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**INTER-CONTINENTAL PATTERNS IN THE FINE-SCALE
SPATIAL ECOLOGY OF RAIN FOREST TERMITES**

By

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in partial fulfilment for the degree of

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Olivia I Scholtz
Inter-Continental Patterns in the Fine-Scale Spatial Ecology
of Rain Forest Termites

Abstract

In this thesis I describe fine-scale spatial patterns in rain forest termites, from the colony to the assemblage level, sampled from one hectare plots in Central African and South East Asian lowland rain forest. By so doing the ecological interactions that structure this functionally important and abundant soil community were identified. The African termite assemblage, dominated by soil-feeding termites, saturated the upper soil profile (collected from 90% of soil pits) In contrast termites were collected from <50% of soil pits in Asia, with this difference reflecting the lower species densities and abundances of soil-feeding termites in Asian forests. Territoriality and inter-specific competition was shown to be important between colonies of soil-feeding species in the African plot. The termite assemblages were spatially associated with several environmental properties. However these could not explain the spatial patterns in the functional components of the assemblages. Wood-feeding termites were highly patchily distributed, due to the heterogeneous nature of their food material, but also due to possible competitive interactions for this. Humus-feeding termites were homogenously structured, due to the continuous nature of soil as their feeding and nesting material. True soil-feeding termites, unique to the African assemblage, were heterogeneously distributed despite the equally continuous nature of their feeding and nesting material. This structure may arise from facilitative interactions, such as co-operative defence against ant predation which may be intense in African systems, or through the transfer of soil material at different stages of decomposition. Competition for space is apparent in both regions, both at the colony level among soil-feeding genera, and between aggregations of functional groups. Positive and negative biotic interactions, operating at various spatial and functional scales, appear to be important in influencing how assemblage composition is spatially structured. If indeed facilitation is important in maintaining the taxonomic and functional diversity in termite assemblages, it would be valuable to confirm the mechanism(s) that drives this (i.e. predation and/or food transfer), as these may then influence ecosystem stability.

Contents

List of figures.....	ix
List of tables.....	xiv
Acknowledgements.....	xvi
Author's declaration.....	xix
Abbreviations and acronyms	xx
1 General Introduction	1
1.1 Overview.....	1
1.2 Scale in ecological patterns and processes.....	2
1.2.1 Historical considerations of local assemblage composition.....	2
1.2.2 Interpreting local-scale spatial patterns.....	3
1.3 Ecological interactions in soil communities.....	4
1.4 Termites.....	8
1.4.1 General background.....	8
1.4.2 Feeding and nesting strategies	9
1.4.3 Rainforest termites and biogeographic history	11
1.5 Thesis outline.....	14
2 Fine-scale environmental conditions in an African and Asian rain forest. 17	
2.1 Summary	17
2.2 Introduction.....	17
2.3 Methods.....	21
2.3.1 Study site selection and description	21
2.3.2 Daqum Valley Conservation Area, SE Asia.....	22
2.3.3 Ivindo National Park, Central Africa.....	23
2.3.4 Environmental Measurements.....	25
2.3.5 Data exploration	29
2.4 Results.....	30
2.4.1 Relationships between C_{tot} and C_{org}	30
2.4.2 Frequency distributions and differences.....	30
2.4.3 PCA data exploration	33
2.5 Discussion	38
2.5.1 Comparison of environmental conditions	38
2.5.2 Environmental relationships	42
2.6 Conclusions	44

3	Soil-dwelling macrofaunal assemblages. composition, occupancy and co-occurrence..	46
3.1	Summary...	46
3.2	Introduction .	47
3.3	Methods.	49
3.3.1	Sampling design.....	49
3.3.2	Spatial scale	51
3.3.3	Field sampling .. .	52
3.3.4	Taxonomic identification.....	54
3.3.5	Functional group assignment.....	55
3.3.6	Ant identification and classification..	57
3.4	Results.....	57
3.4.1	Termite assemblage composition and occupancy rates ..	57
3.4.2	Soil occupancy patterns ..	63
3.4.3	Ant assemblage composition	64
3.4.4	Macrofaunal co-occurrence patterns.....	68
3.5	Discussion	70
3.5.1	Termite assemblage representativeness	70
3.5.2	Occupancy and co-occurrence patterns of NSF and SF termite ...	72
3.5.3	Occupancy and co-occurrence patterns of termites and ants ..	73
4	Colony extent and inter-specific interactions in mound-building rain forest termites (<i>Cubitermes</i> -group, Termitidae).....	76
4.1	Summary.	76
4.2	Introduction.....	77
4.3	Methods.....	80
4.3.1	Data collection... ..	80
4.3.2	Microsatellite genotyping	81
4.3.3	Spatial analysis of mound and pit samples	82
4.4	Results	83
4.4.1	Genetic markers and parental genotypes .. .	83
4.4.2	Microsatellite assignment of pit samples to mounds	85
4.4.3	Community description and spatial structure	88
4.4.4	Carbon concentrations	90
4.5	Discussion	91

4.5.1	Foraging distances and mound dispersion.....	91
4.5.2	Mound aggregation	94
4.5.3	Population processes and species co-existence.....	95
4.5.4	Scale of ecosystem services	96
4.5.5	Microsatellite markers	97
4.6	Conclusions	98
5	Spatial patterns in rain forest termite assemblages; an examination of abiotic and biotic interactions.....	100
5.1	Summary	100
5.2	Introduction.....	101
5.2.1	Environmental relationships	103
5.2.2	Inter-feeding-group facilitation.....	106
5.2.3	Predator-prey interactions.....	107
5.2.4	General hypotheses	108
5.3	Methods.....	109
5.3.1	Spatial and Statistical analysis	110
5.4	Results.....	114
5.4.1	SADIE red-blue structure	114
5.4.2	Environmental relationships	116
5.4.3	Inter-feeding-group relationships.....	120
5.4.4	Predatory-ant/termite assemblage relationships	122
5.5	Discussion	124
5.5.1	Environmental relationships	124
5.5.2	Inter-feeding-group relationships.....	130
5.5.3	Predator-prey relationships	133
5.5.4	Synthesis of spatial structure and ecological interactions	135
5.5.5	Biotic interactions in termite assemblages	137
6	Fine-scale assembly rules in rain forest termites; genus-level co-occurrence patterns are dependent on spatial scale and biogeographic history	139
6.1	Summary	139
6.2	Introduction.....	140
6.2.1	Resource availability gradient	142
6.2.2	Biogeographic history.....	143
6.2.3	Co-occurrence patterns.....	144

6.3	Methods	146
6.3.1	Null model analysis	147
6.3.2	Partitioning community variance into spatial and environmental components.....	148
6.3.3	Scale of spatial structure in community composition. ..	152
6.4	Results	153
6.4.1	Generic richness	153
6.4.2	Co-occurrence patterns	154
6.4.3	Variance partitioning analysis	156
6.4.4	Scale of assemblage spatial structure.....	157
6.5	Discussion	159
6.5.1	Resource availability gradient.	159
6.5.2	Biogeographic history....	162
6.5.3	Interpreting the co-occurrence patterns	163
6.5.4	Fine-scale assembly rules.....	167
7	Final discussion.....	172
7.1	Summary	172
7.2	Fine-scale rain forest structure	172
7.3	Colony extent and intra- and inter-specific interactions in soil-feeding termites	175
7.4	Feeding-group spatial structures	176
7.4.1	Wood-feeding termites	176
7.4.2	Humus-feeding termites	177
7.4.3	True soil-feeding termites	178
7.5	Scale-dependency of positive and negative interactions	179
7.6	Predatory-ant/termite interactions.....	180
7.7	Ecosystem services	181
7.8	Final conclusions	183
8	References.	185

List of figures

- Figure 1.1 Mean per transect species richness apportionment (mean±SE) between the four termite feeding-groups in undisturbed lowland equatorial forests (drawn from replicate samples between sea level and 1000m elevation) across S America, Africa and SE Asia. Feeding groups are coded as follows: group I, open column; group II, diagonal hatching; group III, horizontal hatching; group IV, black column. (taken from Davies *et al.*, 2003a, Fig. 2a. Permission to reprint this has been granted by John Wiley and Sons).13
- Figure 2.1 a) Location of Sabah in Borneo. b) Location of DVCA in Sabah. c) Significant features in the 'Danum' plot. Arrows indicate downslopes.23
- Figure 2.2 a) National Parks of Gabon with Ivindo National Park located in central Gabon. b) Langoué Field station in southern Ivindo N.P. c) Significant features in the 'Ivindo' plot. Arrows indicate downslopes.25
- Figure 2.3 Survey plot, divided into 64 sub-plots. Environmental variables were either measured from the 25cm x 25cm, x 15cm depth soil pit, or the 2m x 2m sample point as indicated.26
- Figure 2.4: Linear regression plot of Soil C_{tot} and C_{org} (from randomly selected sample pits) in Danum (n=58) and Ivindo (n=36).30
- Figure 2.5 Frequency distributions of soil variables from Danum (black) and Ivindo (red), with an additional combined normal distribution plot, that illustrates the differences in mean and variance between Danum and Ivindo. The sample mean and standard deviation of non-transformed data is included.32
- Figure 2.6 Combined frequency distributions of vegetation and dead plant material variables from Danum (black) and Ivindo (red). The sample mean and standard deviation is included.33
- Figure 2.7 PCA axis 1 vs axis 2 plot of environmental relationships. a) Danum, b) Ivindo. LL, leaf-litter; GC, ground vegetation cover.34

Figure 2 8 PCA environmental relationships without soil C_{tot} and N for Danum
(a, b, c) and Ivindo (d, e, f). a) & d) PCA axis 1 vs axis 2 plot LL, leaf-litter,
GC, ground vegetation cover b) & e) Contour plot of sample point axis 1
scores. c) & f) Contour plot of sample point axis 2 scores35

Figure 2 9 PCA axis 3 vs axis 4 plot of environmental relationships a) Danum,
b) Ivindo. LL, leaf-litter; GC, ground vegetation cover 37

Figure 2.10 The soil C and N relationship that explains the subsequent co-
correlation with C/N ratio in each site. Danum, black line; Ivindo, red
dashed line41

Figure 2 11 Schematic diagram summarizing the main environmental
relationships detected in axes 1 and 2 of the PCA analyses 44

Figure 3.1 Termite generic richness by feeding-group from the plot (Danum),
and PF* (two pooled transects in primary forest (Eggleton *et al.*, 1997)). 59

Figure 3.2 Danum rank abundance (number of hits per genus) distribution (on a
log scale) 60

Figure 3.3 Termite generic richness by feeding-group from the plot (Ivindo) and
PF* (two pooled transects in primary forest, Republic of Congo (Eggleton *et al.*, 2002b))
..... .. .62

Figure 3.4 Ivindo rank abundance (number of hits per genus) distribution (on a
log scale)63

Figure 3 5 Proportion of pits occupied by termites grouped by generic richness
per pit NSF, Non-soil-feeding (FGI and FGII); SF, soil-feeding (FGIII and
FGIV) 64

Figure 3.6 Ant genera rank order abundance (number of hits per genus)
distribution (on a log scale), with predatory ant genera highlighted a)
Danum, and b) Ivindo67

Figure 3.7 Proportion of pits occupied by ants grouped by generic richness per
pit. 68

- Figure 3.8 Soil-pit occupancy and overlap of termites (T), ants (A) and worms (W). Circle sizes approximately represent the relative proportions indicated as a percentage for each section.....69
- Figure 3.9 Soil pit occupancy and overlap of soil-feeding termites (SF), non-soil-feeding termites (NSF) and predatory-ants (PA). Shape sizes approximately represent the relative proportions indicated as a percentage for each section. An ellipse is used in lvingo 'PA' in order to retain representation of the proportions, including overlap with 'SF', 'NSF+SF', and 'NSF'.....70
- Figure 4.1 Upper section: Each row represents one of the 19 soil pits with full MS data. The distance to the nearest assigned mound (parental genotype) is represented along the x axis and indicated by the black circle. Green circles represent the distance from the soil pit to the nearest mound, e.g. pit #2, contained two offspring with full MS data which assigned to mounds ~70m away, while the mound closest to the pit was <5m away. In most cases offspring were assigned to their closest mound. Lower section: Frequency distribution of the distance between pit offspring and their nearest assigned mounds in 5m distance classes, e.g. 20 offspring were assigned to mounds 0 - 5m away.86
- Figure 4.2 Location of *C. severus*. Black cross, pit offspring that were assigned to a mound parental genotype; black circles, mounds with MS data; red circles, mounds lacking full MS data. Connecting lines are between offspring that do not assign to their closest mound, with the numbering corresponding to the pit # in Figure 4.1 and lack mound parental genotypes from their closest mound, or putative closest mound outside the plot. Dashed circles indicate offspring assignments to their closest mounds. ...87
- Figure 4.3 left to right. *Cubitermes* mound "against-tree", *Cubitermes* mound "free-standing", *T. macrothorax* mound.88
- Figure 4.4 Relative neighbourhood density (Omega) by distance of *C. severus* pit sample, and *T. macrothorax* pit sample. $\Omega_x=1$ for random distribution, $\Omega_x>1$ for aggregated distributions, $\Omega_x<1$ for dispersed distributions. Tails represent 95% confidence limits. Insert left: position of *C. severus* pits (red

circles) and mounds (open circles). Insert right. position of *T. macrothorax* pits (black circles) and mounds (open circles)..89

Figure 4.5 Relative neighbourhood density (Omega) by distance of all mounds, and a pooled sample of *C. severus* and *T. macrothorax* pits. $\Omega_x=1$ for random distribution, $\Omega_x>1$ for aggregated distributions, $\Omega_x<1$ for dispersed distributions. Tails represent 95% confidence limits 90

Figure 4.6 C_{tot} concentrations for soil samples from 'pits', soil pits not adjacent to a mound, 'pit by mound', soil pits adjacent to a mound, and 'mound', samples from *Cubitermes* spp mounds. Boxes indicate the interquartile range, horizontal lines within boxes indicate the medians, whiskers include all points to 1.5 times the interquartile range, asterisks indicate outlying values.91

Figure 5.1 SADIE red-blue plots, from Danum and Ivindo, for the full assemblage, and by feeding-group. I_a , Global index aggregation (from Table 5.2) is included in each plot 115

Figure 5.2 Site-specific and common significant SADIE spatial relationships between the termite assemblages and environmental variables +ve, positive association; -ve, disassociation. Ter, full assemblage, FGII, wood-feeding; FGIII, humus-feeding, FGIV, true soil-feeding. Arrows highlight where associations were opposing, either between feeding-groups within sites (highlighted in purple), or between sites... . 119

Figure 5.3 Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th a_u percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k . a) Danum FGII vs FGIII, $a_l=-2.73$, $a_u=2.71$. b) Ivindo FGII vs FGIII, $a_l=-2.800$, $a_u=2.841$ c) Ivindo FGIII vs FGIV, $a_l=-2.522$, $a_u=2.417$ 121

Figure 5.4 Association results of predatory ants (*P. Ants*) vs termite assemblage a) and b) Danum. c), d) and e) Ivindo a) and c) SADIE red-blue plot for predatory ants b) and d) Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th a_u

percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k . b) Danum, $a_l=-2.488$, $a_u=2.443$. d) Ivindo, $a_l=-2.560$, $a_u=2.146$. e) Additional plot taken from Ivindo (d) presenting only the significant local associations; black line envelopes ant patches (black dot and open circle); orange line envelopes termite patches (black dot and X). 123

Figure 6.1 Contour plots of the broadest and finest spatial vectors from PCNM analysis at two scales (cell sizes). 4m x 4m cell size a) PCNM vector 1 b) PCNM vector 403. 12m x 12m cell size c) PCNM vector 1 and d) PCNM vector 44. 150

Figure 6.2 C-Score index co-occurrence SES values at four cell sizes. a) Danum, b) Ivindo. FGII, wood-feeding; FGIII, humus-feeding; FGIV; true soil-feeding; Comm, full assemblage. Significant results exceed the upper and lower SES limits ($SES > 1.96$, lower co-occurrence than random i.e. exclusion; $SES < -1.96$, higher co-occurrence than random i.e. aggregation) with the critical limits represented by the parallel black dotted lines, and specific statistically significant results indicated by a black dot. 155

Figure 6.3 Plot of the PCNM vectors retained in a forward selection with the 8m x 8m full assemblage data, with dots representing retained vectors from the original matrix of 102 PCNM vectors. Low values represent broad spatial structure; retained vectors between 1 and 10 represent the broad spatial model, and retained vectors between 11 and 102 represent the medium spatial model. Contoured plots of PCNM vector 10 and 47 plots are positioned above their respective location. The pie charts present the $adjR^2$ values of the 'broad' scale and 'medium' scale models, as well as unexplained community variance 'none', in the RDA analyses. 158

Figure 6.4 Schematic diagram of spatially structured processes occurring at various scales between feeding-groups (FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding) in Ivindo and Danum. Black outlines indicate inter-genus aggregation, dashed in Ivindo as two-tailed test was not significant (see Figure 6:2). Arrows for exclusion indicate direction of exclusion. 170

List of tables

Table 1.1 Regional generic richness of lower termite families, and higher termite sub-families (compiled from Jones and Eggleton, 2010, unpublished).....	14
Table 2.1 Summary data of dead plant material and understorey vegetation ..	31
Table 2.2 Percentage of environmental variance explained in PCA axes .	34
Table 3 1 Danum termite genera. NG, nesting-group, h, hypogaeal-; e, epigeal-; w, wood-; a, arboreal-nesting FG, feeding-group; L(F), leaf-litter (fungus-harvesting); S/W, soil-wood interface.	58
Table 3.2 Ivindo termite genera. NG, nesting-group; h, hypogaeal-, e, epigeal-, w, wood-; a, arboreal-nesting FG, feeding-group; L(F), leaf-litter (fungus-harvesting) .	61
Table 3 3 Danum ant genera, and trophic description, with genera classified as predatory in bold (Brown, 2000).	65
Table 3.4 Ivindo ant genera, and trophic description with genera classified as predatory in bold (Brown, 2000).	66
Table 3.5 Generic richness by feeding-group in Danum and Ivindo, total rain forest richness in Indomalaysia and Africa (Jones and Eggleton, 2010, unpublished), and the proportion (prop.) of this sampled in the survey plots .	71
Table 4.1 Summary of the number of samples-points (and individual workers in brackets) with DNA extracts, with PCR products at loci 19, 34 and 36, and of these the average # workers per sample point .	84
Table 5.1 Local spatial relationships (χ_k): contour colours and symbols used in plots of association tests between biotic data ..	114
Table 5 2 SADIE red-blue analyses summary statistics.....	114
Table 5 3 Danum SADIE global index aggregation (I_a) for the environmental variables, and SADIE global association index (X) from association	

analyses between the environmental variables and the termite assemblage, FGII and FGIII.....	117
Table 5.4 Ivindo SADIE global index aggregation (I_a) for the environmental variables, and SADIE global association index (X) from association analyses between the environmental variables and the termite assemblage, FGII, FGIII and FGIV.	118
Table 6.1 Environmental data treatment during pooling of sample points. x , value recorded at sample point as described in Chapter 2; P/A, presence/absence data; Dan, Danum; Ivi, Ivindo.	151
Table 6.2 Mean number and standard deviation of genera at each cell size sample. FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding; Comm, full assemblage.	154
Table 6.3 Adjusted R^2 values (as percentage) for the pure environment component (PE), spatially-structured environment component (SSE), and pure space component (PS) in the VPA on the full and feeding-group assemblages at four cell sizes.	157
Table 6.4 Summary of hypothesized ecological interactions, operating at various functional levels and spatial scales. Full, full assemblage; FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding, scale of interactions in parenthesis.	168

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At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

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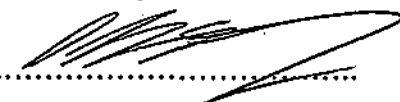
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Abbreviations and acronyms

DVCA	Danum Valley Conservation Area
EMMA	Electron Microscopy and Mineralogy Analysis
FGI	Wood-feeding non-Termitidae termites
FGII	Wood-feeding Termitidae termites
FGIII	Humus-feeding termites
FGIV	True soil-feeding termites
GC	Ground vegetation cover
H-W	Hardy-Weinberg equilibrium
LL	Leaf-litter
NHM	Natural History Museum
NSF	Non-soil-feeding termites
PA	Predatory ants
PCA	Principal components analysis
PCNM	<i>Principal co-ordinates analysis of neighbourhood matrices</i>
PCR	Polymerase chain reaction
RDĀ	Redundancy analysis
SADIE	Spatial analysis by distance indices
SES	Standardised effect size
SF	Soil-feeding termites
VPA	Variance partitioning analysis

1 General Introduction

1.1 Overview

Termites (Termitoidae) are particularly abundant in tropical rain forests, where they are one of the most important arthropod decomposers (Wood & Sands, 1978; Collins, 1983; Watt *et al.*, 1997; Bignell & Eggleton, 2000; Yamada *et al.*, 2005). Global patterns in termite diversity have been described (Eggleton *et al.*, 1994; Eggleton, 2000b), and within-region influences such as habitat disturbance on termite assemblage composition, have been the focus of considerable previous research (e.g. Eggleton *et al.*, 1999; Jones *et al.*, 2003). The local spatial patterns of rain forest termites, and the ecological processes that drive these are however largely unknown. From an applied perspective, we lack critical descriptive information on the scale at which the functional components of rain forest termites contribute to ecosystem services. From a theoretical perspective, efforts by soil ecologists to establish generalities of the important ecological processes in soil communities (e.g. Bardgett *et al.*, 2005; Decaëns, 2010) are constrained, partly due to a paucity of field-based studies. The aims of this thesis are to: 1) quantify spatial structure in rain forest termites, 2) gain insights into the spatial scale at which a number of key ecological interactions are operating, and 3) consider the role of historical biogeographic factors in influencing spatial patterns.

