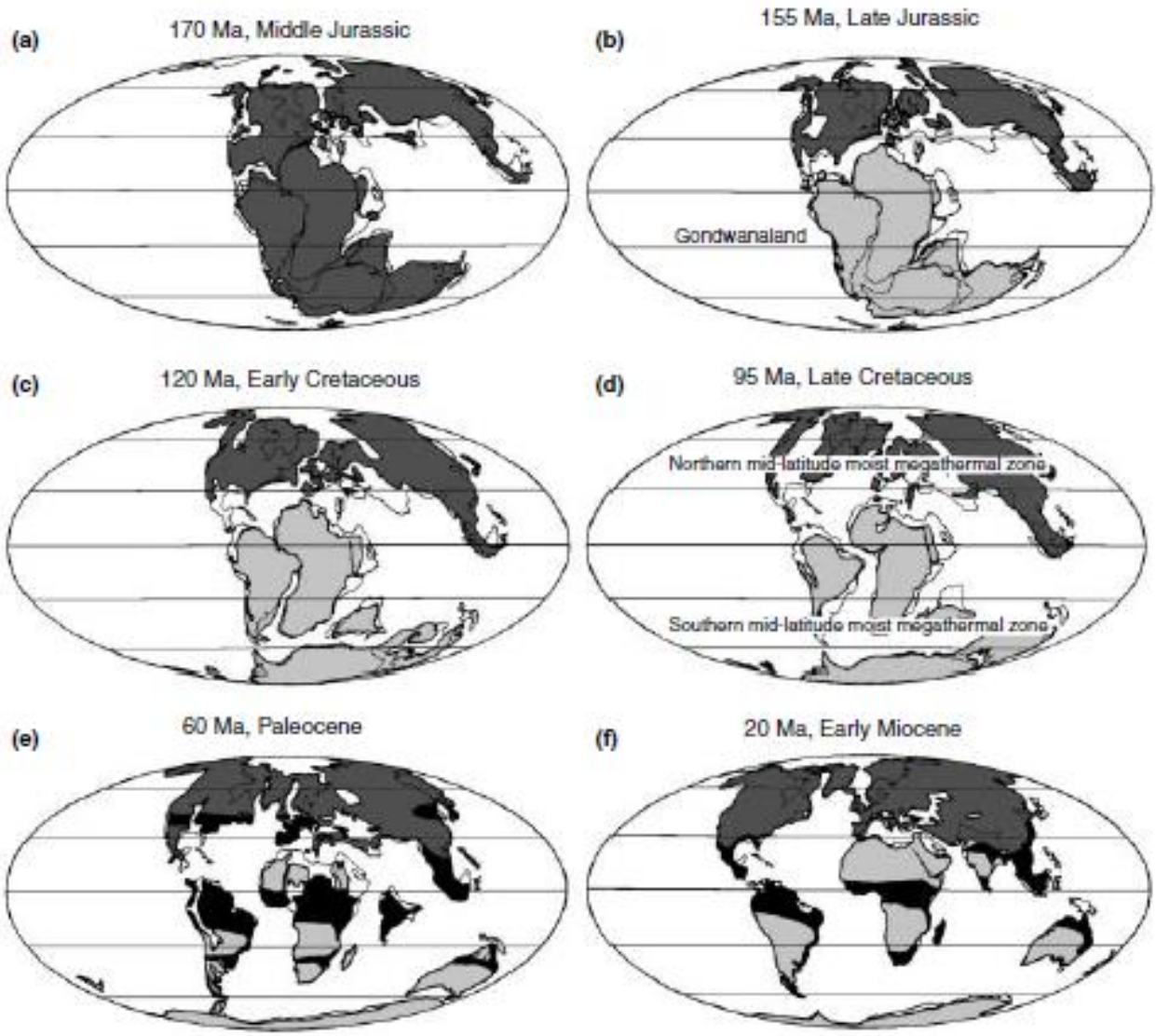

Figure 2.2. Movements of the tectonic plates though time edited slightly from Davies et al. (2003a). Dark grey: Pangaea and non-Gondwanan continental fragments; light grey: Gondwana and Gondwanan continental fragments; black areas: distribution of tropical closed canopy forests. Termitidae evolved on the isolated African continent. (a) Pangaea when termites first evolved; (b) Gondwana was formed; (c) connection between Africa and South America after break up of Gondwana; (d) connection between Africa and South America lost; (e) closed canopy tropical forests were thought to have been widespread; (f) the Indian plate had reached Eurasia along with termite fauna from Gondwana.

Today, non-Termitidae wood-feeding (FGI) termites have the widest distribution, e.g. they are the only functional group to colonise temperate rain forests (Jones & Eggleton 2011), which may be due to the split of the Pangaea before the evolution of Termitidae (Figure 2.2) (Davies et al. 2003a). More generally wood-feeding termites (FGI and FGII) are often better dispersers than soil-feeding termites (FGIII and FGIV) because they have adapted more readily to arid environments (Davies et al. 2003a) and because they feed on, and sometimes live within, dead wood (Eggleton 2011) which enables dispersal across oceans or other bodies of water (Gathorne-Hardy et al. 2000). Due to the low dispersal rate of soil-feeding termites, particularly the true soil-feeding (FGIV) termites that depend on the buffered environment that closed canopy forests provide (Davies et al. 2003a), endemism in soil-feeders is higher than for wood-feeding termites. However, although fungus-growing termites forage for wood and litter and are highly adapted to arid environments (Macrotermitinae increase as a proportion of the overall termite population as environments become more arid (Jones et al. 2003, Dosso et al. 2013)) they have failed to colonise South America (Aanen & Eggleton 2005). The low dispersal success of fungus-growing termites is likely to be due to their dependence on fungal spores from *Termitomyces* that they need for decomposition of organic matter (Aanen & Eggleton 2005, Nobre et al. 2011a). Although, species in the genus *Microtermes* (and *Macrotermes bellicosus*) are able to transport fungal spores in their digestive tracts (Nobre et al. 2010) most fungus-growing species depend on foraging workers to provide the fungal spores from the new environment when they are settling in a new area.

Termite biogeography has been relatively well documented using standardised sampling protocols (e.g. see Jones & Eggleton 2000) which have revealed a difference in species and functional diversity across regions with highest diversity of termite species in Africa followed by South America and then south east Asia (Davies et al. 2003a). It has also

been shown that soil-feeding termites are more diverse in Africa while wood and litter-feeding termites are more dominant than the soil-feeding termites in South America and south east Asia (Davies et al. 2003a). These data are important as they provide insights into the differences between regions which may be linked to evolutionary dispersal patterns and so to potentially ecosystem functioning. However, although species diversity is important for understanding assemblage structure and ecosystem processes, in order to quantify the role of termites in ecosystem functioning biomass and abundance data are needed. Comparable termite biomass and abundance data are sparse (Eggleton et al. 1996, 1999, Bignell & Eggleton 2000, Jones & Eggleton 2011) and further comparable data sets are needed in order to gain a broader understanding of how important termites are in tropical rain forests.

2.4. Termite gut symbiosis and morphology

Termites feed on dead plant matter that is hard to break down due to its high cellulose and lignin content (Brune 2010). To enable decomposition of these complex molecules termites harbour specialised microbial gut symbionts at high densities, reaching up to 10^{11}cells mL^{-1} (Brune & Ohkuma 2011) in their hindgut, where most of the decomposition takes place (Figure 2.3). The hindgut morphology (Figure 2.4) and composition of gut microbiota (Figure 2.5) vary with feeding habits (Miyata et al. 2007) with generally simpler morphology and composition of gut microbiota in termites outside the Termitidae family (wood, litter and plant-feeding (FGI) termites) (Brune 2010, Dietrich et al. 2014).

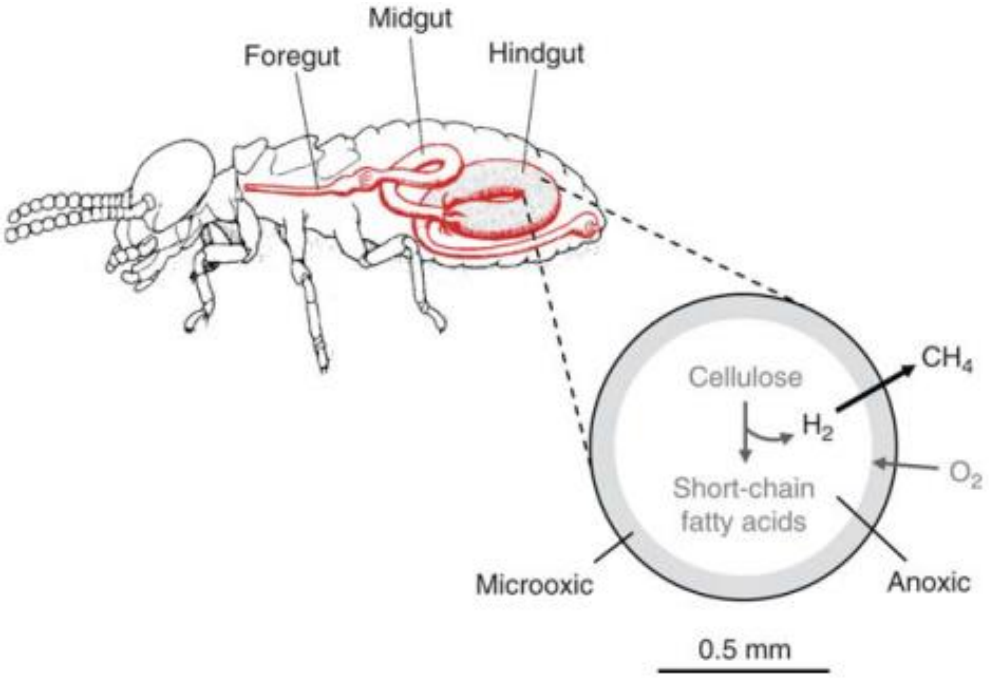

Figure 2.3. Outline of the gut of a worker termite. The majority of the decomposition process takes place in the midgut and hindgut. Modified from Brune 2010.

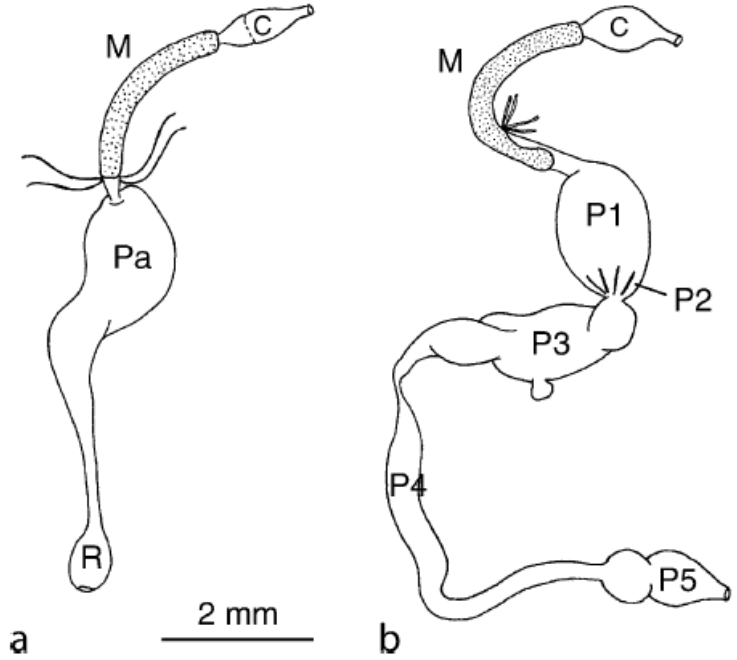

Figure 2.4. The gut morphology of (a) non-Termitidae termites (*Reticulitermes* sp.) and (b) termites within the Termitidae (*Cubitermes* sp.). C = crop, M = midgut, Pa = paunch, R = rectum, P1 = first proctodaeal segment, P2 = second proctodaeal segment (enteric valve), P3 third proctodaeal segment, P4 = fourth proctodaeal segment, P5 = rectum. From Brune 2010.

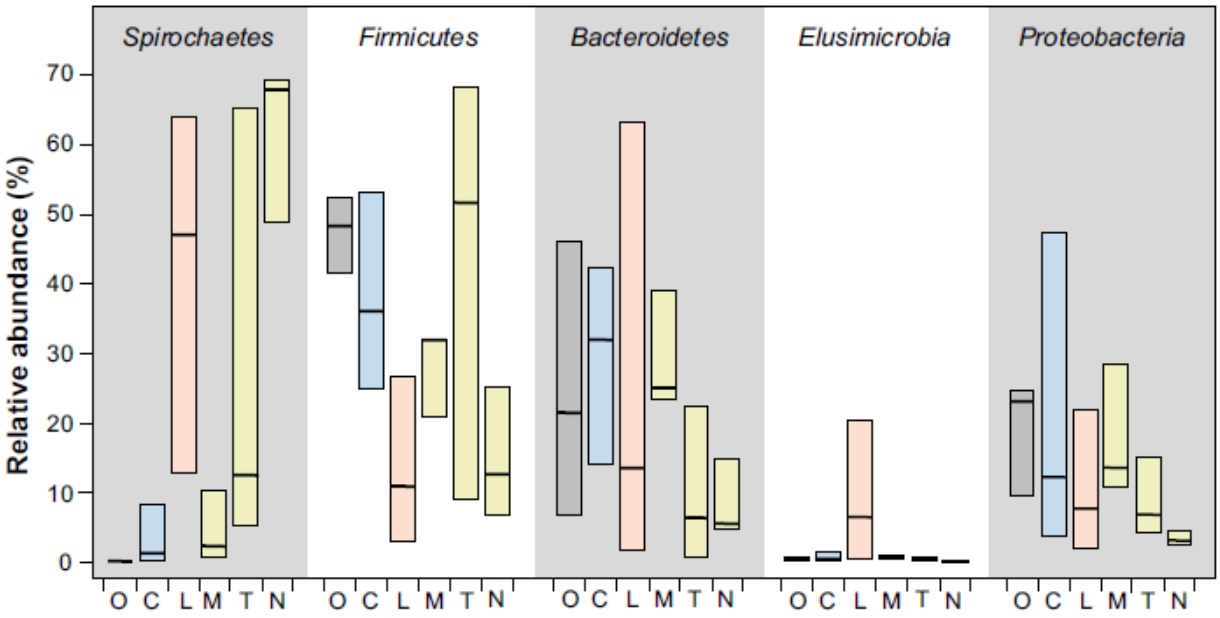

Figure 2.5. Relative abundance of bacteria phyla in the gut of different host groups. O = other insects, C = cockroaches, L = non-Termitidae termites, M = Macrotermitinae (fungus-growing termites), T = Termitinae, N = Nasutitermitinae. The horizontal lines show the median numbers of the sequence reads for each bacterial strand as a measure of relative abundance with variance shown by the bars. From Dietrich et al. (2014).

2.4.1. Gut microbiota and external fungi

Wood-feeding (FGI) termites are a sister group of the wood-feeding cockroaches *Cryptocercus* (Lo et al. 2000) which share symbiotic gut flagellated protozoa (Inward et al. 2007a, Dietrich et al. 2014). While all termites contain bacteria and archaea the flagellated protozoa were lost in the Termitidae family which is thought to have enabled a wider range of feeding habits (Cleveland 1926). The fungus-growing termites (Macrotermitinae; Termitidae) have developed a symbiotic relationship with external fungi, particularly species of *Termitomyces* (Nobre et al. 2011a). However, other wood-feeding termites, such as *Reticulitermes* (Rhinotermitidae), have been shown to depend on fungal conditioning of the

wood before they consume it (Rouland-Lefèvre 2000). Potential ingestion of bacteria has also been recorded in some soil-feeding (FGIII) termites (Fujita & Abe 2002).

The assemblage structure of the bacterial gut microbiota has been shown to vary in the short-term depending on the quality of the substrate (from wood with high lignin content to simple glucose molecules) (Miyata et al. 2007), although termites with different feeding-habits have been shown to be associated with different bacterial phyla (Dietrich et al. 2014). Phylogenetic analyses of bacterial composition placed Macrotermitinae closer to the cockroaches without flagellated protozoa while the bacterial composition of the wood-feeding roach *Cryptocercus* was more closely related to the wood-feeding termites than other cockroaches (Figure 2.6). The Termitidae family, with the exception of fungus-growing termites, made its own cluster with wood and soil-feeding termites separated within the cluster (Figure 2.6) (Dietrich et al. 2014).

The role of the fungal symbionts of the Macrotermitinae is far from understood, and may vary with genus or even species. Nobre and Aanen (2011b) argue that the termite serves the fungus by distributing its conidia evenly in the fresh forage, thus reducing potential competition from other fungi, while the consumption of old mycelium is an N-reward for the termite. The termite's carbon metabolism is autonomous, as the endogenous enzymes and gut microbiotas are similar to other wood-feeders in the Termitidae.

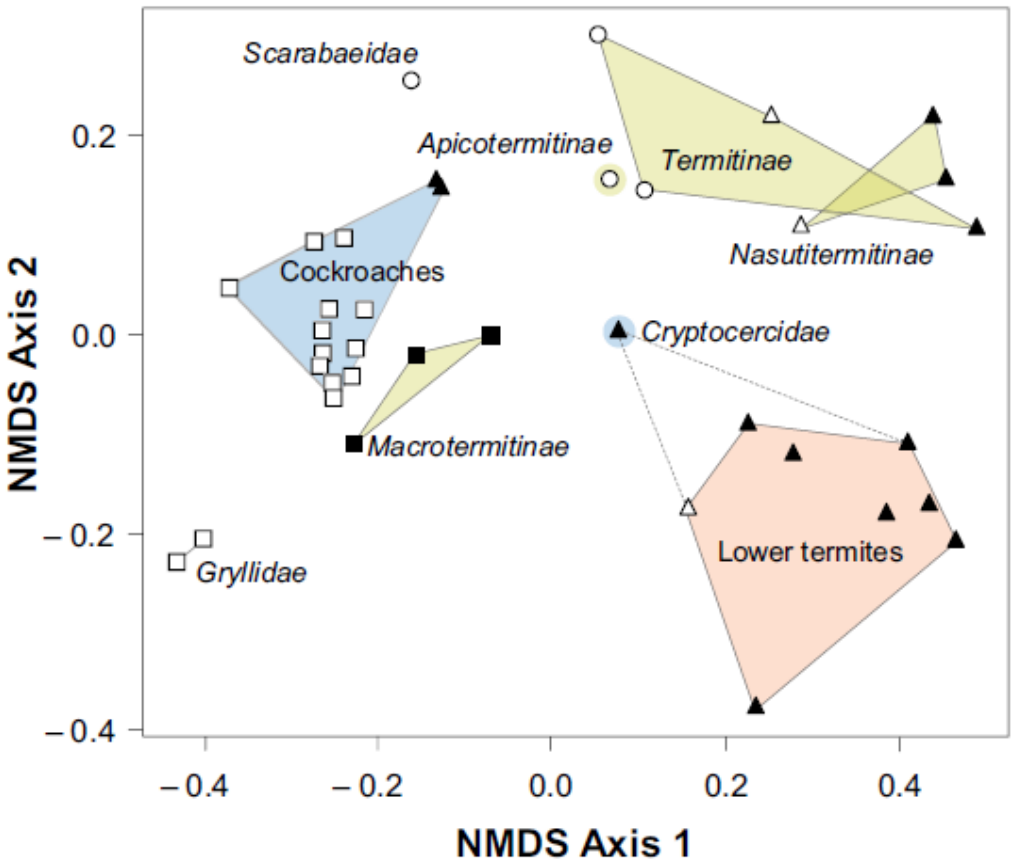

Figure 2.6. Phylogenetic analysis of bacterial phyla. White squares = generalists (most cockroaches), black triangles = grass-feeders, white triangles = wood-feeders, white circles = soil/humus-feeders, black squares = fungus-growing termites. From Dietrich et al. (2014).

2.4.2. Gut morphology

The gut structure of non-Termitidae termites is simpler than that of termites in the Termitidae family and may be divided into three sections: crop, paunch and rectum (Figure 2.4); while the gut structure within the Termitidae may be divided into the crop and five hindgut segments: P1-P5 where P1 and P3 are the first and third proctodeal segments; P2 is the enteric valve housing which divides the hindgut compartments (P1 and P3); P4 is the posterior colon and P5 is the rectum (Figure 2.4) (Eggleton 2011).

The segments become more sophisticated with the ingestion of humified matter which may be observed in the enteric valve in particular. The enteric valve lies between the first and

third proctodeal segments and consists of six ridges with more or less sclerotisation. The enteric valve has little importance in wood-feeding termites where it is less developed while the enteric valve is highly sophisticated and variable between species in the true soil-feeding (FGIV) termites (Donovan 2002). Although the function of the enteric valve is poorly understood modern technology such as Scanning Electron Micrography has been used to examine the three-dimensional structure of the valve (Donovan 2002). From these advances it has been suggested that the enteric valve structures, particularly in true soil-feeding (FGIV) termites, separate fine particle material which is richer in adsorbed organic matter towards the periphery of the P3, where bacterial populations are very dense (Figure 2.7) (Donovan 2002).

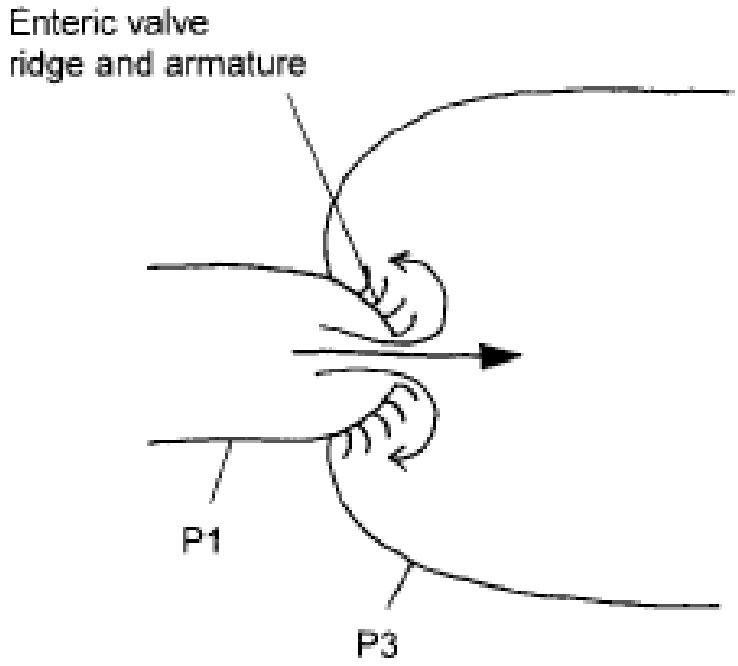

Figure 2.7. Ingested soil passing through the enteric valve in a termite gut from the P1 to the P3. The smaller arrows represent small soil particles that are thought to be slowed by the enteric valve armature once it has entered the P3. The larger arrow represent the larger coarse soil particles that are thought to pass through the gut at a faster rate as they are not affected by the enteric valve armature. From Donovan (2002).

Although both humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites feed on soil with overlapping stable isotope composition (Bourguignon et al. 2009) their gut morphologies are very different. Humus-feeding termites, feeding on soil with visible plant material, have more or less sclerotised enteric valve cushions while true soil-feeding termites have conspicuous spines (Donovan 2002) (Figure 2.8). The true soil-feeding termites also have a more complex gut which may sometimes contains a diverticulum that expands and contracts when coarse soil particles pass though the gut (Eggleton 2011). While the highly complex gut of the true soil-feeding termites *Cubitermes* have been well studied (Donovan et al. 2001b, 2004, Donovan 2002) the guts of humus-feeding termites and other true soil-feeding termites are less well known.

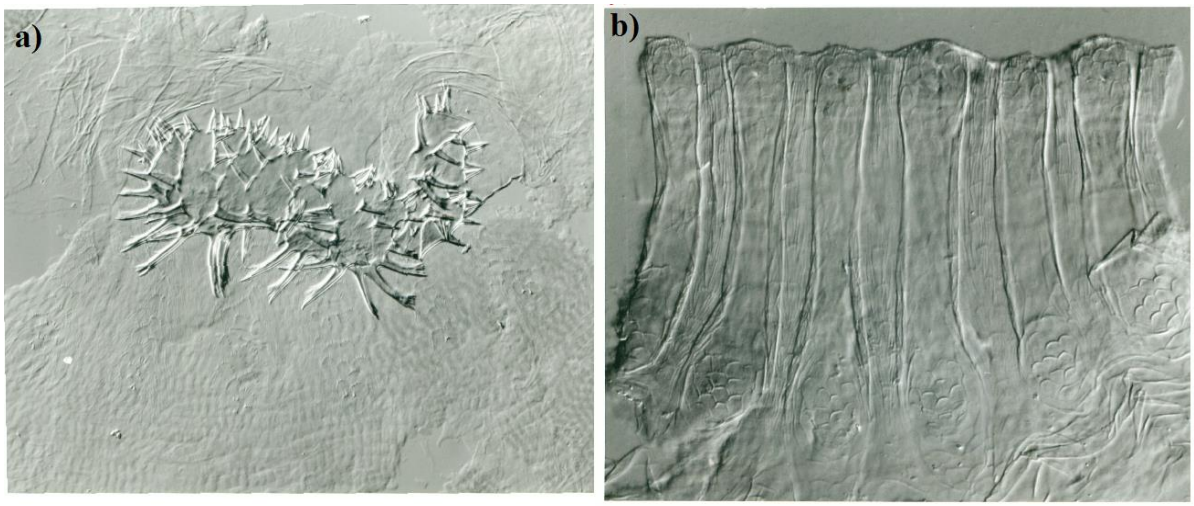

Figure. 2.8. Enteric valve structures in (a) true soil-feeding (FGIV) termite *Aoplotermes parvus* and (b) humus-feeding (FGIII) *Anoplotermes* sp *K*. From L.M. Hernández's (unpubl.) key to the Apicotermitinae of the Guiana Shield.

2.5 Energy flow and C:N balance in termites

Eggleton et al. (1998) showed that there is a difference in how energy is distributed in different termite feeding groups (soil-feeding termites and wood-feeding termites). In wood-feeding termites the highest energy throughput was shown to be in medium to small-bodied

species while large-bodied soil-feeding termites were shown to have higher energy throughput per unit area than expected by their body mass (Eggleton et al. 1998). The difference in energy distribution among species of different sizes may be linked to the availability and quality of the feeding substrate (Eggleton & Tayasu 2001). Wood and soil are very different both in quality and availability; while wood is a patchily distributed high carbon high energy substrate, soil is highly available but energetically and nutritionally poor. Due to the differences between the substrates Eggleton et al. (1998), argue that the optimal size for the two feeding groups is different. Wood-feeding termites benefit from being small-bodied as this is linked to smaller mandibles that will enable wood to be broken into smaller pieces which increases the surface to volume ratio. The higher surface area to volume ratio may in turn contribute to higher energy and nutrient uptake (Eggleton & Tayasu 2001). Soil-feeding termites that feed on a poor quality but highly available substrate benefit from being large-bodied as larger guts have been shown to increase the retention time of the substrate increasing nutrient uptake (Illius & Gordon 1992, Müller et al. 2013).

The C:N ratio in the body tissue of termites may differ depending on the species but lies between 5:1 and 12:1 (Matsumoto & Abe 1979, Higashi et al. 1992) while wood may be seriously N depleted with a ratio greater than 200:1 (Tayasu et al. 1997). Soil on the other hand have relatively high N content with C:N ratio between 9:1 and 14:1 (Tayasu et al. 1997). The termite functional groups therefore face different challenges in balancing the C:N ratio; e.g. while single-piece nesting (the most primitive form of nesting restricted to a single piece of wood, Inward et al., 2007) wood-feeding termites often fix N in order to make up for the low N content in wood (Eggleton & Tayasu 2001), true soil-feeding (FGIV) termites and humus-feeding (FGIII) termites, that feed on soil which is a highly available substrate with relatively low C:N ratio, do not need to acquire additional N from the atmosphere (Higashi et

al. 1992). This suggests that N and C emissions/fixation by termites vary depending on the termite feeding group and nesting type.

2.6. Termites as ecosystem engineers

Ecosystem engineers modify, maintain and create habitats by substantially changing the chemical and physical composition of substrates (Jones et al. 1994). Termites are particularly important ecosystem engineers as they manipulate the ecosystem e.g. by building complex mounds and nests (Korb 2011), acting as bioturbation agents by constructing tunnels and runways (Jouquet et al. 2011) and being one of the most important decomposer macrofauna organisms in tropical forests (Bignell & Eggleton 2000).

2.6.1. Mounds and nests

Termite nesting structures may be categorised into four different types: epigeal mounds (part of the nest is a mound on the surface or above the ground, Figure 2.9.), subterranean nests, nests in dead wood and arboreal nests (nests in trees) (Abe 1987, Korb 2011). Mounds and nests are architecturally complex structures that are constructed to condition the inside environment by controlling air quality and temperature, and provide protection (Korb 2011). Although the chemical composition of termite nesting structures depends on the original composition of the building material (Garnier-Sillam & Harry 1995, Brossard et al. 2007) they are normally rich in nutrients and organic compounds (N, P and C) and mineral nutrients (e.g. Ca^{2+} and Mg^{2+}) (López-Hernández 2001, Ackerman et al. 2007, Rückamp et al. 2010, Mujinya et al. 2010, Jouquet et al. 2011, Joseph et al. 2013a) due to the abundance of organic matter within the nesting structures (Jouquet et al. 2011).

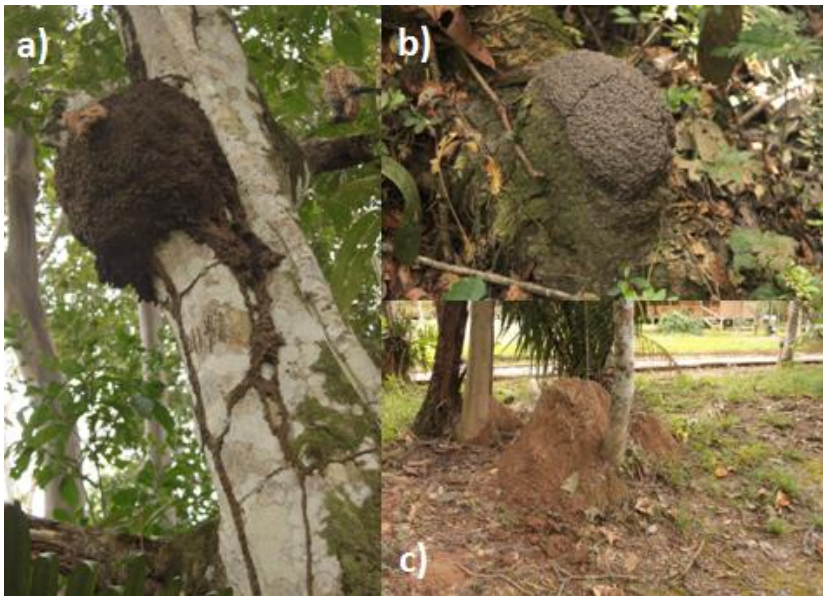

Figure 2.9. Termite nests and mounds in Tambopata, Peru. (a) arboreal nest; (b) mound on the root of a tree; (c) epigeal mound.

Due to the accumulation of clay and nutrients in termite nesting structures, particularly in epigeal mounds (Jouquet et al. 2002), these may act as islands of nutrition or refugia for organisms such as plants, mammals and other invertebrate species (Moreira et al. 2009, Jouquet et al. 2011). The concentrations of clay minerals and nutrients are particularly important for the growth of grasses and woody vegetation in nutritionally poor areas such as savannah and dry land areas (Sileshi & Arshad 2012). Indicator plant species that grow on mounds have been shown be associated with higher clay content and animal seed dispersal (Joseph et al. 2013a). In areas where fire is an important disturbance factor the presence of large termitaria (termite mounds) has been found to protect and promote the growth of large trees through higher soil moisture and richer soil nutrient composition (Joseph et al. 2011, 2013b).

Construction of mounds contributes to bioturbation through mixing of the substrate and redistribution of nutrients. Erosion of termite nesting structures is also important for the redistribution of nutrients in the habitat as nutrients are deposited into the soil from the

eroded mound and new soil is incorporated to repair them (Rückamp et al. 2010, Jouquet et al. 2011). The concentration of nutrients, difference in pH and termite activity around the nesting structures contribute to habitat heterogeneity (Joseph et al. 2013a) which supports a range of different organisms, and hence influences biodiversity. However, while above-ground mounds and nests are relatively well described, below-ground nesting structures are poorly understood which may, in part, be due to the difficulty of finding diffuse subterranean nests and tunnels and observing them *in situ*.

2.6.2. Decomposers

Termites are decomposer organisms that feed on dead organic plant derived matter at different stages of decomposition (Donovan et al. 2001a). Through the breakdown of organic matter termites promote nutrient turnover, redistribution and transformation into forms which may be utilised by plants or by higher trophic levels (Jouquet et al. 2011). The range of termite functional groups (Donovan et al. 2001a) as well as their specialised mandibles and gut microbiota (Hongoh 2010) make them one of the most effective decomposers, particularly in lowland tropical forests where their abundance is high (Bignell & Eggleton 2000).

2.6.2.1 Wood and litter decomposition

Wood and litter decomposition by termites has been shown to vary with habitat and substrate quality (Didham 1998, Takamura 2001, Martínez-Yrízar et al. 2007) and termite species composition (Schuurman 2005). Changes in wood and litter chemical composition are thought to be the main effects of decomposition by termites (Songwe et al. 1995, Didham 1998, Takamura 2001, Martínez-Yrízar et al. 2007, Coq et al. 2010) with lower decomposition rates generally seen with higher lignin content. These results suggest that

certain plant species may act as C and nutrient sinks due to their lower decomposition rates (Songwe et al. 1995).

Decomposition has been shown to increase with disturbance in Africa with highest decomposition of cellulose baits in secondary forests (Kagezi et al. 2011, Olugbemi 2013). These patterns (from African studies) may be due to the increase in the abundance of fungus-growing termites with land-use intensification (Olugbemi 2013). Fungus-growing termites play an important role in wood and litter decomposition (Wood & Sands 1978), particularly in Africa and Asia, where they are abundant (Eggleton et al. 1996, 1999, Aanen & Eggleton 2005). Fungus-growing termites have higher annual wood consumption than non-fungus-growing termites, 35.5 g m^{-2} and 20.0 g m^{-2} respectively, much of which is needed to support the strong aerobic respiration of the fungus garden and is directly mineralised without creating a humification chain (Wood & Sands 1978). Decomposition rates from regions without fungus-growing termites (South America) are, however, sparse with most studies conducted in Brazil (Vasconcellos & Moura 2010). Here the decomposition rate of dry wood by *Nasutitermes* has been estimated at 6.7 g m^{-2} (Vasconcellos & Moura 2010).

2.6.2.2 Soil processes and decomposition

Soil-feeding and soil-dwelling termites are important for plant growth through their effect on soil processes, such as nutrient decomposition and availability, by affecting soil microclimate and habitat heterogeneity that have been shown to enhance plant growth (Donovan et al. 2001b). Soil processes influenced by termites include redistribution of nutrients through decomposition of organic matter and bioturbation through construction of tunnels and runways, which also increase air and water flow (Jouquet et al. 2011).

Perhaps the most studied group of soil-feeding termites is the true soil-feeding *Cubitermes* -group which are endemic to Africa (Donovan et al. 2001b, Ji & Brune 2001,

Ndiaye et al. 2004, Ngugi et al. 2011) which may be due to their high species abundance (Eggleton et al. 1996) and their conspicuous mounds (Korb 2011), compared with the diffuse below-ground nests inhabited by soldierless soil-feeding termites. The effects of *Cubitermes* are predominantly seen in old-growth lowland forests in Africa where they are the most abundant (Eggleton et al. 1996). In these habitats *Cubitermes* has been shown to increase pH in acidic soils as well as the content of organic carbon and water (Donovan et al. 2001b). Their mounds are high in SOM which is thought to induce microbial activity which may increase nitrogen (N) mineralisation, ammonification and denitrification (Ndiaye et al. 2004). Although, denitrification may reduce the soil N content (N_2) other *Cubitermes*-induced-processes, such as ammonification and N mineralisation, are thought to increase N availability for plant uptake (Ngugi et al. 2011). Studies from other regions are sparse but are needed to gain a better understanding of soil processes in areas without *Cubitermes* (outside of Africa).

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CHAPTER III

STUDY SITE AND METHODS

3.1 Study site

Experiments and sampling took place in Tambopata National Reserve (12˚49.434'S, 069˚15.791'W) in Peru (Figure 3.1). The reserve protects 274,690 ha of old-growth lowland tropical forest and the fieldwork was based at Explorer's Inn, which is one of the oldest eco lodges along the Tambopata river. Explorer's Inn was founded in 1976 and has a long history of supporting researchers and conservation. The site has an average altitude of 190 m and the average annual temperature and rainfall are 24.4˚C and 1900 mm, respectively (Malhi et al. 2014). Two field campaigns were carried out in Tambopata in 2011 and 2012.

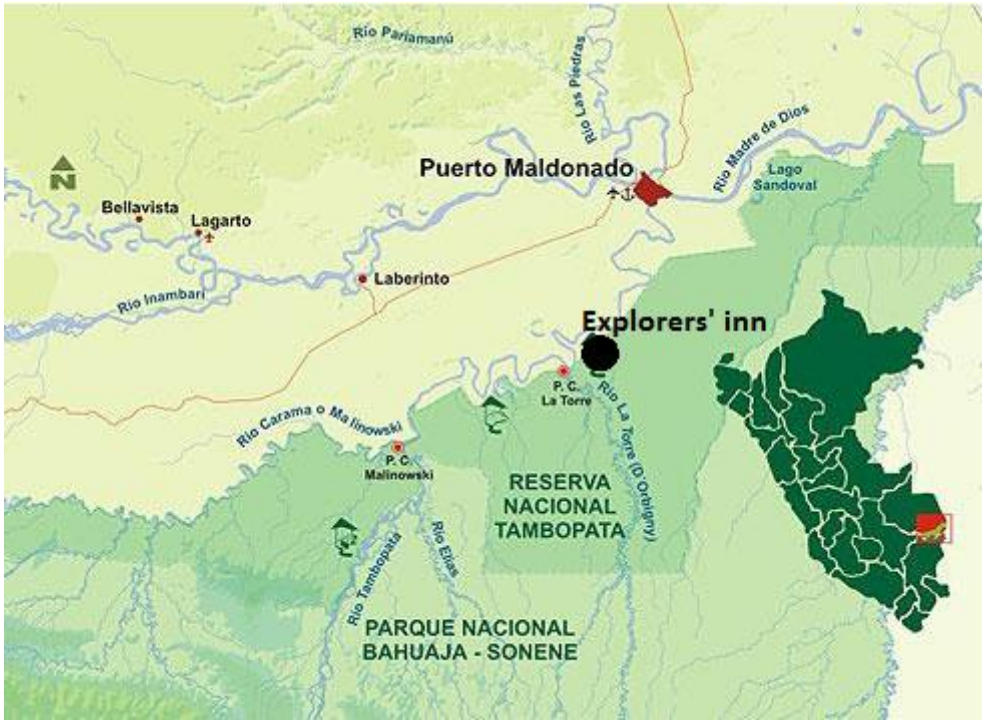

Figure 3.1. Map of Tambopata, and the Explorers' Inn lodge, in the Madre de Dios region in Peru.

Although the lodge is primarily a tourist lodge, and the trails are walked and cleared of vegetation almost every day, the trails are narrow (Figure 3.2) and so do not notably affect the forests structure as a whole. The forest has a patchy canopy structure with dense canopy being broken up by large gaps due to naturally occurring tree falls. The soil structure is

variable with high clay content in soil on higher elevation and further away from the river or lake while soil at lower elevation close to bodies of water had higher sand content. The plots were chosen to represent the patchy canopy structure and deliberately chosen to have soil with high clay content as soil-feeding termites depend on the clay to support their nesting structures.

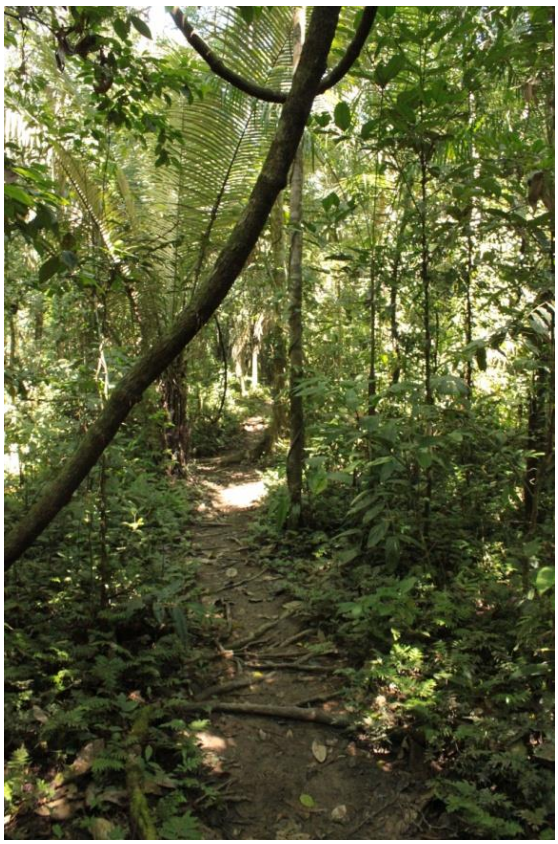

Figure 3.2. Main trail in Explorers' Inn, Tambopata National Reserve.

3.2 Experimental design

In Tambopata, Peru, six plots (70 m × 50 m) were laid out at least 300 m apart along two of the main trails (Figure 3.3 & 3.4). Each plot was located at least five metres from the trail and divided into seven sub-plots (10 m x 50 m each). Two sampling methods (transect and quadrat) and one exclusion experiment were carried out in two sub-plots each in each plot. The sub-plots in which the same method was conducted were spaced 30 m apart (Figure 3.3). The transect and quadrat sampling methods were conducted in the same year, in 2011, while

the exclusion experiment was conducted the following year, in 2012. The distance between the different sampling regimes (at least seven metres) was considered large enough not to cause any disturbance to termite communities in the different sub-plots.

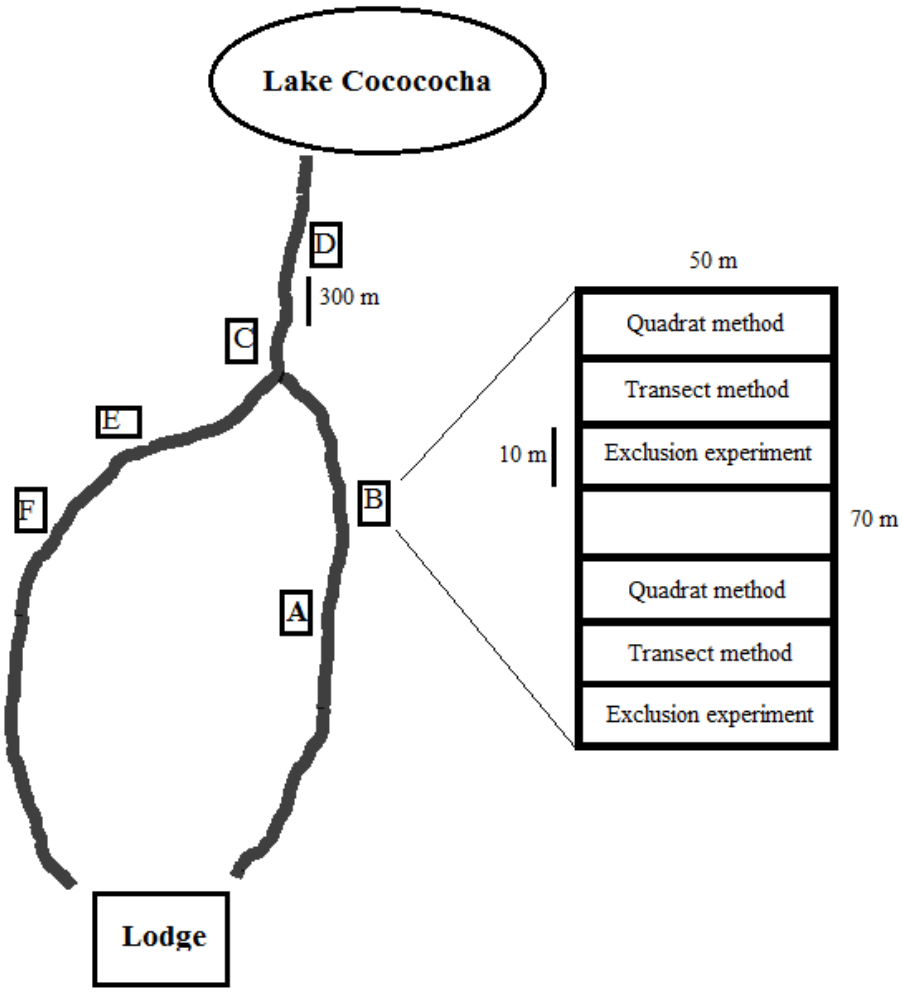

Figure 3.3. Schematic layout of the six plots along the two trails from Explorers' Inn Lodge to Lake Cococha. The plots were at least two kilometres from the lodge and a kilometre from the lake and placed at least 300 metres apart. The plots were divided into seven sub-plots for either one of two sampling protocols or one experiment. Each activity was conducted in two sub-plots 30 m apart.

Figure 3.4 Geographical positioning of the six plots along the two trails from the Explorers' Inn Lodge (on the far left) and Lake Cococha (on the right). The GPS coordinates for each plot are: A 12˚50.132"S 069˚16.342"W, B 12˚49.622"S 069˚16.087"W, C 12˚49.526"S 069˚15.910"W, D 12˚49.434"S 069˚15.791"W, E 12˚49.539"S 069˚16.120"W and F 12˚49.605"S 069˚16.249"W.

3.2.1. Quadrat method

Abundance and biomass data from the quadrat method (QM) (Eggleton et al., 1996), from three sites in Peru, Cameroon and Malaysia, with slight differences in sampling regimes (see table 3.1), were used in this thesis. While the quadrats were located randomly within the plots in Cameroon and Malaysia, a grid system was employed in Peru, with five quadrats placed five metres apart in each sub-plot (Figure 3.5). Each sub-plot was located 30 metres apart due to the number of sampling regimes and experiments taking place within the same plot. Although the location of the quadrats in Peru were not random they were neither chosen subjectively but allocated a pre-determined pattern prior to the selection of each plot location. While the grid sampling may have contributed to sampling of a smaller proportion of the plots the autocorrelation between quadrats is thought to have been low due to the relatively large distance between each quadrat. Donovan et al (2007) show that patterns of soil-feeding

termites could be observed at a minimum distance of two metres which suggests that the quadrats in the Peruvian site (spaced five metres apart) may be considered as individual samples.

Termite workers in all dead wood >0.2 cm diameter, up to breast height, were sampled within each quadrat. Large logs (>50 cm long and >10 cm diameter) were sub-sampled and the number of termites extrapolated. All termites were also sampled from a 25 cm × 25 cm × 10 cm soil pit in the centre of each quadrat. The termites were placed in tubes with 70% ethanol and identified by the author (CALD) at the Natural History Museum (NHM) in London.

Table 3.1. Different sampling regimes in the three study sites Cameroon, Malaysia and Peru.

Study site	Number of plots	Plot size (m)	Number of quadrats/ plot	Size of soil pit (m)
Cameroon	4	30 × 20	10	0.2 ×0.2 ×0.5
Malaysia	6	50 ×50	20	0.3 ×0.3 ×0.25
Peru	6	70 ×50	10	0.25 ×0.25 × 0.1

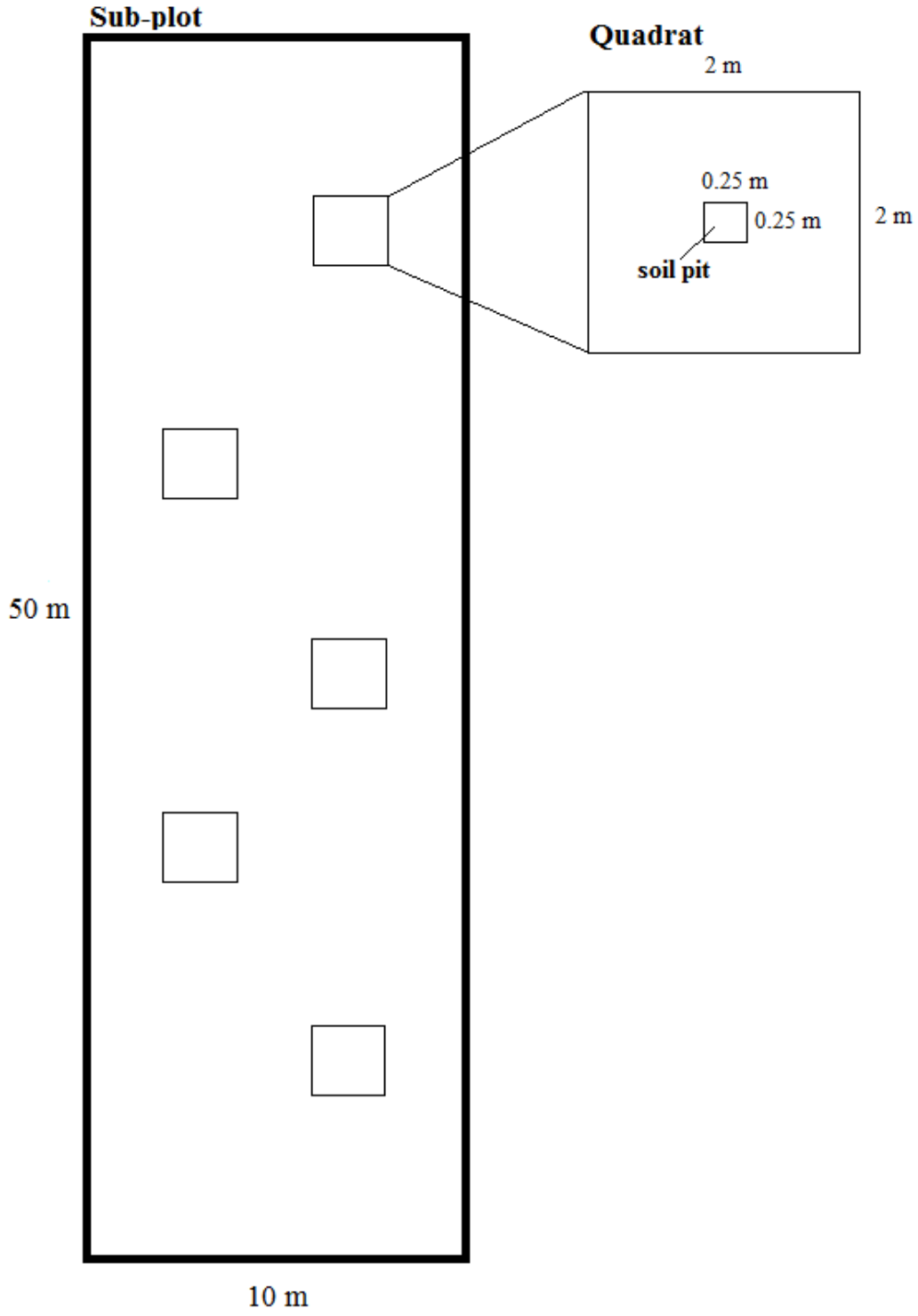

Figure 3.5. Outline of the quadrat method in a sub-plot. Five quadrats were placed five metres apart in each sub-plot (10 sub-plots per plot). All termites were collected from all dead

wood in each of the 2 m × 2 m quadrats and from the soil in the 0.25 cm × 0.25 cm × 10 cm soil pits in the centre of each quadrat.

3.2.2. Transect method

A standardised transect protocol (Jones & Eggleton 2000) was used to collect termite species density data. Six full transects (100 m × 2 m) were sampled across the six plots with a half transect in each sub-plot (Figure 3.6). In each sub-plot the 50 m × 2 m half-transect was divided into ten 5 m × 2 m sections. Termite species representatives (~15 soldiers and workers) were collected from 12 (12 cm × 12 cm × 5 cm) soil pits (scrapes) as well as runways, nests and dead wood at chest height. Each section was sampled for one-person hour (i.e. sampling by one person for an hour) totalling a sampling time of 20 h per each full 100 m transect. The termites were placed in tubes with 70% ethanol and identified by the author (CALD) at the NHM in London.

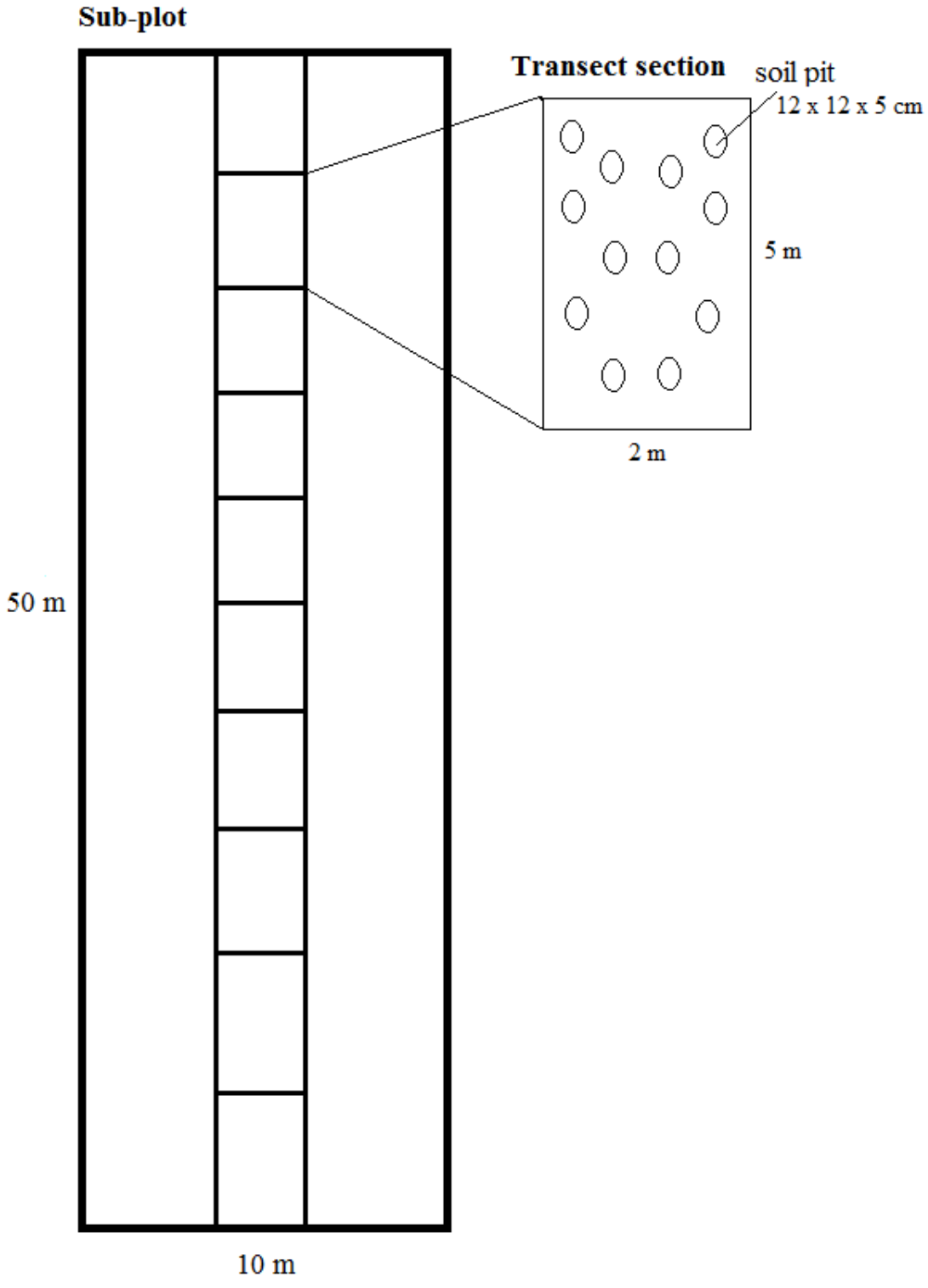

Figure 3.6. Outline of the transect method in a sub-plot. Half-transect (50 m × 2 m) divided into ten (5 × 2 m) sections in the sub-plot. Termites from twelve soil-pits, dead wood, runways and nests were collected in each section.

3.2.3. Macrofauna exclusion experiment

The exclusion experiment was conducted using three baits: wood, leaf litter and soil. Local Cedro wood was used, instead of the planned Aspen wood due to issues in the Peruvian customs, leaf-litter was collected from the five most common species in the site and organic rich soil (high carbon (C) and high nitrogen (N)) was collected from a montane forest site in Wayqecha (3000 m asl) and translocated to the lowland primary forest site in Tambopata (190 m asl). These baits were used in order to investigate the impact of termites and other macrofauna in decomposition of different organic matter. Wood and leaf-litter were placed in coarse (5 mm) and fine (0.3 mm) nylon mesh bags (30 cm × 30 cm) while soil was placed in cylindrical plastic containers (10 cm diameter and 5 cm height) where the top and bottom had been replaced by coarse and fine mesh for inclusion and exclusion of macrofauna, respectively. In total, 90 leaf litter samples and 90 soil samples of each mesh treatment were sampled across all six plots (Figure 3.7). Slightly fewer wood samples (60 samples of each mesh size) were sampled across the plots due to the higher cost of wood.

All baits were placed in two rows in each sub-plot alternating between different baits so that the same bait was at least 10 m apart (Figure 3.7). The baits were placed 2.5 m from the short side of the sub-plot (we made sure that the sub-plot started slightly further into the forest to avoid disturbance of the path) and five metres from the edges of the neighbouring sub-plots. In each plot, three pseudoreplicates of each mesh treatment of leaf-litter and soil, and two preudoreplicates of wood, were collected at each of five sampling occasion 7, 14, 28, 56 and 112 days after the start of the experiment.

The data for wood and leaf-litter did not provide significant results and will therefore only be discussed in Chapter VIII. The soil exclusion experiment, however, provided significant results and will be described here in more detail.