In this chapter I begin by providing a brief background on the scale-dependency of the processes influencing local assemblage composition, and factors that generate spatial patterns. Soil systems support particularly high species diversities (Heywood, 1995; Giller, 1996), and I outline the ecological processes considered important in soil communities. I then introduce the study taxon,

termites, their basic biology, taxonomic diversity and biogeographic history
Finally I provide an outline on the remainder of the thesis

1.2 Scale in ecological patterns and processes

1.2.1 Historical considerations of local assemblage composition

Species diversity patterns are the product of numerous scale-dependent processes structured in a hierarchical fashion, as summarized by Ricklefs and Schluter (1993). Global patterns are generated by past stochastic events such as evolutionary novelties, mass extinctions, and adaptive radiations, termed 'historical processes', which are frequently associated with geographic isolation, climatic shifts, and adaptation into empty niches. These therefore represent augmented or divergent evolutionary histories at the global scale. Nested within this, regional influences include geographic and ecological dispersal over evolutionary time. At the landscape scale species pools are constrained according to particular habitat preferences. At local scales, species interactions such as competition and predation are important in structuring assemblages, with facilitation also increasingly recognized as an important structuring mechanism (Callaway & Walker, 1997; Bruno *et al.*, 2003).

When considering the factors that structure local assemblages, one therefore needs to either explicitly incorporate, or control for, these scale-dependent influences. One on-going ecological question concerns the relative role of historical influences versus local ecological interactions in determining assemblage composition (Tokeshi, 1999), and this can be extended to their role in influencing spatial ecological patterns in local assemblages. In this thesis I address this question for termites in rain forests, where termite assemblages

from two tropical lowland rain forest blocks, Central Africa and South East Asia, were examined; the physiognomic similarities of these forest blocks means that habitat-type is largely controlled for (Morley, 1999; Corlett & Primack, 2006), while the termites themselves, as well as the floral communities, have different evolutionary histories within these forest blocks (Morley, 1999; Davies *et al.*, 2003a).

1.2.2 Interpreting local-scale spatial patterns

The spatial aspect of ecological processes are now more frequently being integrated into ecological theory, for instance meta-population dynamics (Gilpin & Hanski, 1991), and the role of species' spatial distributions in the species-area relationship (He & Legendre, 2002). From an analytical perspective, spatial patterns or structures in ecological data (i.e. spatial distributions of species or assemblage composition) are used to infer or generate hypotheses of causal processes (Fortin & Dale, 2005). Spatially-explicit ecological studies allow one to identify the scale at which patterns are structured, which, not only sheds light on the scale at which various processes are operating, but also the scale at which communities or species provide ecosystem services.

Spatial ecological patterns are generally considered to be the product of two factors: exogenous factors that are generated by an independent variable, and endogenous factors which are an inherent property of the study taxa (Legendre & Legendre, 1998; Fortin & Dale, 2005). First then, species and communities will be spatially structured according to the spatial structure of deterministic environmental factors, such as those associated with a particular habitat type. Second, intrinsic biotic processes, such as dispersal can generate aggregated patterns, for instance when dispersal abilities are limited. Abiotic and biotic

processes operate at various nested scales, and therefore the relative importance of these factors will depend on the scale being considered. As this thesis concerns historical (the biogeographic history between regions is outlined below) versus local ecological processes, local-scale spatial patterns in the termite assemblages will be quantified, encompassing within-site environmental heterogeneity and localized biotic interactions. An additional important ecological consideration in these assemblages is the soil environment itself (where termite species richness predominates, Roisin *et al.*, 2006), which presents both unique ecological opportunities and limitations, compared with the above-ground environment (Bardgett *et al.*, 2005)

1.3 Ecological interactions in soil communities

Below-ground systems are known to support a high biological diversity of *microbes and fauna, often much greater than found in above-ground communities* (Heywood, 1995, Giller, 1996). The high diversity found in soil systems is often explained by a hypothesized reduction of competitive interactions that occurs in the soil environment. This results from spatial properties of both. 1) population processes (such as reproduction) and 2) the soil environment, that promote spatio-temporal resource partitioning and co-existence of ecologically similar species (Ettema & Wardle, 2002, Wardle, 2002; Decaens, 2010). Reproduction and limited dispersal abilities through the soil matrix generates intra-specific aggregation, and therefore spatial separation of potentially competing species (O'Connell & Bolger, 1998). Microhabitat heterogeneity in the soil environment promotes greater spatial resource partitioning (Anderson, 1975, Giller, 1996). This resource patchiness and microsite heterogeneity is further added to by the biogenic structures produced

by soil ecosystem engineers (Decaëns, 2010) e.g. worm casts and termite nests, that provide nutrient patches and aggregates of soil particles.

The scale at which soil organisms are spatially structured is dependent on numerous intrinsic biotic factors such as body size and dispersal abilities. For instance microbial communities are typically structured at a few tens of centimeters to a few meters (Lavelle & Spain, 2001; Ettema & Wardle, 2002), while multi-species aggregates of earthworms are typically structured at tens of meters (e.g. Decaëns & Rossi, 2001; Rossi, 2003a, 2003b). In earthworm assemblages, limited dispersal abilities results in mixed-species aggregations independent of environmental conditions, while soil compaction, soil carbon (C) and root biomass also correlate with assemblage spatial patterns (Decaëns & Rossi, 2001). Indeed, much of our understanding of the spatial patterns and ecological processes in soil macrofaunal communities has been gained from earthworm and ant studies.

In a recent scale-dependent study on earthworm assemblages in France, habitat determined by land-use practices filtered assemblages at the habitat scale, while competition further constrained assemblages at the local scale (Decaëns *et al.*, 2008). As a result of competition, earthworm species that have high niche overlap tend to occur in separate resource patches, while those with limited ecological similarity co-exist within patches (Jimenez & Rossi, 2006; Jimenez *et al.*, 2006b; Decaëns *et al.*, 2009). In ant communities, territoriality and inter-specific competitive interactions results in over-dispersion of colonies, whereby colonies are positioned further apart than would be expected by chance (Levings & Traniello, 1981; Traniello & Levings, 1986). Competition is generally considered to be an important structuring mechanism in ant

assemblages (Holldobler & Wilson, 1990) Spatio-temporal resource partitioning between individual colonies was demonstrated as being important in reducing competitive exclusion and therefore facilitating co-existence (Albrecht & Gotelli, 2001) Apart from evidence in ants and earthworms, carabid beetles and terrestrial molluscs also show evidence for competition (Brandl & Topp, 1985, Barker & Mayhill, 1999) Therefore although competition is generally considered to be a weak ecological force in soil organisms (as suggested in the reviews of Anderson (1975) and Bardgett et al (2005)), in macrofaunal groups it may be a more significant interaction.

Other important biotic interactions in soil communities have been outlined by Wardle (2006) Facilitative interactions between biota can lead to inter-specific aggregation (Purves & Law, 2002; Tirado & Pugnaire, 2005) Evidence for facilitative interactions in soil communities has been documented in fungal communities. Components of the fungal communities specialize on fresh dead plant material, and as these fungi break down the recalcitrant carbohydrates, this provides the food for sugar fungi (Frankland, 1969) One might then expect that such a food-mediated facilitation would generate aggregated patterns between the functional components of the decomposer community. Predation has frequently been shown to be important in population density regulation in soil systems (summarised in Wardle, 2002). Spatial patterns of predation have not explicitly been examined in soil communities; yet as predicted by the Janzen-Connell spacing hypothesis (Janzen, 1970, Connell, 1971), density-dependent predation can generate spatial dispersion, thereby reducing competitive interactions

There is relatively little published information on the ecological interactions in rain forest termites, which can comprise up to 95% of soil insect biomass (Watt *et al.*, 1997). The particularly high species densities found in rain forest assemblages, is supposed to be a result of micro-habitat heterogeneity (Deblauwe *et al.*, 2008), however without any evidence. Based on the available information on earthworms and ants, one can speculate as to the important ecological processes that might operate in termites. As decomposers, termites and earthworms can be considered functionally analogous, and heterogeneity in soil conditions important for earthworms, for instance soil C, moisture regimes and soil texture (e.g. Phillipson *et al.*, 1976; Lee, 1985; Rossi, 2003a), may also be important for termites, and thus influence assemblage spatial patterns. On the other hand termites and ants, which are two of the most ecologically successful and dominant animal groups in rain forests (Wilson, 1993; Watt *et al.*, 1997), have undergone remarkable convergent evolution to eusociality. Population processes known to be important in ants, e.g. spatial dispersion due to territoriality, and higher dispersive abilities (relative to other soil organisms) from alates that found new colonies, are also likely to be important factors that influence spatial patterns in termites.

Collectively termites, ants and earthworms are considered "ecosystem engineers", due to the role they play in affecting the structure and dynamics of soils, including contributing to: soil microhabitat heterogeneity and stability, the distribution of organic matter, water retention, and the stimulation of micro-organisms (Lavelle *et al.*, 1997; Hastings *et al.*, 2007). As abundant, largely subterranean, and detritivorous animals, termites are important in several ecosystem processes which include: decomposition, nutrient cycling, nitrogen fixation, carbon fluxes, soil creation and soil distribution (Bignell & Eggleton,

2000; Holt & Lepage, 2000; Sugimoto *et al.*, 2000). Mounds and nests persist after the colonies have died, providing habitats for other soil biota, while also improving soil fertility, and generating microhabitat heterogeneity in the soil environment (Eggleton & Bignell, 1997, Donovan *et al.*, 2001b; Ji & Brune, 2006) The contribution of termites to these ecosystem functions is largely dependent on the local assemblage composition, which as described below, varies between habitats and regions, and on the spatial structure of the local assemblage This thesis provides some of the first efforts to describe the spatial structure of termite assemblages in rain forests, and identify the important ecological interactions occurring in these systems.

1.4 Termites

1.4.1 General background

Over 2,600 species of termites from approximately 280 genera have been described (Engel & Krishna, 2004) Phylogenetic analyses have confirmed that the termite clade (previously classified as the order Isoptera) is nested within the cockroach order, Blattodea (Inward *et al.*, 2007a), and is now classified as the epifamily, Termitoidae (Eggleton *et al.*, 2007) The major evolutionary transition leading to termites was to eusociality, with permanent families, overlapping generations, and sterile worker and soldier castes (Roisin, 2000). A mutualism with cellulolytic flagellates that allowed wood-feeding was established in an ancestor of the termites, and required prolonged parental-offspring contact for the transfer of flagellates between generations (Nalepa *et al.*, 2001).

Colonies are typically founded by a pair of alates, although colony budding and colony fusion also occurs (Husseneder *et al.*, 1998; DeHeer *et al.*, 2005). Most of the studies on the family structure of termites demonstrate that monogamy is typical (e.g. DeHeer *et al.*, 2005; Dupont *et al.*, 2009; Roy *et al.*, 2010). The worker caste is responsible for foraging and feeding the colony, tending the brood, and building and repairing the nest. The guts of worker termites are adapted for the digestion of dead plant material, and are the site of mutualisms with a huge concentration and diversity of microorganisms which help to aid this process (Bignell, 2000; Brauman *et al.*, 2000). The soldier caste is responsible for colony defence, both from predators, and in inter-colonial warfare (Matsuura, 2002; Thorne *et al.*, 2003). Morphological structures and chemical secretions are adapted for defence within the colony's nest (Deligne *et al.*, 1981; Prestwich, 1984), e.g. the soldier head capsule blocks subterranean tunnels from raiding predators (Matsuura, 2002), which would predominantly be ants. In one termite clade, the Apicotermiinae, the soldier caste is largely absent (Inward *et al.*, 2007b), which may have resulted, in part, from the energetic constraints of their feeding strategies (Eggleton & Tayasu, 2001).

1.4.2 Feeding and nesting strategies

Termites consume dead plant material from across the 'humification gradient' i.e. material that is in various states of decay. A classification exists based on morphological characters associated with the contents of worker guts (Donovan *et al.*, 2001a). This places termite species into one of four feeding-groups along the humification gradient, from dead wood (higher up the gradient) and leaf-litter material, to organically depleted clay-mineral soil (lower down the gradient). This range of food material differs in its energetic quality (carbon:nitrogen (C:N)

ratio) and quantity (C and N concentration and distribution of material). These patterns of food quality and availability then relate with colony nesting and foraging strategy (Eggleton & Tayasu, 2001), with two examples provided below to illustrate this. The nesting strategy classification system was provided by Abe (1987), who identified three strategies: single-piece, intermediate and separate-piece nesters, according to the degree of spatial overlap between the nest and food material, i.e. single-piece is where the colony consumes the same material that it nests in.

Fungus-growing termites (Macrotermitinae) are separate piece-nesters where the workers forage away from the nest to collect dead wood, grass or leaf-litter material. This material has a high C:N ratio but can be relatively patchily distributed. Within the colonies' nests, they have a mutualism with microorganisms (an external rumen system (Nalepa *et al.*, 2001)) that burns off excess C to reduce the C:N ratio in the collected material (Higashi *et al.*, 1992). Species within this sub-family frequently have epigeal mounds with elaborate architecture for thermal-regulation (Noirot & Darlington, 2000). Colonies can live of up to fifteen to twenty years (Collins, 1981), with subterranean foraging distances of around 50m (Pomeroy, 1976, Darlington, 1982).

By contrast soil has a low C:N ratio, with low absolute concentrations of C and N. As result of its low energetic quality soil-feeding termites live on an energetic knife-edge (Eggleton *et al.*, 1998), yet soil is a continuous resource available in profusion. As foraging and nest construction incurs energetic costs, soil-feeding termites frequently are single-piece nesters, living in diffuse colonies in the upper soil profile, and colony turn-over may be very high. The nutritional ecology of termites therefore has a major influence on their life-history, ecology

and evolution. Arguably the most successful feeding strategy in terms of the proportion of taxonomic richness are soil-feeding termites, (c. 50% of all known species are soil-feeding (Brauman *et al.*, 2000)), most of which are confined to tropical rain forests (Eggleton, 2000b).

1.4.3 Rainforest termites and biogeographic history

The 'higher' termites, the Termitidae, make up approximately 71% of the known total species diversity and 85% of known genus richness of termites (Collins, 1989; Kambhampati & Eggleton, 2000). This group is composed of Macrotermitinae, Formaminitermittinae, Apicotermittinae, Syntermittinae, Nasutitermittinae, and the Termitinae, which, as this is paraphyletic (Inward *et al.*, 2007b), its taxonomic status is currently under review (P. Eggleton, personal communication). The higher termites encompass a range of feeding habits, from wood- to soil-feeding. The phylogenetically basal families, termed the 'lower' termites, are exclusively wood-feeding. The onset of higher termites was accompanied by a shift to soil-feeding and fungus-growing, with subsequent reversion to wood-feeding having occurred repeatedly within a number of clades (Inward *et al.*, 2007b).

Based on phylogenetic data the Termitidae is considered to have originated on the African continental shelf during the early Tertiary (65Ma). The stable micro-climatic conditions found in moist megathermal closed-canopy forests, which were widespread by the Paleocene (60 Ma) (Morley, 1999), appears to have been the pre-requisite for the evolution of true soil-feeding in termites (termites that consume highly humified plant material in clay-mineral soil) (Davies *et al.*, 2003a). As soil-feeding termites are confined to stable moist forests, dispersal in this group would have been severely limited. Dispersal to the South American

continental shelf may have occurred by island hopping during much cooler periods of the Oligocene (35Ma) and later periods, when ocean levels would have been at their lowest. Subsequent radiation of soil-feeding termites has occurred there, whereas in Africa, stable closed-canopy forests have had a long history (Morley, 1999). It is hypothesized that the higher termites dispersed onto the Indian plate, which subsequently drifted from near Africa to Asia from the Paleocene to the early Miocene (Davies *et al.*, 2003a). Stable megathermal forests are relatively young in SE Asia relative to African and S American forests, arising after a period of monsoonal climate during the Himalayan orogeny. The relatively species depauperate SE Asian Termitidae fauna may be due to the short length of geological time for evolution and speciation in stable forest, once the climate had returned to being perhumid.

As a result of energetic and dispersal limitations, specifically associated with the most species rich soil-feeding clades, global patterns of taxonomic and functional diversity (feeding-groups present from across the humification spectrum) are asymmetrical (Eggleton, 2000b), which I refer to later in this thesis as the 'diversity anomaly'. African forests have the highest species densities, dominated by true soil-feeding (FGIV) termites, South American forests are intermediate, with a particularly high diversity of humus-feeding (FGIII) termites, while Asian forests are relatively species depauperate, with a higher proportion of wood-feeding (FGI and FGII) termites (see Figure 1.1 for local species richness by feeding-group, and Table 1.1 for regional taxonomic representation).