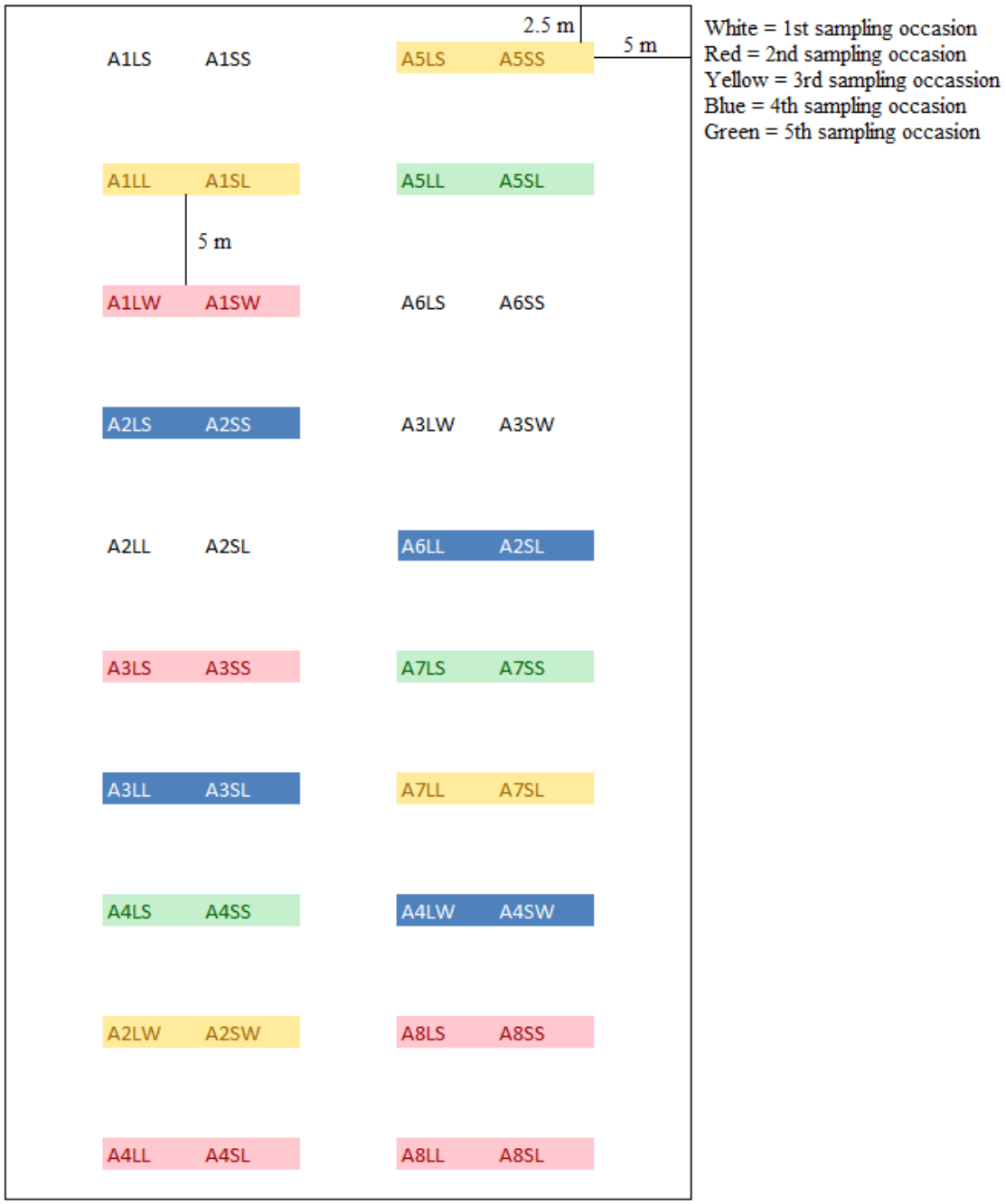

Figure 3.7. Outline of the sampling of the macrofauna exclusion experiment. The first letter in the code indicates the plot (A), the number represents the sample number (n), the second letter indicates the sample treatment (coarse = L, fine = S) and the last letter in the code indicates whether the bait is soil (S), leaf litter (L) or wood (W). The colours represent the different sampling occasions 7, 14, 28, 56 and 112 days after the start of the experiment, respectively.

3.2.3.1. Soil macrofauna exclusion experiment

Translocated organic rich soil from highland forests, where decomposition rates are low, provides a suitable habitat for macrofauna in lowland forests where decomposition rates are higher (Zimmermann et al. 2010). Soil from a montane rain forest in Wayqecha (13˚11'24S, 71˚35'13"W) (at 3000 m elevation), where termites are absent (Palin et al. 2010), was therefore translocated to the Peruvian lowland site in Tambopata (at 190 m elevation).

Rocks, roots, leaves and visible macrofauna were removed from the soil before it was dried to constant temperature and weighed prior to the start of the experiment. A cylindrical plastic container (10 cm diameter and 5 cm height) was filled with the sorted soil which was then dried to constant temperature, at no more than 70˚C. A full container worth of soil was measured and dried to make sure that the containers were filled when placed in the field. This was done to enable termites to enter the microcosm through the mesh both at the bottom and top of the container. The mean weight of the dried soil samples was 193 grams. Once dried and weighed the soil was placed in plastic bags and rehydrated with 100 ml of water for the purpose of an infiltration rate experiment that took place once the samples were installed. As equipment to measure specific moisture content in the sample soil was not available 100 ml was decided upon as it provided enough moisture for all of the soil to retain the water yet enough to provide moisture for the whole soil sample. The rehydration process was done to ensure that the microcosm contained moisture when the infiltration experiment was conducted once the samples had been installed. Rehydration was decided upon after water was poured over completely dry soil as the infiltration was very fast which may have introduced noise into the data as time was recorded manually with a stop watch. The bags were labelled and transported into the field where microcosms for each mesh treatments were paired. The soil was poured into the plastic containers and placed in two holes with the lid at ground level (Figure 3.8). The location was marked with a coloured peg and the containers

were covered with two centimetres of soil. One data logger was placed in each plot to record temperature and moisture (Figure 3.8), although, the data from these were recorded with high errors, perhaps due to battery failure, and so were not used in the study.

The samples were collected without replacement after 7, 14, 28, 56 and 112 days and placed in plastic bags for transportation to the laboratory at the lodge. All macrofauna were collected from the samples and placed in tubes with 70% ethanol for identification by CALD at the Hope Department for Entomology in Oxford. Thereafter the soil was dried to constant temperature and weighed. The soil was ground to a fine structure with a pestle and mortar and a sub-sample was taken for carbon and nitrogen analyses at the NHM in London.

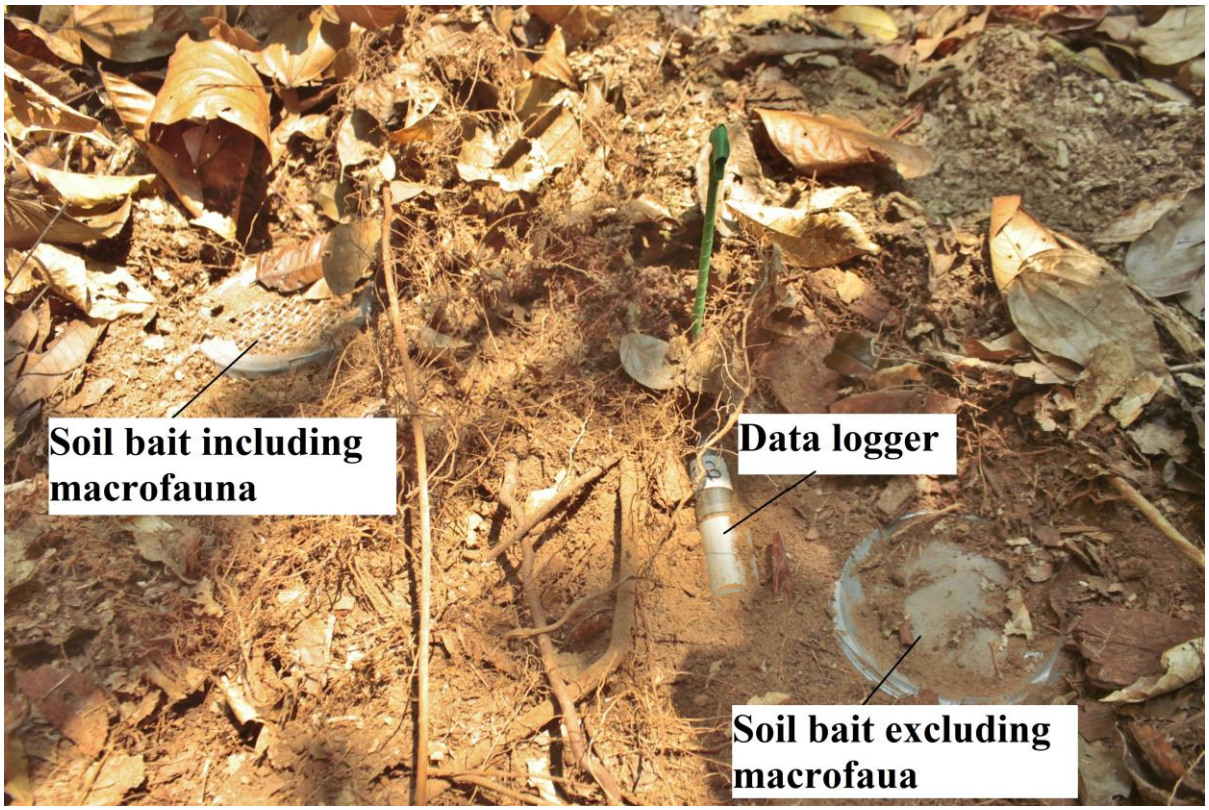

Figure 3.8. Illustration of soil samples *in situ.* The soil samples were placed in plastic containers where the bottom and lid had been replaced by fine (right) and coarse (left) mesh. The two mesh treatments were placed in pairs with a total of 15 samples of each mesh treatment per plot and 90 samples in total. The colour of the peg indicates the sampling occasion (5th sampling occasion in this case after 112 days).

3.2.4. Environmental data

Environmental variables were collected in each quadrat during sampling with the quadrat method. Soil temperature was measured with a probe thermometer at 5 cm depth and moisture was measured using a Delta-T theta probe type ML2x, Delta-T Inc., Cambridge, UK over a depth 0- 5 cm once in each quadrat. Soil samples were taken from each quadrat for chemical analysis of carbon (C) and nitrogen (N). Total soil C and N content were analysed using a Thermo Finnigan Flash Elemental Analyser 1112 at the Imaging and Analysis Centre (IAC) at the Natural History Museum (NHM) in London. The plot coordinates (latitude and longitude) were estimated with a GPS in the field and used to collect plot specific elevation data from Google Earth. The distance from each plot to the main river and the distance to the lake in the study area were collected using the 'ruler' tool in Google Earth.

3.2.5. Spatial data

The spatial variables included GPS data for latitude and longitude from each of the plots. Cubic trend surface regressions (x^2, xy, y^2, x^3, x^2y, xy^2, y^3) were analysed as variables influencing termite species composition in addition to the basic geographical coordinates (x and y) (Legendre 1990). The cubic trend surface regression adds spatial dimensions that enables non-linear relationships with species composition to be detected.

3.3 Functional group classification

Functional group classifications may be seen as simplifications of termite functionality that differ from species to species, however, they may be useful if the hypothesis of a study is focused on the function of a group of species. Generally termite functional groups may be defined by their nesting habits (Abe 1987) or feeding habits (Donovan et al. 2001, Inward et al. 2007, Bourguignon et al. 2009). In this study we use a combination of the functional

groupings from Donovan et al. (2001) and Inward et al. (2007) that identify five functional groups depending on where along the humification gradient they feed , i.e. the level of decomposition of their respective feeding structures (Donovan et al. 2001). For the purpose of discussing ecosystem functioning, through decomposition of organic matter and bioturbation, this classification of functional groups is suitable as it is based on both termite gut content and gut morphology (Donovan et al. 2001). Bourguignon et al. (2009) show that the food substrate of humus-feeding (FGIII) and true soil-feeding (FGIV) termites does not differ in $\delta^{13}C$ and $\delta^{15}N$ isotopic ratio, however, due to the difference in particle size and SOM content as well as the difference in gut morphology (Donovan et al. 2001) we treat humus-feeding (FGIII) and true soil-feeding (FGIV) termites as separate functional groups.

3.3.1 Non-Termitidae (FGI) species

All termite species outside the Termitidae are classified as FGI-feeding termites feeding at the top of the humification gradient on sound wood, litter and other plant material (Donovan et al. 2001). Species within this functional group differ from other functional groups in that they have a simpler gut morphology with flagellate protists, along with Archaea and bacteria, as part of their symbiotic gut microbiota (Eggleton & Tayasu 2001, Ohkuma 2008, Hongoh & Ohkuma 2010).

3.3.2. Wood and litter-feeding termites (FGII)

Wood and litter-feeding termites of FGII belong to the Termitidae family only. Along with all other functional groups within the Termitidae these species have lost their gut flagellates and protists (Ohkuma & Brune 2011). These wood and litter-feeding species have a more complex gut than the termites from FGI (Inward et al. 2007) which enables for a more diverse diet slightly further down the humification gradient.

3.3.3. Fungus-growing termites (FGIIF)

The fungus-growing termites evolved from the wood (FGI) feeding termites and lost their gut flagellates, possibly through ingestion of soil when constructing their mounds (Davies et al. 2003, Nobre et al. 2011a). Fungus-growing termites belong to the sub-family Macrotermitinae and decompose organic matter of similar humification to the diet of FGII. The termites produce endogenus cellulases for decomposition of the organic matter that they place on the fungus gardens after which fungal spores are introduced (genus *Termitomyces*) (Aanen & Eggleton 2005, Nobre et al. 2011b). While the fungi produce N-enriched fruiting bodies the termites reduces the potential competition from other fungi by grooming the fungus comb and regularly introducing new fungal spores. Fungus-growing termites evolved in Africa (Aanen & Eggleton 2005) and exist in African and south east Asian regions while they are absent from South America (Davies et al. 2003).

3.3.4.Humus-feeding termites (FGIII)

Humus-feeding termites feed further down the humification gradient than wood and litter-feeding termites (FGII and FGIIF) and have a more sophisticated gut structure with slightly sclerotised enteric valve structures (Donovan 2002). They feed on soil with visible plant material (Donovan et al. 2001) and many species, particularly in South America, do not have a soldier caste e.g. *Anoplotermes*-group.

3.3.5. True soil-feeding termites (FGIV)

True soil-feeding termites feed at the bottom of the humification gradient, i.e. on mineralised soil that is at a late stage of decomposition (Donovan et al. 2001). The gut of soil-feeding termites is the most sophisticated of the termite functional groups with highly sclerotised enteric valve structures with armature such as spines (Donovan 2002).

3.4 Identification

All termites collected in Peru were identified by the author of this thesis (CALD) at the Natural History Museum in London and the Hope Department for Entomology in Oxford. Termites with soldier castes were identified to genera using a key to Neotropical genera (Constantino 2002) and to species by using available keys (e.g for *Neocapritermes* see Krishna & Araujo (1968)) and the collection at the NHM in London. Soldierless termites were identified to genus and species level with L.M. Hernández's key to the Apicotermitinae of the Guyana Shield (unpubl. data). The soldierless species were identified by features such as gut morphology and enteric valve structures. When only workers of termites with a soldier caste could be found these were identified by comparing enteric valve structures and head widths.

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CHAPTER IV

Describing termite assemblage structure in a Peruvian lowland tropical rain forest: a comparison of two alternative methods

Overview

Data on termite assemblage structure are known to be relatively sparse for South America with little temporal and spatial replication within sites. In order to gain better understanding of termite species and functional composition within a site in Peru I sampled termite species density, abundance and biomass data from six spatially replicated plots in a lowland tropical rain forest. Two standardised sampling protocols, one using transects (100 × 2 m) (TM) and one using quadrats (2 × 2 m) (QM), were used to sample termite species density (TM), abundance (QM) and biomass (QM). In this chapter I investigate the drivers of the composition of species in the Peruvian site and explore the effectiveness of the two sampling methods and their strengths and weaknesses.

Cecilia Dahlsjö wrote the paper with comments from Paul Eggleton, Yadvinder Malhi, Kate Parr and Patrick Meir. Cecilia Dahlsjö set up the sampling plots in Tambopata, Peru, and collected all data with the help of Henry Siccos and Hugo Lopez. This chapter was submitted as a full paper to *Insectes Sociaux* (in review).

Paper details

Title: Describing termite assemblage structure in a Peruvian lowland tropical rain forest: a comparison of two alternative methods

Keywords: environmental variables; quadrat method; species composition; spatial variables; Termitoidae; transect method

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Abstract

Termites are frequently dominant invertebrate decomposers and bioturbators in lowland tropical forests and therefore strongly influence ecosystem processes favouring soil stability, porosity and nutrient retention. In this study we provide the first spatially replicated dataset on termite assemblage composition, abundance and biomass in a Peruvian rainforest by sampling six separate plots. In addition, two alternative sampling methods (transect method-TM and quadrat method-QM) were used to sample termite species density that was compared among the plots. The relationships between a range of environmental and spatial variables and species composition were examined using Canonical Correspondence Analysis (CCA) variation partitioning. We found that the TM captured a higher proportion of the known species in the site (85%) compared with the QM (69%). Additionally, 56% of the species sampled by TM were common between the plots while only 18% of species overlapped using the QM. The QM may therefore potentially have undersampled the species pool. Environmental variables were shown to explain a larger proportion of the species patterns than the spatial variables with elevation, soil temperature and distance to the river being the most important. We discuss the impacts of the environmental and spatial variables on termite species composition.

4.1. Introduction

A better understanding of species diversity and composition in tropical rain forests, and the drivers behind the observed patterns, may provide insights into ecosystem functioning as well as enabling predictions of how ecological systems are likely to respond to environmental changes. This is particularly important in the case of decomposer organisms as the recycling of organic matter is one of the most important ecosystem processes (Gessner et al., 2010).

Termites inhabit subtropical and tropical regions and are particularly abundant in lowland tropical rain forests (Bignell and Eggleton, 2000). They exhibit a wide range of feeding habits, from single-piece wood-feeding to true soil-feeding, that are often classified into five functional groups (the Donovan et al., (2001) and Inward et al., (2007) systems, see Table 4.1). Although, other functional group classifications are available, based on nesting habits (Abe, 1987) or $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios (Bourguignon et al., 2011b), the Donovan/Inward system takes account of both gut morphology and gut contents and thus reflects the digestive process as well as the substrate ingested. Termites are ecosystem engineers (Jones et al., 1994), acting as bioturbation agents and affecting soil nutrient availability and turnover (Jouquet et al., 2011); additionally, the range of functional groups and the abundance of termites in lowland tropical forests make them one of the most important decomposer organisms in those habitats (Bignell and Eggleton, 2000). Termite compositional and diversity data are therefore important for a better understanding of the role termites play in ecosystem processes, such as nutrient availability and distribution and physical alterations of the habitat, and for the understanding of the functioning of the ecosystem as a whole.

Despite their importance to ecosystem function, data on termite species and functional diversity from tropical forests are restricted (Eggleton et al., 1996, 1999), particularly for

South America (Martius, 1992; Martius and Ribeiro, 1996; Apolinário and Martius, 2004; Bourguignon et al., 2011a; Cancello et al., 2014), and existing studies tend to examine single plots within different regions or land uses, with limited temporal or spatial replication (Jones, 2000; Davies et al., 2003a; Huising et al., 2008; Palin et al., 2010; Dahlsjö et al., 2014).

Two standardised sampling protocols are recognised for termites in humid tropical forests (Bignell, 2009), the transect method (TM) (Jones and Eggleton, 2000) and the quadrat method (QM) (Eggleton et al., 1996). The TM is based on representative sampling in sequential adjacent sections, limited by time (1 person-hour per section, 20 h per transect). Thus different sites are addressed by a sampling exercise which is equal in effort as well as being logistically efficient (Jones and Eggleton, 2000; Bignell, 2009). This method is not exhaustive, but provides encounter data, which may be used to estimate termite species density (species richness per transect). In contrast, data from the QM are based on a higher point-scale sampling effort in a number of small separated quadrats, where all individuals are collected to provide absolute termite abundance (indiv m^{-2}), which may then be used to estimate biomass. However, the requirement to show confidence intervals for estimates of absolute abundance and biomass may mean that a large number of quadrats are sampled, and the logistical investment per site is generally greater (Eggleton et al., 1996; Bignell, 2009). The TM has been used extensively to provide better understanding of termite species diversity both regionally (Eggleton et al., 1995, 2002; Jones, 2000; Jones and Eggleton, 2000; Jones et al., 2003) and globally (Davies et al., 2003a); while the QM, although less often deployed (Eggleton et al., 1996, 1999; Dahlsjö et al., 2014), has provided important insights into termite abundance and biomass for better understanding of their impact on ecosystem processes (Dahlsjö et al., 2014). Based on work in the humid forests of Malaysia and Cameroon Jones and Eggleton, (2000) showed that the TM could compile a comparable number of species to the QM in about one tenth of the field time, however, comparable

studies have not been carried out in South America. A further complication arises from the lack of genuine replication in many previous studies, that is the restriction of sampling to a single plot within a defined land use within a gradient of land uses, rather than separate replicated plots within the same land use and site. Thus there is limited understanding of how species composition differs among plots within the same land use, or across a single site in relation to topographical or other environmental factors. In this study the diversity and compositional patterns of termites within a Neotropical lowland rain forest in Peru were examined using two sampling methods, the TM and the QM. The results demonstrate the degree to which the two methods reveal similar patterns, and permit an evaluation of the strengths and weaknesses of each method. Environmental and spatial drivers behind the observed compositional patterns are also considered.

Table 4.1. Classification of termite functional groups and respective feeding substrates within tropical rain forests. Modified from Donovan et al. (2001) and Inward et al. (2007).

Functional group	Feeding substrate
FGI	Sound wood
FGII	Wood and leaf litter
FGIIF	Wood and leaf litter on which fungi are grown and harvested (Macrotermitinae only, not found in South America)
FGIII	Organic material-rich soil and humus, with visible plant structures
FGIV	Mineral soil with no visible plant structures (true soil-feeding termites)

4.2. Methods

4.2.1. Study site

Sampling was conducted in a lowland old-growth tropical forest in Tambopata National Park, Peru (12˚49.434'S, 069˚15.791'W). The site (approximately 100 ha) is adjacent to the Tambopata river at an average elevation of 190 m with a mean annual temperature of 24.4˚C and a mean annual rainfall of 1900 mm (Malhi et al., 2014). Sampling took place in the dry season from June to August in 2011. Six plots were marked out in areas that represented the mosaic structure of naturally occurring tree fall gaps and dense canopy. To ensure the presence of soil-feeding termites, plots were deliberately chosen to be in areas with high soil clay content as this benefits the galleries that soil-feeding termites construct and inhabit.

4.2.2. Sampling

4.2.2.1. Plots and sampling methods

Sampling took place in six replicated rectangular plots (50 m × 70 m) spaced approximately 300 m apart (Fig. S4.1). Each plot was divided into seven parallel (50 m × 10 m) sections, in four of which two standard sampling protocols were conducted: the Transect Method (TM) and the Quadrat Method (QM). Each sampling method was conducted in two sub-plot sections spaced 30 m apart (Fig. S4.1).

The transect method (TM) was used to estimate termite species density (species richness per transect), using two half standardised belt transects (100 m × 2 m) (Jones and Eggleton, 2000; Davies et al., 2003b) located 30 m apart in each plot. Each transect was divided into twenty 5 m × 2 m sections in which active searching for termites took place for one person-hour (sampling by one person for an hour), using twelve scrapes (12 cm × 12 cm × 5 cm soil pits) and by inspection of all dead wood, nests and runways. The total number of

encounters for each species was recorded as a measure of relative abundance (as specified in Jones and Eggleton (2000)). Using the TM, a total of 6 transects and 1200 m^2 were sampled over a total period of 120 hours. Species density, absolute abundance and biomass were estimated using a standardised quadrat sampling protocol (QM) (Eggleton et al., 1996; Dahlsjö et al., 2014). These estimates are based on sampling of termites in ten 2 m × 2 m systematically placed quadrats per plot (5 quadrats in each sub-section with each quadrat 5 m apart). All worker termites that were encountered in dead wood (>20 mm diameter) were collected. Small branches were broken open, while larger logs were sampled with a saw before being split open to extract all, or a subsample of all, termites. Large logs (>20 cm diameter and >150 cm long) were sub-sampled by only collecting termites in 50% of the log, or in 25% of larger logs or trees. This may have underestimated the abundance of termites in some logs while it may have overestimated the abundance in others. Additionally, all termites in one 25 cm × 25 cm × 10 cm depth soil pit in the centre of each quadrat were collected. A total of 60 quadrats and 240 m^2 were sampled using the QM.

4.2.2.2. Environmental variables

Soil temperature and moisture were measured using a probe thermometer and a Delta-T theta probe type ML2x, Delta-T Inc., Cambridge, UK, respectively, at a depth of 5 cm once in each quadrat. One soil sample was collected from each quadrat (60 sampled in total), at a depth of 5 cm, for chemical analysis of carbon (C) and nitrogen (N). Total soil C and N content were analysed using a Thermo Finnigan Flash Elemental Analyser 1112 at the Imaging and Analysis Centre (IAC) at the Natural History Museum (NHM) in London. The plot coordinates (latitude and longitude) were estimated with a GPS in the field and used to collect plot specific elevation data from Google Earth. The distance from each plot to the main river and the distance to the lake in the study area were measured using the 'ruler' tool in Google Earth.

4.2.2.3. Spatial variables

The spatial variables included GPS data for latitude (x) and longitude (y) from each of the plots. The higher order components of the cubic trend surface regression (i.e. x^2, xy, y^2, x^3, x^2y, xy^2, y^3) that are used on larger spatial scales (Legendre, 1990) were redundant in this study due to the small scale approach (within site). The coordinates were converted into decimal degrees before analysis for compatibility purposes with CANOCO (version 5).

4.2.3. Identification

Termites were identified by the first author (CALD) at the Soil Biodiversity lab at the Natural History Museum (NHM), London, UK (see Table S1 for full species list). Termites with soldier castes were identified to genus using a key to Neotropical genera (Constantino, 2002) and to species using available keys (e.g for *Neocapritermes* see Krishna & Araujo (1968)) and the collection at the NHM. Soldierless termites were identified to genus and species level with an unpublished key to the Apicotermitinae of the Guyana Shield (unpubl. data) which features gut morphology and enteric valve structures (Hernández, L. M. unpubl. data). When only workers of termites with a soldier caste were found (soldiers absent from the sample but present within the species), these were identified by comparing enteric valve structures and head widths.

4.2.4. Data analyses

Data from the quadrats within each plot (QM only) were analysed using a split-plot design and pooled to make them directly comparable with the TM. The proportion of known species captured with the TM and QM in Peru compared with data from Malaysia (Eggleton et al., 1999) and Cameroon (Eggleton et al., 1996) was examined using ANOVA and post hoc Tunkey HSD tests (R, version 2.15.3). Species turnover was calculated among plots for data

collected with both the TM and the QM using Bray-Curtis similarity (BCS), calculated by subtracting the Bray-Curtis dissimilarity (BCD) measure from one (1 - BCD = BCS). The BCS was used instead of BCD as it is an easier index to interpret. 0 (zero) means that the plots do not share any common species while 1 (one) means that the plots have the same species composition. Analyses were conducted using the *bray* method in the *vegdist* command in R (version 2.15.3). The *rarefaction* method in the *specaccum* command (vegan) in R was used to generate species accumulation and standard deviation values. The values were used to visualise the effectiveness of estimating species diversity with the two sampling methods (TM and QM) across plots (area) and over time (person hours).

For the QM, two initial Monte Carlo Canonical Correspondence Analysis (CCA) permutation analyses (Lepš and Šmilauer, 2003) were conducted in order to test which environmental and spatial variables were significantly associated with species compositional data (at the plot level) in wood and soil separately in CANOCO (version 5). Due to potential sampling errors (no temporal replication of temperature measurements and potential low accuracy using distance measurements in Google Earth), only variables that were highly significant (≤ 0.01) were included. As the environmental and spatial variables were collected in the quadrats it was not possible to do these analyses using the TM data.

Variation partitioning analyses (Lepš and Šmilauer, 2003) were conducted using species composition in wood and soil and the significant environmental and spatial variables identified with the Monte Carlo analyses of the QM data. The proportion of the variance that each environmental and spatial variable explained were examined using a split plot CCA analysis (a constrained, unimodal ordination method) with log-transformed response variables and hierarchical permutation parameters for species composition in wood and soil separately (CANOCO, version 5). The effect of elevation and soil carbon content in each plot

on species diversity was examined using ANOVA (R, version 2.15.3) and analysed at the plot level.

4.3. Results

4.3.1. Comparison of sampling regimes

In total 94 species were found in the Peruvian lowland rain forest site using both the TM and QM (Table S4.1). Neither of the sampling methods yielded all species found in the site, although the addition of previously unsampled species by the TM was greatly reduced at the end of the study (Fig. 4.1). The efficiency of the two sampling methods differed with the TM capturing ~85% of the total number of species collected (Table 4.2) while the QM captured ~69% (Table 4.2). The efficiency of the TM in this study was significantly higher than the efficiency of the TM in methodologically similar studies in Cameroon (Tukey HSD *post hoc*: $P = 0.03$) and Malaysia (Tukey HSD *post hoc*, $P = 0.02$) (Table 4.2), while the proportion of species captured with the QM in Peru did not differ significantly from the proportion of the termite populations captured with the QM in Cameroon and Malaysia (ANOVA, $P > 0.05$).

In Peru, species diversity within each of the functional groups was similar using the TM and QM for all groups except for humus-feeding (FGIII) termites (refer to Table 4.1 for functional group terminology) with the number of species collected using the TM being FGI = 4, FGII = 15, FGIII = 42, FGIV = 14 and with the QM being FGI = 1, FGII = 14, FGIII = 32, FGIV = 15. Twelve additional species of humus-feeding termites were encountered using the TM compared with the QM. A total of 75 species and 16 genera were collected with the TM over 120 person-hours (20 person-hours per plot) (Fig. 4.1) with mean (± SE) termite species richness per transect of 43 ± 1.7 spp. The mean species similarity index among plots was BCS = 0.56 ± 0.017, where 1 is complete similarity (Table 4.3).

Using the QM a total of 62 species and 15 genera were collected over 360 person-hours (~ 60 person-hours per plot) (Fig. 4.1). The mean (± SE) termite species richness per plot (10 quadrats) was 24.7 ± 2.7 sp, while termite abundance and biomass collected with the QM were 130 ± 39 indv m^{-2} and 0.35 ± 0.10 g m^{-2} respectively. The species similarity indices in soil and wood among quadrats (within plots) were very low with mean similarity in soil being BCS = 0.02 ± 0.01 and in wood BCS = 0.02 ± 0.008. These low similarity values suggest that termites are very patchily distributed at the quadrat level. At the plot level the mean similarity of species composition among plots was higher with BCS 0.18 ± 0.025 (Table 4.3), although still much lower than the similarity found in the TM data.

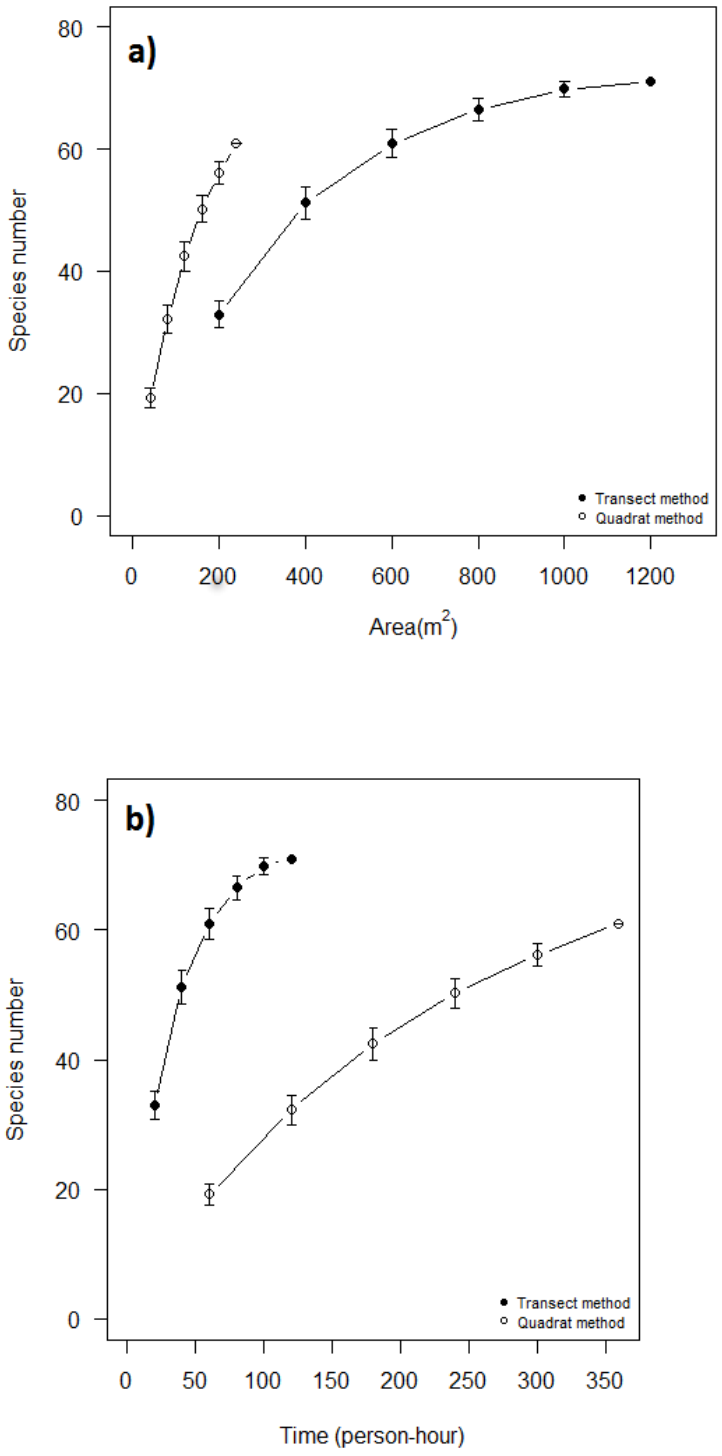

Figure 4.1. Rarefaction curves for species accumulation (± SD) across (a) area (m^2) and (b) over time comparing the number of species collected with the transect and quadrat methods. Time is expressed in person-hours i.e. sampling by one person for an hour.

Table 4.2. Species richness sampled with the TM and the QM from three forest sites in Peru, Malaysia and Cameroon. The proportion of the total fauna sampled with the two sampling regimes is based on the total number of known species from available records (Cameroon and Malaysia) and field sampling as described in this study (Peru).

Sampling method	Species sampled	Total known species	Proportion of total fauna (%)
Transect Method			
Tambopata, Peru (transect 1)	47	90*	52.2
Tambopata, Peru (transect 2)	44	90*	48.9
Tambopata, Peru (transect 3)	46	90*	51.1
Tambopata, Peru (transect 4)	35	90*	38.9
Tambopata, Peru (transect 5)	43	90*	47.8
Tambopata, Peru (transect 6)	43	90*	47.8
Danum Valley, Malaysia (transect 1)	31	93#	34.4
Danum Valley, Malaysia (transect 2)	33	93#	35.5
Mbalmayo, Cameroon (transect 1)	46	136ˣ	33.8
Mbalmayo, Cameroon (transect 2)	53	136ˣ	39.0
Quadrat Method			
Tambopata, Peru (plot 1, 10 quadrats)	24	90*	26.7
Tambopata, Peru (plot 2, 10 quadrats)	19	90*	21.1
Tambopata, Peru (plot 3, 10 quadrats)	20	90*	22.2
Tambopata, Peru (plot 4, 10 quadrats)	21	90*	23.3
Tambopata, Peru (plot 5, 10 quadrats)	37	90*	41.1
Tambopata, Peru (plot 6, 10 quadrats)	27	90*	30.0
Danum Valley, Malaysia (plot 1, 20 quadrats)	29	93#	30.2
Danum Valley, Malaysia (plot 2, 20 quadrats)	28	93#	30.1
Mbalmayo, Cameroon (plot 1, 10 quadrats)	30	136ˣ	22.1
Mbalmayo, Cameroon (plot 2, 10 quadrats)	36	136ˣ	26.5

*This study, see appendix Table S4.1.

#(Eggleton et al., 1997, 1999).

ˣEggleton et al., (1995, 1996); Jones & Eggleton, (2000).

Table 4.3. Bray-Curtis similarity results for species composition collected with the quadrat method (**bold**) and the transect method. 0 (zero) means that the plots (A-F) do not share any common species while 1 (one) means that the plots have the same species composition.

		Quadrat					
		A	B	C	D	E	F
Transect	A	--	**0.06**	**0.03**	**0.22**	**0.24**	**0.20**
	B	0.42	--	**0.17**	**0.31**	**0.20**	**0.29**
	C	0.52	0.48	--	**0.06**	**0.05**	**0.12**
	D	0.5	0.55	0.59	--	**0.28**	**0.22**
	E	0.54	0.52	0.62	0.62	--	**0.27**
	F	0.57	0.52	0.58	0.65	0.66	--

4.3.2. Environmental variables

Species composition in soil was significantly associated with soil temperature, soil carbon content, elevation and the distance to the main river (Fig. 4.2, Table 4.4). Temperature had a significantly positive association with *Anoplotermes-group* sp. AD, *Anoplotermes pacificus* and *Anoplotermes-group* sp. HE while it had a negative association with *Embiratermes neotenicus*. *Longustitermes manni* and *Anoplotermes* sp. V had a significantly negative association with the distance from the river. Elevation and soil carbon content were not significantly associated with particular species, however, the number of species was significantly higher (ANOVA, F = 9.1, P = 0.04) in the soil in plots with higher carbon which may have had an effect on species composition.

In wood, species composition was significantly associated with soil temperature, soil moisture, elevation, distance to the main river and distance to the lake (Fig. 4.2, Table 4.4). *Cylindrotermes brevipilosus, Cylindrotermes caata, Labiotermes pelliceus, Neocapritermes talpa* and *Nasutitermes* sp. I had a significantly negative association with temperature while the association with temperature was significantly positive for *Embiratermes neotenicus*. Both *Cylindrotermes caata* and *Labiotermes pelliceus* had a significantly positive association with moisture and *Nasutitermes* sp. III had a significantly negative association with elevation. *Atlantitermes snyderi* and *Anoplotermes* sp. F had a positive association with the distance from the river while *Anoplotermes-group* sp AD, *Labiotermes longilabius, Nasutitermes* sp. II, *Nasutitermes* sp. III *and Nasutitermes* sp. VIII had a positive association with the distance from the lake.

Among the spatial variables, *x* (latitude) was the only variable significantly associated with species composition in soil while *y* (longitude) was associated with species composition in wood (Fig. 4.2, Table 4.4). Variation partitioning showed that all environmental variables put together explained a larger proportion of the termite species community patterns in both soil and wood than the spatial variables (Table 4.5).

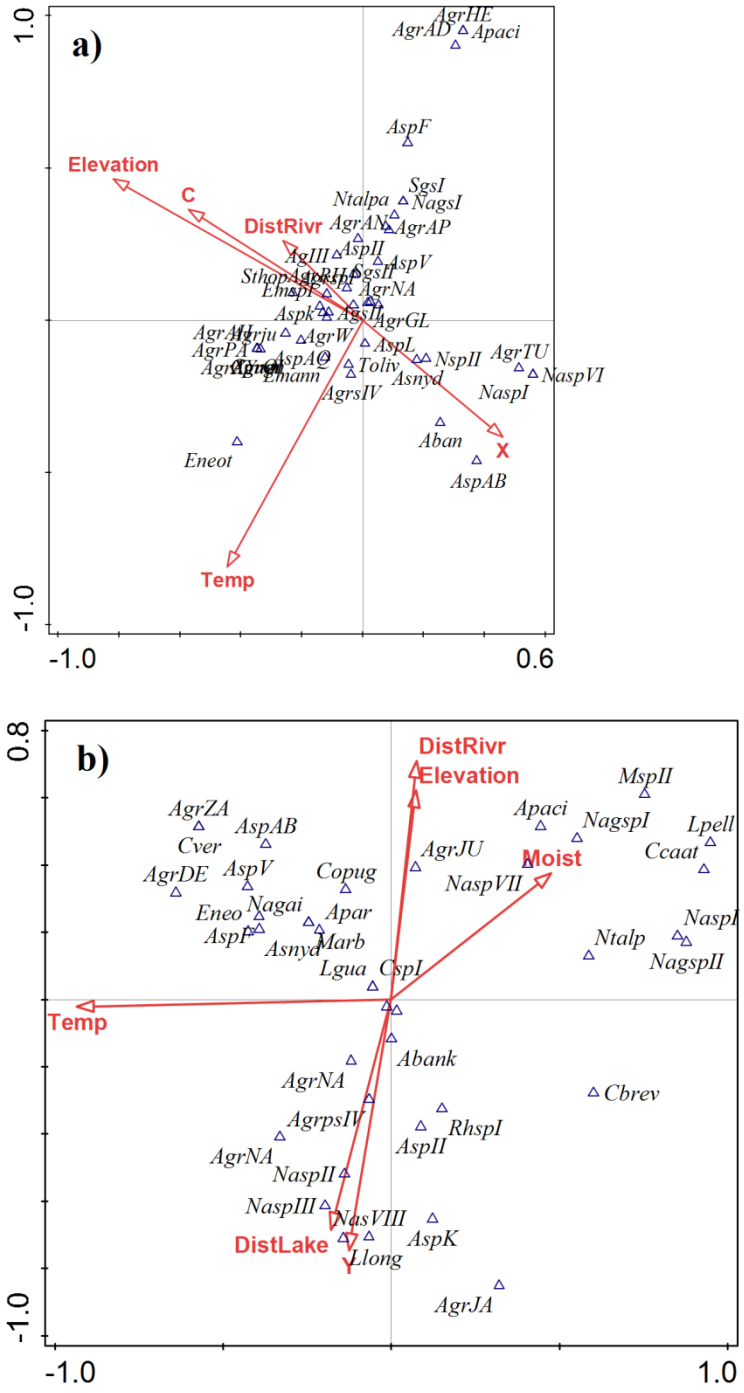

Figure 4.2. Canonical Correspondence Analyses (CCA) ordination plots for species composition in (a) soil and (b) wood and the environmental and spatial variables with a significant effect on the species composition. DistRivr = distance from the plot to the Madre de Dios river, DistLake = distance from the plot to the Cococha lake, Elevation = the elevation of the plot, Moist = soil moisture, Temp = soil temperature, C = soil carbon content (%), X = latitude, Y = longitude. Please, refer to Table S1 for complete species names.

Table 4.4. Canonical Correspondence Analysis (CCA) permutation test results examining the association between species composition in soil and wood with environmental and spatial variables. Data were collected using the quadrat method. *variables that were highly significant (i.e. ≤0.01) and used in the partitioning of variation analyses.

	Species composition in soil			Species composition in wood		
Conditional effects	Explains %	Pseudo-F	P	Explains %	Pseudo-F	P
Environmental variables						
Temperature	3.8	2.3	0.006*	4.5	2.8	0.003*
Moisture	2.2	1.5	0.17	3.0	1.9	0.005*
Elevation	4.7	2.9	0.002*	3.2	2.0	0.002*
Distance to river	2.8	1.8	0.01*	3.7	2.3	0.002*
Distance to lake	2.4	1.5	0.014	2.0	1.9	0.005*
Nitrogen	3.0	1.9	0.046	--	--	--
Carbon	2.9	1.9	0.002*	--	--	--
Spatial variables						
Latitude	4.6	2.8	0.006*	2.9	1.8	0.047
Longitude	2.5	1.5	0.06	3.6	2.2	0.002*

Table 4.5. Canonical Correspondence Analysis (CCA) variation partitioning of environmental and spatial data and the interaction between the two factors for termite species composition in wood (W) and soil (S). Data were collected using the quadrat method.

	Variation (adj)		% explained		% of all		Df		Mean square	
Fraction	W	S	W	S	W	S	W	S	W	S
Environmental	0.80	0.57	78.4	65.8	7.2	5.6	5	4	0.33	0.29
Spatial	0.06	0.18	6.3	20.5	0.6	1.8	1	1	0.23	0.32
Environmental vs spatial	0.16	0.11	15.3	13.8	1.4	1.2	--	--	--	--
Total explained	0.86	0.69	100.0	100.0	9.2	8.6	6	5	0.34	0.33
All variation	11.11	10.04	--	--	100.0	100.0	59	59	--	--

4.4. Discussion

4.4.1. Comparison and effectiveness of the transect and quadrat methods

The proportion of the total number of known species encountered in each site using the TM was significantly higher in Peru compared with the broadly comparable studies in Malaysia and Cameroon. This may be due to the augmentation of TM and QM by casual sampling in the latter studies. The total number of species (i.e. the site pool) may therefore have been underestimated for the Peruvian site. However, in the Peruvian work the equivalent of one standard transects (two spatially separated half-transects) were run per plot, and this may have mitigated the autocorrelation effects known to be a disadvantage of transect methods (Bignell, 2009). Additionally, as sampling in Peru was restricted to breast height microhabitats such as suspended dead wood were not sampled which may have reduced the potential of finding some species e.g. Kalotermitidae known to be associated with this microhabitat. The significant difference in the proportion of known species captured with the TM among the three globally separated sites may therefore be due to undersampling of the total species pool. This suggests that the efficiency of the TM and QM are similar among sites and that the two sampling protocols, therefore, provide robust methods for estimating termite species diversity.

In Peru, the similarity of the species composition among the plots was much higher when using the TM (56%) compared with the QM (18%), although, presumably the same species pool was sampled. The humus-feeding termites, that were the most abundant in the site, were particularly better represented by the TM. This may be due to the presence of humus-feeding termites in specialised microhabitats, such as the suspended soil in understory palms (Davies et al., 2003b), that may be better represented with the TM as it covers a greater area and a larger number of points (12 scrapes per section) per plot.

The TM and QM may be used to estimate termite abundance although the TM provide relative abundance (encounters of species) rather than absolute abundance (indv m^{-2}) that the QM provides. Relative abundance may be useful when comparing transects and total encounters across different regions or gradients of land use intensity (Eggleton et al., 1995, 2002) or altitude (Palin et al., 2010) and may serve as a proxy for species abundance; however absolute abundance, which requires exhaustive sampling of soil and woody materials, is still required to provide a fuller understanding of the role of termites in ecosystem functioning, since process rates are assumed to be proportional to biomass. The TM is logistically preferable (Eggleton and Bignell, 1995; Lawton et al., 1998) and has therefore been much more widely deployed across the humid tropics (see Davies et al., 2003a for a summary) while the QM is less well represented in the literature (Eggleton et al., 1996, 1999; Dahlsjö et al., 2014). Among the advantages of the TM is a relatively rapid sampling time of 20 person-hours per transect, a larger sampling area (200 m^2 per transect) and greater efficiency at capturing a larger proportion of the termite population (Table 4.6). Against this, the QM provides absolute abundance and biomass data and reduces autocorrelation effects, although high variance at the point scale complicates the statistical presentation and treatment of results. Due to the smaller quadrat sampling area (10 quadrats = 40 m^2) the encounter of termite species with patchy distributions may be lower than transects that include a larger sampling area and explore a larger variety of microhabitats. A list of the encounters, abundance and biomass of all species collected in the site in Peru is given in the supplementary material (Table S4.1).

Table 4.6. Comparison of the data collected with the transect method (TM) and quadrat method (QM).

	Sampling time/plot (person-hours)	Species density	Absolute abundance	Biomass	Global data set available	Local data set available
TM	20	✓	×	×	✓	✓
QM	~60	✓	✓	✓	×	✓

4.4.2. Environmental and spatial drivers of species composition patterns

4.4.2.1. Environmental variables

The total proportion of the termite species compositional patterns explained by individual environmental variables accounted for a larger proportion of the variance than when the environmental variables were analysed together with variation partitioning. The same was true for the spatial variables suggesting that some of the variables may have explained similar species patterns. Individually, the environmental variables shown to be most important for termite species composition in soil and wood were soil temperature, elevation and distance to the main river. Canopy structure, may have had an effect on the quadrat soil temperature microclimate (Gehlhausen et al., 2000; Szarzynski and Anhuf, 2001) as gaps in the canopy from natural tree falls, may have increased the temperature and reduced the 'buffer' effect that the canopy provides (Chen et al., 1999; Davies et al., 2003b; Jones et al., 2003). In soil, the termite species abundances of four humus-feeding (FGIII) species were significantly associated with temperature with the majority of humus-feeders showing a positive trend. In contrast to the present results, studies of termite assemblage structure along disturbance gradients where temperature and canopy cover are key variables, show that soil-feeding termites decline in areas associated with higher soil temperature (Eggleton et al., 1999, 2002;

Bignell and Eggleton, 2000; Guil et al., 2008; Vasconcellos et al., 2010). Although a higher number of species were encountered in plots with the lowest temperatures, the difference between plots was not significant. As temperature was only sampled once in each of the quadrats the data may not be fully representative of the natural fluctuations within the plots.

The elevation of the plot and the distance to the main river may both be related to the height of the water table, soil type, and the flooding of the plots. Mound building termites have been shown to build their nesting structures on higher land e.g. on top of soil mounds, inactive termite mounds (de Oliveira-Filho, 1992) or nutrient poor crests in dry-savannah habitats (Davies et al., 2014). It has also been shown that mound density is higher on land at higher elevation in relation to the surrounding area (Meyer et al., 1999; Davies et al., 2014). Elevation was significantly associated with the abundance of *Nasutitermes* sp. III (FGII), which decreased with elevation. The predominantly arboreal nesting genus *Nasutitermes* are dominant in South American floodplain forests (Mill, 1982; Martius, 1994; Martius et al., 1994) which may be due their consequent resilience to flooding.

Two species each in soil and wood (all FGIII) were shown to be significantly associated with the distance from the river. As seasonal inundation may destroy their nesting galleries, humus-feeding termites in the soil were expected to increase away from the river. However, species in soil were shown to have a negative relationship with the distance from the river while the association was positive in wood. These results suggest that the four humus-feeding species may have been principally affected by other factors such as soil type, which showed high heterogeneity throughout the forest. Species composition in soil was also affected by soil C content that may be linked to the proportion of plant-derived matter in the soil. No particular species were associated with soil carbon content, however, the number of species in plots with high carbon were significantly higher than in plots with low carbon (ANOVA, $F = 9.1$, $P = 0.04$). The distance from the lake showed a positive association with

particularly *Nasutitermes* (FGII) species which may be due to habitat heterogeneity. Plot heterogeneity may have affected nesting patterns due to spatial density and quality of dead organic tissues leading to higher site-level diversity of functional groups (Hasemann and Soltwedel, 2011) and species (see Eggleton 2011).

4.4.2.2. Spatial variables

Spatial variables explained a fifth of the variation in species composition in soil while the interaction of environmental and spatial variables explained a higher proportion of species composition in wood than the spatial variables alone. Although the spatial variables do not account for a large proportion of the factors affecting termite species composition they may reflect variables that were not sampled and may be related to the geography and topography of the plots. While *x* (latitude) was the only spatial variable that affected species composition in soil, *y* (longitude) alone had a significant relationship with species composition in wood.

4.4.3. Conclusion

The TM and QM have different merits which were highlighted by comparison of the two methods by sampling the same assemblage. While the QM appeared to undersample high diversity feeding-groups such as the humus-feeding termites the TM obtained a higher number of species from the same species pool. Spatial replication of the TM within the site provided insights into the difference in species composition among plots that is likely to change with environmental variables. Replication of these sampling methods is therefore recommended to ensure comprehensive understanding of species patterns within the same land use site. The spatial scale of this study may have affected the results due to the relative proximity of plots (i.e. replicated sampling within the same, contiguous, land use); however, the understanding of the impact of environmental and spatial drivers on termite species patterns identified in this study provide better understanding of how termite assemblages may

be affected by climate or habitat change and the potential impact this may have on ecosystem processes.

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4.7 Supplementary material

Table S4.1 Species list of encounters (encounters/transect), abundance (individuals/m^2) and biomass (mg/m^2) found in Peru. Classifications follow Krishna et al. 2013[*] and Davies et al. 2003[#].

	Abbreviated name used in Fig. 2	FG	Species encounters (TM) (encounters/ transect)	Abundance (QM) (individuals/m^2)	Biomass (QM) (mg/m^2)
RHINOTERMITIDAE					
Rhinotermes sp. I	RhspI	I	1	0.7	2.6
Rhinotermes sp. II		I	0.5	-	-
Heterotermes sp. I		I	1.3	-	-
Heterotermes sp. II		I	0.7	-	-
TERMITIDAE					
TERMITINAE					
Microcerotermes arboreus	Marb	II		0.1	0.4
Microcerotermes sp. I	MspI	II	2.3	-	-
Microcerotermes sp. II	MspII	II	0.7	0.3	0.8
Neocapritermes sp. I	NspI	II	0.3	-	-
Cylindrotermes brevipilosus	Cbrev	II	0.5	0.8	2.2
Cylindrotermes caata	Ccaat	II	-	1.1	3.0
Crepititermes verruculosus	Cver	III	0.2	2.8	5.2
Crepititermes sp. III	CrspIII	III	1.3	-	-
Neocapritermes talpa	Ntalpa	III	4.2	8.5	29.0
SYNTERMITINAE					
Cornitermes pugnax	Copug	II	0.2	24.9	149.5
Embiratermes neotenicus	Eneo	III	4.8	17.1	55.5
Embiratermes sp. I	EspI	III	0.7	5.6	14.9
Embiratermes sp. II		III	0.2	-	-
Embiratermes sp. III		III	4.5	-	-
Embiratermes sp. IV		III	2.2	-	-
Embiratermes sp. V		III	0.2	-	-
Armitermes-grp sp. I	ArgrsI	III	-	3.2	9.3

Armitermes-grp sp. II	ArgrsII	III	-	0.07	0.2
Armitermes-grp sp. III	ArgrsIII	III	-	6.9	15.5
Armitermes-grp sp. IV	ArgrsIV	III	-	0.004	0.009
Macuxitermes. sp. I		III	0.2	-	-
APICOTERMITINAE					
Anoplotermes banksi	Aban	III	1.8	15.7	31.8
Anoplotermes pacificus	Apaci	III	2.3	1.2	3.2
Anoplotermes turricola	AspTUR	III	0.3	-	-
Anoplotermes sp. K	AspK	III	6.2	54.9	111.3
Anoplotermes sp. F	AspF	III	0.5	14.9	28.0
Anoplotermes sp. V	AspV	III	14.7	19.2	39.0
Anoplotermes sp. L	AspL	III	2.3	39.7	92.0
Anoplotermes sp. AB	AspAB	III	3.3	14.1	30.0
Anoplotermes sp. BU	AspBU	III	4.5	-	-
Anoplotermes sp. AQ	AspAQ	III	1.7	9.6	20.8
Anoplotermes sp. II	AspII	III	0.5	5.1	11.0
Anoplotermes-grp. sp. DE	AgrDE	III	2	5.5	16.7
Anoplotermes-grp. sp. JU	AgrJU	III	2.5	6.3	13.6
Anoplotermes-grp. sp. NA	AgrNA	III	11	65.9	143.1
Anoplotermes-grp. sp. AM	AgrAM	III	0.2	-	-
Anoplotermes-grp. sp. AD	AgrAD	III	4.5	5.9	17.9
Anoplotermes-grp. sp. IN	AgrIN	III	0.8	-	-
Anoplotermes-grp. sp. TUC	AgrTUC	III	0.7	34.9	72.4
Anoplotermes-grp. sp. XY	AgrXY	III	3.5	7.5	19.4
Anoplotermes-grp. sp. AP	AgrAP	III	3.7	8.0	25.5
Anoplotermes-grp. sp. AH	AgrAH	III	2	1,9	3.8
Anoplotermes-grp. sp. AG		III	1.8	-	-
Anoplotermes-grp. sp. AO		III	0.5	-	-
Anoplotermes-grp. sp. FR		III	0.8	-	-
Anoplotermes-grp. sp. AN	AgrAN	III	1.5	8.3	17.1
Anoplotermes-grp. sp. GL	AgrGL	III	3	4.3	12.3
Anoplotermes-grp. sp. HE	AgrHE	III	0.8	0.8	2.1
Anoplotermes-grp. sp. RH	AgrRH	III	10	20	43.4
Anoplotermes-grp. sp. YU		III	0.7	-	-
Ruptitermes sp. A		III	0.3	-	-
Ruptitermes sp. B		III	0.7	-	-
Longustitermes manni	Lmann	IV	12.8	70.7	102.2

Anoplotermes parvus	Apar	IV	3.7	10.0	21.6
Anoplotermes-grp. sp. JA	AgrJA	IV	0.3	8.2	17.9
Anoplotermes-grp. sp. ZA	AgrZA	IV	0.3	0.04	0.07
Anoplotermes-grp. sp. W	AgrW	IV	5.8	1.3	2.9
Anoplotermes-grp. sp. OI	AgrOI	IV	0.5	0.8	1.2
Anoplotermes-grp. sp. AC		IV	4.7	-	-
Anoplotermes-grp. sp. PA	AgrPA	IV	2.5	27.2	74.8
Tetimatermes oliveirae	Toli	IV	2	8.8	22.9
NASUTITERMITINAE					
Nasutitermes gaigei	Nagai	II	-	0.6	1.7
Nasutitermes-grp. sp. I	NagsI	II	1.2	28.2	136.7
Nasutitermes-grp. sp. II	NagsII	II	1.7	1.3	4.4
Nasutitermes-grp. sp. III	NagsIII	II	0.5	12.2	8.1
Nasutitermes-grp. sp. IV	NagsIV	II	0.2	0.08	0.2
Nasutitermes-grp. sp. V	NagsV	II	-	0.6	1.8
Nasutitermes-grp. sp. VI	NagsVI	II	1	14.8	131.7
Nasutitermes-grp. sp. VII	NagsVII	II	1	0.6	1.9
Nasutitermes-grp. sp. VIII	NagsVIII	II	-	0.8	2.5
Nasutitermes-grp. sp. IX		II	0.7	-	-
Nasutitermes-grp. sp. X		II	0.2	-	-
Nasutitermes-grp. sp. XI		II	0.5	-	-
Nasutitermes-grp. sp. XII		II	0.5	-	-
Nasutitermes-grp. sp. XIII	NagsXIII	II	-	0.04	0.1
Nasutitermes-grp. sp. XIV		II	0.8	-	-
Subulitermes thompsonae	Stho	III	0.8	0.08	0.1
Atlantitermes guarinim	Agua	III	0.5	2.9	5.0
Atlantitermes snyderi	Asny	III	-	5.8	10.0
Convexitermes sp. I		IV	0.2	-	-
Convexitermes sp. II		IV	0.7	-	-
Subulitermes-grp sp. I	SgsI	IV	0.2	0.3	0.9
Subulitermes-grp sp. II	SgsII	IV	1.3	1.1	2.3
Cortaritermes sp. I	CspI	IV	-	0.1	0.1
Labiotermes guasu	Lgua	IV	-	0.004	0.02
Labiotermes longilabius	Llong	IV	-	0.2	1.1
Labiotermes pelliceus	Lpell	IV	-	0.9	2.6
Labiotermes leptothrix		IV	1.5	-	-

*Krishna, K., Grimaldi, D. A., Krishna, V. and Engel, M. 2013. Treatise on the Isoptera of the world. *Bulletin of the American Museum of Natural History*. **4**: 973-1495.

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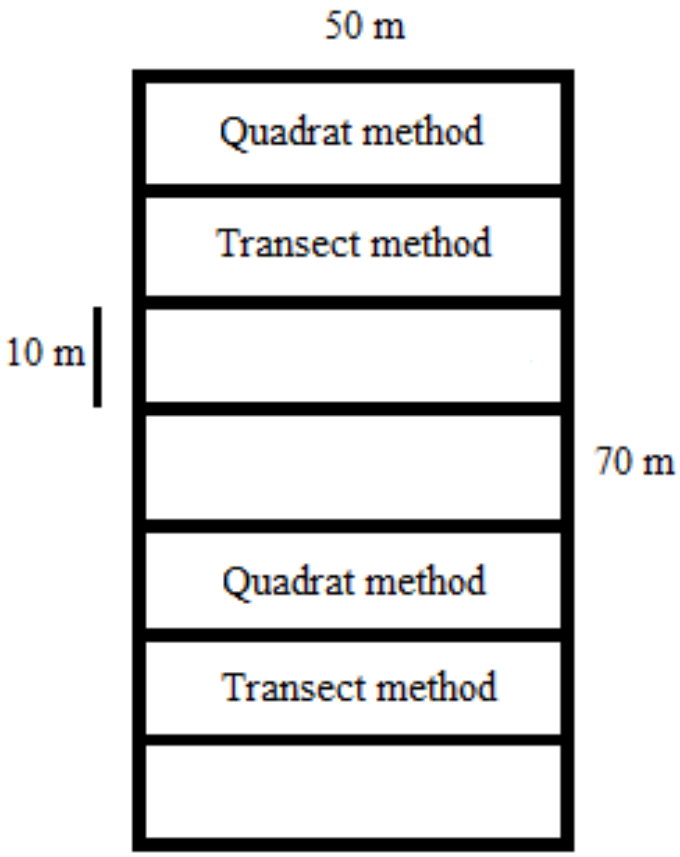

Figure S4.1. Plot layout. The quadrat method and transect method were divided into two sub-sections 30 m apart in each plot.

CHAPTER V

First comparison of quantitative estimates of termite biomass and abundance reveal strong intercontinental differences

Overview

In chapter IV I discussed the drivers of the composition of termite species in a lowland tropical rain forest site in Peru and the strengths and weaknesses of the two sampling methods (quadrat and transect). In this chapter I use the biomass and abundance data collected with the quadrat method to make the first intercontinental comparison of termite biomass and abundance by complementing the already published data from Cameroon and Malaysia.