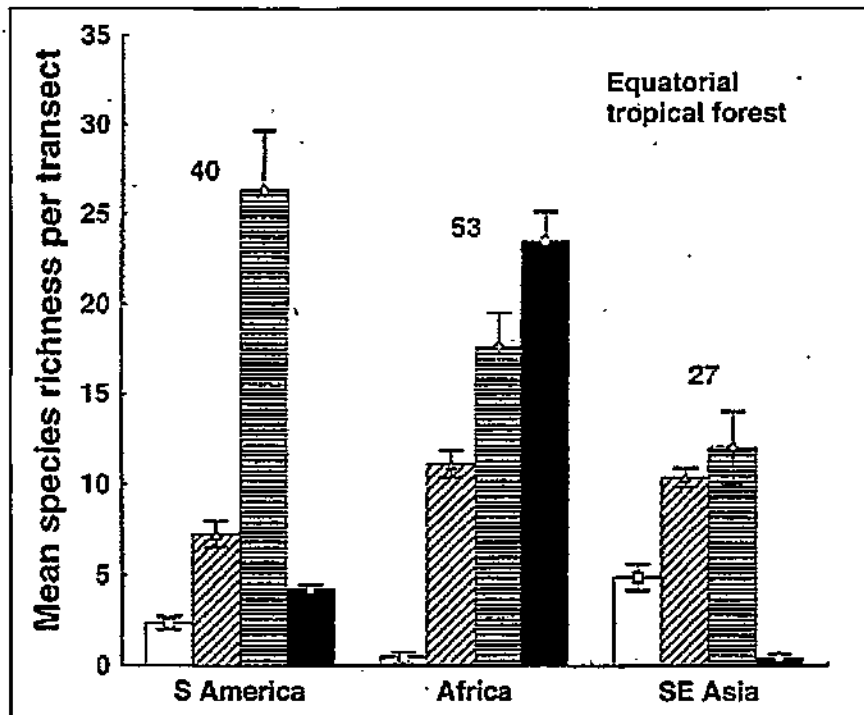


Figure 1.1 Mean per transect species richness apportionment (mean \pm SE) between the four termite feeding-groups in undisturbed lowland equatorial forests (drawn from replicate samples between sea level and 1000m elevation) across S America, Africa and SE Asia. Feeding groups are coded as follows: group I, open column; group II, diagonal hatching; group III, horizontal hatching; group IV, black column. (taken from Davies *et al.*, 2003a, Fig. 2a. Permission to reprint this has been granted by John Wiley and Sons).

Against this biogeographic back-drop, where equatorial rain forests have been the site of most of the important evolutionary shifts, it is therefore not surprising that within-region species richness and functional diversity is also concentrated in closed-canopy rain forests (Davies *et al.*, 2003a). Divergence from the stable climatic conditions associated with closed-canopy forest e.g. through disturbance, or habitat shifts along altitudinal or rainfall gradients, sees a general reduction in diversity, mostly seen in a decline in soil-feeding termites (Dibog *et al.*, 1999; Donovan *et al.*, 2002; Jones *et al.*, 2003).

Table 1.1 Regional generic richness of lower termite families, and higher termite sub-families (compiled from Jones and Eggleton, 2010, unpublished).

	Global	Neotropical	Afrotropics	Indomalay
Mastotermitidae	1	0	0	0
Termopsidae	5	1	2	2
Hodotermitidae	3	0	3	1
Kalotermitidae	21	12	9	9
Serritermitidae	2	2	0	0
Rhinotermitidae	14	6	4	10
Termitidae	236			
Macrotermitinae	14	0	10	6
Foraminitermitinae	2	0	1	1
Sphaerotermitinae	1	0	1	0
Apicotermitinae	54	5	43	6
Termitinae	101	32	35	23
Nasutitermitinae	89	23	16	29

African and Asian rain forests were selected for this present work, as termite assemblages to represent the extremes of biogeographic history and contemporary diversity patterns within tropical forests (Figure 1.1). The inter-continental differences are also reflected in termite abundances and biomass, which is far higher in African forest systems than in Asian ones (Eggleton *et al.*, 1999). Therefore termites may be contributing more to ecosystem services in Africa, where also any changes in the termite assemblages, e.g. due to disturbance or climate change, would presumably have more significant ecological implications (discussed in Eggleton *et al.*, 1999, Davies *et al.*, 2003a).

1.5 Thesis outline

In this thesis I describe and investigate ecological spatial patterns at the local scale, which involved sampling a 96m x 96m plot in both an Asian (Danum) and African (Ivindo) tropical rain forest site.

Chapter 2 introduces the two study sites, and details the field surveying methods. It summarises the environmental heterogeneity measured from each site, with an emphasis on identifying the scale at which this heterogeneity was spatially structured, and the major habitat similarities and differences that may explain termite spatial patterns. Chapter 3 describes the termite sampling and identification protocols. It provides a summary of the sampled termite and ant assemblage composition and occupancy, and considers whether these samples are representative of the known within-in region functional diversity patterns. These two chapters provide the context for comparing and interpreting the ecological patterns detected in later chapters, from the two sites.

In Chapter 4, genetic tools and spatial analyses are employed to estimate the spatial extent of *Cubitermes* sp. colonies, a true soil-feeding genus confined to Africa. Using the spatial patterns the scale-dependency of intra- and inter-specific interactions were inferred.

In Chapters 5 and 6, spatial patterns and relationships in generic richness and composition of the assemblages from the two sites are examined. By comparing them, I will identify whether these patterns either: 1) pertain to habitat conditions or biotic interactions unique to each site, and therefore due to biogeographic history, or 2) are consistent between sites, and therefore due to similar localised ecological processes. In Chapter 5 I describe spatial structure of generic richness asking the following questions: 1) what are the important environmental factors? 2) is there evidence for facilitative interactions between components of the feeding-groups? 3) is there evidence for a predator-prey interaction between ants and termites? In Chapter 6 I explore how termite assemblage composition is spatially structured, by considering genus-level co-

occurrence patterns at a series of nested scales, from which local-scale assembly rules for termites could be constructed.

Chapter 7 provides a final synthesis of the major findings, outlining their relevance to broader ecological factors, and I make recommendations for future research

2 Fine-scale environmental conditions in an African and Asian rain forest

2.1 Summary

Due to their physiognomic similarities, the tropical rain forests of Africa and Asia are considered to be habitat analogues, despite having very different evolutionary and climatic histories (Morley, 1999). The aim here is to examine the extent to which one hectare plots in an Asian (Danum) and African (Ivindo) rain forest, present similar environmental and microhabitat conditions, which may be important for the soil-dwelling termite assemblages. Variables measured were designed to capture heterogeneity in the quality and availability of termite food material (soil C_{tot} and N, wood, and leaf-litter), soil properties, and understorey vegetation, most of which are known to effect termite assemblages at broader environmental gradients. The 'food' variables and soil pH were extremely similar (means and frequency distributions) between the two sites. Trees were more abundant, soils wetter, and soil infiltration rates lower in the Asian site, probably due to differences in soil texture and region-specific plant species richness patterns. Environmental relationships, as measured by Principal Components Analyses and the spatial scale at which these were structured, were broadly the same between sites in the first two PCA axes. The heterogeneity in soil properties correspond with shallow slopes, and the vegetation relationships are likely to result from tree-fall events. These results suggest that similar microhabitats exist in the Danum and Ivindo study plots.

2.2 Introduction

Termite species richness is greatest in rain forest habitats (Bignell & Eggleton, 2000). It is in this habitat type that termites appear to have undergone repeated.

evolutionary shifts in feeding strategies, such as consuming soil and fungus-harvesting (Davies *et al.*, 2003a, Aanen & Eggleton, 2005), followed by radiation. Multistratal closed-canopy equatorial forest provided stable microclimate regimes which appears to have been a pre-requisite for these shifts and may explain the success of termites in these habitats (Eggleton, 2000a, Davies *et al.*, 2003a).

Some of the environmental conditions important in structuring termite assemblages have been established from numerous previous studies that examine communities along disturbance or altitudinal gradients. Increasing rainfall and reduced temperatures associated with altitude affect termite assemblage composition and abundance (Gathorne-Hardy *et al.*, 2001, Donovan *et al.*, 2002, Palin *et al.*, 2010). It is also not surprising then that canopy cover is important (Dibog *et al.*, 1999; Roisin & Leponce, 2004), as this improves the regulation of soil moisture and temperature regimes, but may also provide a buffering to water-logging during intensive rainfall. Along a disturbance gradient, termite diversity is positively correlated with plant heterogeneity and above-ground habitat complexity (Gillison *et al.*, 2003), which may translate into below-ground microhabitat complexity that supports a greater termite species richness. Food quality and availability has not yet been examined in any detail, although they appear to be important for fungus-growing termites (Attignon *et al.*, 2005). Indications of this factor are the results of a study following experimental habitat disturbance, where the amount of woody material and potentially the quality of soil organic material, influenced recovery rates of termite assemblages (Davies *et al.*, 1999).

It is consistently the soil-feeding component of local assemblages that are most sensitive to altered primary rain forest conditions (e.g. Martius, 1994; Eggleton *et al.*, 1997; Eggleton *et al.*, 2002a). Wood-feeding species richness is generally less impacted by habitat disturbance (e.g. Attignon *et al.*, 2005; Norgrove *et al.*, 2009). It would appear, then, that the functional and taxonomic components of termite assemblages differ in their environmental requirements and tolerances, which is linked with the feeding and nesting strategies. Due to the ecological importance of termites, the implications of these compositional changes are often estimated, for instance in terms of termite-mediated carbon mineralization and decomposition rates (e.g. Martius, 1994; Eggleton *et al.*, 1999; Yamada *et al.*, 2005). It would be valuable to know whether more localized environmental heterogeneity, will also be influencing the spatial structure of termite assemblages, and hence whether this is important for determining the scale at which termites contribute to these services.

Relationships between biotic communities and environmental conditions are scale dependent. Therefore the environmental relationships with termites known from across habitat gradients e.g. with canopy cover, soil moisture and habitat complexity, may have little or no impact at the within-habitat scale, while other factors may be more significant. For example within a Neotropical forest, the abundance of understorey palms, and the associated soil pH and humus depth was found to have a greater influence on termite assemblage composition than forest fragmentation (Davies *et al.*, 2003b). In the only other spatially-explicit study of termite assemblages, from a rain forest in Borneo, environmental relationships depended on the feeding-group; soil-feeding termites were positively associated with humus depth and negatively with root-matt density,

while no environmental relationships were found with the wood-feeding termites (Donovan *et al.*, 2007).

Spatial structure in soil communities can be determined by, amongst other factors, the spatial heterogeneity of the environmental conditions that affect the community (Ettema & Wardle, 2002). Here the spatial relationships of termite assemblages with environmental properties from comparable habitat types, equatorial primary rain forest, in two continents, Africa and SE Asia, will be considered. The aim is to determine whether there are similar environmental relationships at the local scale in these two sites, despite the known differences in termite abundance and species richness. This assumes therefore that the sites are habitat analogues with, to a greater degree, similar within-plot micro-habitat heterogeneity that might be affecting termite community structure, or indeed vice versa. The environmental variables measured fall into three main categories which may be important for termites: 1) the quality and availability of food material, 2) soil properties, and 3) understorey vegetation. In this chapter the focus is on explaining the selection of study sites and plot location, and the measurement of environmental variables. I go on to compare between the two sites: the variation in the environmental data, the environmental relationships, and the spatial structure of these relationships. Therefore the major similarities and differences in the environmental properties from the two sites will be assessed.

2.3 Methods

2.3.1 Study site selection and description

A primary aim in this study was to characterize the fine-scale spatial structure of the termite assemblages in each region. This determined the two dimensional sampling design, spatial extent of the study plot (96m x 96m), and lag of the sample points (contiguous sample points every 2m x 2m), explained in further detail in Chapter 3. For simplicity the plot size will be referred to as "one hectare plots" except when specified as 96m x 96m, for the remainder of the thesis. The high sample size per plot (n=2304) meant it was not logistically possible to survey more than one plot per site. To over-come this limitation of no replication, certain criteria were used to determine plot location, in order that: 1) the collected termite assemblage would be representative of generic richness typically found in rain forest assemblages within each continent, and 2) microhabitat heterogeneity in the plot could be comparable between regions. In addition to being in equatorial lowland forest, the following criteria were used for site location:

- The parent material and soil conditions are those that are typical for rain forests in each region, i.e. acidic and clay-based, as termite assemblage composition are sensitive to differences in these (Jones *et al.*, 2010).
- Within a substantial block of closed-canopy forest in order to avoid the possible influence of habitat fragmentation on the termite assemblage (Davies *et al.*, 2003b).
- Within primary forest with no records of anthropogenic impacts that would effect the vegetation structure and therefore potentially the termite

assemblage (Gillison *et al.*, 2003), such as logging in recent history (<100 years)

In addition to these criteria, the location of the study plots was chosen to avoid major topographic or hydrological features that 1) could have a large effect on the localised termite assemblage structure, and 2) may not be directly comparable between the two regions. Therefore streams, gullies and rocky outcrops were avoided, and effort was made to position the plot in a relatively flat area, where any slopes were gentle (<5° slope). Other small-scale features that are typical of closed-canopy forest, such as animal trails and tree falls were not avoided, and were present in both plots.

2.3.2 Danum Valley Conservation Area, SE Asia

The study plot, referred to throughout as 'Danum', was located in the Danum Valley Conservation Area (DVCA), in the eastern Malaysian state of Sabah, Borneo (N 05° 01' E 117° 49') (Figure 2 1a & b). DVCA spans approximately 44,000 hectares, comprising mostly lowland evergreen forest (<760m asl) (Marsh & Greer, 1992) The lowland forest vegetation is dominated by canopy trees within Dipterocarpaceae, while species of Euphorbiaceae and Rubiaceae often dominate the understorey. The study plot was located in the area of DVCA on the 'Kuamut geological formation' that is a mix of sedimentary sandstone and volcanic rocks. The soils here are ultisol (Acrisol-Alisol in the FAO-UNESCO system) and have a predominantly clay-loam texture within the plot, measured using the hand texturing method (Dubbin, 2001).

Climate conditions are equatorial. Mean annual temperature is 26.8°C, with a narrow range in mean monthly temperatures of between 25.8 and 27.6°C. Mean

annual precipitation (as recorded from the DVCA Field Centre) is 2,825 mm, with two rainy and two dry seasons, although these seasons are non-distinct. Sampling was carried out from March to June 2007, during the transition from a dry (March - April) to wet (May - June) season. Total monthly rainfall during the collection period ranged from a low of 89 mm in April to a high of 337 mm in June. The plot was characterized by a gentle south-easterly aspect, with a flatter ridge on a north-south axis in the western part of the plot, and a small gully that continues to the west of the plot. A small footpath dissected the plot from north to south (Figure 2.1c).

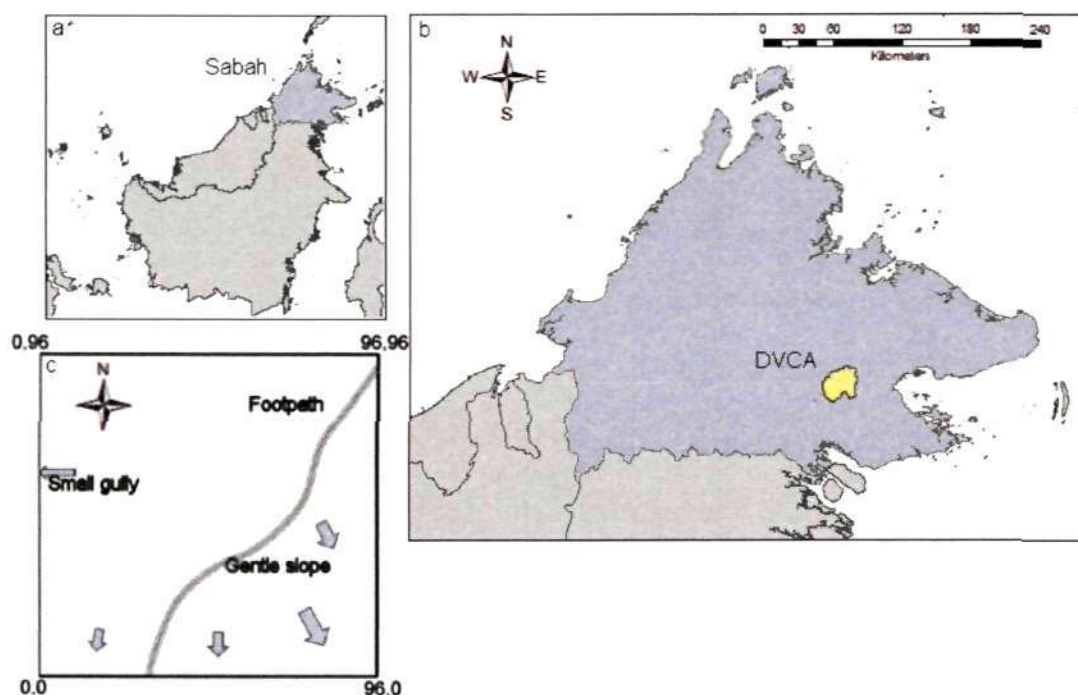


Figure 2.1 a) Location of Sabah in Borneo. b) Location of DVCA in Sabah. c) Significant features in the 'Danum' plot. Arrows indicate downslopes.

2.3.3 Ivindo National Park, Central Africa

The Central African plot, referred to throughout as 'Ivindo', was located towards the southern end of Ivindo National Park, central Gabon (S 00° 10' E 12° 32') (Figure 2.2a and b). The park covers an area of approximately 300,000

hectares of closed-canopy forest. The vegetation is predominantly semi-evergreen lowland forest, and represents a transition between the Congo forest ecotone to the north and east, and the Atlantic forest ecotone in western Gabon. The soils are oxisol (Ferralsols in the FAO-UNESCO) (USDA-NRCS, 2005) on a sedimentary sandstone parent material (Vande-Weghe, 2006), and within the study area had a predominantly sandy-clay-loam texture.

Temperature remains relatively stable throughout the year, with a monthly minimum of 21.7°C in July and a monthly maximum of 25°C in April (Vande-Weghe, 2006). The climate is equatorial, with two distinct dry and wet seasons, and annual precipitation ranging from 1300mm to 2000mm (Vande-Weghe, 2006). Surveying was carried out from February to May in 2008, which is during the transition from the small dry (February – March) to small wet (April – May) season. Total monthly rainfall ranged from a low of 108 mm in February to a high of 296 mm in May. The Ivindo plot was flat in most of the western half, and sloped gently downwards towards the east. Other noticeable features were a large canopy gap following tree fall in the north eastern corner, and an active elephant trail dissecting the plot from the north-western towards the south-eastern corners (Figure 2.2c).

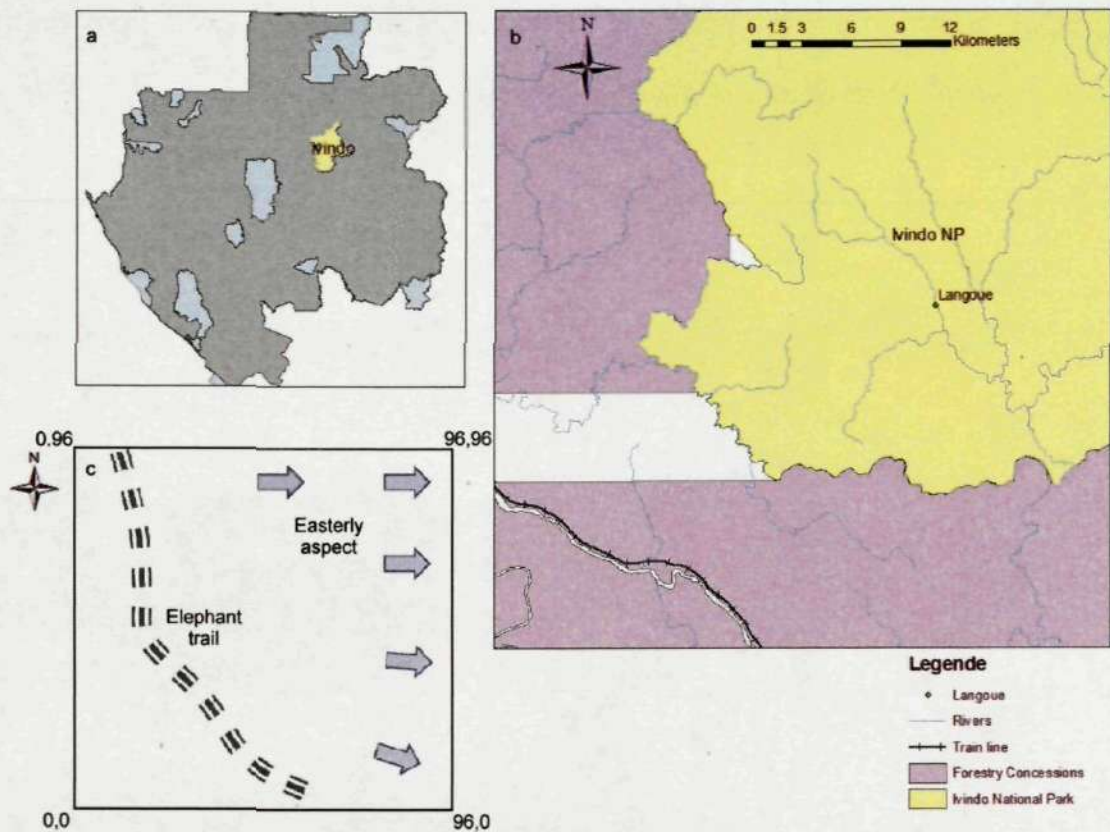


Figure 2.2 a) National Parks of Gabon with Ivindo National Park located in central Gabon. b) Langoué Field station in southern Ivindo N.P. c) Significant features in the 'Ivindo' plot. Arrows indicate downslopes.