Cecilia Dahlsjö wrote this paper with comments from Paul Eggleton, Yadvinder Malhi, Kate Parr, David Jones and Patrick Meir. Cecilia Dahlsjö collected all data from the Peruvian site with the help of Henry Siccos and Hugo Lopez. Data from Cameroon were collected by Paul Eggleton and published in Eggleton et al. (1996) and data from Sabah were collected by Homathevi Rahman. This chapter was published as a full paper in *Journal of Tropical Ecology* in March 2014. doi:10.1017/S0266467413000898

Paper details

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Abstract

Termite species and functional groups differ among regions globally (the functional-diversity anomaly). Here we investigate whether similar differences in biomass and abundance of termites occur among continents. Biomass and abundance data were obtained with standardised sampling in Cameroon, Malaysia and Peru. Data from Peru were original to this study, while data from Cameroon and Malaysia were compiled from other sources. Species density data were sampled using a standardised belt transect (100 × 2 m) while the biomass and abundance measurements were sampled using a standardised protocol based on 2 × 2-m quadrats. Biomass and abundance data confirmed patterns found for species density and thus the existence of the functional diversity anomaly: highest estimates for biomass and abundance were found in Cameroon (14.5 ± 7.90 g m^{-2} and 1234 ± 437 ind m^{-2}) followed by Malaysia (0.719 ± 0.193 g m^{-2} and 327 ± 72 ind m^{-2}) and then Peru (0.345 ± 0.103 g m^{-2} and 130 ± 39 ind m^{-2}). The biomass and abundance for each functional group were significantly different across the continental sites for most termite functional groups. Biogeographical distribution of lineages was the primary cause for the functional diversity anomaly with true soil-feeding termites dominating in Cameroon and the absence of fungus-growing termites from Peru. These findings are important as the biomass and abundance of functional groups may be linked to ecosystem processes. Although this study allowed for comparisons between data from different regions further comparable data are needed to enhance the understanding of the role of termites in ecosystem processes on a global scale.

5.1. Introduction

Termites (Blattodea: Termitoidae) are dominant invertebrate decomposers of dead organic matter in tropical and subtropical terrestrial regions (Bignell & Eggleton 2000). They are important ecosystem engineers that affect physical and chemical composition of soil through the breakdown and fixation of carbon and nitrogen, as well as the translocation of soil via the construction of mounds, tunnels and runways (Brussaard 1997, Jones *et al.* 1994, Jouquet *et al*. 2006, 2011). Termites feed on a range of dead organic plant-derived matter and have been classified into five functional groups depending on the humification (decomposition) of the substrate that they feed on (Donovan *et al*. 2001a, Inward *et al*. 2007) (Table 5.1).

At present we have a relatively good understanding of tropical termite diversity patterns through sampling of termite species density using a standardised transect protocol (Davies *et al.* 2003, Eggleton *et al.* 1999, Palin *et al.* 2010). Studies have shown that there is a clear difference in termite functional diversity among the main tropical rain-forest regions: for example, large-bodied soil-feeding termite lineages dominate in Africa (Davies *et al.* 2003, Eggleton *et al.* 1994), and Macrotermitinae (fungus-growing termites) are completely absent from South America (Aanen & Eggleton 2005, Davies *et al*. 2003, Eggleton *et al.* 1994, Jones & Eggleton 2011). These functional differences have been referred to as the 'termite functional diversity anomaly' (Davies *et al*. 2003). The functional diversity anomaly has been shown to exist even when different types of land (cleared and lacking canopy to old-growth forests) have been compared (Davies *et al.* 2003, Eggleton *et al.* 1994).

Table 5.1. Classification of termite functional groups and respective feeding substrates within tropical rain forests. Modified from Donovan *et al*. (2001a) and Inward *et al*. (2007).

Functional group	Feeding substrates
FGI	Sound wood
FGII	Wood and leaf litter
FGIIF	Wood and leaf litter (fungus-growers: Macrotermitinae only)
FGIII	Organic rich soil and humus, with visible plant structures
FGIV	Mineral soil with no visible plant structures (true soil-feeding termites)

Although data on density of termite species and variation among continents in key functional groups are important for our understanding of assemblage structure and ecosystem processes, we do not yet know exactly how biomass and abundance are distributed among species. Therefore, the documented differences in functional diversity among regions (Davies *et al*. 2003) need to be supplemented with biomass and abundance data if the impact of termites on ecosystem processes is to be quantified. However, comparable biomass and abundance data on termites are sparse (Bignell & Eggleton 2000, Eggleton *et al.* 1996, 1999; Jones & Eggleton 2011) because these data are exceptionally time consuming to collect. Combining data from the literature with newly collected data from Peru, our study is novel in that we provide the first preliminary data to test whether the termite functional anomaly is found also for biomass and abundance across the equatorial regions.

We compare biomass and abundance estimates across three equatorial tropical forest regions (Africa (Cameroon), south-east Asia (Malaysian Borneo), South America (Peru)) to investigate whether the functional diversity anomaly exists for biomass and abundance data within functional groups. We aimed to (1) compare species density data for functional groups

from the three study sites to confirm the existence of the functional diversity anomaly across our study areas, (2) compare biomass and abundance data for termite functional groups across the three sites, (3) explore the potential causes (termite evolutionary history or present day climate) of the uncovered differences, and (4) discuss the implications of these differences for ecosystem processes across the main tropical forest blocks.

5.2. Methods

5.2.1.Compilation of data

Biomass and abundance data from Cameroon and Malaysia were obtained from Eggleton *et al*. (1996) and Eggleton *et al*. (1999), respectively. Samples for the Peru data were obtained by CALD in 2011.

5.2.2. Study sites

Sampling was conducted in relatively undisturbed tropical rain-forest sites in Cameroon, Malaysia (Sabah, Borneo), and Peru. Full site details are provided in Table 5.2.

5.2.3. Sampling

In each site species density measurements (the number of species per square metre) were sampled using a standardised belt transect (100 × 2 m) (Eggleton *et al*. 1995, Jones & Eggleton 2000). Each transect was divided into twenty sections (5 × 2-m) in which termites from 12 soil pits (12 × 12 × 5 cm) and from all dead wood, nests and runways were collected for one person-hour. Four transects were sampled in Malaysia (Eggleton *et al*. 1999) and Cameroon (Eggleton *et al*. 1995) while six transects were sampled in Peru by CALD.

Sampling for biomass and abundance took place in four plots in Cameroon (two old-growth forest plots and two old regenerating forest plots), and six plots each in Malaysia

(three old-growth forest plots and three regenerating forest plots) and Peru (six old-growth forest plots). Non-old-growth forest plots were chosen to be as comparable as possible to old-growth forests. At all sites plots were chosen to represent the main forest type and to take into account the natural variability of vegetation structure. A standardised quantitative sampling protocol based on 2 × 2-m quadrats was used in all three study sites following Eggleton *et al*. (1996). Broadly, the same method was used across all sites with slight variation in soil pit volume, and size and number of quadrats (Table 5.2). The effect of the differences in sampling effort on species encounters were examined by species rarefaction curves. The rarefaction curves clearly showed that Cameroon had the highest species richness while Malaysia had the lowest species richness despite the low sampling effort in Cameroon and the high sampling effort in Malaysia (Figure 5.1). As these results did not affect the outcome of this study, all values were made comparable by scaling them to unit area (m^2). As this is the first time data from the Peruvian site has been published, a detailed account of the sampling methods is given below.

In Cameroon, four 30 × 20-m plots were created in old-growth and old regenerating forest. Termites from all dead wood in ten quadrats per plot were sampled as well as all termites in 20 × 20 × 50-cm soil pit in the centre of each quadrat.

In Malaysia, six 50 × 50-m plots were set-up in old-growth and two ages of regenerating forest. No significant composition or abundance differences were found between the forest types (Homathevi, unpubl. data).Termites were sampled in dead wood in 20 quadrats per plot. Termites in 30 × 30 × 25-cm soil pits in the centre of each quadrat were also sampled (see Eggleton *et al*. 1996 and Eggleton *et al*. 1999 for a more detailed description of the sampling methods in Cameroon and Malaysia).

In Peru, six 70 × 50-m plots were set-up at least 300 m apart. Each plot was divided into six subplots (10 × 50-m each) of which two in each plot were used for the surveys reported in this paper. Those were spaced 30 m apart. Ten 2 × 2-m quadrats, spaced 5 m apart, were placed in each plot and split between the two subplots, five quadrats in each. Within each quadrat, the total number of worker termites in all dead wood greater than 20 mm diameter were subsampled and extrapolated. Small branches were broken open while larger logs were subsampled with a saw before being split open to extract the termites. In addition, all termites were manually extracted from one soil pit (25 × 25 × 10-cm depth) in the centre of each quadrat. Termites were preserved in 70% alcohol and processed and identified at the Natural History Museum in London (NHM).

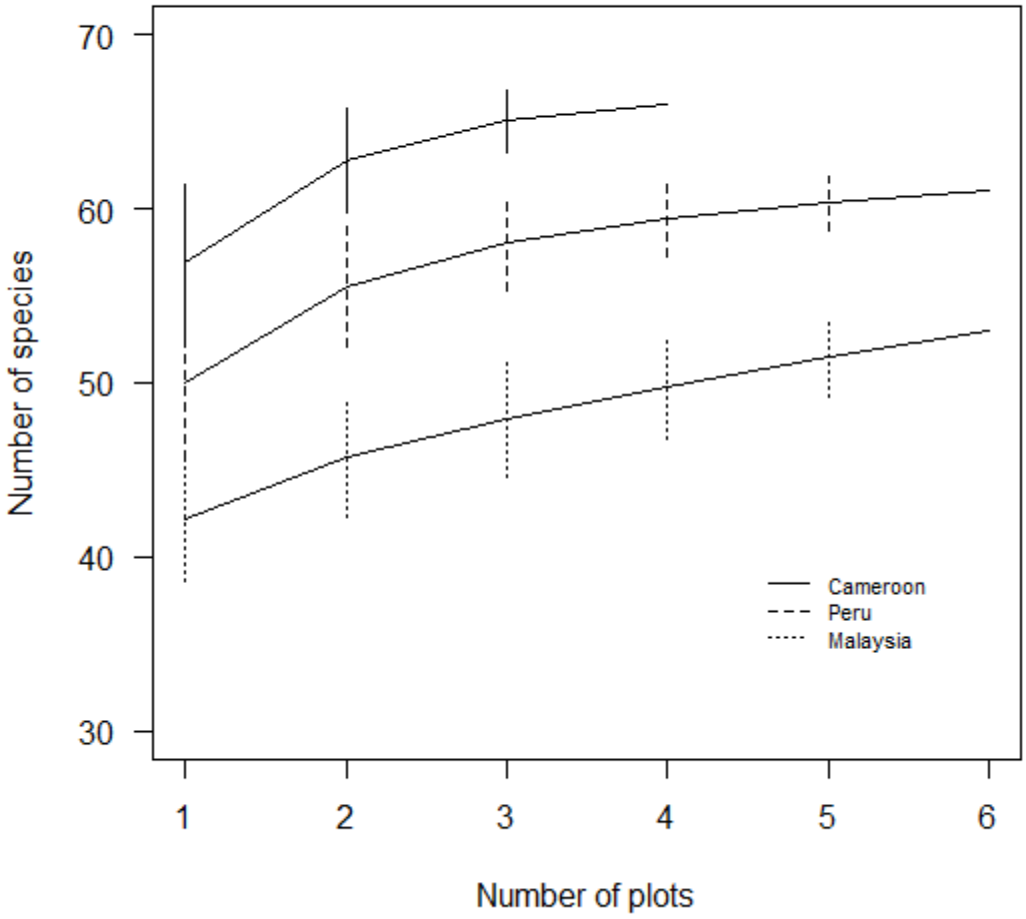

Figure 5.1. Species rarefaction curves (± SD) from Cameroon, Peru and Malaysia. Species richness data were collected in quadrats (2 × 2 m). Although Cameroon had the lowest number of plots it had the highest number of species. Malaysia with six plots and the highest number of quadrats (20 per plot) had the lowest number of species suggesting that Cameroon may have increased its dominance over Malaysia and Peru had the sampling effort been equal.

Table 5.2. Site descriptions and data sources. Many of the tropical rain forests in Africa are at a higher elevation than lowland forests on other continents as they are located on the central continental plateau (see Davies *et al.* 2003 and Eggleton *et al.* 2002 for examples of African forest site altitudes). It can therefore be argued that most African forests at an altitude similar to the one in Cameroon are considered lowland forests and therefore justifies the comparison of Cameroon with Malaysia and Peru.

Region	Lat	Long	Number of plots (plot size m^2)	Mean annual rainfall (mm^{-1})	Mean annual temp (C˚)	Altitude (m)	Forest type	Data source
Cameroon	3°31' N	11°25' E	4 (600)	1520	24.05	650	Tropical (old growth, old regenerating)	Eggleton *et al.* (1996)
Malaysia	4°58' N	117°48' E	6 (2500)	2700	26.7	100–150	Tropical moist (old growth, old and young regenerating)	Eggleton *et al.* (1999), Homathevi (unpublished)
Peru	12°49' S	69°16' W	6 (3500)	2272	24.6	190	Tropical moist (old growth)	This paper

5.2.4 Identification

Details of the identification methods for the Cameroonian and Malaysian termites are given in Eggleton *et al*. (1996) and Eggleton *et al*. (1999). Termites sampled in Peru were identified by CALD at NHM. Existing species names were given to as many of the specimens as possible. Where soldiers were present these were identified to genus with the key to Neotropical termite genera by Constantino (2002), and to species level with identification keys and the NHM collection. Where soldiers were absent, worker gut morphology (including the enteric valve structure) was compared with samples in NHM collection. Soldierless termites were identified to genus and species level with L.M. Hernández's (unpubl.) key to the Apicotermitinae of the Guiana Shield.

5.2.5. Functional group classification

Termites can be classified into five feeding groups by the level of 'humification' (decomposition) of the organic matter upon which they feed (Donovan *et al*. 2001a, Eggleton & Tayasu 2001). The groups range from wood-feeding to soil-feeding termites (Table 5.1). Wood-feeding termites in FGI feed at the top of the humification gradient and include all wood-feeding termites outside the Termitidae. All other feeding groups, including wood-feeding termites in FGII, fungus-growing termites in FGIIF, humus-feeding termites in FGIII and true soil-feeding termites in FGIV (Donovan *et al*. 2001a, Inward *et al*. 2007), are in the Termitidae. Only FGIIF use external fungi (*Termitomyces:* Basidiomycotina) for decomposition of organic matter and produce endogenous cellulases in the same way as other wood-feeding Termitidae. They also have, along with all other termites, a complex community of symbiotic gut bacteria, Archaea and protists (Hongoh 2010) which vary in composition and abundance with the degree of humification of the feeding substrate (Brauman *et al*. 2001).

5.2.6. Analysis

Biomass and abundance data were estimated for worker termites only as soldiers represented a small proportion of the total number of individuals. In the majority of the termite species in this study soldiers represented less than 5% of the individuals while 30%-40% of the species did not include soldiers at all (*Anoplotermes*-group). *Nasutitermes* (and other Nasutitermitinae) is the exception with approximately 25% of all individuals being soldiers (Vasconcellos & Moura 2010). The biomass and abundance measurements for *Nasutitermes* may therefore have been underestimated, however, this was favoured over the potential error caused by comparing species which did not have soldiers to species with soldiers.

Rarefaction curves were produced using species richness data collected from quadrats in order to examine the effect of the different sampling efforts across sites. The mean masses of worker termites were calculated using the equation $M = 3.72w$, where M is the mass in mg and w is the mean head width in mm (modified slightly from Eggleton *et al*. 1996). The equation constant (3.71) was produced by regressing species head width and body mass data and forcing the slope through zero (to prevent small-bodied speices having negative masses). As termite worker morphology is conservative the mass equation was used to calculate the mass of species in this study. The biomass density was calculated as the product of M and abundance (ind m^{-2}). Biomass and abundance data from the quadrats in each plot were pooled and log(x+1)-transformed prior to analysis. The replicate unit is the individual plot. One-way ANOVAs were used to examine statistical differences in mean biomass and abundance among the biogeographical areas examining each feeding group separately. Phylogenetic structure in the data was visualised using a phylogenetic tree based on the trees in Lo & Eggleton (2011). Analyses were conducted using R (version 2.15.3).

5.3. Results

The highest termites species locality total and mean (± SE) species density, from transects, were found in Cameroon with a total of 101 species and 50.3 ± 2.6 spp per transect, respectively; followed by Malaysia with a total of 86 species and species density of 29.2 ± 1.6 spp per transect then Peru with a total of 73 species and species density of 43 ± 1.7 spp per transect (Figure 5.2). Species richness (± SD), from quadrats, was highest in Cameroon, when sampling effort was accounted for, followed by Peru and then Malaysia despite Cameroon having the smallest sampling area (Figure 5.1). Cameroon had the highest mean (± SE) biomass and abundance with 14.5 ± 7.90 g m^{-2} and 1234 ± 437 ind m^{-2}, respectively, followed by Malaysia with 0.719 ± 0.193 g m^{-2} and 327 ± 72 ind m^{-2} and then Peru with 0.345 ± 0.103 g m^{-2} and 130 ± 39 ind m^{-2}.

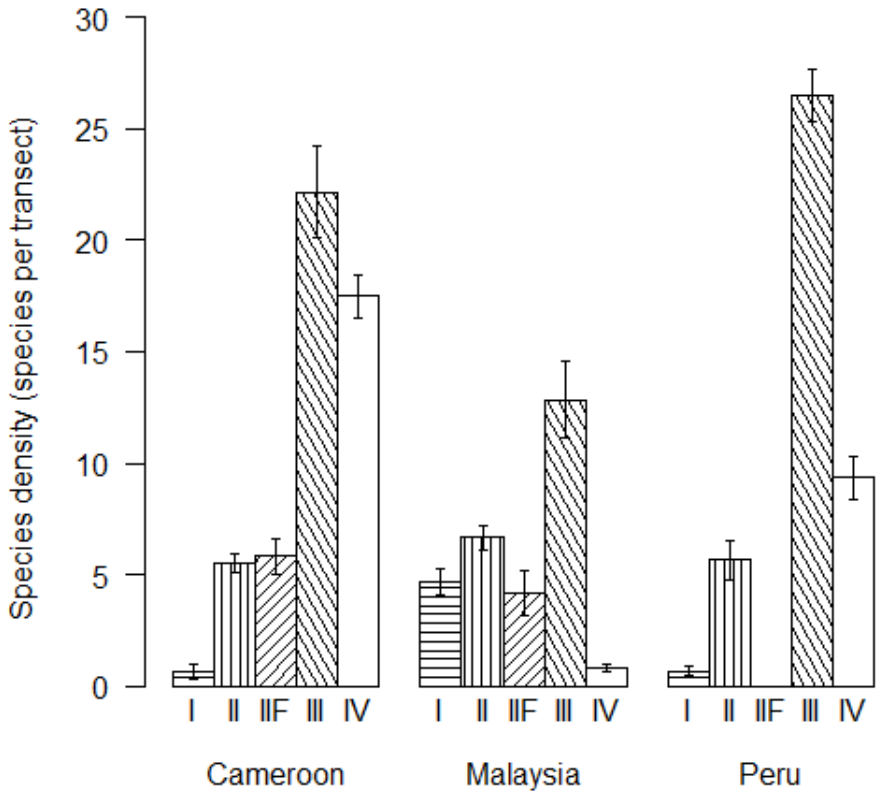

Figure 5.2. Termite species density (species per transect) (mean ± SE) for functional groups FGI and FGII wood-feeders, FGIIF fungus-growers, FGIII humus-feeders and FGIV true soil-feeders across the three sites, Cameroon, Malaysia and Peru, as estimated by standardised transects (data from Eggleton *et al*. (1996, 1999) and from the Peruvian site).

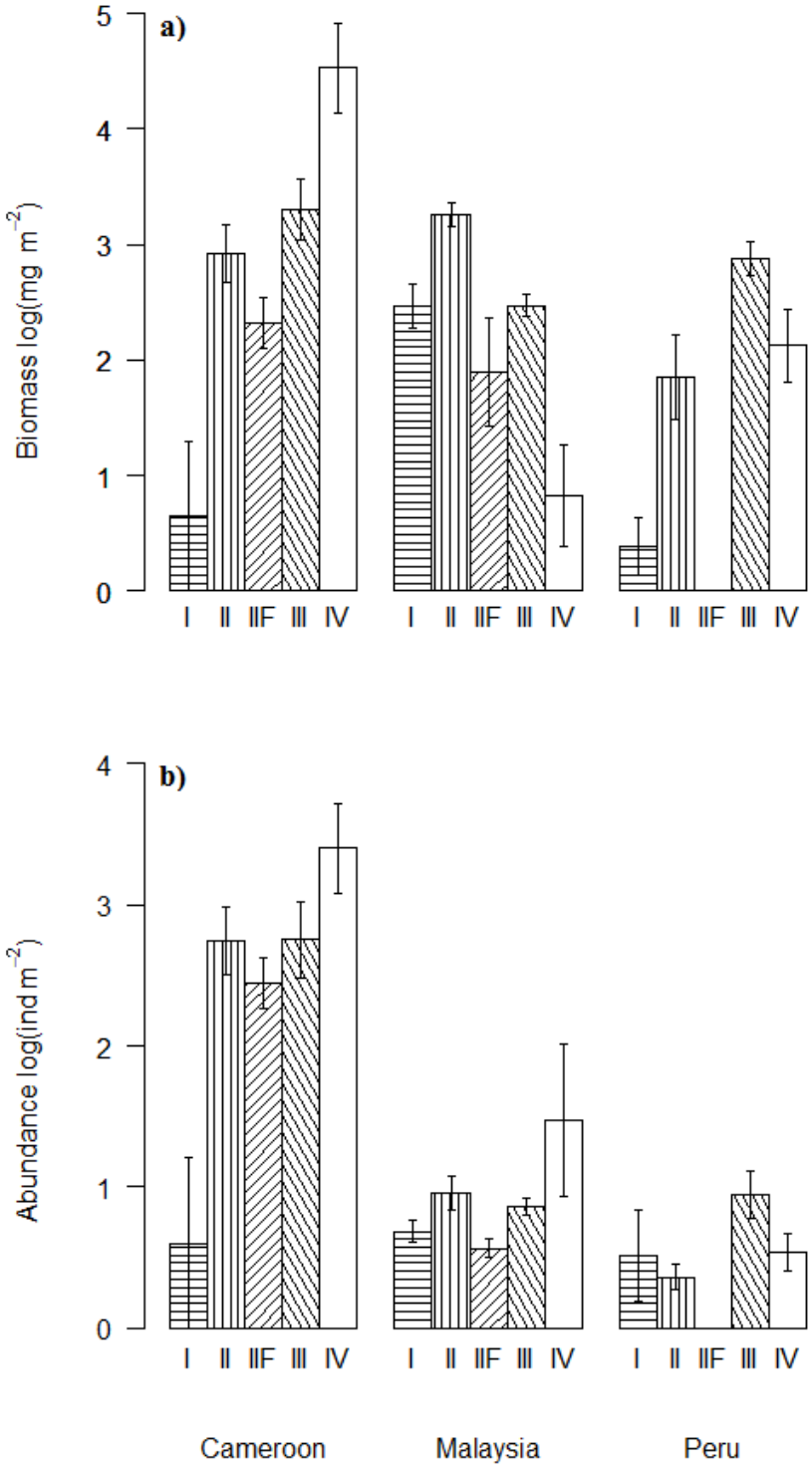

Figure 5.3. Termite biomass (mg m^{-2} (log(x+1))) (a) and abundance (ind m^{-2} (log(x+1))) (b) (mean ± SE) for functional groups FGI and FGII wood-feeders, FGIIF fungus-growers, FGIII humus-feeders and FGIV true soil-feeders across the three sites, Cameroon, Malaysia and Peru.

Soil-feeding termites (FGIII & FGIV) had their highest biomass density in Cameroon while 'wood-feeding' termites (FGI, FGII and FGIIF) had their highest biomass in Malaysia (Figure 5.3a). Regionally, FGIV dominated in Cameroon while within Malaysia and Peru FGII and FGIII had the highest biomasses, respectively (Figure 5.3a). Abundances of all functional groups, with the exception of FGI, were by far the highest in Cameroon (Figure 5.3b). The high biomasses of wood-feeding termites in both Malaysia and Peru when compared with their relatively low abundances were due to the large body-size of a few wood-feeding termites in those sites (Figure 5.4). Wood-feeding termites were small-bodied in Cameroon while large-bodied in Malaysia and Peru, while soil-feeding termites were large-bodied in Cameroon and small-bodied in Malaysia and Peru (Figure 5.4). Regionally, the functional group with highest abundance matched the biomass patterns, except for the high abundance of one species of FGIV in some plots in Malaysia (Figure 5.3b). The biomass for all functional groups was significantly different across the three continents (Table 5.3). The same pattern was shown for termite abundance across all functional groups with the exception of wood-feeding termites (FGI) which did not differ among continents (Table 5.3).

Table 5.3. Results from one-way ANOVA comparing termite biomass and abundance for each functional group across the sites (n) Cameroon, Malaysia and Peru. *P < 0.05, **P < 0.01, ***P < 0.001.

			Biomass	Abundance
	n	df	F-value	F-value
FGI	3	2	12.2**	0.07
FGII	3	2	8.09**	68.4***
FGIIF	3	2	15.0***	194***
FGIII	3	2	6.41*	36.8***
FGIV	3	2	20.1***	12.1***

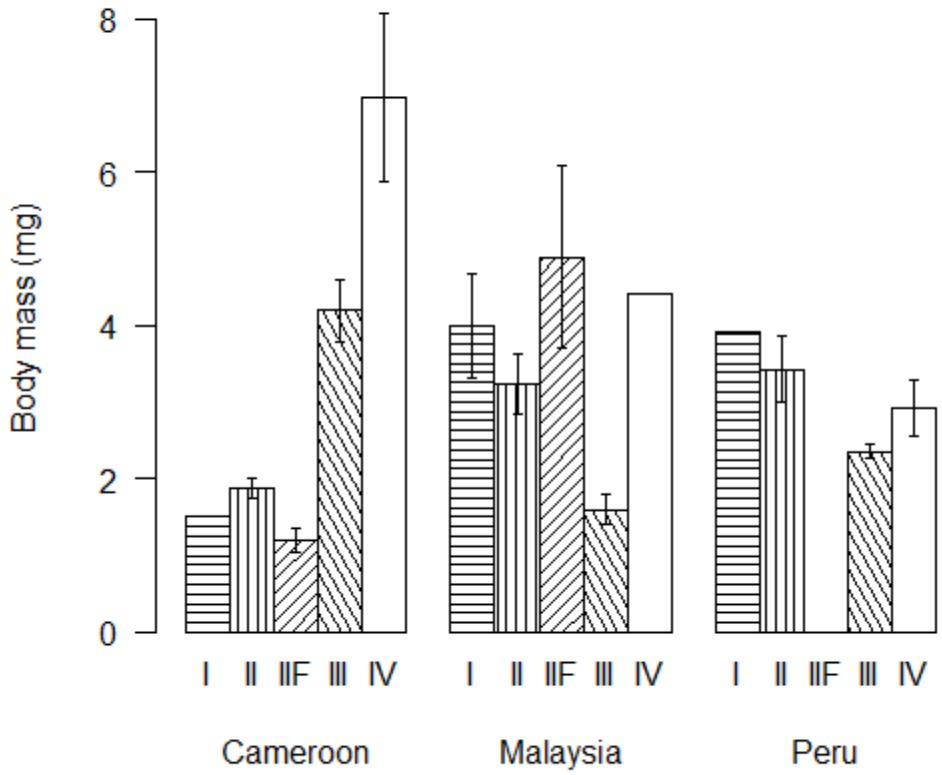

Figure 5.4. Individual termite body mass (mg) (mean ± SE) in each of the five functional groups, FGI and FGII wood-feeders, FGIIF fungus-growers, FGIII humus-feeders and FGIV true soil-feeders , across the three sites, Cameroon, Malaysia and Peru.

Cameroon had the highest presence of lineages with high biomass concentrated in particularly two lineages, the *Cubitermes*-group and *Apicotermes*-group, while those lineages were not found in any of the other sites (Figure 5.5). The biomass of litter-feeding termites (FGII) in Malaysia was high and concentrated particularly in the *Nasutitermes*-group (Figure 5.5). The number of lineages in the Peruvian site was relatively low, with a highest biomass of humus-feeding (FGIII) termites, particularly those in the *Anoplotermes*-group and *Amitermes*-group (Figure 5.5).