2.3.4 Environmental Measurements

Environmental measurements were recorded from every 2m x 2m sample point (see Chapter 3). Except where specified, the environmental variables were measured while sampling the biotic communities at each sample point. The 96m x 96 m study plot was divided into 12m x 12m sub-plots (see Figure 2.3). One sub-plot was surveyed per day, with the order of surveying the sub-plots randomly determined. The large sample size (n=2304) placed limitations both on what could be analyzed, and how variables could be measured. Environmental measurements were therefore selected that would capture information within each category (food, soil structure and vegetation) with the greatest efficiency. They were measured either from within the 2m x 2m sample

point, or from a soil pit located in the centre of the sample point, from which termites and ants were first collected (Figure 2.3).

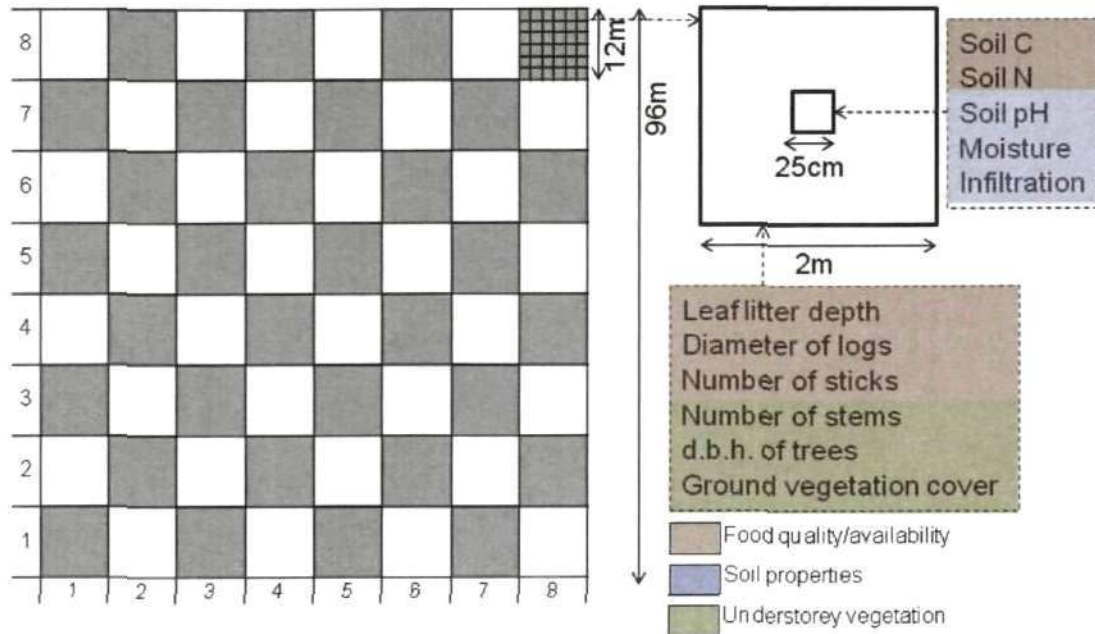


Figure 2.3 Survey plot, divided into 64 sub-plots. Environmental variables were either measured from the 25cm x 25cm, x 15cm depth soil pit, or the 2m x 2m sample point as indicated.

Food material

Large dead wood. Dead wood items with a diameter of >15cm were termed 'logs', and the number lying on the ground in each 2m x 2m sample area were counted, and their diameter measured.

Small dead wood. Wood items with a diameter of <15 cm were considered 'sticks', and the number of sticks on the ground within the 2m x 2m sample area were counted.

Leaf-litter depth. The depth of leaf-litter, 'LL' was measured in categories from the surface of the soil to the height of upper leaf in the litter layer; 0, 0cm LL; 1,

1-2cm LL; 2, 2-5cm LL; 3, >5 cm LL. The most common estimation from four made with the 2m x 2m sample area was taken as the final measurement.

Soil Organic Material. Soil samples were collected from the 25cm x 25cm, x 10cm depth soil pit (see Chapter 3 for details of sampling grain size) in each sample point, which were dug and first hand-sorted for termites and ants. All animals, pieces of large organic debris such as sticks and bark, and stones were hand removed. In Danum the soil samples were oven dried overnight, and in Ivindo samples were dried under a small constructed greenhouse left in an open area. The dried samples were first sieved at 2mm to small debris, then ground using a pestle and mortar into a fine powder, which were further sieved using a fine mesh. These samples were stored for later analysis in the Electron Microscopy and Mineralogy Analysis (EMMA) Laboratory at the Natural History Museum (NHM), London. A Thermo Finnigan Flash EA1112 Elemental Analyzer was used to measure soil carbon and nitrogen concentration as a percentage of 4-5mg sub-samples. As the dried soil samples had been ground and sieved, this sub-sample was assumed to be representative of the pit soil sample. It was not possible to measure C_{org} due to additional steps, and therefore time involved, of acidification that removes the inorganic material prior to analysis. Instead all the soil samples were analyzed for C_{tot} , and a randomly selected set of soil samples (Danum n=58, Ivindo n=36) were also analyzed for C_{org} . The relationship between the C_{tot} and C_{org} measurements was then analyzed using linear regression models.

Soil properties

Soil pH. Fractions of the soil samples collected from the pits were also used for measuring the soil pH at each sample point. In Danum this was carried out on a

daily basis following field-work, therefore the samples were not first dried. In Ivindo this was not possible, and therefore the dried, ground and stored soil samples were analyzed on completion of field work at the NHM, London. In both cases the soil samples were suspended in de-ionised water at a 1:1 ratio of soil and water (Thomas, 1996), and the pH measured from the solution using a hand-held pH meter, calibrated to pH4 and pH7 buffer solutions on a daily basis.

Soil porosity. A measure of 'infiltration rate' (ml/second) was used to indicate soil porosity in the top 5cm of the soil profile. This was calculated from the time taken for 75ml of water to pass through a core ring (circumference of 15cm), driven 5cm into the soil profile. For very dense soil cores measurement of the time was capped at 10 minutes. The core was placed directly next to the soil pit. Due to time restrictions, infiltration rate was measured in only half of the plot in Danum, after completing all other surveying. In Ivindo infiltration was measured while sampling all other variables and therefore data were collected for the entire plot.

Soil moisture. This was measured as a percentage of volume of pore space, using a ThetaProbe Soil Moisture Sensor, submerged into the soil directly adjacent to the soil pit.

Vegetation

Mature trees. The number of trees with a dbh (diameter at breast height) of >10cm were counted in each 2m x 2m sample point, and their dbh noted.

Stems. The number of stems (trees with a dbh <10 cm) were counted in each 2m x 2 m sample point.

Ground vegetation cover. The amount that vegetation with a height of <50 cm covered the ground in each 2m x 2m sample point was estimated as a percentage within categories of 10%.

2.3.5 Data exploration

The frequency distributions of all measured variables were plotted. In the case of continuous variables with heavily right-skewed distributions, these were $\log_{10}(x+1)$ transformed and their frequency distributions re-plotted to indicate whether the data were normally distributed.

To examine the relationships between the environmental variables within each site, Principal Components Analyses (PCA) were performed using CANOCO 4.5 (ter Braak & Šmilauer, 2002), with all variables centered and standardized. In order to compare environmental relationships between the sites, the same set of environmental variables were included for each pair (Danum and Ivindo) of analyses. There was a large amount of missing data for infiltration rate in Danum, and so this was not included in any of the PCA analyses. Soil C_{tot} and soil N strongly co-correlated, and as the C/N ratio is derived from these variables, the first PCA axes mostly explained strong co-variance in those three variables. The analyses were therefore repeated with soil C_{tot} and N removed. The proportions of variance explained by the first four axes were recorded. The spatial structure and scale of the environmental relationships described in PCA analyses were visualized using a Loess non-parametric fit model for contour plotting the sample-point PCA axes scores into the plot x-y space using CANOCO (ter Braak & Šmilauer, 2002).

2.4 Results

2.4.1 Relationships between C_{tot} and C_{org}

In both sites the relationship between soil C_{tot} and C_{org} appear linear with similarly high R^2 values in the linear regression (Figure 2.4). Soil C_{tot} is therefore reasonable indicator of C_{org} concentrations, as an indirect measure of soil organic material consumed by soil-feeding termites.

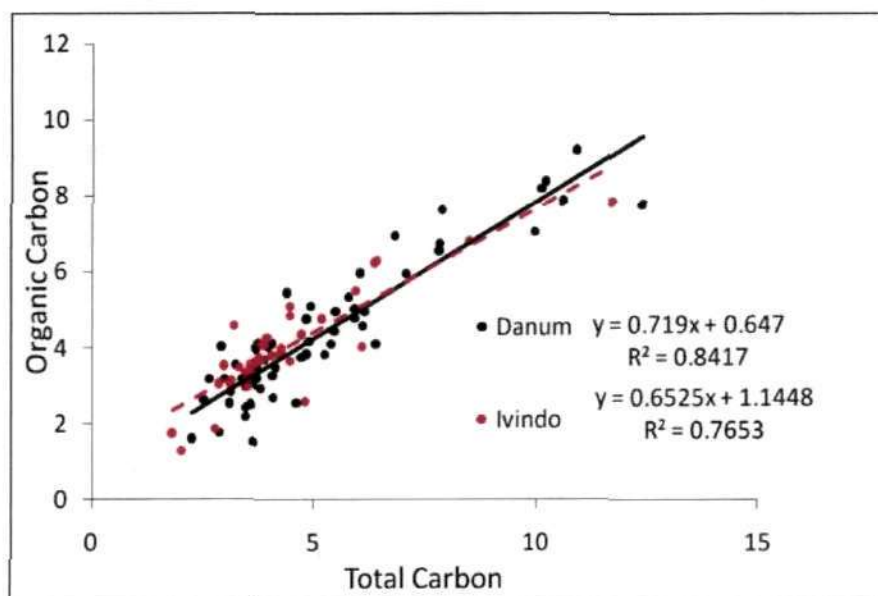


Figure 2.4: Linear regression plot of Soil C_{tot} and C_{org} (from randomly selected sample pits) in Danum ($n=58$) and Ivindo ($n=36$).

2.4.2 Frequency distributions and differences

Of the continuous environmental variables, pH, soil moisture, and C/N ratio are normally distributed (Figure 2.5). The frequency distributions of soil C_{tot} and N are heavily right skewed, and are more normally distributed when $\log_{10}(x+1)$ transformed. Infiltration rate is also heavily right skewed, and there is an artificial lower tail due to the 10 minute cap in measuring the time of water passing through the soil core. Soil pH, soil C_{tot} and N had very similar means and distributions in Danum and Ivindo. Danum soils were generally wetter, and

less porous, while soil C/N ratio was higher with greater variance, due to both marginally higher soil C_{tot} and lower soil N concentrations (Figure 2.5).

The remaining variables are categorical with frequency distributions that are right skewed (Figure 2.6). The majority of sample points lack a tree or a log, therefore in the PCA analyses these are converted to nominal variables. Danum had fewer sticks, while the leaf-litter layer and the number of logs were remarkably similar in both sites (Figure 2.6 and Table 1.1). The vegetation is characterized by more, smaller trees in Danum compared with Ivindo, accompanied by a higher frequency of young trees (stems) (Table 2.1), while ground vegetation cover appeared lower (Figure 2.6).

Table 2.1 Summary data of dead plant material and understorey vegetation.

Environmental variable	Danum	Ivindo
Total number of logs	488	473
Total number of sticks	5468	6089
Total number of trees	370	224
Mean tree dbh	22.8 ± 24.6	32.4 ± 24.4
Total number of stems	5547	2495

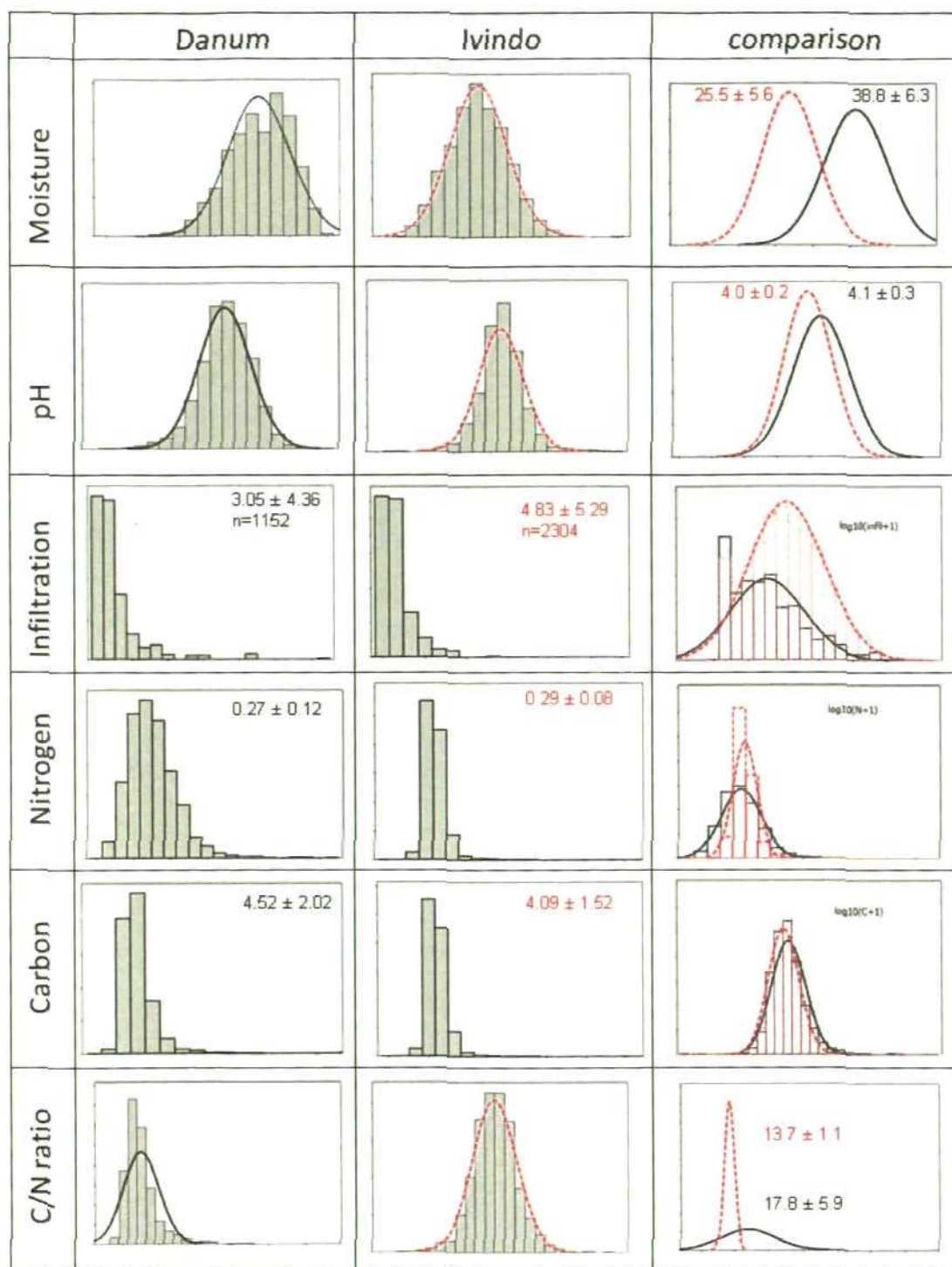


Figure 2.5 Frequency distributions of soil variables from Danum (black) and Ivindo (red), with an additional combined normal distribution plot, that illustrates the differences in mean and variance between Danum and Ivindo. The sample mean and standard deviation of non-transformed data is included.

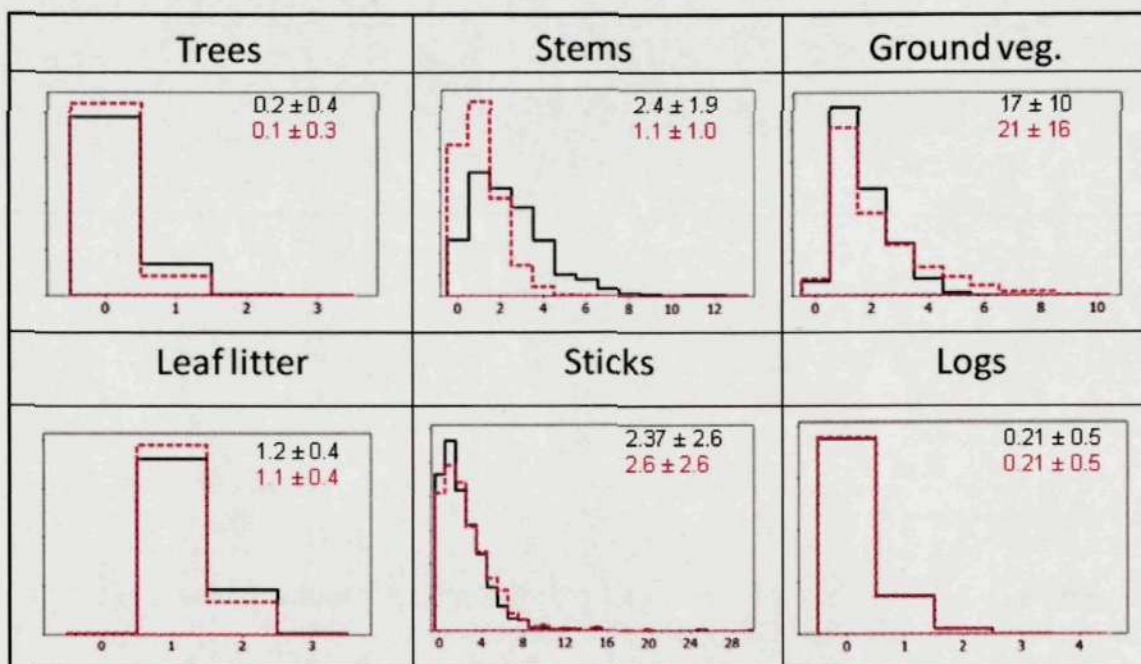


Figure 2.6 Combined frequency distributions of vegetation and dead plant material variables from Danum (black) and Ivindo (red). The sample mean and standard deviation is included.

2.4.3 PCA data exploration

The initial PCAs in both sites included soil C_{tot} and N, as well as the soil C/N ratio. The first axis in both describe the co-variance between these three measurements; in Danum the C/N ratio negatively co-varies with soil C_{tot} and N, while in Ivindo, all three strongly positively co-vary (Figure 2.7a & b). As the C/N ratio is derived from the soil C_{tot} and N measurements, the analyses were repeated removing the soil C_{tot} and N measurements. The first axes in these repeated analyses explain proportionally less of the total variance (Table 2.2). The variance explained by the second axes increases as a result of removing the strong co-variance between the soil C_{tot} and soil N, while axes 3 and 4 explain only marginally less variance (Table 2.2).

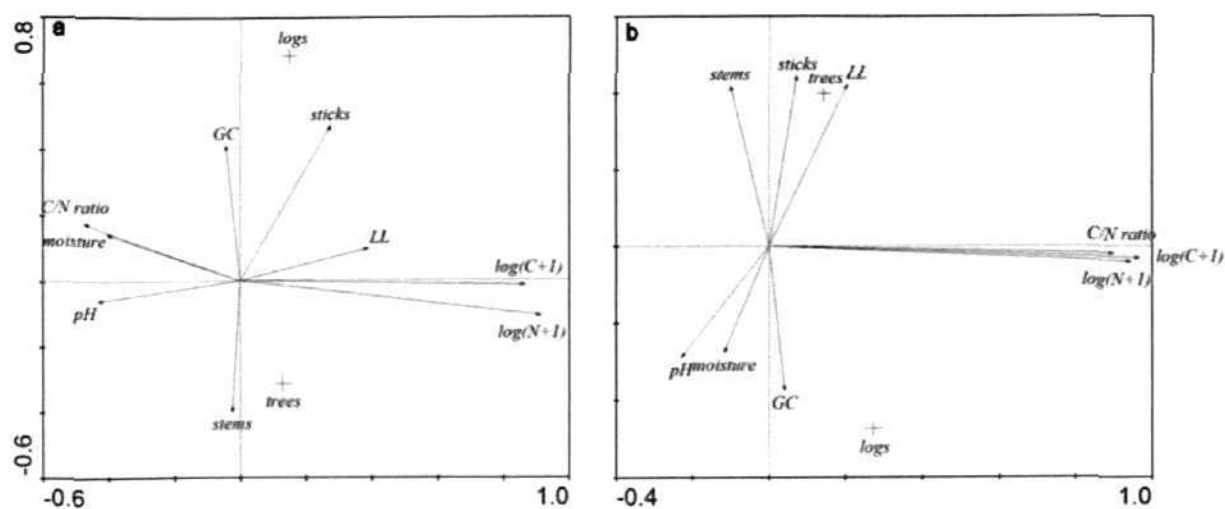


Figure 2.7 PCA axis 1 vs axis 2 plot of environmental relationships. a) Danum, b) Ivindo. LL, leaf-litter; GC, ground vegetation cover.

Table 2.2 Percentage of environmental variance explained in PCA axes.

	Axis 1	Axis 2	Axis 3	Axis 4
Danum: all variables	22.2	11.2	10.4	9.9
Danum: Soil C and N removed	15.6	13.6	12.0	11.5
Ivindo: all variables	25.2	11.2	10.6	9.6
Ivindo: Soil C and N removed	16.4	12.5	11.8	11.7

The first axes of these latter analyses largely describe relationships in soil properties (Figure 2.8a & d) as well as leaf-litter, with similar patterns between sites; soil moisture and pH increase, as the leaf-litter decreases. Soil moisture and pH co-varied positively with soil C/N ratio in Danum (Figure 2.8a), and therefore they had a negative relationship with soil C_{tot} and N (Figure 2.7a). In Ivindo by contrast, soil moisture and pH negatively co-varied with C/N ratio (Figure 2.8d), and therefore as in Danum, these would negatively co-vary with soil C_{tot} and N.

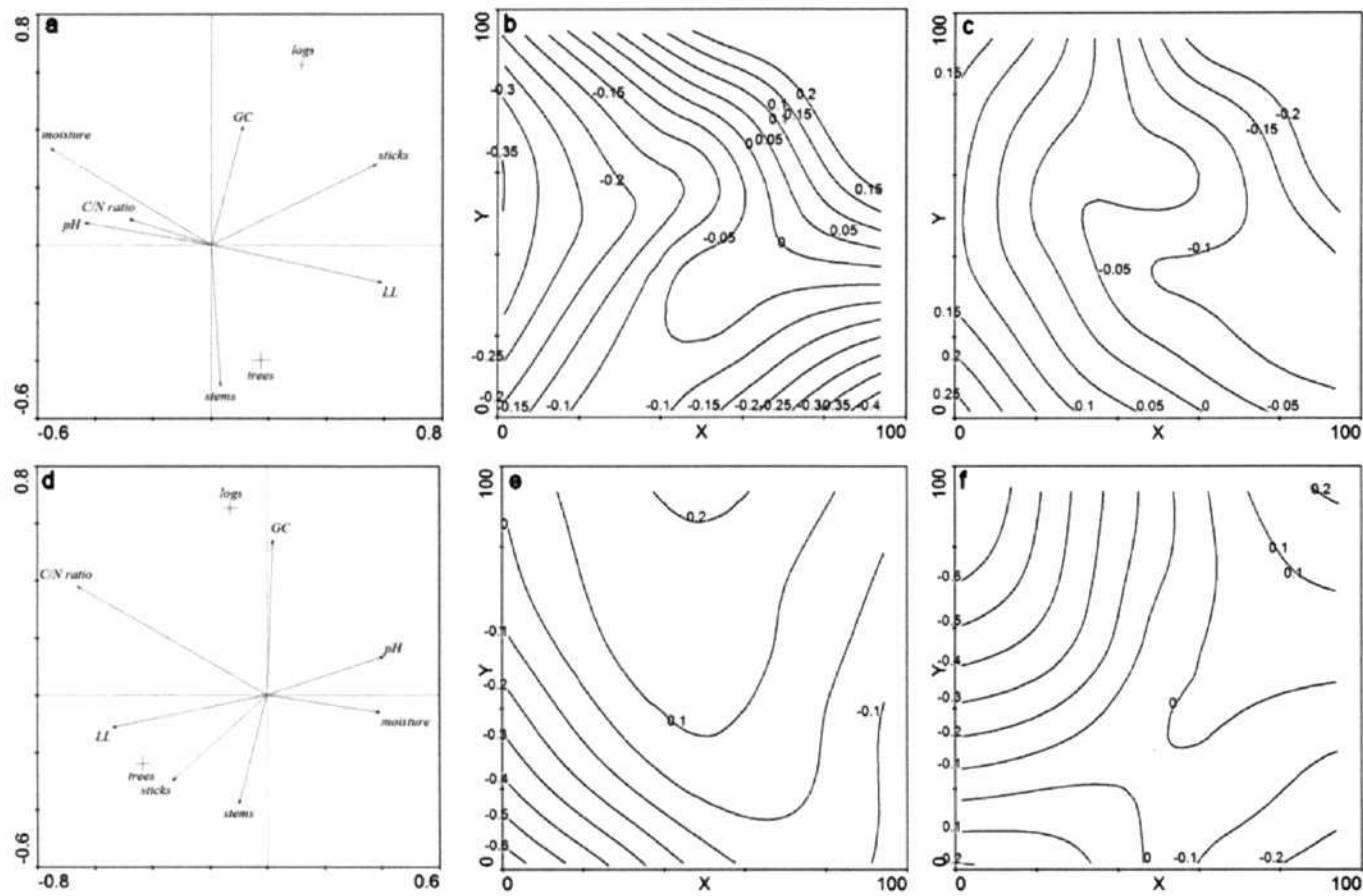


Figure 2.8 PCA environmental relationships without soil C_{tot} and N for Danum (a, b, c) and Ivindo (d, e, f). a) & d) PCA axis 1 vs axis 2 plot. LL, leaf-litter; GC, ground vegetation cover. b) & e) Contour plot of sample point axis 1 scores. c) & f) Contour plot of sample point axis 2 scores.

In both sites the environmental relationships described in the first axis, which are predominately soil variables, correspond with small-scale topographic features within each plot (Figure 2.1c and Figure 2.2c). In Danum the orientation of the negative PCA axis 1 values, that represent high soil moisture, pH and C/N ratio and low leaf-litter (Figure 2.8a & b), corresponds with a gentle southern slope in the south-east of the plot, and a slope towards a small gully in the east of the plot (as indicated in Figure 2.1c). In Ivindo, the positive PCA axis 1 values, representing the same combination of environmental conditions are orientated in the north-east of the plot (Figure 2.8e), which corresponds with a gentle easterly aspect (Figure 2.2c). The negative PCA axis 1 values (representing low soil moisture and pH, and higher leaf-litter and soil C/N ratio), show more spatial structure in the south west of the Ivindo plot (Figure 2.8e), that corresponds with the flat area (see Figure 2.2c).

The second axes of the PCAs mostly describe the vegetation measurements and the presence of logs, with similar relationships in both sites; ground vegetation is denser around logs, there tends to be more stems near trees (although in Ivindo this is weak), and these two groups are inversely related (Figure 2.8a & d). In summary, there are more logs and ground vegetation where the upper and mid canopy vegetation is less dense. These variables are structured as a gradient across the Danum plot: more ground vegetation and logs in the west (+ve PCA axis 2 values) are replaced by more trees and stems towards the east (-ve PCA axis 2 values) (Figure 2.8c). In Ivindo these vegetation associations represent separate patches; the north-west and south-east sections of the plot are characterised by higher stem density and the presence of trees (-ve PCA axis 2 values) (Figure 2.8f).

Apart from the major difference in the direction of the C/N ratio relationships with other soil properties, the number of sticks was the only other variable that did not show consistent relationships between sites. In Danum, stick density correlated with leaf-litter depth, ground vegetation and logs (Figure 2.8a). In Ivindo, sticks also correlate with leaf-litter, but was more strongly associated with trees and stems (Figure 2.8d).

Axis 3 of the PCA analyses explains positive co-correlation of stems and ground vegetation in both Danum and Ivindo (Figure 2.9a & b), which must then be structured in a different spatial manner to the negative co-correlation explained in axis 2 in both sites. There are no other general similarities in environmental relationships between the two sites in axis 3, and none in axis 4, however a negative co-correlation in stems and trees is described in axis 3 of the Danum PCA, and axis 4 of the Ivindo PCA.

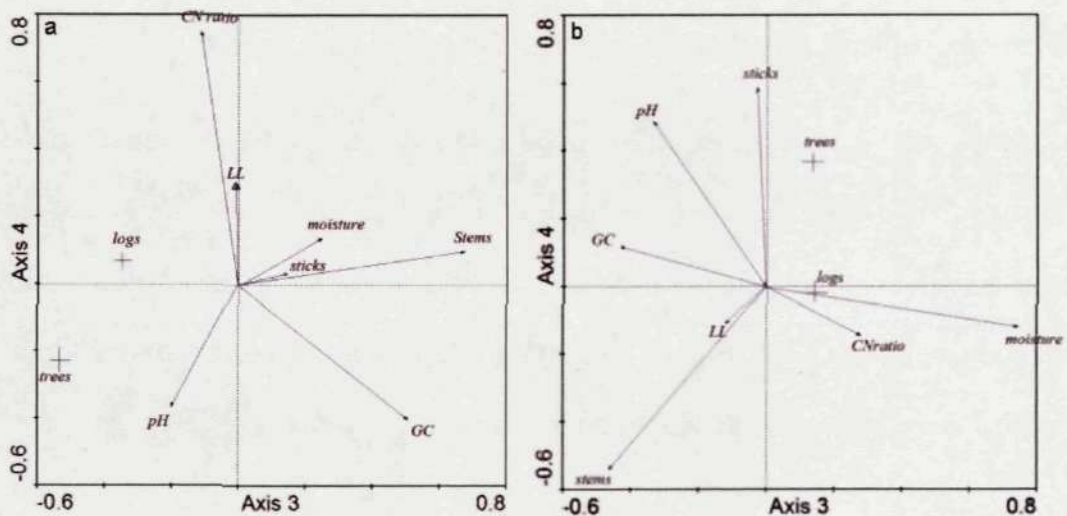


Figure 2.9 PCA axis 3 vs axis 4 plot of environmental relationships. a) Danum, b) Ivindo. LL, leaf-litter; GC, ground vegetation cover.

2.5 Discussion

2.5.1 Comparison of environmental conditions

2.5.1.1 Similarities

The similarity between the sites in the mean and variance of soil C_{tot} and soil N, and pH are remarkable, when one considers comparable measurements from other studies in each region. In Gabon, only 200 km to the west of Ivindo the rain forest soils in Lope National Park had a mean pH value of 4.64 ± 0.34 (Roose-Amsaleg *et al.*, 2005). The means of pH in Danum and Ivindo (4.1 ± 0.3 and 4.0 ± 0.2 respectively, Figure 2.5) are therefore more similar than between rain forest sites within the same region. Using the soil C linear model equation (see Section 2.4.1), the C_{org} mean is calculated to be 3.9% in Danum and 3.8% in Ivindo. These estimates are similar to those from other studies in each region; in a previous study in Danum soil $C_{\text{org}} = 3.7\% \pm 0.87$ (Eggleton *et al.*, 1997), and in a Cameroonian rain forest soil $C_{\text{org}} = 3.5\%$ (Donovan *et al.*, 2001b).

Logs, number of sticks, leaf-litter depth, soil C and N were measured as indicators of the quality and availability of termite food material. The overlapping frequency distributions (Figure 2.6) and similarities in their means and abundances (Figure 2.6, Figure 2.7, and Table 2.1) in these variables suggest that this factor is broadly similar in both plots.

2.5.1.2 Differences

Differences between the means and frequency distributions are more apparent for the remaining environmental variables, which measure vegetation structure and other soil properties. The factors that determine soil moisture and infiltration rates are complex and operate at various spatial scales. Soil texture influences

infiltrations rates and moisture levels (Foth, 1990), and the sandier soil texture in Ivindo may explain the higher infiltration rates and lower soil moisture levels recorded there. The mounds of termites have been shown to both increase and decrease soil porosity depending on the species being considered, while organic enrichment in mounds increase water storage capacity (Holt & Lepage, 2000). These effects of termite mounds on soil would be occurring at fine spatial scales. The high density of termites in African rain forest soils (Eggleton *et al.*, 1999) may increase infiltration rates throughout the upper soil profile due to tunneling from termites.

Annual precipitation rates in Danum are far higher than in Ivindo, however a similar range of rainfall was recorded during the collection periods. This suggests that the soil moisture differences recorded here (Danum= 38.8 ± 6.3 , Ivindo= 25.5 ± 5.6) were not due to rainfall events during the sampling period, raising an important point. The response of rain forest termite communities to rainfall is not consistent in studies that examine this relationship; in a Cameroonian study rainfall had a negative effect on termites at short time-scales (Dibog *et al.*, 1998), while in a dry evergreen forest in Thailand, no significant effect was found (Inoue *et al.*, 2001). It may be that termites migrate further down into the soil profile briefly if soil becomes temporarily water-logged. Given the large differences between sites in soil water content, it would be reasonable to conclude that any short-term changes to this resulting from rainfall events during the study period, are unlikely to have had vastly different impact on the sampled termite assemblages.

The Danum plot had a higher density of trees and stems, which may relate to the higher tree species richness per hectare in Asian rain forests compared with

African (Latham & Ricklefs, 1993). At global scales, tree and termite species richness in rain forests therefore show opposing patterns (Davies *et al.*, 2003a). At a local scale however, termite diversity was related to the greater habitat complexity and tree species richness in forests from across a disturbance gradient (Gillison *et al.*, 2003). At such local scales, tree heterogeneity may then also have a positive influence on the termite community, by increasing micro-habitat heterogeneity. Alternatively the root matt associated with a higher density of trees, may occupy space in the soil, and therefore have a negative effect on the termite community, as Donovan *et al.* (2007) have previously observed.

The higher C and lower N concentrations, although small, explain the higher soil C/N ratio recorded in Danum (Danum mean=17.8, Ivindo mean=13.7). The PCA analyses demonstrate that the soil C/N ratio is inversely related to soil C_{tot} and soil N in Danum, while in Ivindo these are positively related (Figure 2.7a & b). In order for these patterns to occur, the rate at which soil C_{tot} and soil N co-vary must differ between sites, as indicated in Figure 2.10. Although soil C/N ratio is influenced by numerous factors, it is frequently used as an indicator of decomposition rates (Foth, 1990). Enriquez *et al.* (1993) demonstrated from across a range of habitat types that decomposition rates increase with decreasing C/N ratio. If these relationships are applied to the patterns in Danum and Ivindo, this suggests that where soil C and N concentrations are high, decomposition rates are also high in Danum. In Ivindo, however, decomposition rates are low where soil C and N concentrations are high.

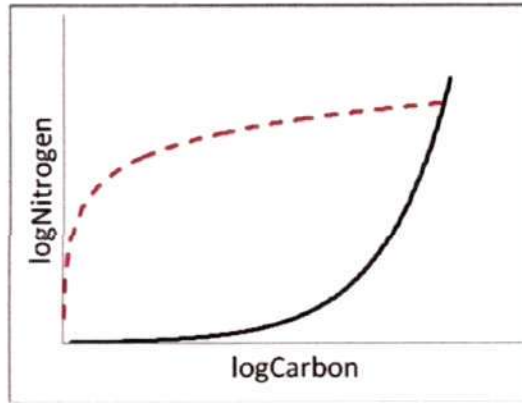


Figure 2.10 The soil C and N relationship that explains the subsequent co-correlation with C/N ratio in each site. Danum, black line; Ivindo, red dashed line.

Considerations of the importance of the C/N ratio in food material consumed by termites, are in the context of overall termite feeding strategies (Eggleton & Tayasu, 2001). For instance wood-feeding and fungus-growing termites consume dead plant material that has a high C/N ratio; these termites are N limited but are efficiently able to burn-off excess C. Soil-feeding termites live on an energetic knife-edge, and high consumption rates of soil, which relative to woody material has a low C/N ratio, is necessary for sufficient marginal energetic gains (Eggleton *et al.*, 1998). Within soil-feeding termites the heterogeneity in soil C/N ratio, may be less important, however, than the availability of highly stable humic substances, and specifically the proteinaceous fractions of this, which have been shown to be selectively digested by soil-feeding termites (Ji *et al.*, 2000). In this study, I assume that soils with higher soil C_{tot} have proportionally higher concentrations of organic compounds that can be digested by termites.

In summary, indirect measures of food material i.e. soil C and N for soil-feeding termites, and availability of dead plant material for non-soil feeding termites, are

very similar in both plots. Understorey vegetation, soil moisture and soil porosity differ the most. Biogeographic history, rather proximate ecological factors such as these explain the regional differences in termite species richness (Davies *et al.*, 2003a), however at fine spatial scales, they may influence the heterogeneity of termite assemblages in a variety of ways, and this will be examined in Chapters 5 and 6.

2.5.2 Environmental relationships

The third and fourth axes of the PCAs explained only marginally less variance than axes two and three (Table 2.2), demonstrating that the environmental variables co-vary in a complex fashion in both plots. Despite this, it is interesting that the first two axes (i.e. those that explain proportionally more variance) explain largely similar environmental relationships in both sites, while relationships in the subsequent axes are mostly idiosyncratic to each site. The largely consistent relationships described in the first two axes (Figure 2.8a & d), suggest that microhabitat patches, characterised by similar environmental conditions, are present in both plots. Figure 2.11 summarises the relationships described by axes 1 and 2 which, as indicated by the contour plots (Figure 2.8b, c, e & f), are broadly structured across each plot.

Soil properties correlate, with soil tending to be wetter, less acidic, and of lower carbon quantity on slopes, and leaf-litter tending to be denser on flat ridges. Similar patterns have been noted in rain forests across a broader altitudinal range (>300m) by Tsui *et al.* (2004). In that study it was suggested that the constant transport and accumulation of water and solutes generated the higher pH, and lower C_{org} and N in the lower slopes and depositional areas. The higher soil organic matter concentrations on the summit in the Tsui *et al.* (2004) study,

was also attributed to the lower temperature which would slow decomposition processes, along with higher leaf-litter quantity. The results from this study suggest that spatial heterogeneity in soil properties due to water flow and leaching may be detectable at much finer scales. Less leaf-litter on the slopes in this study may be due to vegetation properties or by litter being gently dragged down slopes during heavy rainfall. This greater accumulation of leaf-litter on the flat areas may explain the associated higher soil C and N.