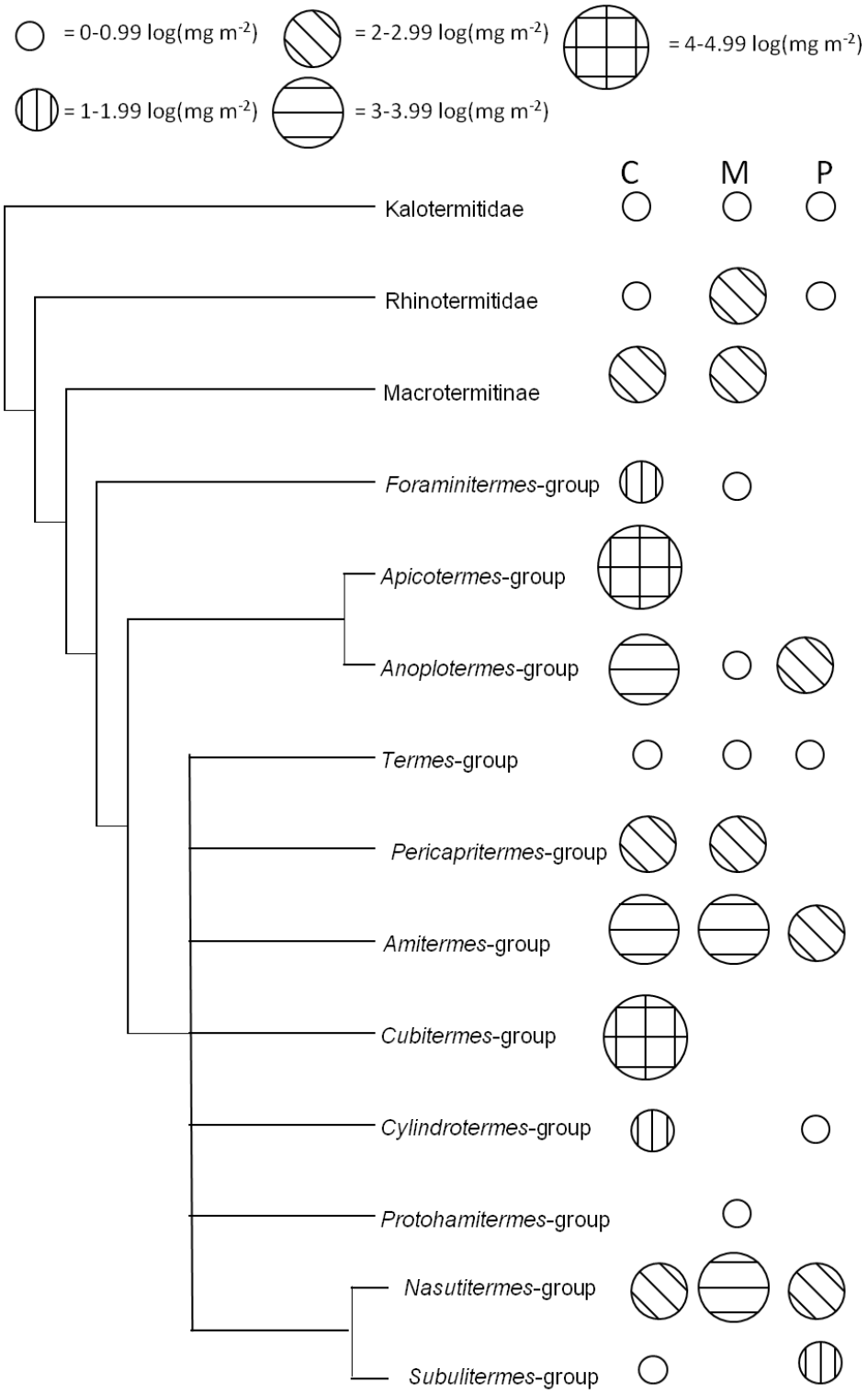

Figure 5.5. Phylogenetic tree including termite lineages from each sites. The log transformed biomass (mg m^{-2}) of each lineage is represented by the size and hatched lines within the circles. No circle means that the lineage is absent from the region while lineages with white circles may be absent or have low biomass in the site. The three columns of circles represent each of the sites in Cameroon (C), Malaysia (M) and Peru (P).

5.4. Discussion

5.4.1. Comparison of termite assemblage patterns

The main objective of this study was to investigate the existence of the functional diversity anomaly for biomass and abundance of termite functional groups across the three equatorial regions. Although other biomass and abundance data are available (e.g. see list in Bignell & Eggleton 2000), only data from the three sites in this study are directly comparable. The termite functional structure across the three sites in this study are consistent with large-scale comparisons of species density data (Davies *et al.* 2003) which show that there is a large difference between feeding groups across sites. The differences in functional group composition were also consistent with biomass and abundance data which confirms the existence of the functional diversity anomaly for termite biomass and abundance. In particular, there was a high biomass of FGIV termites (particularly in the *Cubitermes*-group and the *Apicotermes*-group) in Cameroon while fungus-growing termites (Macrotermitinae) were absent from Peru.

5.4.2. Potential causes of the functional diversity anomaly

Some of the observed diversity differences across the sites may be influenced by differences in body size distribution within particular lineages. Biomass is influenced both by the body size of individual termites and the abundance of individuals in each species. While Cameroon had the highest abundance of all functional groups, except for FGI, the biomass of wood-feeding termites (FGI & FGII) in Malaysia was higher than the biomass of wood-feeding termites in Cameroon. The difference between the biomass and abundance patterns is explained by differences in body-size distributions for each functional group among the sites. Cameroon had relatively larger-bodied soil-feeding termites and relatively smaller-bodied wood-feeding termites compared with Malaysia and Peru. Size distribution across the

functional groups is associated with the presence or absence of particular lineages. The high species density of the large-bodied species in the *Cubitermes*-group and *Apicotermes*-group (Jones & Eggleton 2011) contributed disproportionately to the high biomass of FGIV termites, and the biomass overall, at the Cameroonian site.

Fungus-growing termites are absent from the whole of South America (Aanen & Eggleton 2005), while humus-feeding and litter-feeding *Anoplotermes*-group and *Nasutitermes*-group termites (FGIII & FGII) had high biomasses in the Peruvian site. Additionally, FGIII were small-bodied but with high abundance while FGII were large-bodied with low abundance. In Malaysia the presence of FGIV was low, with only one species recorded; while the dominance of wood-feeding termites in Malaysia was influenced by the presence of particularly Macrotermitinae and Rhinotermitinae. The dominance of the two large-bodied FGIV lineages in Cameroon, the absence of Macrotermitinae in Peru, and the low abundance of true soil-feeding termites (FGIV) in Malaysia strongly contributed to the different patterns of biomass and abundance across sites.

The presence or absence of certain termite lineages therefore appears to be an important correlate of biomass and abundance patterns, as some lineages are widely distributed (*Nasutitermes*-group and the *Amitermes*-group) while others are restricted to certain regions (*Cubitermes*-group, *Apicotermes*-group and Macrotermitinae). Our data therefore support earlier suggestions (Bignell & Eggleton 2000, Davies *et al*. 2003, Jones & Eggleton 2011) that present-day termite distributions are driven by the evolutionary history of termites and not present-day climate. Although temperature and moisture may influence regional termite assemblages (Eggleton *et al*. 1996, 1999; Palin *et al*. 2010), the distribution of feeding groups is more likely to be linked to termite evolutionary history through differential patterns of both dispersal and the regional diversification of functional groups within lineages (Aanen & Eggleton 2005, Eggleton *et al.* 1994, Jones & Eggleton 2011). In

addition, the climatic similarity of the studied habitats, all lowland tropical rain forests, suggests that climate is not the most important factor in explaining the functional diversity anomaly. Moreover, climate can only act as a filter to allow or exclude species through their environmental tolerances. This filter can only act on the regional pool of species and that composition of that regional pool is dependent on historical factors that usually predate the onset of contemporary climates. In this case the regional pools are fundamentally distinct at the major lineage level and those lineages are dated to be several million years old (Eggleton, unpubl. data).

The Termitidae (FGII-FGIV) probably evolved and dispersed from Africa with higher dispersal rates for wood-feeding termites compared with soil-feeding termites (Aanen & Eggleton 2005, Jones & Eggleton 2011). Soil-feeding termites such as the *Cubitermes*-group and the *Apicotermes*-group are probably more dependent on the buffered environment within tropical rain forest, which offer less fluctuation in temperature and moisture compared with non-forest habitats (Davies *et al*. 2003). Therefore, arid and semi-arid habitats such as woodland, savanna and desert would be more likely to be barriers to dispersal for those groups. Wood-feeding termites on the other hand (with the probable exception of fungus-growing termites) are more likely to have been able to disperse across different types of barrier, including bodies of water, because of their rafting abilities (Gathorne-Hardy *et al*. 2000). These activities are probably dependent on their harder and thicker exoskeletons, which support their foraging behaviour (Nalepa 2011) and therefore the likelihood of allowing dispersal across suboptimal habitat types. The biogeographical patterns of wood-feeding termites may therefore have evolved through a wider range of dispersing types than soil-feeding termites, which may have had relatively low dispersal rates. However, it seems likely that soil-feeding (particularly FGIII) termites may have evolved independently from rafting wood-feeding termites on several occasions across the continents (Inward *et al*. 2007,

Jones & Eggleton 2011) leading to the relatively depauperate humus- and soil-feeder assemblages of the non-African sites.

Macrotermitinae (fungus-growing termites) seem to have evolved in African tropical forests (Aanen & Eggleton 2005) and although four dispersal events from Africa to South-East Asia appear to have taken place, fungus-growing termites have failed to colonise South America. Macrotermitinae are hypothesised as poor dispersers, as they depend on their close mutualistic relationship with *Termitomyces,* a fungus, which breaks down organic matter within the termite mound (Aanen & Eggleton 2005). Generally termites depend on the presence of the reproductive caste (king and queen), however, the species of Macrotermitinae also need spores of *Termitomyces* to be available in their new environment. The genus *Microtermes* (along with a single species of *Macrotermes, M. bellicosus*) is able to store fungal spores in their digestive tracts and so pass them on vertically from generation to generation while other species depend on foraging workers to provide fungal spores from the environment when they settle in a new area (Nobre *et al*. 2010). This ability makes species of *Microtermes* more efficient dispersers and, as a result, species of that genus are found in areas where few Macrotermitinae are present, e.g. on Madagascar (Nobre *et al*. 2010). The successful colonisation of Asia but their failure to inhabit South America contributes to the diversity anomaly of functional groups across the equatorial regions.

5.4.3. Possible implications of biomass and abundance patterns on ecosystem processes

The patterns of biomass and abundance uncovered here are likely to affect ecosystem processes across equatorial sites differentially because of the differential dominance of particular functional groups (Ji & Brune 2001, Jouquet *et al*. 2011, Schuurman 2005). While it was shown that true soil-feeding (group IV) termites dominated the Cameroonian site, litter-feeding and humus-feeding (group II & III) termites and humus-feeding (group III)

termites dominated the sites in Malaysia and Peru, respectively. This biomass and abundance anomaly may have an effect on the processes of soil and wood decomposition and in turn the turnover and availability of nutrients in the respective sites.

True soil-feeding termites (group IV) are not only physiologically distinct from wood-feeding termites but also have more complex guts than humus-feeding (group III) termites (Ji & Brune 2005). In theory FGIV termites are thought to break down bacterial polysaccharides as a carbon energy source while stimulating the mineralisation of soil cellulose and protein (Ji & Brune 2001, 2005). True soil-feeding (group IV) *Cubitermes* species have also been shown to influence soil pH, organic carbon content and water content (Donovan *et al.* 2001b). Further, group IV termites have been shown to stabilise nitrogen in a form which plants can use, releasing no more than 3% to the atmosphere compared with other macrofauna (e.g. earthworms) for which emission of N_2 gas is higher (Ngugi & Brune 2012). Tropical forest soils are however generally neither nitrogen nor carbon limited (pers. comm. Malhi 2014), so these termite effects may only be of local importance, for example, by enhancing soil heterogeneity (Donovan *et al*. 2001b). Phosphorus (P), on the other hand, is in short supply (Aragão *et al*. 2009) but seems to accumulate in termite mound and nest material (Chapuis-Lardy *et al.* 2011, Rückamp *et al*. 2010). Mound and nest erosions may increase soil P content through, for example, leaching (Chapuis-Lardy *et al.* 2011), although erosion rates have been shown to vary greatly both within and across species (Brossard *et al*. 2007). We therefore predict that the presence of true soil-feeding termites, particularly of the genus *Cubitermes*, may affect soils by influencing soil heterogeneity.

Macrotermitinae (fungus-growing termites) have been shown to be very important for the decomposition of wood. Results from African studies in savanna woodlands have shown that 90% of the termite wood decomposition was due to fungus-growing termites, and *Macrotermes* in particular (Buxton 1981, Schuurman 2005, Wood & Sands 1978). Both

Cameroon and Malaysia had fungus-growing termites (Eggleton *et al.* 1996, 1999) while these were absent from Peru altogether. We suggest it is likely therefore that sites with Macrotermitinae may have higher wood decomposition rates than the sites without fungus-growing termites, holding all other factors constant. For example, annual consumption by species of Macrotermitinae was recorded as 35.5 g m^{-2} and 669 kJ m^{-2} compared to only 20.0 g m^{-2} and 377 kJ m^{-2} for other wood-feeding species (Wood & Sands 1978).

5.4.4. Conclusion

The biomass and abundance patterns across the three sites were broadly similar to the already established global species density patterns. This strongly supports the existence of the functional diversity anomaly as an ecologically meaningful phenomenon. The importance of the presence or absence of certain lineages for the patterns of functional groups in each region strongly suggests that termite functional distributions are a consequence mainly of evolutionary factors, including chance dispersal events. These findings are important as the biomass and abundance of functional groups may be linked to ecosystem processes which in turn may influence the regional ecosystems as a whole. The three study sites have allowed us to compare data sets from different regions; however, further comparable studies are needed to create a broader data set that will enhance the understanding of the impact and drivers of the biomass and abundance of termite functional groups. These ecological predictions made from the anomaly also clearly need to be tested as soon as is practicable.

5.5. Acknowledgements

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CHAPTER VI

Density-body mass relationships: inconsistent intercontinental patterns among termite feeding-groups

Overview

In chapter V the intercontinental comparison of termite biomass and abundance data showed that there was a difference in the functional composition among the three sites in Peru, Cameroon and Malaysia. Termite evolutionary history was identified as the main cause behind the patterns as the presence or absence of certain lineages, dominance of endemic soil-feeding termites in Cameroon and the absence of fungus-growing termites from Peru, were shown to have the greatest effect on the results. In this chapter I show how the intercontinental patterns may be linked to resource distribution examined through allometric scaling laws of body mass and population density. Additionally, I discuss how the allometric body size relationships may be used to gain better understanding of the role termites play in ecosystem processes.

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Abstract

Allometric relationships are useful for estimating and understanding resource distribution in assemblages with species of different masses. Damuth's law states that body mass scales with population density as $M^{-0.75,}$ where M is body mass and -0.75 is the slope. In this study we used Damuth's law ($M^{-0.75}$) as a null hypothesis to examine the relationship between body mass and population density for termite feeding-groups in three different countries and regions (Cameroon, West Africa; Peru South America; and Malaysia SE Asia). We found that none of the feeding-groups had a relationship where $M^{-0.75}$ while the data suggested that population density-body mass relationships for true soil-feeding termites in Cameroon ($M^{2.7}$) and wood-feeding termites in Peru ($M^{1.5}$) were significantly different from the expected values given by Damuth's law. The dominance of large-bodied true soil-feeding termites in Cameroon and the absence of fungus-growing termites from Peru suggest that these allometric patterns are due to heterogeneities in termite biogeographical evolution. Additionally, as these feeding-groups have higher population density than expected by their body masses it may be suggested that they also have a higher energy throughput than expected. The results presented here may be used to gain further understanding of resource distribution among termite feeding-groups across regions and an insight into the importance of evolutionary history and biogeography on allometric patterns. Further understanding of population density-body mass relationships in termite feeding-groups may also improve understanding of the role these feeding-groups play in ecosystem processes in different regions.

6.1. Introduction

6.1.1. Allometric scaling laws

Body mass is one of the most studied physiological traits in ecology as, among other things, it influences metabolic rate, abundance, and growth rate (Brown et al., 2004). The relationship between body mass and energy flow is important for understanding resource distributions within assemblages with species of different masses (Damuth, 1981; Eggleton et al., 1998; Lewis et al., 2008; Maurer and Brown, 1988). According to metabolic scaling theories the metabolic rate is a power law function of body mass (Brown et al., 2004). The species-specific metabolic rate of the individual $\dot{B}$ is calculated as

$$\dot{B} = \bar{M}^b \tag{6.1}$$

where $\bar{M}$ is the average mass of a species and b is the scaling exponent.

It is frequently observed across a range of organisms that $b \sim 0.75$, a relationship referred to as Kleiber's law (Kleiber, 1947). The West, Brown, and Enquist (WBE) model suggests that the mechanism behind this law is the regulation of metabolic rate by the geometry of vascular networks that supply cells with energy from mammalian aortae to vascular systems in plants (West et al., 1997). This is supported by the mass scaling exponent $b \sim 0.75$ for the cross-section area of aortae or tree trunks (West et al., 1997). Critics of this law have argued, however, that the scaling exponent is not always 0.75 (Chown et al., 2007; Riveros and Enquist, 2011). An alternative model, the cell size model (Chown et al., 2007), suggests that Kleiber's law is only true at a wider interspecific level with a range of scaling exponents between 0.6 and 1.0 found within species or genera (Chown et al., 2007).

The energy flow in a species population (total metabolic rate) can be described as the product of species-specific metabolic rate $\dot{B}$ and population density of a species N:

$$\dot{B}_{tot} = \dot{B} \cdot N \quad (6.2)$$

N is proportional to $\overline{M}^{-a}$, where $\overline{M}$ is the average mass of a species and *a* is the power law coefficient of the relationship between population density and mean individual mass. It is commonly observed that smaller organisms have higher population density while larger organisms have lower population density. The power constant *a* is frequently observed to be ~-0.75 described as Damuth's law (Damuth, 1981).

6.1.2. Allometry in termites

Termites are one of the most important invertebrate decomposers, particularly in the tropics where their abundance and range of feeding-groups are high (Bignell and Eggleton, 2000; Donovan et al., 2001a; Eggleton et al., 1999, 1996) partly due to their symbiotic relationship with gut biota (Hongoh, 2010). The termite gut is a specialised habitat for bacteria, archaea, and protists which, along with termites' specialised guts and mandibles (wood-feeders), make them highly efficient decomposers (Eggleton, 2011; Hongoh, 2010). Termites have been categorised into five feeding-groups depending on the humification (decomposition) of the material they feed on (Donovan *et al.* 2001). These feeding-groups range from wood-feeding termites, which feed on sound dead wood, to true soil-feeding termites, which feed on soil organic matter in mineral soil with no visible plant remains (Table 6.1). The difference in particle size of the diets of humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites, although no difference in isotope composition has been found (see Bourguignon et al. (2011) for C and N stable isotope ratios), may mean that the two feeding-groups metabolise their substrates in different ways. It is known, for example, that FGIV feeders have a more complex gut than FGIII feeding termites to allow the decomposition of nutritionally poorer soil (Ji and Brune, 2005). Species of *Cubitermes* (FGIV soil-feeding termites) have been shown to stabilise nitrogen in a form which plants can use by increasing

soil ammonia content (Ngugi et al., 2011; Ngugi and Brune, 2012). Through decomposition of organic matter and the construction of tunnels, runways and nesting structures (e.g. mounds) termites influence nutrient availability and distribution which affects water and air movement through the soil and promote plant growth (Jouquet et al., 2011, 2006). These activities make termites important ecosystem engineers as they contribute to the structural and chemical composition of their habitat (Brussaard et al., 1997; Jones et al., 1994).

Table 6.1. Classification of termite functional groups and respective feeding substrates within tropical rain forests. Modified from Donovan *et al*. (2001) and Inward *et al*. (2007).

Functional group	Feeding substrates
FGI	Sound wood
FGII	Wood and leaf litter
FGIIF	Wood and leaf litter on which fungi are grown and harvested (Macrotermitinae only)
FGIII	Organic material-rich soil and humus, with visible plant structures
FGIV	Mineral soil with no visible plant structures (true soil-feeding termites)

Eggleton *et al.* (1998) investigated the relationship between total metabolic rate and body mass in two termite feeding-group assemblages (wood-feeding and soil-feeding termites) in Cameroon. Their analysis showed that small to medium-bodied wood-feeding termites had higher metabolic rates (O_2 consumption per unit weight combined with population density to give energy use per unit area) than large-bodied species while large-bodied soil-feeding species had the highest metabolic rates. The latter indicates that the larger-bodied soil-feeding termites in Cameroon have a larger energy throughput (Damuth, 1981) than species of other mass classes due to their proportionally higher metabolic rate.

Recent biomass estimates across the three study sites (Dahlsjö et al., 2014) show that termite biomass varies among regions with highest biomass per unit ground area being found for large-bodied soil-feeding termites (*Cubitermes*-group & *Apicotermes*-group) in Cameroon. These very large soil-feeding termites are absent from Asia and South America.

Since the Eggleton *et al.* (1998) study, a number of advances have been made in the field of termite ecology, particularly in the development of comparable sampling techniques and a more sophisticated feeding-group classification (Jones & Eggleton 2000; Donovan *et al.* 2001; Davies *et al.* 2003; Bourguignon *et al.* 2011; Hyodo *et al.* 2011). These developments have provided better estimates of termite diversity patterns and functional groupings. Additionally, there are now sufficient data to compare biomass and abundance patterns of assemblages from sites in the three main tropical regions (Africa, Asia, and South America) (Dahlsjö et al., 2014; Eggleton et al., 1999, 1996). These advances allow us to explore the termite population density - body mass relationship in more detail and to compare and contrast across the three major tropical continents for the first time. This paper considers population density - body mass relationships in termite feeding-groups using data from Cameroon, Peru and Malaysia. As population density is, according to Damuth's law, approximately reciprocal to individual metabolic rate (Damuth, 1981) investigating population density-body mass relationships in termite feeding-groups may enhance our understanding of the role termites play in ecosystem processes, such as nutrient turnover, availability and distribution (Jouquet et al., 2011), among regions.

In this study we (a) treat Damuth's law as a null hypothesis (Isaac et al., 2013), by testing the observed slope values for population density and body mass against the predicted value (-0.75) of Damuth's law, for three feeding-groups (true soil-feeding termites FGIV, humus-feeding termites FGIII and wood-feeding termites FGI, FGII and FGIIF) across three regions (Cameroon, Peru and Malaysia) and (b) discuss the causes of the observed patterns

(biogeography and evolution) and the potential implications on ecosystem processes. We predict that the dominance of large-bodied true soil-feeding (group IV) termites in Cameroon will greatly impact on the population density-body mass relationships and is, therefore, expected to diverge from Damuth's law. The population density - body mass relationships in all other feeding-groups are expected to follow Damuth's law.

6.2. Methods

6.2.1. Study site

Sampling of termite abundance and biomass was conducted in relatively undisturbed tropical forest sites in Peru (South America), Cameroon (Africa), and Malaysia (south-east Asia). Each site consisted of a set of plots (four in Cameroon and six each in Peru and Malaysia), from which population density and body mass data were calculated and pooled to create a dataset for each site within each region. Data from Cameroon (3°31' N, 11°25' E) and Malaysia (4°58' N, 117°48' E) were compiled from Eggleton *et al.* (1996) and Eggleton *et al.* (1999) respectively, while data from Peru were collected by the first author (CALD) in 2011 in Tambopata National Park (12˚49.434'S, 069˚15.791'W). See Dahlsjö et al. (2014) for more detailed information.

6.2.2. Sampling

Broadly, the same method was adopted in all the three sites with slight variations in quadrat size and number (Table 6.2). This variation in sampling approach was overcome by scaling the data in each case to unit area (m^2). Data from Cameroon and Malaysia were compiled from Eggleton *et al.* (1996) and (1999), respectively, while data from Peru were collected by the first author (CALD). In Peru, six 70 m × 50 m plots were set-up at least 300 m apart. Each plot was divided into six sub-plots (10 m x 50 m each) of which two in each plot were

used for the surveys reported in this paper. Those were spaced 30 m apart. Ten 2 m x 2 m quadrats, spaced five metres apart, were placed in each plot and split between the two sub-plots, five quadrats in each. Within each quadrat, the number of termites in all dead wood greater than 20 mm diameter were sub-sampled and extrapolated. Small branches were broken open while larger logs were sub-sampled with a saw before being split open to extract the termites. In addition, all termites were manually extracted from one soil pit (25 cm × 25 cm × 10 cm depth) in the centre of each quadrat. Termites were preserved in 70% alcohol and identified by CALD at the Natural History Museum (NHM) in London.

Table 6.2. Summary of the differences in sampling methods across the study sites.

Study site	Number of plots	Plot size (m)	Number of quadrats/ plot	Size of soil pit (m)
Cameroon	4	30 × 20	10	0.2 ×0.2 ×0.5
Malaysia	6	50 ×50	20	0.3 ×0.3 ×0.25
Peru	6	70 ×50	10	0.25 ×0.25 × 0.1

6.2.3. Feeding-groups

Termites were classified into five feeding-groups by the level of humification (decomposition) of the organic matter they feed on (Donovan *et al.* 2001). The feeding substrates of the feeding-groups range from wood at the top of the humification gradient and soil at the bottom of the humification gradient. FGI feed on wet and dry wood and include all termite families except the Termitidae. FGII and FGIIF feed on wood and leaf litter, but only FGIIF, the fungus-growing subfamily Macrotermitinae, use external symbiotic fungi (*Termitomyces:* Basidiomycotina) for decomposition (Table 6.1) (Aanen and Eggleton, 2005;

Nobre et al., 2011). FGIII feed on soil with microscopically visible plant material while FGIV (true soil-feeding termites) feed at the bottom of the humification gradient on low quality soil with high mineral content.

6.2.4. Data analyses

A total of 186 species of termites were used in this study representing all five feeding-groups. FGI, FGII and FGIIF (Table 6.1) were grouped as wood-feeders due to the relatively low number of representatives in each feeding-group particularly in Peru and to an extent in Cameroon. In Peru, only FGI and FGII were pooled as fungus growing (FGIIF) termites are absent from Peru, and from the whole of South America (Aanen and Eggleton, 2005). Humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites were analysed separately (note that there are very few FGIV termites in Malaysia). Here, the population density represents the average number of individual termites of a feeding-group found per square metre.

Only worker termites were used for estimates of abundance and biomass in this study in order to make unbiased comparisons between species with highly different proportions of soldiers. Termite soldiers represented less than 5% of the individuals in most species, with the exception of *Nasutitermes* (and other Nasutitermitinae) with approximately 25% of all individuals being soldiers (Vasconcellos and Moura, 2010), while the *Anoplotermes*-group, that represented 30% - 40% of all species in the sites, are soldierless.

We used termite worker head width and body mass data from Malaysia (Eggleton et al., 1999) to calculate the average mass of individual species. Nalepa, (2011) shows that worker head width has an exponential relationship with body mass and as worker termites have very conservative morphology we are therefore able to estimate the body mass of worker termites outside of Malaysia using the equation:

$$M = 0.5378e^{1.637w} \quad (6.3)$$

where *M* is the mass in mg and *w* is the head width in mm (Figure 6.1). Equation (6.3) was used to calculate the average mass of each species found in the plot in Peru (see Eggleton et al., (1999 and 1996) for mass estimates in Malaysia and Cameroon). The head widths of at least ten individuals from each species were used to create the average mass estimates.

The slope of the relationship between population density and body mass was tested against the value proposed by Damuth's law (a = -0.75) using *slope.test* in the *smatr* package in R (version 2.15.3). All data were $\log_{10}$ transformed and regressed with ordinary least square (OLS) regression models. The standard error (SE) of the slope was calculated using the LINEST function in Excel.

6.3. Results

None of the termite feeding-groups had population density-body mass relationships where $M^{-0.75}$ as proposed in Damuth's law (Figure 6.2, Table 6.3). However, only population density-body mass relationships in large-bodied true soil-feeding (FGIV) termites in Cameroon (*slope.test*: $M^{2.7}$, R^2 = 0.44, P = 0.0007) and large-bodied wood-feeding (FGI & FGII) termites in Peru (*slope.test*: $M^{1.5}$, R^2 = 0.46, P = 0.005) were significantly different from the expected values given by Damuth's law (Figure 6.2, Table 6.3). Population density and body mass showed weak correlations in the humus-feeding termites in all sites (Table 6.3) which is likely to be due to variations in population density with little variation in body mass (Figure 6.2). The non-significant population density-body mass relationships in soil-feeding termites in Peru may be due to the small number of samples and the large scattering of data points around the mean (Figure 6.2 and Table 6.3). True soil-feeding termites were rare in Malaysia with only one species encountered in the plot. The small data set for true soil-feeding termites in Malaysia did not contribute to the analyses and may have restricted the overall comparison

of true soil-feeding termites across the three regions. Additionally, while the wood-feeding termites in all sites were well represented the large scattering of the data around the mean in Cameroon and Malaysia may have contributed to the non-significant results in those sites.

Table 6.3. Allometric scaling relationships between log body mass and population density in humus-feeding, true soil-feeding and wood-feeding termites in Cameroon, Peru and Malaysia. The scaling relationships were significant tested against the value -0.75 predicted by Damuth's Law. ** P < 0.01, *** P < 0.001, NA = insufficient data.

Geographic region	Functional group	n	R	R^2	Slope (OLS)
Cameroon	humus	20	-0.19	0.038	-1.0
	soil	29	0.66	0.44	2.7***
	wood	18	-0.56	0.31	-1.7
Peru	humus	34	-0.06	0.003	-1.0
	soil	13	-0.10	0.01	-1.2
	wood	15	0.68	0.46	1.5**
Malaysia	humus	19	0.24	0.00061	0.1
	soil	1	NA	NA	NA
	wood	32	-0.23	0.12	-2.1

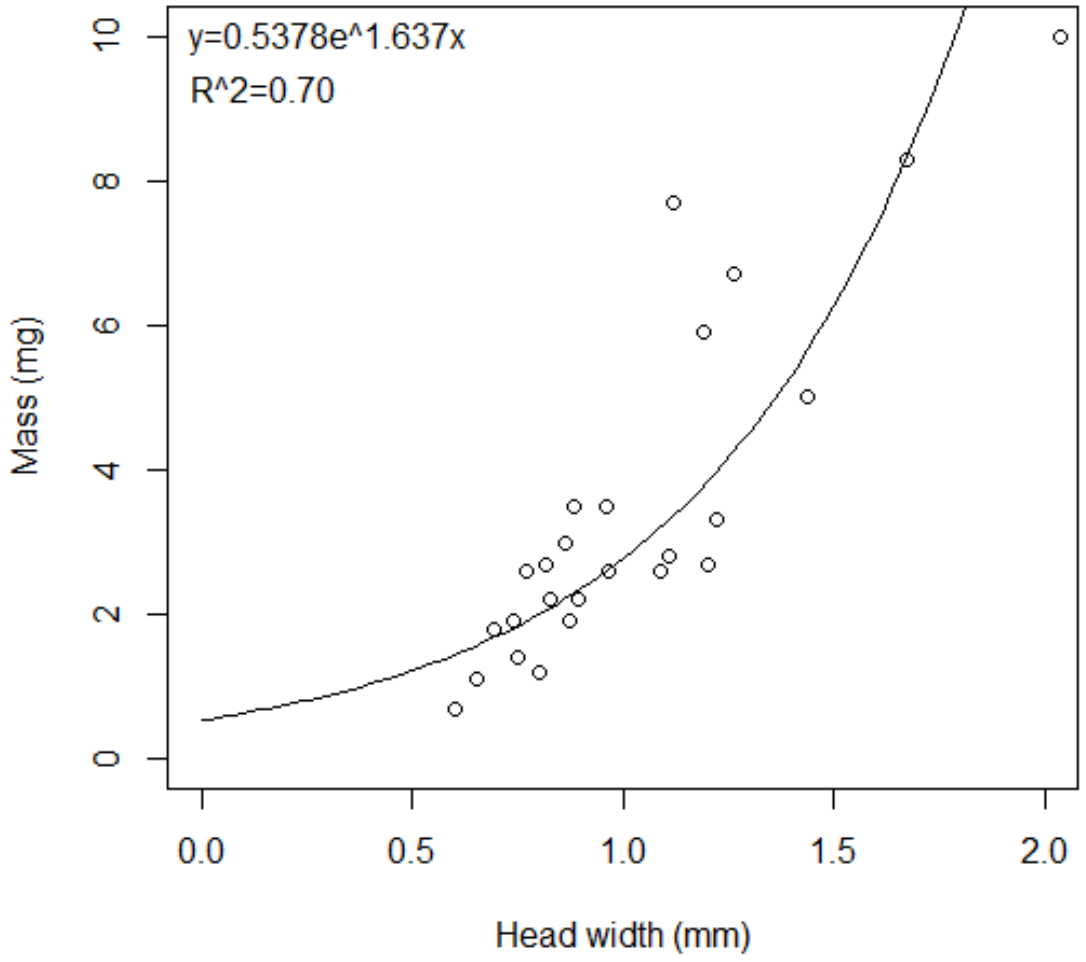

Figure 6.1. Termite worker head width and body mass data from Malaysia. The worker termite head width - body mass regression was used to calculate the mass of worker termites in the sites in Peru.