The most plausible explanation for the described correlations of the vegetation properties is tree-fall events. The subsequent aggregation of logs and branches may persist for some time following the tree-fall, and a fragmented canopy would result in dense understorey vegetation. Condit et al (2000) demonstrated that the vast majority of tropical tree species in a Neotropical rain forest are strongly aggregated at short distances, likely due to dispersal limitations. Where adult trees are aggregated, one might also expect a high density of young trees (stems), explaining the association between trees and stems. The spatial structure of the vegetation patterns do not obviously correspond with plot topography. Leaf-litter is denser among the trees and stems, while in Ivindo, the number of sticks is also greater with more trees.

The main difference between the two sites is the C/N ratio pattern, which is higher in wetter soil in Danum, therefore corresponding with slopes (Figure 2.11). Typically decomposition rates (therefore a lower C/N ratio) increase with soil moisture (Liang *et al.*, 2003), however this is reversed when soil becomes water-logged due to the anaerobic conditions (Tiquia *et al.*, 1996). The higher overall moisture content in Danum relative to Ivindo may mean that the wettest

soils in Danum are actually water-logged and the rates of decomposition are thus reduced.

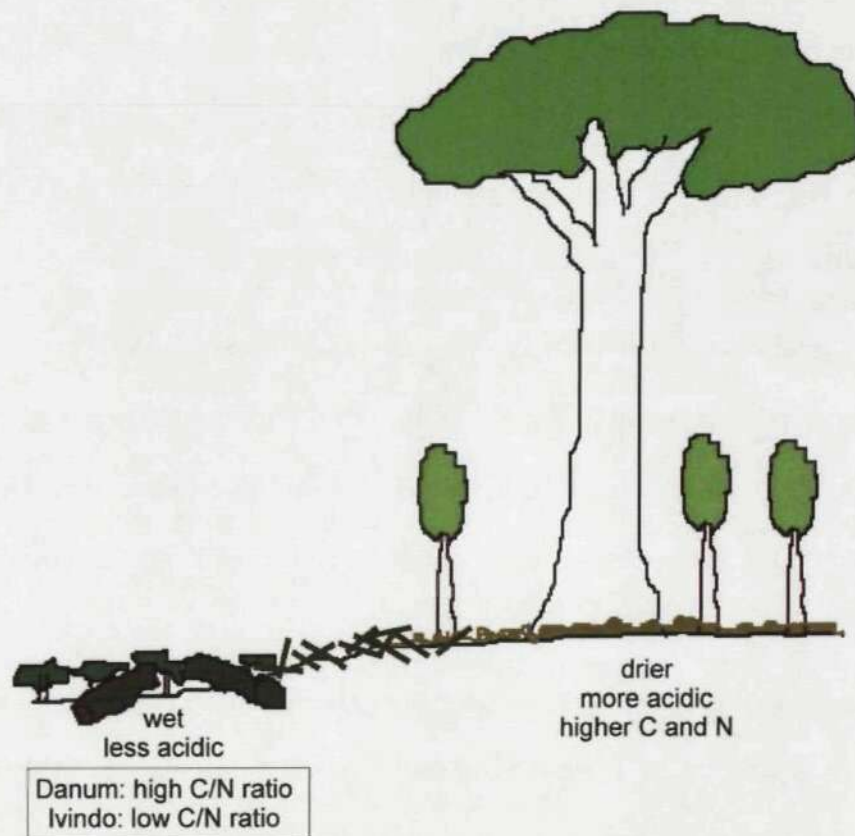


Figure 2.11 Schematic diagram summarizing the main environmental relationships detected in axes 1 and 2 of the PCA analyses.

2.6 Conclusions

All equatorial rain forests are characterized by extremely wet and warm climatic conditions, multistratal closed-canopy vegetation, and extremely high species diversity. Of all the tropical rain forest systems, those of Africa and SE Asia have perhaps the most dissimilar climatic and evolutionary histories (Morley, 1999). These habitat similarities and historical differences are reflected in the patterns of similarity and difference in environmental conditions within the one hectare study plots. Soil C and N concentration, pH, and measures of plant

debris are most similar, while vegetation and soil structure differ the most between study plots. These differences may then have variable influences on the termite assemblages, for instance changes in soil moisture may have a greater impact on termites in Danum due to the higher water content of the soils, and therefore possible tendency to water-logging.

The environmental relationships and the scales at which these are structured, were, to a certain degree, similar in both forest plots. Therefore the termite assemblages have been sampled from plots that present a similar suite of microhabitats conditions in both study sites. Chapter 5 will examine the relationships between the termite assemblages and environmental variables. The question there will be whether the detected environment-termite associations are either due to: 1) overall microhabitat heterogeneity, or 2) site- or region-specific environmental conditions that were outlined in this chapter, and/or differences in the termite assemblages as outlined in the following chapter.

3 Soil-dwelling macrofaunal assemblages: composition, occupancy and co-occurrence

3.1 Summary

In Chapters 4 and 5, the spatial structure and a series of ecological patterns of rain forest termite assemblages will be examined, in the context of the known regional differences in rain forest termites. The purpose of this chapter is to: 1) describe the surveying methods and identification protocols, 2) assess whether the sampled termite assemblages represent the known regional differences in taxonomic and functional diversity from African and Asian rain forests, and 3) describe the occupancy and co-occurrence patterns of the termite and ant assemblages. The Ivindo (African) and Danum (Asian) assemblages sampled here accurately reflect the known region-specific differences in taxonomic (generic) richness and functional (feeding) diversity. Soil-feeding termites were particularly abundant (measured as pit encounter rates) and genus-rich in Ivindo. There was also a high degree of overlap within pits (or co-occurrence) of non-soil-feeding termites with soil-feeding termites. In Danum, soil-feeding termites were far less abundant, with less co-occurrence of the feeding-groups in individual pits. Although ant generic richness was greater in Danum, occupancy rates were similar in both sites, while predatory ants occupied marginally more pits in Ivindo. In Ivindo predatory ants were found to almost fully co-occur with termites, and in particular with soil-feeding termite, while predatory ant co-occurrence with termites was less in Danum. This baseline data provide contextual information to interpret the ecological patterns examined in later chapters.

3.2 Introduction

Watt *et al.* (1997) estimated that termites comprise up to 95% of soil insect biomass in a southern Cameroon forest. Other estimates, such as 10% of all animal biomass in the tropics being composed of termites (Wilson, 1993), are equally staggering. Although an accurate estimate from rain forest systems is still lacking, the underlying message remains; termites are an extremely abundant and significant component of tropical rain forest soil systems (Wood *et al.*, 1982; Eggleton *et al.*, 1996; Eggleton *et al.*, 1999), matched possibly only by ants.

We know, however, that a search for termites in African forests yields very different results from an Asian forest, i.e. this high abundance and diversity is not uniformly distributed across the equatorial rain forest blocks (Eggleton, 2000a; Davies *et al.*, 2003a). Rather an inter-continental gradient exists; African assemblages are particularly abundant and taxonomically rich, while S. American assemblages are intermediate, and Asian rain forest assemblages are relatively depauperate (Davies *et al.*, 2003a). As outlined in Chapter 1, the functional diversity also differs between regions. African assemblages are dominated by termites that consume highly humified soil, while this feeding preference is almost completely absent in Asian assemblages.

Global patterns of termite diversity have thus been well characterized, and these are attributed to biogeographic rather than ecological processes (Davies *et al.*, 2003a). Within-region factors such as habitat type and disturbance, and altitude, have a large impact on local assemblage structure (e.g. Jones, 2000; Jones & Prasetyo, 2002; Eggleton *et al.*, 2002a), and the resulting assemblage changes appear to be consistent between regions (Eggleton *et al.*, 1999).

However of the studies that examine ecological processes and interactions at the local scale, relatively few are of rain forest termites (exceptions include: Davies *et al.*, 2003b; Roisin & Leponce, 2004; Donovan *et al.*, 2007; Deblauwe *et al.*, 2008), and none consider whether similar processes occur across the inter-equatorial rain forest diversity anomaly.

To address this, in this thesis I compare and contrast ecological patterns from an African and Asian assemblage, chosen for their extreme differences in local assemblage structure. The additional aim was to quantify the spatial structure of the assemblages, and to understand the spatial scales at which interactions are occurring. To address these questions a single one hectare plot was surveyed in each region, and due to time constraints within-region replication was not possible. Intensive, spatially explicit studies of biotic communities are more common for plants, surveyed from vegetation plots that exceed 16 hectares (e.g. Condit, 1995; He *et al.*, 1996; Legendre *et al.*, 2009), and where, as a result of the high surveying effort, replication is not possible. To minimize the implications of lack of replication, sampling criterion identified in this study were for the sampled assemblages to: 1) adequately represent the inter-continental differences and 2) be typical of lowland forest assemblages known from each region, in terms of their taxonomic richness and functional diversity. In Asia it was possible to select a site where the termite fauna has been well characterized (Danum Valley Conservation Area). In Africa, however, it was not possible to return to a previously well studied site, Mbalmayo in Cameroon, as originally intended, due to continued disturbance and fragmentation of the forest.

The aims in this chapter are to:

1. Describe the biotic field sampling protocol and identification process.
2. Assess whether the taxonomic richness, functional composition and abundance of the sampled termite assemblages, reflect the known inter-continental differences and local patterns typical of primary lowland rain forests.
3. Compare the occupancy and co-occurrence patterns of the non-soil-feeding and soil-feeding termites in the Danum (Asian) and Ivindo (African) assemblages.
4. Compare the occupancy and co-occurrence patterns of termites and ants in the Danum and Ivindo assemblages.

Aims 3 and 4 provide precise local data on relative abundance and occupancy, which is valuable for interpretations of the ecological interactions, i.e. trophic cascades and ant predation, examined in later chapters. In addition this provides comparative data of soil-dwelling termites and ants from an Asian and African rain forest that has not previously been examined in this level of detail.

3.3 Methods

3.3.1 Sampling design

The most frequently employed sampling method of tropical termite assemblages is the linear 2m x 100m 'belt' transect, divided into contiguous quadrats (e.g. Deblauwe *et al.*, 2008; Dosso *et al.*, 2010; Jones *et al.*, 2010). This method has been demonstrated to effectively sample the taxonomic and functional diversity of local assemblages (Jones & Eggleton, 2000). It has been particularly useful in that, as a standardised method, comparisons and meta-

analyses are possible between local assemblages sampled from across large spatial and temporal scales (e.g. Davies *et al.*, 2003a). Roisin & Leponce (2004) recommended altering the quadrat frequency along non-linear transects depending on local species density, with the aim of more fully characterising local assemblage patterns. This later method however suffers from the loss of standardised sampling effort between sites for inter-site comparisons (Jones *et al.*, 2006).

The lack of spatial referencing in the "quadrat-along-transect" methods prevents any identification and description of the spatial structure in a population or local assemblage. Quantifying spatial ecological patterns can include identifying: spatial patterns or distributions of a local population, the spatial scale of heterogeneity, and multi-species aggregations, which for sample data is frequently collected from regularly spaced sample points in a two-dimensional sample design (Fortin & Dale, 2005). Ecological processes operate at a number of spatial scales generating spatial patterns at these hierarchical scales; at broad scales climate and landscape-scale heterogeneity generate spatial patterns, while at fine scales biotic interactions are important in generating spatial patterns (Ettema & Wardle, 2002). Therefore the scale of sampling is determined based upon the particular ecological questions. As outlined in the introduction, the aim of this study was to: 1) describe spatial structure of the local assemblages, i.e. those typically characterised in the standardised transects, 2) understand the ecological processes that generate these, in particular the biotic processes which are essentially unknown in rain forest termites, and 3) assess whether similar patterns and therefore rules exist in assemblages from different continents. A two-dimensional plot, the dimensions

of which are described below, was selected to reflect these aims. An alternative approach would have been a series of transects or quadrats positioned at regular intervals at a broader spatial scale, however the main ecological patterns would have reflected habitat-scale environmental heterogeneity such as topography, more so than biotic interactions. While this would also be novel information, an inter-continental comparison may be limited due to potential differences in the spatial scale and magnitude of this within-habitat heterogeneity.

3.3.2 Spatial scale

The scale and resolution of any spatial patterns in data is determined by the scale of sampling parameters used relative to the study organism in question (Dungan *et al.*, 2002). The choice of grain size (area of the sampling unit), lag (spatial position of the sampling unit) and extent (area of plot) were here based on recommendations from previous termite studies. Of particular relevance is the only other spatially explicit study of termite assemblages in a rain forest, carried out by Donovan *et al.* (2007) also in Danum Valley Conservation Area (DVCA). That study specifically examined how the choice of lag and extent impacted the ability to detect spatial patterns in the assemblage.

Grain. A soil pit of 25cm x 25cm x 10cm deep is a standard grain size demonstrated to capture soil-dwelling termites efficiently (Eggleton *et al.*, 1997; Jones & Eggleton, 2000). The disadvantage of sample designs that describe spatial patterns is the high required sample size in two-dimensions (see below), which placed limitations on the microhabitats that could be sampled here. In addition to soil pits, leaf-litter, woody debris and termite 'run-ways' are also searched by the standardised transect method, which was not possible here. In

rain forest systems the majority of termite species are soil nesting (Eggleton *et al.*, 2002b), and therefore given the limitation to a single microhabitat in this study, searching soil pits is the most effective method to sample the largest proportion of termite assemblage composition within the study area.

Lag. Pits were sampled at a lag of every 2m x 2m, which was demonstrated to more effectively capture significant spatial structure of a termite assemblage, compared with a lag of 0.5m or 4m (Donovan *et al.*, 2007).

Extent. A minimum extent of 64m x 64m was shown to be necessary to capture significant spatial structure of the termite assemblage (Donovan *et al.*, 2007). Here an extent of 96m x 96m was selected based on these recommendations and the dimensions of sub-plots; the plot was divided into contiguous sub-plots of 12m x 12m, which was considered suitable for sampling one sub-plot per day. 8 x 8 sub-plots were sampled therefore requiring a minimum of 64 field surveying days to survey each plot. The order in which sub-plots were surveyed was randomized, thereby preventing any temporal shifts in the termite assemblage from being interpreted as a gradient within the spatial data.

3.3.3 Field sampling

In total 2304 pits per plot were sampled. Each pit was dug and hand-sorted for 10 minutes, thoroughly sifting through the soil material for termites and ants. Field sampling was carried out with the assistance of two to three long-term field assistants in each site. To standardize sampling effort between field samplers, the soil material in each pit was divided in two, with each half sorted for five minutes. When termites and ants were encountered, a representative sample was collected and stored in 95% alcohol. Soldier termites generally

have more easily identifiable taxonomic characters, and wherever possible both termite soldiers and workers were collected to aid identification. Identification to species or genus is not possible in the field, and therefore care was made to collect a representative number of individuals (minimum of 5) that differed in overall size, shape and structure in the workers and soldiers, for both the termites and ants. The number of individuals per pit was not counted, due to the very high densities frequently encountered which would render count estimates as inaccurate. It is also not possible to quantify colony frequency. In subsequent summary statistics and analyses, presence of a taxon within a soil pit is considered an 'hit' or encounter, and taxon abundance refers to the frequency of encounters. Abundances therefore are neither a measure of absolute abundance per unit area, nor of the number of colonies, but an intermediate measure of relative taxon frequency.

The surveying protocol was limited to pits as: 1) the major components of termite assemblages in rain forests of both regions are ground-nesting (Eggleton *et al.*, 1997; Eggleton *et al.*, 2002b), and 2) given the large sample size it would not have been logistically possible to survey additional microhabitats e.g. foraging runways and dead wood across the sampling area in a standardized manner.

Worms encountered in pits were also collected and stored in 4% formalin solution. Identification was not carried out because: 1) the majority of samples were juveniles and therefore lacking in characters necessary for taxonomic identification, and 2) there was a particularly low occupancy rate in Danum (Figure 3.8), and therefore it was unlikely that significant spatial structure could

be detected. The worm occupancy data are presented here for completeness, but no further analyses of the worms are included in subsequent chapters.

3.3.4 Taxonomic identification

Taxonomic identification of the termites and ants was standardized to genus level. This was necessary due to time constraints in identifying the Ivindo assemblage, where the high hit rates and taxonomic diversity meant that species-level identification would have been prohibitively time consuming. It is generally considered that closely related species are ecologically and functionally more similar than distantly related species (Slingsby & Verboom, 2006; Swenson *et al.*, 2007), and that ecological interactions are phylogenetically conserved (Gomez *et al.*, 2010). As this study uses genus- rather than species-level data, and in the absence of congeneric niche information for termites, it is assumed that congeneric species are ecologically more similar than species from different genera. Therefore I assume that genus-level data approximately equates to species-level data, when considering assemblage level ecological interactions.

The Danum termite samples were identified to genus using the taxonomic works of Thapa (1981), Gathorne-Hardy (2001), and Ahmad and Akhtar (1981), and the reference collections of University Malaysia Sabah and the Natural History Museum, London. Identification of the Ivindo samples were carried out using the taxonomic works of Sands (1972; 1998), Bouillon and Mathot (1965), and the reference collections at the Natural History Museum, London. In African assemblages the *Anoplotermes*-group (Apicotermatinae) are small soldierless termites, that are particularly species rich (e.g. Eggleton *et al.*, 2002b; Deblauwe *et al.*, 2008). For taxa within this group of genera that feed on highly

humified soil, genus-level identification is reliable and based on armature of the enteric valve in the worker gut (Sands, 1972). However, those genera that feed on humus soil lack this character and are taxonomically less tractable. This is particularly the case for *Astalotermes*, which occupies a transitional position between other genera, in terms of its taxonomic characters (Sands, 1972). Following Eggleton et al. (2002b), *Astratotermes* and *Acidnotermes* are placed within *Astalotermes* due to the lack of any unique combination of characters within the first two genera.

3.3.5 Functional group assignment

A feeding-group classification exists that places termites into groups defined by the stage of decomposition (termed the “humification gradient”), of their food material. Termite genera are assigned to feeding-groups (FG) based on morphological characters of the worker, which correlate with the proportional amounts of plant tissue and silica in the worker gut (Donovan et al., 2001a).

FGI: Lower termite families. These termites are all dead wood and grass-feeding.

FGII: Representatives of the Termitidae family that consume a range of non-soil food material including dead wood, grass, leaf-litter, micro-epiphytes. Fungus-harvesting Macrotermitinae are also placed in this group, and these termites have fungal mutualism in order to partially decompose collected leaf-litter material prior to consumption. For simplicity I refer to this group as ‘wood-feeding’ throughout the thesis.

FGIII: Representatives of the Termitidae family that consume soil material with a high organic content, and wood material that is heavily decayed and has become soil-like. They can be termed 'humus-feeders'.

FGIV: Representatives of the Termitidae family that consume heavily decomposed mineral soil with low organic content. These are termed the 'true soil-feeders'.

For genera that were not included in the Donovan et al. (2001a) study, assignment to feeding-groups were as follows:

Globitermes (Termitinae, Danum), which previously has been classified as a wood-feeder, was placed in FGII following Donovan et al. (2007).

Homalotermes, *Prohamitermes* and *Termes* (Termitinae, Danum), that previously have been classified as soil-wood interface feeders were placed in FGIII.

Anenteotermes and *Aderitotermes* in the *Anoplotermes*-group (Apicotermitinae, Ivindo) include FGIII and FGIV species based on the absence or presence of enteric valve armature respectively, which is an important character used to distinguish between FG assignment (Donovan *et al.*, 2001a). Due to the feeding ecology differences of species within the two genera, in later chapters each of these genera is divided into two, and therefore treated as separate genera (e.g. *Anenteotermes* FGIII and *Anenteotermes* FGIV) when the analyses were conducted by feeding-group.

3.3.6 Ant identification and classification

Ants were identified to genus level using the taxonomic resources of Bolton (1994), Antbase (www.antbase.net), CSIRO (2010), and Hashimoto (2007). Brown (2000) provides a summary list of genus-level feeding preferences in ants. Ant genera that are obligate termitophages, as well as those defined as generalist predators and therefore likely to include termites in their diet, were assigned to a predatory ant (PA) group.

3.4 Results

3.4.1 Termite assemblage composition and occupancy rates

3.4.1.1 Danum

Twenty-nine termite genera from two families were recorded in Danum (Table 3.1). The *Mirocapritermes*-group was very genus rich, and was largely composed of soil-feeding genera that live in subterranean (hypogean) nests, or mounds that extend above the soil surface (epigeal). There were also several representatives of the Nasutitermitinae sub-family that encompass a number of different feeding and nesting strategies. This included termites that nest in wood, while foraging separately for wood, litter and epiphytic material and are therefore not necessarily soil-dwelling.

Table 3.1 Danum termite genera. NG, nesting-group; h, hypogeal-; e, epigeal-; w, wood-; a, arboreal-nesting. FG, feeding-group; L(F), leaf-litter (fungus-harvesting); S/W, soil-wood interface.

Family Sub-family	Genus	Hits	NG	FG
Rhinotermitidae				
	<i>Heterotermes</i>	6	h	I
	<i>Parrhinotermes</i>	3	w	I
	<i>Schedorhinotermes</i>	1	w	I
Termitidae				
Macrotermitinae	<i>Macrotermes</i>	37	e	II (L(F))
	<i>Odontotermes</i>	26	h	II (L(F))
Foraminitermitinae	<i>Labritermes</i>	2	h	III
Apicotermitinae	<i>Euhamitermes</i>	5	h	III
Termitinae				
Amitermes-group	<i>Globitermes</i>	285	h	II (W)
	<i>Microcerotermes</i>	9	e/a	II
	<i>Prohamitermes</i>	101	h	III (S/W)
Mirocapritermes-group	<i>Coxocapritermes</i>	57	h	III
	<i>Dicuspitermes</i>	84	e	III
	<i>Homallotermes</i>	9	w	III (S/W)
	<i>Malaysiocapritermes</i>	18	h	III
	<i>Mirocapritermes</i>	24	h	III
	<i>Oriencapritermes</i>	122	h	III
	<i>Pericapritermes</i>	72	h	III
	<i>Procapritermes</i>	85	h	III
Termes-group	<i>Termes</i>	8	h	III (S/W)
Nasutitermitinae	<i>Bulbitermes</i>	57	w	II
	<i>Hiritermes</i>	2	w	II
	<i>Hospitalitermes</i>	2	w	II (L)
	<i>Laccessitermes</i>	11	w	II (L)
	<i>Leucopitermes</i>	1	h	III
	<i>Longipeditermes</i>	11	w	II (L)
	<i>Malaysiotermes</i>	51	h	III
	<i>Nasutitermes</i>	35	a	II
	<i>Oriensubulitermes</i>	28	h	III
	<i>Subulioditermes</i>	1	h	III

Three of the four feeding-groups (FG) were represented, the exception being the true soil-feeding-group (FGIV), which typically is very rare in SE Asia. The order of generic richness per feeding-group was: FGIII (16) > FGII (10) > FGI (3). Figure 3.1 compares the FG generic richness with the Eggleton et al. (1997) survey, carried out in approximately the same location in Danum Valley

Conservation Area. The primary forest (PF*) assemblage is pooled from two standardized transects of 100m x 2m, where a range of microhabitats including soil pits are sampled (Jones & Eggleton, 2000). Overall generic richness is greater in the Danum plot, due to an almost doubling of the frequency of FGIII genera.

The most frequently encountered termite was *Globitermes*. The species collected here, *Globitermes globosus*, constructs discrete subterranean nests, and consumes wood that is partially decomposed but not yet soil-like. Most of the remaining non-soil-feeding (NSF) genera (FGI and FGII) do not exceed 40 encounters each. Several, in particular the Rhinotermitidae genera, are rare (<10 hit rate). Compared with the non-soil-feeding-group, generic richness is higher, and the rank abundances (encounter rates) appear to be more evenly distributed in the soil-feeding (FGIII) component of the assemblage (Figure 3.2).

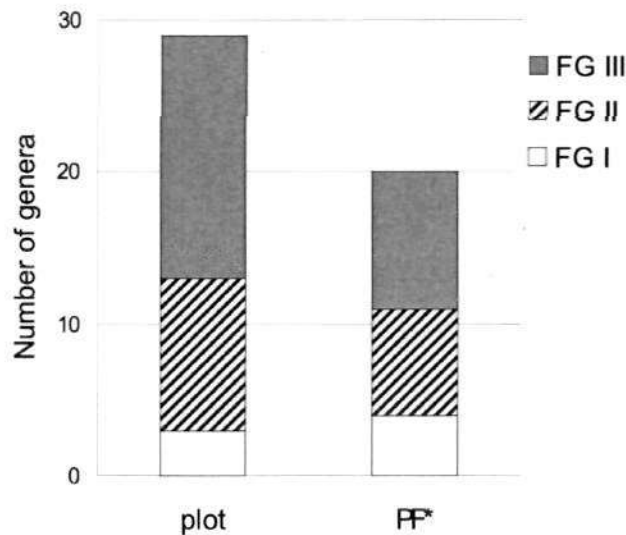


Figure 3.1 Termite generic richness by feeding-group from the plot (Danum), and PF* (two pooled transects in primary forest (Eggleton *et al.*, 1997)).

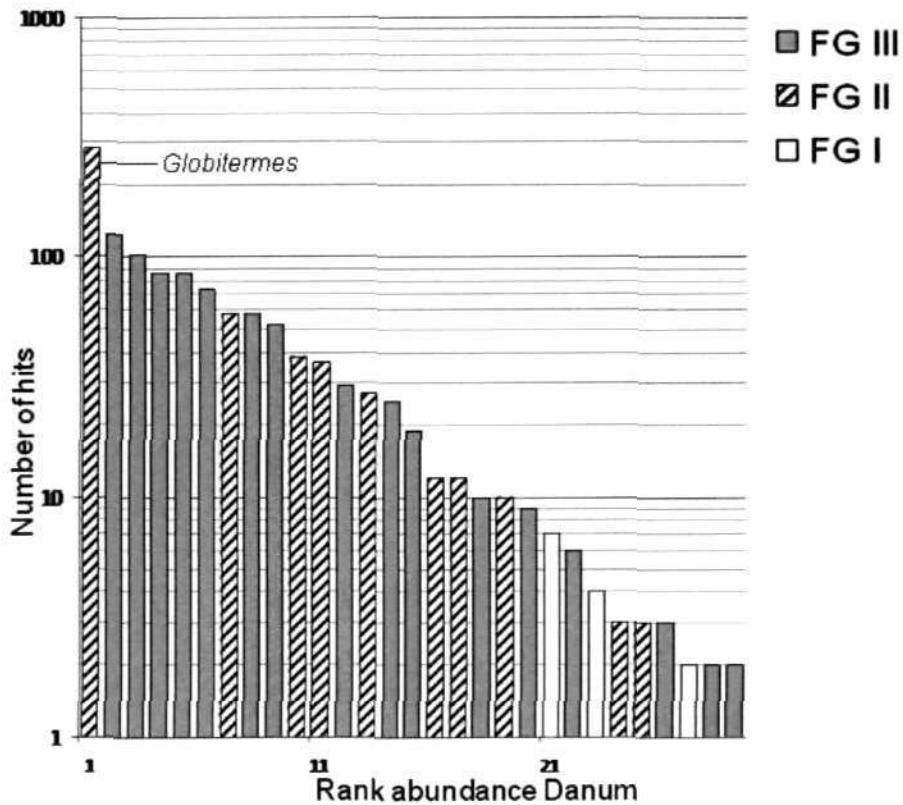


Figure 3.2 Danum rank abundance (number of hits per genus) distribution (on a log scale).

3.4.1.2 Ivindo

Termites were identified from 43 genera (Table 3.2), with only a single non-Termitidae genus, *Schedorhinotermes* (Rhinotermitidae), which was extremely rare. Soil-feeding and hypogeal-nesting termites in the Apicotermitinae subfamily and *Cubitermes*-group (Termitinae) typically dominate African rain forest assemblages (e.g. Eggleton *et al.*, 1996; Eggleton *et al.*, 2002b; Deblauwe *et al.*, 2008), and here make up a large component of the generic richness. The soil-feeding genera were by far the most significant component of the Ivindo assemblage (Figure 3.3). FGIV comprises >50% of total generic richness, with the order of feeding-group generic richness as follows: FGIV (29) > FGIII (8) > FGII (7) > FGI (1).

Table 3.2 Ivindo termite genera. NG, nesting-group; h, hypogeal-; e, epigeal-; w, wood-; a, arboreal-nesting. FG, feeding-group; L(F), leaf-litter (fungus-harvesting).

Family Sub-family	Genus	Hits	NG	FG
Rhinotermitidae				
	<i>Schedorhinotermes</i>	2	e/h	I
Termitidae				
Macrotermitinae	<i>Acanthotermes</i>	17	e/h	II (L(F))
	<i>Odontotermes</i>	2	e	II (L(F))
	<i>Microtermes</i>	397	h	II (L(F))
	<i>Protermes</i>	1	h	II (L(F))
	<i>Pseudacanthotermes</i>	8	h	II (L(F))
Foraminitermitinae	<i>Foraminitermes</i>	372	h	III
Apicotermitinae				
Apicotermes-group	<i>Acutidentitermes</i>	1	h	IV
	<i>Coxotermes</i>	25	h	IV
	<i>Duplidentitermes</i>	4	h	IV
	<i>Eburnitermes</i>	267	h	IV
	<i>Jugositermes</i>	26	h	IV
	<i>Labidotermes</i>	2	h	IV
	<i>Machadotermes</i>	1	h	IV
	<i>Phoxotermes</i>	1	h	IV
	<i>Rostrotermes</i>	1	h	IV
Anoplotermes-group	<i>Astalotermes</i>	844	h	III
	<i>Adaiphrotermes</i>	205	h	III
	<i>Aderitotermes-FGIII</i>	55	h	III
	<i>Aderitotermes-FGIV</i>	57	h	IV
	<i>Alyscotermes</i>	23	h	III
	<i>Amicotermes</i>	82	h	IV
	<i>Anenteotermes-FGIII</i>	218	h	III
	<i>Anenteotermes-FGIV</i>	103	h	IV
	<i>Apagotermes</i>	3	h	IV
	<i>Ateuchotermes</i>	77	h	IV
Termitinae				
Amitermes-group	<i>Microcerotermes</i>	49	w	II
Cubitermes-group	<i>Apilitermes</i>	125	e	IV
	<i>Basidentitermes</i>	23	h	IV
	<i>Cubitermes</i>	169	e	IV
	<i>Euchilotermes</i>	1	h	IV
	<i>Fastigitermes</i>	139	h	IV
	<i>Furculitermes</i>	2	h	IV
	<i>Mucrotermes</i>	3	h	IV
	<i>Basidentitermes</i>	14	h	IV
	<i>Profastigitermes</i>	1	h	IV
	<i>Noditermes</i>	19	e	IV
	<i>Orthotermes</i>	102	h	IV
	<i>Thoractotermes</i>	48	e	IV
	<i>Unguitermes</i>	178	h	IV
Mirocapritermes-group	<i>Pericapritermes</i>	532	h	III
Termes-group	<i>Termes</i>	1	e	III
Nasutitermitinae	<i>Nasutitermes</i>	27	a	II
	<i>Postsubulitermes</i>	11	e/h	IV
	<i>Verrucositermes</i>	4	e/h	IV

No transect data exist from Ivindo, which has never previously been surveyed for termites. A termite assemblage sampled by the standardized transect method (pooled data from two 100m x 2m transects) in primary forest from Mayombe (Republic of Congo) (Eggleton *et al.*, 2002b), is used here as the comparative assemblage to examine FG generic richness. Both assemblages exhibit similar patterns of high generic richness (>40), dominated by soil-feeding termites and in particular FGIV genera. The major difference between the Ivindo plot and the Mayombe transect (PF*) is a conspicuous higher frequency of FGIV genera.

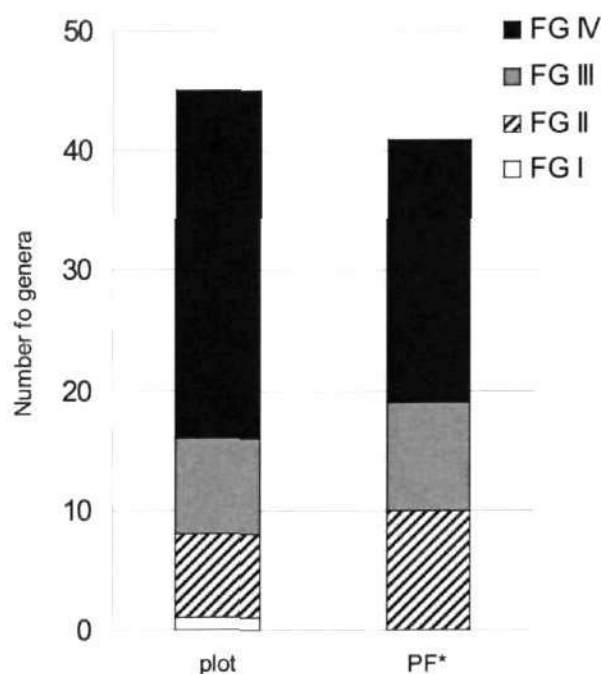


Figure 3.3 Termite generic richness by feeding-group from the plot (Ivindo) and PF* (two pooled transects in primary forest, Republic of Congo (Eggleton *et al.*, 2002b)).

The non-soil-feeding termite genera were mostly found in low abundances, although *Microtermes*, a hypogean nesting Macrotermitinae that foragers on small wood debris, was a notable exception, and was one of the most common termites found. The most frequently encountered termites belonged to FGIII

genera (Figure 3.4), in particular from the *Anoplotermes*-group (Apicotermittinae). *Astalotermes* was the most abundant termite in the assemblage. The tail of the abundance distribution is dominated by FGIV genera (Figure 3.4); 12 of the 17 rare genera (hit rate <10) are FGIV.

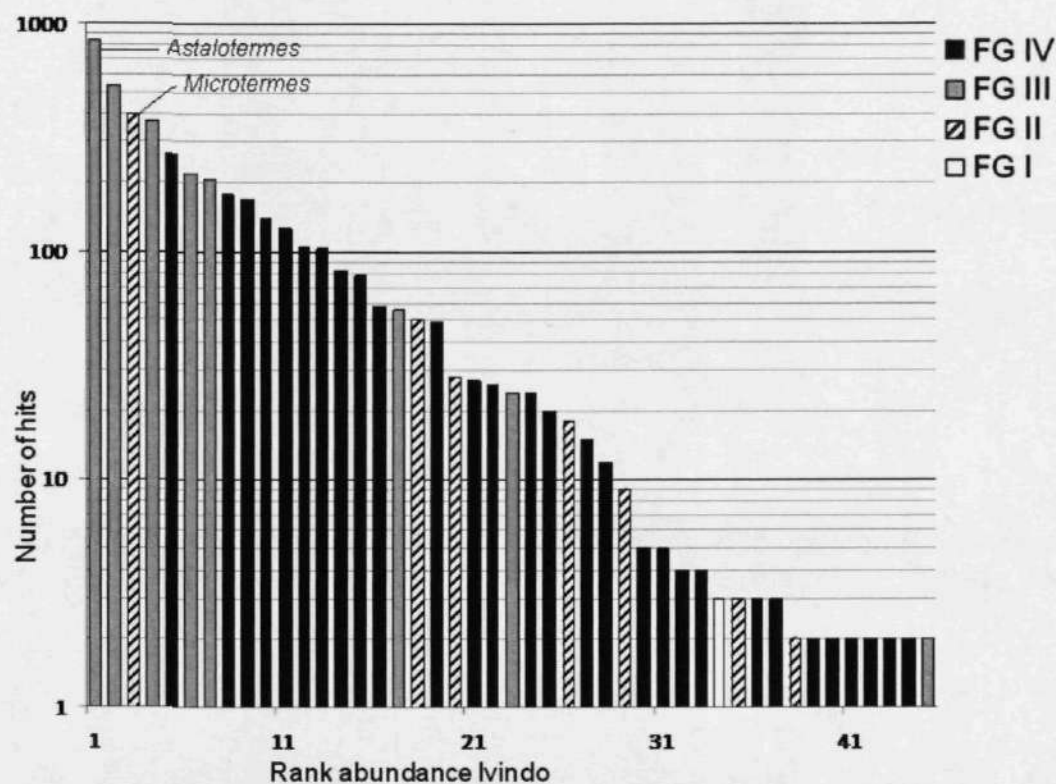


Figure 3.4 Ivindo rank abundance (number of hits per genus) distribution (on a log scale).

3.4.2 Soil occupancy patterns

Termites occupy a far greater proportion of pits in Ivindo (90%) than in Danum (42%), due to the greater occupancy of soil-feeding termites (FGIII and FGIV) (Figure 3.5). The non-soil-feeding termite occupancy patterns are similar in both plots; mostly a single genus in ~20% of pits (Figure 3.5). In Danum, the maximum number of genera found in a single pit was four, although pits were mostly occupied by a single genus. By contrast up to seven genera were collected from a single pit in Ivindo, and >50% of pits had more than one genus.

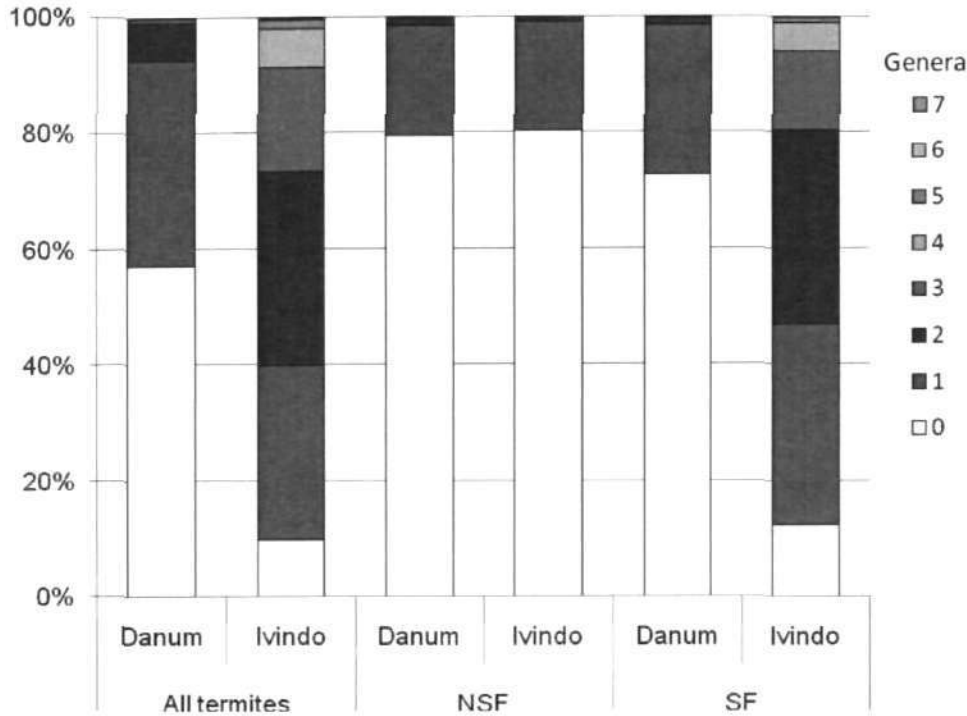


Figure 3.5 Proportion of pits occupied by termites grouped by generic richness per pit. NSF, Non-soil-feeding (FGI and FGII); SF, soil-feeding (FGIII and FGIV).