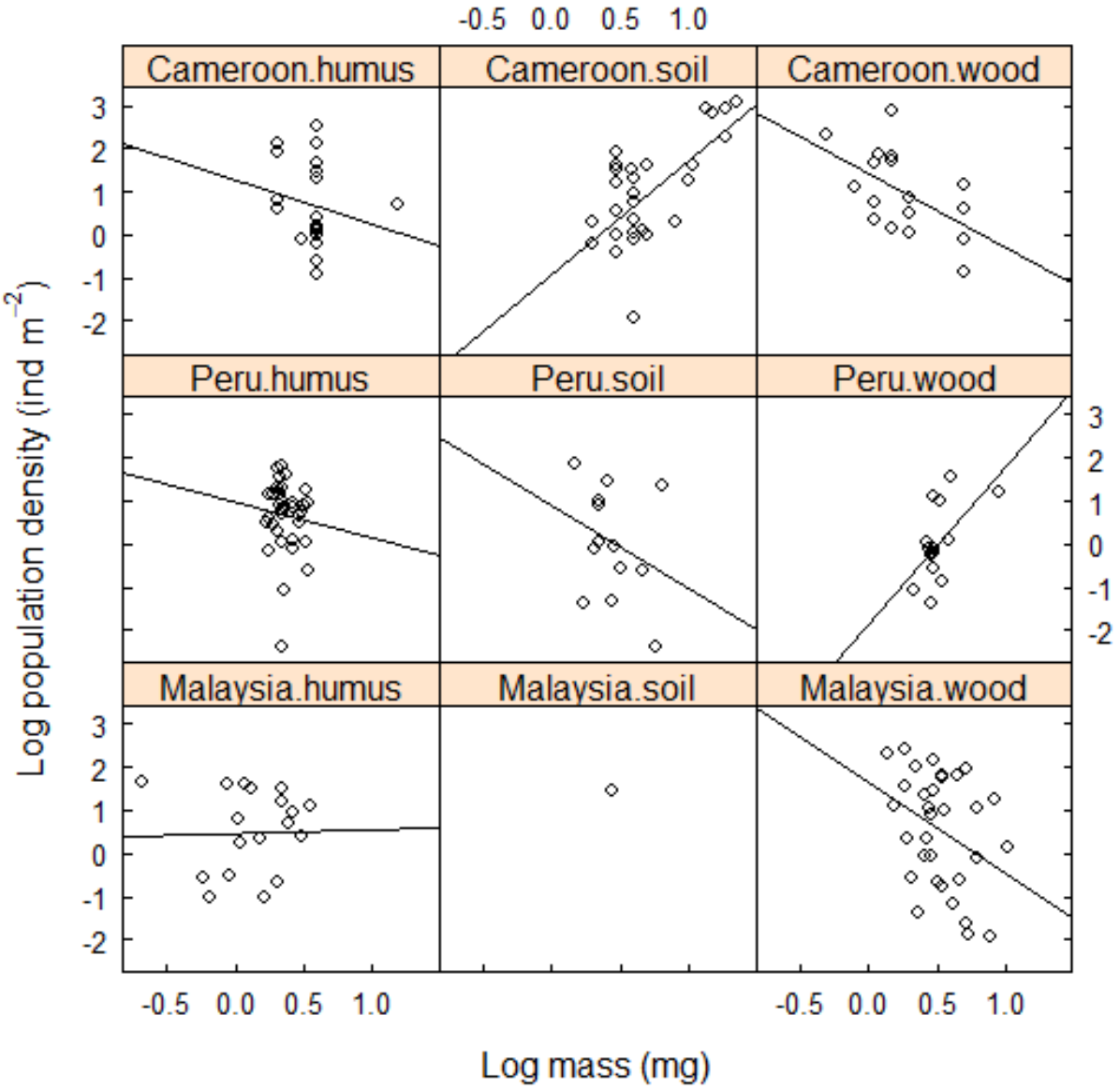

Figure 6.2. Allometric scaling relationships between log body mass (mg) and log population density for humus-feeding termites, true soil-feeding termites and wood-feeding termites in Cameroon, Peru and Malaysia.

6.4. Discussion

Although, none of the feeding-groups had the same scaling exponent as proposed by Damuth's law ($M^{-0.75}$) our results suggest that the largest (significant) diversion from the expected value (-0.75) was found in large-bodied true soil-feeding termites in Cameroon, with a slope of 2.7±0.6 SE, and large-bodied wood-feeding termites in Peru with a slope of 1.5±0.7 SE. These results suggest that the larger-bodied species of true soil-feeding termites in Cameroon and wood-feeding termites in Peru produce a larger number of individuals per unit area than expected by their body mass and so use more energy than expected by their body mass in a population with species of different sizes (Damuth, 1981).

6.4.1. Biogeography and evolution: potential causes of the allometric patterns

The high energy throughput in large-bodied true soil-feeding termites in Cameroon may be due to the dominance of two large-bodied lineages (the *Cubitermes*- and *Apicotermes*-groups) endemic to Africa (Davies et al., 2003; Jones and Eggleton, 2011). The absence of these lineages from other biogeographical regions may be due to their inability to form colonies in dead wood, and so there is limited potential for dispersal (i.e. by rafting) to other regions (Davies et al., 2003). In addition, they require wet, relatively buffered climatic conditions and so are unlikely to disperse through the arid or semi-arid environments that might have provided land bridges in the past (e.g. between Africa and Asia) (Davies et al., 2003). The dispersal of many soil-feeding termites has been limited in termite evolutionary history and although in many cases humus-feeding (FGIII) termites have evolved from lineages of wood-feeding termites, true soil-feeding (IV) termites have evolved relatively rarely outside Africa (Davies et al., 2003; Jones and Eggleton, 2011). Evolution towards larger-bodied soil-feeding termites in Cameroon may have been due to the enhanced nutrient uptake related to longer retention time that increases with gut size (Illius and Gordon, 1992).

This is particularly important in organisms feeding on a nutritionally poor substrates (Eggleton et al., 1998). The relatively small-bodied soil-feeding termites in Peru and Malaysia may be due to the presence of other evolutionary pressures such as the evolution of closed canopy forests that may have impacted on the development of true soil-feeding termites in those regions (Davies et al., 2003).

The diversity of wood-feeding termites is higher in Malaysia compared with Cameroon and Peru (Dahlsjö et al., 2014; Davies et al., 2003) and fungus-growing (FGIIF) termites are absent from Peru and the whole of South America (Aanen and Eggleton, 2005). While the majority of wood-feeding termites in Peru were small-bodied, a few large-bodied species (e.g., *Nasutitermes* sp. I and sp. VI), had very high population densities. The *Nasutitermes* genus commonly occurs in all the study regions (Jones and Eggleton, 2011), however, only in Peru did body mass have a significantly positive relationship with population density. The low diversity of wood-feeding termites in Peru, influenced by the absence of fungus-growing termites, may have reduced the competition for woody substrates (see Table 6.1) and enabled this genus to thrive. Although, the effect of fungus-growing wood-feeding termites on non-fungus-growing wood-feeding termites has not yet been quantified the absence of this lineage may have affected the population density-body mass relationship for wood-feeding termites in Peru. However, this hypothesis must be tested through exclusion of fungus-growing termites before such a conclusion may be reached.

6.4.2. Allometry in termites and the potential impacts on ecosystem processes

Termites contribute to the breakdown of organic matter, turnover of nutrients, fixation and mobilisation of elements which make them exceptionally important in tropical ecosystems (Jouquet et al., 2011, 2006; Yamada et al., 2006). As body mass may influence the efficiency of nutrient uptake and turnover in different trophic groups the dominance of the true soil-

feeding termites in Cameroon and wood-feeding termites in Peru is likely to have an impact on ecosystem processes. Illius & Gordon (1992) argue that gut retention time is longer in large-bodied animals with large guts which enhances nutrient uptake. Longer retention time play an important role in termites and other organisms feeding on nutritionally poor substrates and may therefore play a particularly important role for true soil-feeding termites. Wood-feeding termites benefit from being small-bodied as smaller mandibles may enable them to break wood into finer pieces and subsequently increase the surface-to-volume ratio that enhance nutrient uptake (Eggleton et al., 1998; Nalepa, 2011). However, wood is also a nutritionally poor substrate and large-bodied *Nasutitermes* may feed on more recalcitrant materials with high lignin content, although no empirical evidence exists, for which increased gut retention time would be advantageous.

The origin and subsequent ecological dominance of the two large-bodied true soil-feeding lineages in Cameroon has clearly influenced the population density-body mass relationship which suggests that the large-bodied true soil-feeding termites have a higher throughput of energy than expected by their body masses. The role that the *Cubitermes*-group plays in soil processes has been relatively well studied (Donovan et al., 2001b; Ji and Brune, 2001; Ndiaye et al., 2004; Wood et al., 1983) compared with true soil-feeding termites outside of Africa. *Cubitermes* mounds have been shown to contain more clay and silt than the surrounding soil and accumulate phosphorous (P), nitrogen (N) and carbon (C) (Ndiaye et al., 2004; Wood et al., 1983) that may be utilised by plants as the mound erodes (Rückamp et al., 2010). Additionally, soil that has been processed by *Cubitermes* has also been shown to affect soil pH and increase soil organic C and water content (Donovan et al., 2001b). The dominance of the *Cubitermes*-group and *Apicotermes*-group and their ability to efficiently utilise and process nutrients, compared with smaller-bodied soil-feeding termites, suggests that the soil processes promoted by these soil-feeding lineages will be higher than in areas

where these lineages are absent. However, more information about true soil-feeding termites both within and outside of Africa is needed in order to gain better understanding of the importance of termites in soil processes.

In both Peru and Malaysia the wood-feeding termites have been shown to be larger-bodied than the true soil-feeding and humus-feeding termites while the opposite has been shown to be true for the different feeding-groups in Cameroon (Dahlsjö et al., 2014). It may therefore be suggested that wood-feeding termites in Malaysia and Peru, to a larger extent, benefit from being large-bodied with potentially longer retention times to decompose woody organic matter while most wood-feeding termites in Cameroon benefit from smaller mandibles. Particularly in savannah habitats fungus-growing termites (Macrotermitinae) have been shown to play a major role in woody litter decomposition (Collins, 1981; Wood and Sands, 1978) with higher decomposition rates than non-fungus-growing wood-feeding termites (Wood and Sands, 1978). However, in Peru, where fungus-growing termites are absent, the dominance of predominantly large-bodied *Nasutitermes* species suggests that the genus plays an important role in wood and litter decomposition. Most Neotropical *Nasutitermes* species build arboreal carton nests that are made out of >90% processed organic material (Thorne et al., 1996). While little data exist on the contribution of arboreal nests to nutrient turnover these nests are commonly seen on the forest floor quickly being integrated into the soil (pers. obs.). The high proportion of organic matter in the nests suggests that *Nasutitermes* contributes to decomposition of woody litter and further to nutrient cycling when the nest falls to the ground and erodes. Further information on wood-feeding termites in tropical forests must be gathered before a general conclusion of the importance of this dominant group may be drawn and due to the small dataset presented in this study the results should be viewed as provisional until additional comparable data become available.

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CHAPTER VII

Termites promote soil carbon and nitrogen depletion: results from an in situ macrofauna exclusion experiment, Peru

Overview

In chapters V and VI I examined the impact of termites in ecosystem processes in relation to termite biomass and abundance as well as the proportion of resources managed by different functional groups in the three regions Cameroon, Malaysia and Peru. In this chapter I examine the direct effect of termites on soil carbon (C) and nitrogen (N) availability through an *in situ* soil macrofauna exclusion experiment. I discuss the impacts of termites and other macrofauna on soil C and N depletion, the difference in depletion rates between microcosms with and without macrofauna as well as the impact of seasonality on depletion rates in different microcosm treatments.

Cecilia Dahlsjö wrote the paper with comments from Paul Eggleton, Yadvinder Malhi, Kate Parr, Patrick Meir. Cecilia Dahlsjö conducted the exclusion experiment in Peru with the help of the co-author Omayra V. C. Chevarria. This chapter has accepted for publication, in part, as a short communication in *Soil biology and Biochemistry*. The chapter is kept as the full paper in this thesis in order to provide a more detailed account of my findings.

Paper details

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Abstract

Termites are dominant invertebrate decomposers in tropical forests, where they affect carbon (C) and nitrogen (N) cycling through breakdown of dead organic matter and bioturbation. In this study we conduct the first *in situ* soil exclusion experiment to examine the impact of termites and other macrofauna in C and N depletion using translocated soil. Experimental soil was translocated from a Peruvian highland site (3000 m asl) to a Peruvian lowland site (190 m asl) and placed in containers where the top and bottom had been replaced with fine (0.3 mm) and coarse (5 mm) mesh for exclusion and inclusion of macrofauna, respectively. Two containers, one of each mesh size treatment, were placed in pairs in six plots and collected at five sampling occasions over four months. The C and N content in the soil at each of the sampling occasions were examined as well as the abundance and biomass of termites and other macrofauna in the microcosms. We found that C and N depletion rates were higher in microcosms that included macrofauna (half life was 177.7 days for C and 212.7 days for N) than in microcosms with microbes alone (half life was 244.6 days for C and 310.1 days for N). We also found that termites colonised the soil microcosms at a higher rate than other macrofauna and had higher abundance and biomass in the bait soils than other groups. Our findings suggest that the presence of termites in soil promotes C and N depletion that may be linked to the passage of soil through the termite gut and the affect termites have on bioturbation and nutrient distribution.

7.1. Introduction

Soils are complex, heterogeneous and highly speciose environments which are vital components of most terrestrial habitats (Wolters 2001, Decaëns et al. 2006, Lavelle et al. 2006). The soil biota are essential for soil functioning, which in turn affects the habitat around them (Ekschmitt & Grif 1998, Wolters 2001). Soils are inhabited by organisms that influence the distribution of water and nutrients by increasing soil porosity, and contribute to nutrient cycling through enhancement of the decomposition of organic matter (Jouquet et al. 2006, 2011). The soil macrofauna in the tropics, particularly in lowland forests, is usually dominated by termites, which are often present at high densities (see e.g. Bignell and Eggleton, 2000; Eggleton et al., 1999, 1996). Termites are classified into five functional groups (Table 7.1), four of which exist in South America (Aanen & Eggleton 2005). These groups feed on dead plant matter at different stages of humification (broadly position along the decomposition successional gradient) (Donovan et al. 2001a, Eggleton & Tayasu 2001, Inward et al. 2007) from sound wood (FGI) to soil organic matter (SOM) in mineral soil (FGIV).

Table 7.1. Description of termite feeding substrates and the presence or absence of functional groups in South America. The table is modified from Donovan et al. (2001a) and Inward et al. (2007).

Functional group	Present in Peru	Feeding substrate
FGI	✓	Sound wood
FGII	✓	Wood and leaf litter
FGIIF	×	Wood and leaf litter (Fungus-growers: Macrotermitinae only)
FGIII	✓	Organic rich soil and humus, with visible plant structures
FGIV	✓	Mineral soil with no visible plant structures (true soil-feeding termites)

In contrast to some wood-feeding termites, which feed on substrates with high C:N ratios, soil and humus-feeding termites feed on substrates with relatively high nitrogen. While single-piece nesting (the most primitive form of nesting restricted to a single piece of wood, Inward et al., 2007) wood-feeding termites often fix N in order to balance the difference in C and N in wood (Eggleton & Tayasu 2001), soil (FGIV) and humus-feeders (FGIII) do not need to acquire additional N from the atmosphere (Higashi et al. 1992). The presence of termites in soil has been shown to reduce the N content of the soil through denitrification (Ngugi et al. 2011, Ngugi & Brune 2012) and reduce C content through the production of CH_4 and CO_2 (Sanderson 1996, Macdonald et al. 1998).

Although numerous studies have investigated the importance of termites in C and N cycling (Yamada et al. 2006, Ackerman et al. 2007, Ngugi et al. 2011, Ngugi & Brune 2012) there are few studies that consider how termites and other macrofauna directly affect C and N availability in soil when compared with microorganisms and smaller invertebrates (i.e. microbes, mesofauna and microfauna) alone (Ngugi & Brune 2012). Most studies measure C and N fluxes, either in laboratory environments (Ngugi et al. 2011) or measured from mounds directly (Holt 1987, Khalil et al. 1990, Donovan et al. 2001b, Ackerman et al. 2007). These methods may have limitations: (i) laboratory experiments do not fully represent the range of natural occurring processes or abundance and biomass of macrofauna in the ecosystem, (ii) C and N emissions only represent the elements which are emitted or being fixed by termites but not how much of the C and N are available to plants within the soil, and (iii) most soil-feeding termites in Peru have diffuse nests within the soil, which are hard to locate, making it difficult to measure emission from the nest of soil-feeding termites directly.

In this study, we collected soil (histic lithosol, inceptisols, USDA soil taxonomy, Malhi et al., 2011) with deep O-horizon (~30 cm) and soil C content of 14.99 %±0.28% from a montane tropical forest (Wayqecha, 13˚11'24S, 71˚35'13"W) in Peru at an altitude of 3000 m asl. No termites were present at this elevation (Palin et al. 2010). The soil was translocated into a termite-inhabited soil (cambic horizon, inceptisols, USDA soil taxonomy, Aragão et al., 2009) with soil C content of 2.72% ±0.15% and a very shallow O-horizon (<3 cm) in a lowland tropical rain forest site (Tambopata, 12˚49.434'S, 069˚15.791'W). The translocated soil was used to conduct a decomposition experiment using two different mesh sizes, with the smaller mesh size excluding macrofauna. Specifically, we investigated (a) the effect of (i) microbes, smaller fauna and macrofauna combined and (ii) microbes and smaller fauna alone on soil C and N

depletion, and (b) the soil colonisation rate of termites and other macrofauna groups and the resulting abundance and biomass of these groups in the large mesh treatment soils.

We predicted that soil C and N depletion would be greater in the microbes- and-macrofauna combined treatment than in the microbes-only treatment due to the combined effect of macrofauna and microbes. We also predicted that the macrofauna effect would be influenced by the presence of termites which have high abundance and biomass in lowland tropical forests e.g. 1234 indv m^{-2} and 14.5 g m^{-2} in Cameroon, respectively, and 130 indv m^{-2} and 0.345 g m^{-2} in Peru (Dahlsjö et al. 2014).

7.2. Materials and methods

7.2.1. Study site

The experiment was conducted in a lowland primary tropical forest in Tambopata National Park in Peru (12˚49.434'S, 069˚15.791'W) at an average altitude of 190 metres asl (local measurements using GPS). The site has mean annual rainfall of 1900 mm $year^{-1}$ and mean temperature of 24.4˚C (Malhi et al. 2014). The site has two seasons, a dry season from April to September, and a wet season from October to March. The experiment was run from July (dry season) to November (wet season), which meant that two of the sampling occasions (56d and 112d incubation) occurred in the wet season. The plots were chosen to represent the mosaic structure of naturally-occurring tree falls and dense canopy in the forest. The soil structure varied across the site with higher sand content close to where streams and rivers were or had been. Plots were deliberately chosen to have a higher soil clay content as this is a requirement for the presence of soil-feeding termites, which depend on the clay to support their nesting structures.

7.2.2. Experimental design

Six plots (50 m × 70 m) were established at least 300 m apart at the site. Each plot was divided into six parallel sections (50 m × 10 m) for the purpose of three different experiments. The experiment reported on in this paper was conducted in two of the six sections spaced 30 m apart in each plot. In each section, a grid was marked out with the position of the sampling points, which were placed in the grid at random (generated with random numbers in excel). The grid consisted of two rows with microcosms spaced five metres apart. The microcosms were placed randomly in the two sections. Fifteen microcosms each of coarse mesh and fine mesh were paired in every one of the plots and divided between the two sections with seven and eight microcosms in each. Each pair was randomly allocated a number between one and five representing the different sampling occasions (7, 14, 28, 56 or 112 days of incubation). On each of the sampling occasions three pseudoreplicates of each pair per plot were collected without replacement. In total 90 microcosms of each mesh size were divided among the six plots. On each sampling occasion the soil microcosms were placed in plastic bags and transported to the laboratory where termites and all other macrofauna (in the microcosms) were extracted manually. The sample organisms were placed in tubes with 70% alcohol for identification by the first author (CALD) at the Hope Department of Entomology at the University of Oxford.

7.2.3. Preparation of soil microcosms

While *in situ* soil macrofauna exclusion experiments are rare mesh bags (Powers et al. 2009) and mesh covered trays (Takamura 2001) have been used elsewhere to exclude and include macro- and mesofauna from leaf-litter and wood. In the soil exclusion experiment in this study the translocated soil was sorted and twigs, rocks, and roots

were removed before it was dried and weighed prior to the start of the experiment. Each microcosm had an average initial dry weight of 193 grams representing a full container of soil. The soil macrofauna exclusion experiment was conducted using fine (0.3 mm) and coarse (5 mm) nylon mesh to exclude and include macrofauna, respectively. When installed at the lowland experimental site, the lid and bottom of plastic containers (10 cm diameter and 5 cm high) were replaced by fine (0.3 mm) and coarse (5 mm) mesh and placed in the plots with the top of the microcosms covered by 2 cm of soil. The soil was transported in labelled bags to the plots and placed in the plastic containers in the field to minimise loss of material prior to the start of the experiment.

7.2.4. Data analyses

In total 85 microcosms excluding macrofauna and 87 microcosms including macrofauna were analysed (five fine mesh treatment microcosms and three coarse mesh treatment microcosms were lost in the field). The C and N content in soil were analysed with Thermo Finnigan Flash Elemental Analyser 1112 at the Imaging and Analysis Centre (IAC) at the NHM, London. Three pseudoreplicates for each sample were analysed to produce standard deviations for detection of potential contamination. Each sample value was calculated as the mean of the three pseudoreplicates. Mean and standard error for each sampling occasion and treatment were calculated using the replication of the microcosms.

Nonparametric ANCOVA was used to test the equality (whether the data for including and excluding macrofauna differed significantly along the y-axis) and parallelism (whether the two curves for including and excluding macrofauna have the same shape) for depletion rates of C and N. A nonparametric, rather than parametric, ANCOVA was used as information about the shape of the curve was unknown due to

the novelty of the experiment. ANCOVA was analysed using the *sm* package in R (version 2.15.3) (Young & Bowman 1995, Bowman & Azzalini 2003) (Young & Bowman 1995, Bowman & Azzalini 2003), with cross-validation used to estimate bandwidths (*h*) for each ANCOVA. Analyses were conducted on logit (log(y/[1-y])) transformed data (as recommended in Warton and Hui (2011)) but, as the results of these analyses are essentially identical to the untransformed data, we present the plots with the C and N data in their untransformed forms (%) as these are easier to interpret.

C and N depletion rates were calculated as the half life (assuming exponential depletion rates) expressed in days as:

$$Ƭ = -1/k \cdot ln(1/2) \quad (7.1)$$

where Ƭ is the half life in days and *k* is the decay constant. Both *k* and Ƭ assume exponential C and N decay rates.

We used a relationship between worker termite head width and body mass to calculate the mean mass of individual termite species (for further information see Dahlsjö et al., 2014):

$$M = 3.71w \quad (7.2)$$

where *M* is the mass in mg and *w* is the head width in mm. The termite species mass estimates were used to calculate termite biomass (gram per bait) using the abundance measurements from the microcosms. The average mass of individual Enchytraeidae (pot worms, the only other macrofauna found in the microcosms), from Schmelz et al. (2013) was used to calculate biomass (gram per bait) using the abundance measurements in the microcosms. Data analyses were conducted using R (version 2.15.3).

Abundance and biomass of termites and pot worms (mean ± SE) were plotted for each sampling occasion in order to visualise colonisation rate, and abundance and biomass after colonisation. While termites were found on all sampling occasions, pot worms occurred only twice (in very low numbers), so statistical tests comparing the abundance and biomass of termites and worms would be statistically unwarranted.

7.3. Results

The loss of soil C and N was higher in microcosms with macrofauna, smaller fauna and microbes combined (total loss of C = 35.4% and N = 30.6%) compared with those with microbes and smaller fauna alone (total loss of C = 27.2% and N = 22.1%). The rates of depletion of C and N were significantly different, in both their gradients (rejecting equality) and the shape of the trend lines (rejecting parallelism), when microcosms including and excluding macrofauna were compared (Figure 7.1). The equality analysis investigates whether data for including and excluding macrofauna shift significantly along the y-axis where the shaded area shows the expected range if the two curves followed the same trend line. The parallelism analysis examines the differences in the shape between microcosms including and excluding macrofauna where the vertical and horizontal lines indicate the modelled parallel limits if the curves were parallel. Microcosms with microbes only had higher C and N content than microcosms with microbes and macrofauna combined (Fig. 7.1). In microcosms with macrofauna the half life of C and N were 177.7 days and 212.7 days, respectively across the sampling period, while C and N had a half life of 244.6 days and 310.1 days, respectively, in microcosms with microbes alone. Highest mean termite abundance and biomass were found in the dry season at day 28 (658.7 indv/bait and 2.2 g/bait, respectively), while the lowest abundance and biomass were reached at the end of the experiment in the wet

season at day 112 (116.7 indv/ bait and 0.2 g/ bait, respectively). However, the difference between the maximum and minimum abundance and biomass were not significantly different. The only other macrofauna encountered in the microcosms were pot worms (Enchtraeidae) which had low abundance and biomass with a maximum of 2.3 indv/ bait and 0.0004 g/ bait, respectively. Termite biomass and the number days after the start of the experiment were significantly correlated with C and N depletion rates (P values < 0.01) while termite abundance did not show a significant correlation (P values >0.05).

Of the termite functional groups only FGII (wood and litter-feeding) and FGIII (humus-feeding) were found colonising the soil microcosms while FGIV (true soil-feeding) termites and FGI (wood-feeding) termites were absent. Pot worms were the only other macrofauna to colonise the soil microcosms. Termites had colonised the soil microcosms in the first week of the experiment and were found on all sampling occasions throughout the experiment while pot worms were found on two sampling occasions (at 28 days and 112 days) (Fig. 7.2). The abundance and biomass of termites in the treatment soil increased throughout the dry period, up to 28d of the incubation period, but declined at the start of the wet season at 56d while the abundance and biomass of pot worms were constantly low (Fig. 7.2).

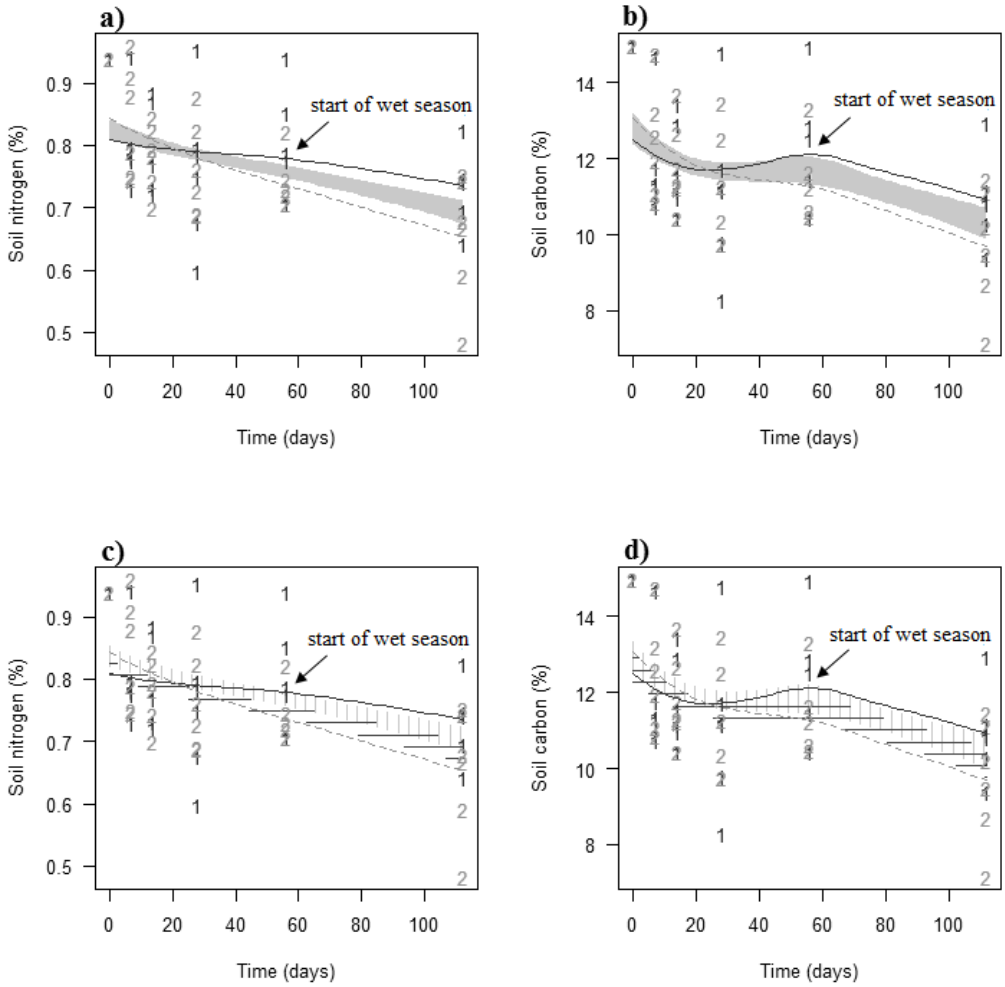

Figure 7.1. Nonparametric ANCOVA results of equality (a-b) and parallelism (c-d) for N and C content comparing microcosms including (hatched line) and excluding (solid line) macrofauna. The numbers 1 (microcosms without macrofauna) and 2 (microcosms with macrofauna) display the range of the data. The equality analysis investigates whether data for including (hatched line) and excluding (solid line) macrofauna shift significantly along the y-axis where the shaded area shows the expected range if the two curves followed the same trend line. The parallelism analysis examines the differences in the shape between microcosms including (hatched line) and excluding (solid line) macrofauna where the vertical and horizontal lines indicate the modelled parallel limits if the curves were parallel. Bandwidths were: h = 18.3** (equality) and h = 18.3** (parallelism) for C and h= 40.0** (equality) and h = 39.2** (parallelism) for N, as estimated by cross-validation. ** P <0.01.

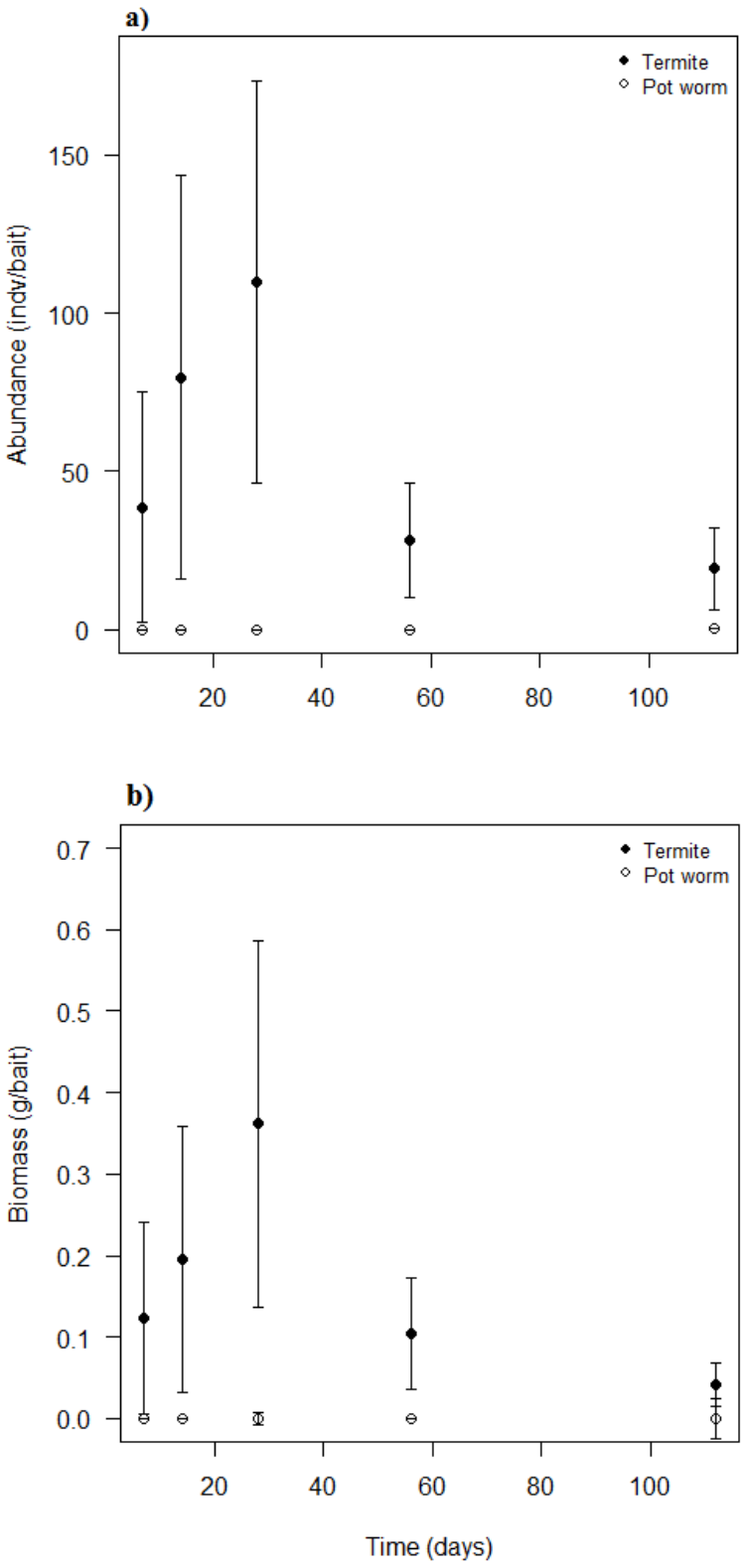

Figure 7.2. Abundance (individuals per bait) (a) and biomass (gram per bait) in all microcosms (b) of termites (filled circle) and pot worms (empty circle) mean ± SE at each sampling occasion (7, 14, 28, 56, and 112 days).

7.4. Discussion

7.4.1. Termite functional groups and decomposition

This study is one of the first *in situ* soil exclusion experiments examining the direct effect of termites and other macrofauna on soil C and N content. Our findings support the termite functional group classification proposed by Donovan et al. (2001a). Of the four functional groups that are present in Peru, only two (FGII and FGIII-feeding termites) were found in the treatment soil microcosms. Termite functional groups are partly classified by the level of humification of the organic matter they feed on (Eggleton & Tayasu 2001), thus the level of humification of a substrate plays an important role in the presence or absence of certain termite functional groups. Because the experimental soil was collected in the Peruvian highlands where termites are absent and decomposition rates are low (Palin et al. 2010, Zimmermann et al. 2010, Salinas et al. 2011), the soil had a high humus content with both large and small visible plant residues, which fits the functional group classification for both FGII and FGIII-feeding termites (Donovan et al. 2001a). The absence of FGI feeding termites is likely due to the lack of woody plant material in the bait soil as most FGI feeding termites in tropical South America feed on sound dead wood. The absence of FGIV-feeding termites throughout the experiment (four months) suggests that the SOM was not sufficiently decomposed to attract true soil-feeding termites that feed on soil with high mineral content.

7.4.2. The role of microbes and macrofauna in soil carbon and nitrogen loss

In this study we found that overall the effect of microbes, smaller fauna and macrofauna combined in C and N depletion was larger than the effect of microbes and smaller fauna alone. This suggests that macrofauna play an important role in the depletion of both C

and N in the bait soils. Depletion rates were highest at the start of the experiment, which may be due to the rapid breakdown of labile C and N pools, which then slowed as the proportion of stable elements became higher (Schwendenmann & Pendall 2008). The rate of C and N decline slowed after day 28 of incubation, particularly in microcosms with microbes and smaller fauna only, which may be due to reduced microbial activity as the labile pools of C and N were depleted (Schwendenmann & Pendall 2008) and the lack of replenished C and N through litter breakdown by macrofauna.

Although a high abundance of earthworms (755 indv/m^2) has been found in forest ecosystems elsewhere (Bartz et al. 2013) only very low abundances of pot worms were found in the soil microcosms suggesting that the macrofauna effect was mainly due to the presence of termites. The split of the decomposition period into two seasons (wet and dry) complicates the interpretation of the results as termites are known to be less active in the wet season (Dibog et al. 1998). While an increase in rainfall changes termite abundance and biomass the overall species composition has been shown to be roughly the same in the dry and wet season (Dibog et al. 1998) suggesting that the effect of termites is reduced with increased rainfall. Yet, soil that had not been inhabited by termites was shown to have lower depletion rates even in the wet season when microbial activity has been shown to increase (Araújo et al. 2013). In contrast, the C and N depletion rates were continuously higher in microcosms including macrofauna even when termite activity decreased in the wet season. These trends suggest that the presence of termites in the soil may promote depletion of C and N which may be linked to the passage of soil through the termite gut and the role termites play as ecosystem engineers (Jouquet et al. 2011) encouraging bioturbation and microbial activity.

7.4.3. Termites and other macrofauna in the treatment soil

Our results show that termites were the most important soil macrofauna in the translocated soil both in colonisation speed, and abundance and biomass after colonisation; although the spatial heterogeneity of termites and rapid colonisation rate also suggest that termites may have colonised microcosms prior to individual sampling occasions and may then have died in the microcosms or migrated away. Pot worms were only present at days 28 and 112 of decomposition with very low abundance and biomass. No other macrofauna were found in the microcosms which suggests that either their abundance and distribution in the habitat are low, or that they are not true soil-colonisers but inhabit the litter layer in a similar way to millipedes and woodlice.

7.4.4. Conclusions

Overall the loss of C and N were largest in microcosms with microbes and macrofauna combined. The high decay rate induced by the presence of macrofauna was likely principally due to the presence of termites in the microcosms; their rapid soil colonisation rate and the high abundance and biomass of termites in the treatment soil are likely to be important factors in the observed decomposition of C and N in the baits. Any general conclusions must, however, be assessed at replicated sites in South America and other rain forest regions.

This study was necessarily limited to the analysis of C and N. However, future investigations should also consider pH and phosphorus (P) as these are commonly known to be affected by termites (Ackerman et al. 2007, Rückamp et al. 2010). The inclusion of soil trace gas emissions (e.g. CH_4, CO_2, N_2), particularly from nests in soil, might lead to a better understanding of C and N cycling. Additionally, as termite activity is higher in the dry season than in the wet season (Dibog et al. 1998), and

because of the turnover effect of soil microorganisms, we suggest that studies of both wet and dry seasons are conducted to further our understanding of the relative importance of termites in decomposition across annual cycles.

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CHAPTER VIII

DISCUSSION AND CONCLUSION

8.1. Discussion

In this thesis I have examined the environmental and spatial factors that act on species composition patterns in a lowland tropical forest in Peru as well as the efficiency of two alternative sampling methods, the transect method (TM) and the quadrat method (QM). Additionally, I have used the data set from Peru to conduct the first intercontinental comparison of termite feeding-group abundance and biomass which also enabled a more detailed study of the body mass-population density relationship among feeding-groups. Finally, the first *in situ* soil macrofauna exclusion experiment was conducted in Peru which provided an insight into the effect of termites on soil C and N loss as well as a method that may be used to further our understanding of the role termites play in soil processes.

South American termite species assemblages are characterised by high diversity of soil-feeding termites (Davies et al. 2003a, Bourguignon et al. 2011a) with particularly high diversity of the *Anoplotermes*-group (Bourguignon et al. 2011a). While a relatively high number of South American termite studies have been conducted the focus has often been on the effect of disturbance (Davies 2002, Vasconcellos et al. 2010), the ecology of wood-feeding termites (Apolinário & Martius 2004, Roisin et al. 2006), termites in Amazonian floodplains (Martius 1992, 1994, Martius et al. 1994) or populations of specific species (Martius & Ribeiro 1996, López-Hernández 2001, Vasconcellos & Moura 2010). Additionally, while the comparison of termite assemblages in different regions or land uses is common (Davies et al. 2003b, Vasconcellos et al. 2010, Souza et al. 2012) the understanding of the factors that influence local termite species and feeding-group assemblages are less well known. The spatially replicated termite assemblage data in this study, therefore, provide a better understanding of the drivers of termite species composition in soil and dead wood on a small spatial scale from an area where little data of this kind are available. Additionally, since

termite density data were collected using two alternative sampling methods (the quadrat method and the transect method), from the same species assemblage, I was able to compare and contrast the two data sets and discuss the efficiency and suitability of the two sampling methods.

I found that environmental variables explained the largest proportion of the species composition in both soil and wood compared with spatial variables. Additionally, I was able to identify the environmental determinants of the species composition. The most important environmental variables for determining species composition in both soil and wood were soil temperature, plot elevation and the distance from the plot to the river. These variables may be related to canopy structure and flooding which have been shown to be some of the major determining factors for termite assemblage structure (Eggleton et al. 1995, 1996, 1999, 2002, Macdonald et al. 1998, Dibog et al. 1999, Davies et al. 2003b). Although, these results may not be surprising, while other studies have focused on habitat effects across sites, our results show that these large scale effects also act on a smaller scale (within site) driven by habitat heterogeneity (Palmer & Dixon 1990, Hasemann & Soltwedel 2011).

Huising et al. (2008) discuss the importance of defining the spatial scales in order to make hypotheses and plan the sampling design. The impact of environmental variables on species composition was examined at two different spatial scales. Elevation, distance from the river, distance from the lake and soil C and N content were measured at the plot level (300 m apart) while soil temperature and moisture were measured at the quadrat level (5 m apart). The recommended distance between plots for the study of termites is 200 m (Bignell 2009) to reduce spatial autocorrelation. Studies have shown that *Reticulitermes* sp. have feeding ranges between 41 m (Grace 1990) and 330 m (Crist 1998) in savannah habitats and so we expect that the majority of species in the Peruvian site forage over shorter distances, within the soil or in dead wood or leaf litter. Plots were therefore established 300 m apart

enabling us to treat the plots as genuine replicates. Further Donovan et al. (2007) show that termite colonies cluster at a spatial scale smaller than four metres and so the quadrats were located five meters apart in each plot in order to reduce autocorrelation. Although, soil samples were collected at the quadrat level for C and N analyses only half of the samples were analysed and pooled to create an average plot value. This was done due to time constraints.

Soil-feeding termites have been shown to have a homogenous distribution in primary forests with dense canopy cover regardless of the spatial scale while the distribution of soil-feeding termites in logged forests have been shown to be aggregated at all spatial scales (Donovan et al. 2007). The primary forest site in Peru (average canopy cover of 89%) features frequent natural tree falls that affects the canopy structure at a scale of 10 m^2. In patches with tree falls the canopy cover may be very sparse (56%) surrounded by dense (99%) canopy (Palin 2008, thesis) which may have an effect on soil temperature and moisture (Gehlhausen et al. 2000, Szarzynski & Anhuf 2001) at the quadrat level where these variables were measured. Moreover, although elevation may be seen as a large scale variable the small differences in elevation (215 - 224 m asl) affected termites species composition in the study. The close proximity of the Tambopata river and the Torre river to the site made lower elevation plots close to the rivers prone to inundation either due to the expansion of the river or due to the height of the water table (Davies et al. 2014).

Further, Huising et al. (2008) also discuss random and non-random sampling linked to the study objectives e.g. whether the average number of species is sought or whether an effect is tested. If the average number of species is of interest a random sampling regime would be suitable as it reduces sample bias and autocorrelation while non-random sampling would be suitable to test e.g. the effect of change on species diversity as sampling areas should be chosen to enable trends, such as land-use change, to be detected. Termite sampling methods

rang from trapping systems like monoliths and pitfall traps to sampling techniques such as quadrats and transects (Huising et al. 2008). Particularly, the standardised transect sampling protocol, introduced by Jones & Eggleton (2000), has been deployed extensively at a global scale (Davies et al. 2003a, Deblauwe et al. 2008, Palin et al. 2010) while quadrat sampling (Eggleton et al. 1996, 1999) and intensive plot sampling (Vasconcellos 2010, Bourguignon et al. 2011b) are much less common. The transect and quadrat sampling methods differ in their sampling approach making them suitable for different types of study objectives. For the transect method (Jones & Eggleton 2000) 100 m x 2 m transects are divided into 20 sections which are actively sampled for one person hour (sampling by one person for one hour) each. This means that sampling may take place over a large area (200 m^2 per transect) and over a relatively short period of time (20 h per transect) while collecting termites from a range of microhabitats (soil pits, dead wood, runways and nests). On the other hand, the quadrat method is based on ten 2 m x 2 m quadrats in each plot (40 m^2 per plot) where all termites in one soil pit and all dead wood in each quadrat are collected. The quadrat method may therefore be very time consuming as the sampling period depends on the abundance of termites in the quadrats.

The quadrat method in this study was based on the randomised standardised sampling protocol in Eggleton et al. (1996), however, due to space limitations and sampling design (see Methods Chapter) the quadrats were necessarily nested within two 10 m × 50 m transect in each plot. Although, the plots were randomly placed in the higher elevation area of the forest the quadrats were located at regular intervals five meters apart in the plots. In the strictest sense the quadrats would therefore be transects (Huising et al. 2008). Randomisation enables unbiased estimates of termite diversity and abundance to be measured, however, as the quadrats were located in two transects (30 meters apart) in randomly located plots five meters apart I argue that autocorrelation between the samples and the bias of the sampling location

was low. Additionally, as the quadrat sampling method requires exhaustive sampling this distinguishes it from the transect method where representatives are sampled from 20 consecutive sections. The transect method provides an efficient sampling technique but suffers from high autocorrelation while the QM is a highly time consuming sampling technique that provides absolute abundances and lower autocorrelation. The difference between the sampling methods was clearly shown in the results suggesting that the transect method is the most efficient method for estimating species density. Additionally, I found that the similarity in species composition between plots was higher using the transect method compared with the quadrat method suggesting that the latter may have underestimated the species diversity in the plots. The transect method is therefore also the most comprehensive sampling method for species composition, although, the quadrat method should still be regarded as an important method for sampling of biomass and abundance data.

Sampling with the quadrat method provided the first comparable termite biomass and abundance data for South America which, along with data from a site each in Cameroon (Eggleton et al. 1996) and Malaysia (Eggleton et al. 1999), enabled the first intercontinental comparison of termite biomass and abundance estimates. Due to the efficiency of the standardised transect sampling method comparable termite species density data are relatively well represented globally (Davies et al. 2003a). However, although species density data are important for understanding termite assemblage structure biomass and abundance data are needed in order to quantify the importance of termites in ecosystem functioning. As data sampled with both the transect method and quadrat method were available for the three regions (Peru, Cameroon and Malaysia) I was able to compare the species density data sampled with the transect method with the global data set from Davies et al. (2003a). As biomass and abundance data were only available from three sites, one in each region, the comparison of species density data with the global data set was done to find out how

representative the data from the three regions were. I found that the species density data from the three sites showed similar patterns to the global species density data, with Africa (Cameroon) having the highest species density followed by South America (Peru) and then southeast Asia (Malaysia).

The biomass and abundance values were, by far, highest in Cameroon followed by Malaysia and then Peru demonstrating that, while species diversity in Peru is high, species abundances is fairly low. The main differences among the sites were identified as the presence or absence of different lineages, particularly the dominance of two endemic soil-feeding lineages (*Cubitermes*-group and *Apicotermes*-group) in Cameroon and the absence of fungus-growing termites from Peru. As the biogeography of termite lineages was determined by evolutionary dispersal events (Gathorne-Hardy et al. 2000, Davies et al. 2003a, Aanen & Eggleton 2005, Nobre et al. 2010) the patterns of termite biomass and abundance are mainly due to termite evolution rather than present day climate, although, the latter may affect local termite assemblage structure (Eggleton et al. 1995, Gathorne-Hardy et al. 2001).

I also noticed that the body masses of the feeding-groups were different in the different regions. Wood-feeding termites in Cameroon were small-bodied and the soil-feeding termites were large-bodied while the opposite was observed in Malaysia and Peru where wood-feeding termites were large-bodied and soil-feeding termites generally small-bodied. As body mass is an important physiological trait affecting abundance, metabolic rate and growth rate (Brown et al. 2004) the difference in body mass for the same functional group may have an effect on the ecosystem processes influenced by termites in different regions. Particularly, as it has been shown that small-bodied wood-feeding termites and large-bodied soil-feeding termites are the most effective at processing their feeding substrate (Eggleton et al. 1998), the body mass of functional groups is likely to play a role in their contribution to ecosystem processes.

The observed body mass and abundance data were tested against the prediction of Damuth's law (that population density scales with body mass as $M^{-0.75}$) for individual feeding-groups. I found that none of the feeding-groups fitted the predicted values perfectly, while only the large-bodied soil-feeding termites in Cameroon and the large-bodied wood-feeding termites in Peru diverged significantly from the expected values. The soil-feeding termites in Cameroon and wood-feeding termites in Peru were the only feeding-groups whose body masses had strong positive relationships with population density suggesting that the large-bodied species in those populations controlled a larger proportion of the energy than expected by their body masses.

In chapter V, I hypothesised that regions with high biomass and abundance of soil-feeding termites would have higher degree of soil process activity, while regions without fungus-growing termites would have lower wood-decomposition. By examining the resource distribution in feeding-group populations with species of different sizes I was able to test the hypothesis using an allometric approach. Large-bodied soil-feeding termites in Cameroon were shown to process the majority of the available resources in their population. As large-bodied animals, feeding on nutrient poor substrates, have been shown to have better nutrient uptake compared with smaller-bodied animals (Müller et al. 2013) the results support the hypothesis suggesting that regions with the large-bodied lineages *Cubitermes*-group and *Apicotermes*-group will have higher rates of soil processes.

I also hypothesised that areas without fungus-growing termites would have lower wood decomposition than areas with fungus-growing termites. The results from chapter VI, using allometric scaling laws, show that large-bodied wood-feeding termites in Peru processed a larger proportion of the resources than expected by their body mass. As fungus-growing termites do not exist in South America their absence may have had an effect on the energy flow in wood-feeding termites. The high proportion of resources managed by the

large-bodied species in Peru suggest that wood decomposition in Peru, without fungus-growing termites, may be higher than might otherwise be predicted.

In the first three results chapters I examine how local and global termite species density, abundance and biomass patterns and allometric relationships may impact on ecosystem processes. To support these results with experimental data a large decomposition experiment including soil, leaf litter and wood was conducted in 2012 with an experimental period of four months. Unfortunately, mass losses of leaf-litter and wood throughout the experimental period were non-significant and subsequently not included in any of the results chapters.

The leaf-litter exclusion experiment was conducted using 30 cm × 30 cm nylon mesh bags with fine (0.3 mm) and coarse (5 mm) mesh to exclude and include macrofauna, respectively. Leaves from five of the most common species in the site (Salinas et al. 2011) were collected and one leaf from each species was placed in each litter bag (~1.4 g). This was recommended (pers. comm. Salinas, 2012) as the experiment was run over a period of four months while 3 g of leaf-litter had been used in the same site over a period of 1.5 years (Salinas et al. 2011). The non-significant results may have been due to the low sample weight as well as the short sampling period which may have contributed to the noise in the data which meant that the results could not be interpreted in any meaningful way.

The wood exclusion experiment was conducted using the same type of mesh bags as in the leaf-litter experiment. I intended to use Aspen wood as it is widely available world-wide and has low density which would have provided decomposition data within the short sampling period (four months). Additionally, the experiment was replicated in Ghana (Africa) with Aspen in order to make an intercontinental comparison of the impact of termites on wood decomposition. Due to permit delays in Peru the intended aspen wood had to be

replaced by local ‘Cedro’ wood. Although the same density wood (0.4) was sought the density of the local wood was much higher than Aspen which may have affected the results. Additionally, we could not control for the chemical composition in the wood that may have deterred termites. After four months there was no notable difference between the wood in either of the mesh treatments in Peru. The results from the Ghanaian study were neither interpretable due to unknown factors. As the sampling in Ghana was done by trained assistants I was unable to identify the root cause of the dubious results. Many of the sampled gained weight and so it is possible that the wood was not dried to constant weight or that sheeting or dirt was left on the wood. Communication with the Ghanaian group did not clarify whether this was the case. If the exclusion experiments with leaf-litter and wood could be conducted again heavier leaf litter samples would be used to reduce the noise in the data. Additionally, wood with the relevant density and chemical composition would be sourced. As particularly the mass loss of wood was very low at the end of the four month experiment a longer decomposition period would be needed for a trend to be recorded (Salinas et al. 2011).

The soil macrofauna exclusion experiment gave significant results and is to our knowledge the first *in situ* experiment of its kind. I translocated soil from a montane forest at 3000 m asl where termites were absent to a lowland termite inhabited site at 190 m asl. The translocated soil had higher carbon (C) and nitrogen (N) content than the soil in the lowland site, which may have attracted termites to the baits. However, as the same soil was used in all samples the use of soil with high organic content may have enhanced the observed effects rather than altering the outcome of the results. The top and bottom of plastic containers were replaced by fine and coarse mesh to exclude and include macrofauna respectively. The plastic containers were placed in the ground with the top being two centimetres below the surface. Termites and other macrofauna were collected from the samples at each sampling occasion to estimate abundance and biomass in the soil samples. The experiment was conducted over

four months and spanning both the end of the dry season and the start of the wet season. The extension of the experiment into the wet season was not intended, but due to delays in the field, the use of the two seasons produced some interesting results.

Abundance and biomass estimates from the samples revealed that termites were the most dominant invertebrates with only pot worms being the other macrofauna found. It is therefore fairly certain that the observed effect seen in samples with macrofauna was mainly due to the presence of termites. The results agree with Dibog et al. (1998) suggesting that termite activity was reduced in the wet season. Yet, soil that had not been inhabited by termites was shown to have lower reduction rates even in the wet season when microbial activity has been shown to increase (Araújo et al. 2013). In contrast, the C and N reduction rates were continuously higher in samples including macrofauna even when termite activity decreased in the wet season. These trends suggest that the presence of termites in the soil may promote loss of C and N which may be linked to the passage of soil through the termite gut and the role termites play as ecosystem engineers (Jouquet et al. 2011) encouraging bioturbation and microbial activity.

The sampling was done with higher sampling frequency at the start of the experiment to detect patterns caused by loss of labile C and N (Schwendenmann & Pendall 2008). The C and N reduction rates were high until day 28 of incubation after which they became slower suggesting that the first two sampling occasions (7 days and 14 days incubation) could have been used at later stages enabling sampling over a longer period of time. Although, the results showed that termites promote C and N loss, even after their reduced abundance and biomass in the wet season, if this experiment was conducted again it would have been restricted to one season, or included both the full dry and wet seasons, to avoid dubious results.

In addition to the soil exclusion experiment a stable isotope experiment was conducted in five separate plots in order to examine the feeding range of wood and soil-feeding termites using C3 and C4 plants with different $\delta^{13}C$ stable isotope levels (C3 = $\delta^{13}C$ -24 to -34‰ and C4 = $\delta^{13}C$ -6 to -19‰). Maize was used as a C3 bait which was expected to change the stable isotope signal in termites that were feeding on predominantly C4 plants. The maize was placed in the centre of each plot and termites were collected before the start of the experiment and every two weeks for a period of six weeks from runways or nests in trees up to 20 m from the bait and from soil pits 1m, 2 m and 4 m from the bait. The aims were to investigate (a) how far away from the bait the C3 isotopes would be detected i.e. the feeding range of wood-feeding termites and (b) the time it takes for the carbon to be utilised by the soil-feeding termites in the soil around the bait. I received a grant in order to analyse the samples at the Centre for Environment and Hydrology at the University of Lancaster. The $\delta^{13}C$ stable isotope levels in termites that had been identified to species level were analysed, however, there was no difference between samples that had been collected before the start of the experiment and samples that had been collected at the three sampling occasions. If this experiment was conducted again $^{13}CO_2$ pulse-labelling of baits may provide better results (Leake et al. 2006).

In this thesis I have begun to show the role termite play in lowland tropical forests. By examining termite assemblage structure and function on local and intercontinental scales we now have a better understanding of what drives termite assemblage structure and how and why termite assemblages may differ across regions. We also have a better understanding of the role different termite lineages play in resource distribution through the paper on allometric scaling relationships. Moreover, I have identified the importance of the presence of termites in soil for nutrient cycling. To conclude, I have showed that termites are important in

ecosystem processes and how their patterns and resource distribution, both taxonomically and functionally, differ globally.

8.2. Future research and recommendations

8.2.1.Further research

The work in this thesis has provided data that may be important for further research into the role of termites in tropical forests and particularly in ecosystem processes. Future research include:

1. Further research into the global biomass and abundance patterns and what they mean for ecosystem functioning through replication of the standardised sampling protocols.

2. Investigation of the role of termite functional groups in ecosystem processes, from wood decomposition to soil bioturbation and nutrient turnover, on a local scale in order to compare global functional patterns.

3. Examination of the role of soil-feeding termites, particularly the soldierless *Anoplotermes*-group that nest in the ground, in soil processes. Data on these termites are sparse but they may play an important role in soil processes in regions, outside of Africa, where the very dominant *Cubitermes*-group and *Apicotermes*-group are absent.

4. Investigation of the role of fungus-growing termites in ecosystem processes though exclusion experiments. This would enable a better understanding of what impact fungus-growing termites have on wood and litter decomposition and resource distribution.

5. Investigation of the effect of termite abundance and biomass on soil microbial composition in tropical forests. By identifying the microorganisms in the samples this experiment would enable a more comprehensive understanding of how termites affect soil processes.

8.2.2. Recommendations

This thesis has provided information and data that may be useful for other studies. My recommendations are:

1. The data from the lowland tropical rainforest site in Peru provide an account of the similarity between plots as well as the environmental effects on assemblage structure. These data may be used as guidelines for other studies in similar sites for determining the replication of plots. The data may also be used to compare species composition in sites in different regions as well as the importance of similar environmental drivers.

2.The use of two comparable sampling methods, the transect and quadrat methods, has provided insights into the use of the two methods. This information may be useful when sampling designs are developed.

3. The data from the intercontinental comparison of termite biomass and abundance data are the first to be presented of its kind. These data may, therefore, be used as references of global termite biomass and abundance patterns for further comparative studies. Recommendations include further replication of data using comparable methods (the transect and quadrat methods) to increase understanding of how termites affect ecosystem processes in different regions.

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