3.4.3 Ant assemblage composition

In Danum 35 ant genera from seven subfamilies were recorded, of which 17 were identified as potential termite predators following the feeding preferences summarized in Brown (2000) (Table 3.3). Some predatory-ant (PA) genera are known to be obligate termitophages e.g. *Centromyrmex*, *Leptogenys* and some *Pachycondyla* species (Wheeler, 1936; Mill, 1982; Leal & Oliveira, 1995). Generalist predatory ants e.g. the 'army ants' *Dorylus* and *Gnamptogenys* are likely to include termites in their predatory diet in an opportunistic manner (e.g. Cogni & Oliveira, 2004; Schoning, 2007). Representatives of the Ponerinae sub-family, that includes *Pachycondyla*, are abundant, and dominate the predatory-ant community (Figure 3.6a).

Table 3.3 Danum ant genera, and trophic description, with genera classified as predatory in bold (Brown, 2000).

Subfamily	Genus	Hits	Description
Dolichoderinae	<i>Tapinoma</i>	23	Generalist foragers
Ectatomminae	<i>Gnamptogenys</i>	21	Predators and scavengers
Formicinae	<i>Acropyga</i>	5	Tend coccids
	<i>Camponotus</i>	18	Generalist foragers
	<i>Euprenolepis</i>	17	Foragers
	<i>Paratrechina</i>	86	Generalist foragers
	<i>Polyrachis</i>	12	Generalist foragers
	<i>Pseudolasius</i>	170	Cryptic foragers
	Ponerinae	<i>Anochetus</i>	50
<i>Amblyopone</i>		4	Predators, esp of Chilopoda
<i>Centromyrmex</i>		2	Cryptic predators of termites
<i>Cryptopone</i>		4	Cryptic predators
<i>Diacamma</i>		26	Predators
<i>Emeryopone</i>		2	Predators
<i>Hypoponera</i>		182	Generalist foragers
<i>Leptogenys</i>		14	Predators, esp of termites
<i>Odontomachus</i>		28	Predators
<i>Odontoponera</i>		5	Predators
<i>Pachycondyla</i>		340	Predators
<i>Ponera</i>		32	Predators of small arthropods
Myrmicinae		<i>Acanthomyrmex</i>	6
	<i>Crematogaster</i>	132	Generalist foragers
	<i>Dilobocondyla</i>	3	
	<i>Lophomyrmex</i>	360	Generalist foragers
	<i>Lordomyrma</i>	3	
	<i>Myrmecia</i>	16	Generalist predators
	<i>Myrmecina</i>	7	Predators of mites
	<i>Oligomyrmex</i>	6	Cryptic foragers, termite thief ants
	<i>Pheidole</i>	359	Seed harvesters, omnivorous
	<i>Pheidologeton</i>	35	Generalist mass foragers
	<i>Proatta</i>	12	Scavengers
	<i>Tetramorium</i>	95	Generalist foragers
Dorylinae	<i>Aenictus</i>	8	Army ants
	<i>Dorylus</i>	8	Army ants
Cerapachyinae	<i>Cerapachys</i>	11	Army ants, predators of other ants

Twenty-seven ant genera were recorded from six sub-families in Ivindo, of which 12 were identified as predatory (Table 3.4). Again, *Pachycondyla* was an abundant predatory-ant, and most of the predatory ants are members of the

Ponerinae sub-family. The ant assemblage was dominated by *Anoplolepis carinata* which was collected from 60% of pits. This species is epigeic (litter dwelling), and was regularly observed raiding termites as the pits were being dug. It has not been included here as predatory-ant despite this observation when disturbance was caused, as species in this genus are omnivorous foragers that consume a variety of material that include Hemipteran honeydew as well as live and dead prey (Haines & Haines, 1978; Kuate *et al.*, 2008).

Table 3.4 Ivindo ant genera, and trophic description with genera classified as *predatory in bold* (Brown, 2000).

Subfamily	Genus	Hits	Description (Predator*)
Dolichoderinae	<i>Tapinoma</i>	30	Generalist foragers
Formicinae	<i>Acropyga</i>	1	Tend coccids
	<i>Anoplolepis</i>	1360	Foragers
	<i>Camponotus</i>	2	Generalist foragers
	<i>Paratrechina</i>	31	Generalist foragers
	<i>Polyrachis</i>	3	Generalist foragers
	<i>Pseudolasius</i>	86	Cryptic foragers
Ponerinae	<i>Anochetus</i>	28	Predators
	<i>Amblyopone</i>	4	Predators, esp of Chilopoda
	<i>Centromyrmex</i>	194	Cryptic predators of termites
	<i>Diacamma</i>	6	Predators
	<i>Hypoponera</i>	35	Generalist foragers
	<i>Leptogenys</i>	19	Predators, esp of termites
	<i>Loboponera</i>	4	
	<i>Odontomachus</i>	10	Predators
	<i>Pachycondyla</i>	409	Predators
Myrmicinae	<i>Atopomyrmex</i>	1	
	<i>Bondroitia</i>	1	
	<i>Crematogaster</i>	129	Generalist foragers
	<i>Dacotinops</i>	6	
	<i>Oligomyrmex</i>	2	Cryptic foragers, termite thief ants
	<i>Pheidole</i>	338	Seed harvesters, omnivorous
	<i>Pristomyrmex</i>	10	Generalist foragers/specialist predators
	<i>Tetramorium</i>	487	Generalist foragers
Dorylinae	<i>Aenictus</i>	1	Army ants
	<i>Dorylus</i>	54	Army ants
Cerapachyinae	<i>Cerapachys</i>	6	Army ants, predators of other ants

Generic richness was greater in Danum (Figure 3.6), while similarities between the ant assemblages include: 1) the proportion of predatory-ant genera to total generic richness is roughly the same in both plots (49% and 44% in Danum and Ivindo respectively), and 2) the most abundant predatory ant in both plots, *Pachycondyla*, had similar encounter rates (340 and 409 in Danum and Ivindo respectively) (Figure 3.6).

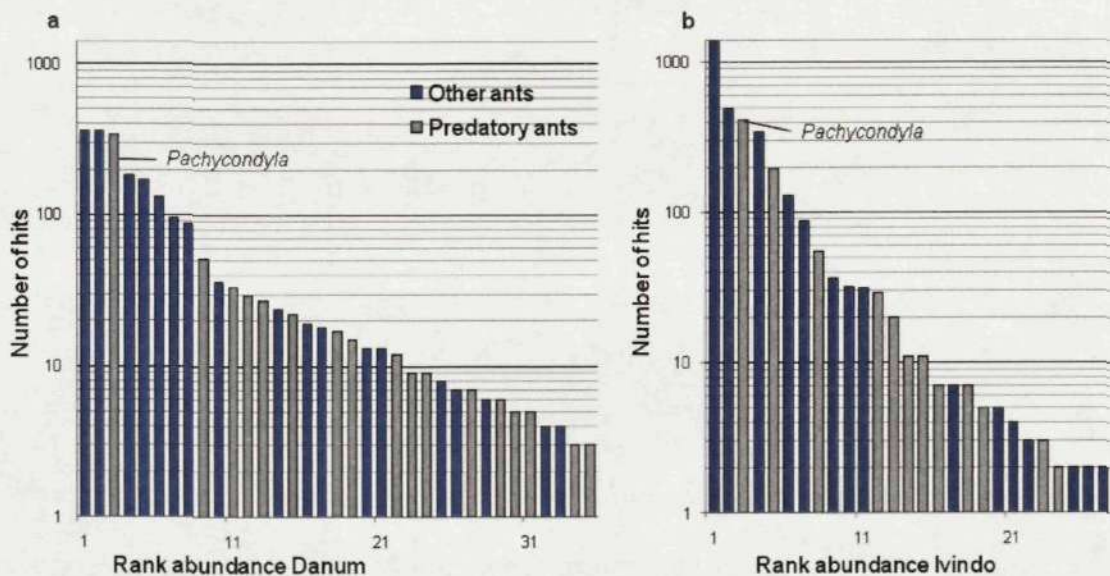


Figure 3.6 Ant genera rank order abundance (number of hits per genus) distribution (on a log scale), with predatory ant genera highlighted a) Danum, and b) Ivindo.

Ants had a higher occupancy rate in Ivindo (85%) compared with Danum (64%), largely due to the ubiquitous species, *Anoplolepis carinata* in Ivindo (Figure 3.7). Despite the higher genus richness in Danum, a maximum of four genera was found in a single pit in Danum, compared with five in Ivindo. Considering only the predatory ants, similar patterns were found; pit occupancy was slightly higher in Ivindo (29% compared with 22%) of the pits, and in most instances these were a single genus. The maximum number of predatory-ant genera in a single pit was three in both plots (Figure 3.7).

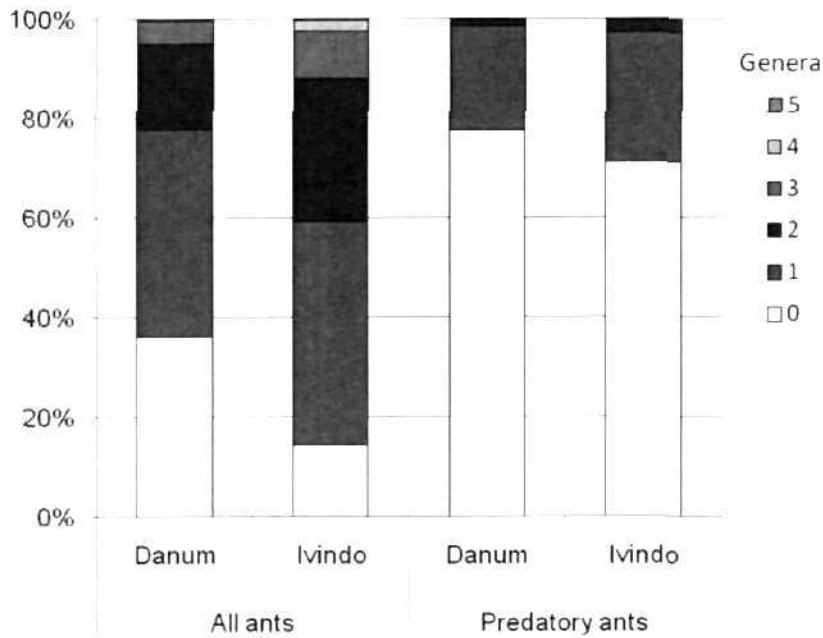


Figure 3.7 Proportion of pits occupied by ants grouped by generic richness per pit.

3.4.4 Macrofaunal co-occurrence patterns

The proportion of soil pit occupancy by faunal categories and over-lap (=co-occurrence within soil pits) of these are presented as Venn diagrams in Figures 3.8 and 3.9, illustrating the major differences in the proportions of occupancy and overlap between Danum and Ivindo. Ants are far more abundant than termites in Danum, and although these two groups co-occur in roughly one quarter of soil pits, in a substantial proportion of pits ants and termites occur separately (Figure 3.8). By contrast, in Ivindo, termites were marginally more abundant than ants, and the two groups mostly co-occur within pits. Collectively ants and termites occupy far more pits in Ivindo than in Danum; only 5% of pits were un-occupied by either in Ivindo. In Danum approximately one third of the termite-ant co-occurrences (26%) were with predatory ants (9%), and approximately half of the predatory-ant encounters are in the absence of termites, i.e. there is little overlap (Figure 3.9). In Ivindo, again one third of

termite-ant co-occurrences (80%) are with predatory ants (27%), by contrast, however, the predatory-ants were rarely found in pits not also occupied by termites (Figure 3.9). In both sites, predatory-ants co-occurred with soil-feeding termites more often than with non-soil feeding-termites (Figure 3.9).

Non-soil-feeding termites mostly co-occurred with the soil-feeding termites in Ivindo, while in Danum there was relatively little over-lap of NSF and SF termites within pits (Figure 3.9). Worms were found in 26% of pits in Ivindo, and frequently with both ants and termites, and in Danum only 9% of pits were occupied by worms.

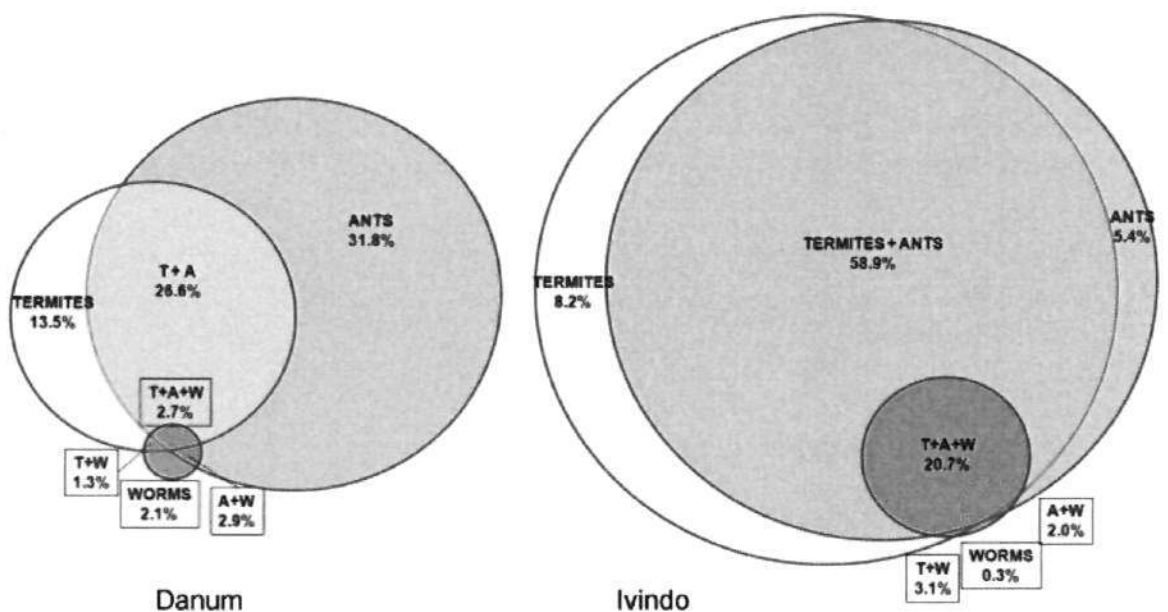


Figure 3.8 Soil-pit occupancy and overlap of termites (T), ants (A) and worms (W). Circle sizes approximately represent the relative proportions indicated as a percentage for each section.

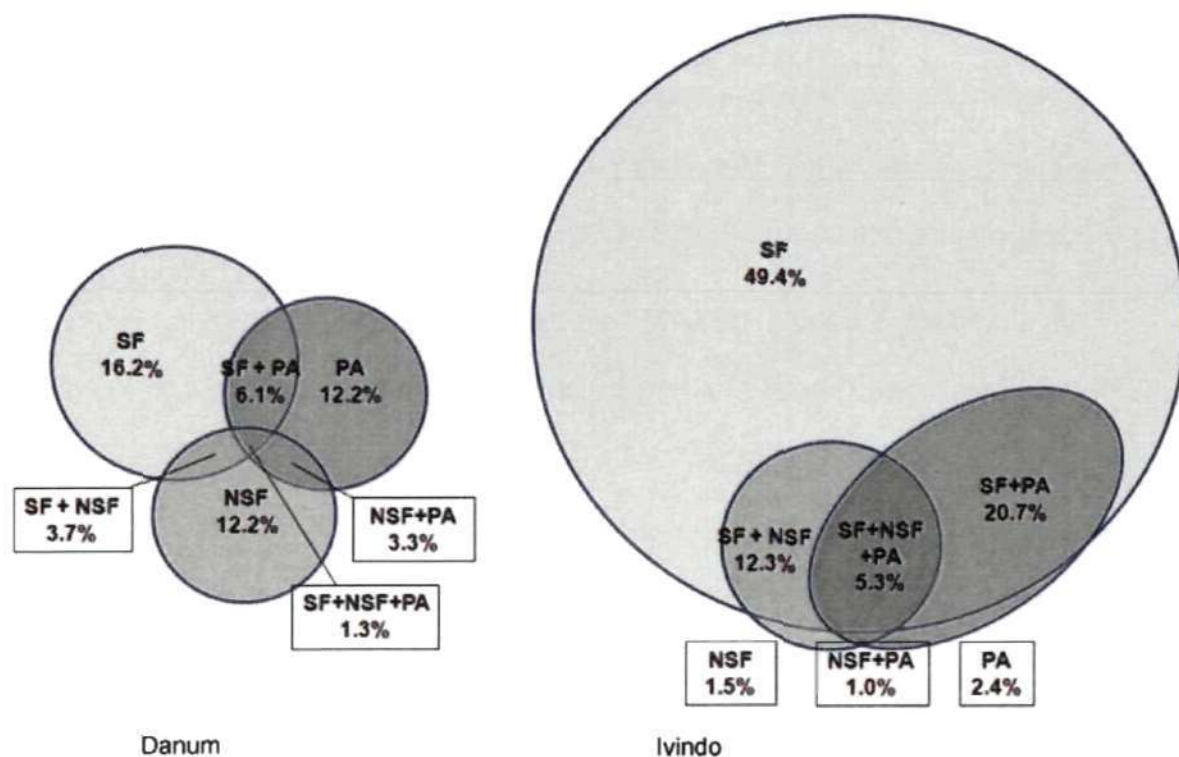


Figure 3.9 Soil pit occupancy and overlap of soil-feeding termites (SF), non-soil-feeding termites (NSF) and predatory-ants (PA). Shape sizes approximately represent the relative proportions indicated as a percentage for each section. An ellipse is used in Ivindo 'PA' in order to retain representation of the proportions, including overlap with 'SF', 'NSF+SF', and 'NSF'.

3.5 Discussion

3.5.1 Termite assemblage representativeness

Termites, and specifically soil-feeding termites, saturate the upper soil profile in Ivindo, where in addition several genera occupy individual pits. If it is assumed the occupancy patterns recorded here are typical of African and Asian rain forest assemblages, this is consistent with estimated termite biomass differences (a factor of 16) from these regions, recorded in a comparative study from a site in southern Cameroon (average = 56.9 g per m²) and Danum Valley Conservation Area (average = 3.5 g per m²) (Eggleton *et al.*, 1999). The

differences in generic richness by feeding-group (Table 3.5) between Danum and Ivindo correspond with the regional patterns described by Eggleton and Tayasu (2001). In summary the assemblages sampled here accurately reflect the previously published region-specific differences in taxonomic richness, functional diversity and abundance.

Table 3.5 Generic richness by feeding-group in Danum and Ivindo, total rain forest richness in Indomalaysia and Africa (Jones and Eggleton, 2010, unpublished), and the proportion (prop.) of this sampled in the survey plots.

	Danum	Indomalay	prop.	Ivindo	Afrotropics	prop.
FGI	3	9	33%	1	5	20%
FGII	10	15	67%	7	12	58%
FGIII	16	17	94%	8	12	67%
FGIV	0	3	0%	29	33	88%
Total	29	44	66%	43	62	69%

The pit-only sampling protocol captured ~68% of rain forest genera known from each region (Table 3.5). FGI genus richness is the most under-represented in both sites, and FGIV was completely un-represented in Danum, otherwise representation generally increases along the humification gradient (Table 3.5). The major differences, when comparing the plot with previously published transect data are an increase in FGII and FGIII genera in Danum, and an increase in FGIV genera in Ivindo (Figure 3.1 and Figure 3.3). The standardized transect protocol (using a single transect) captured ~33% of known local species richness, however within this Apicotermitinae and Nasutitermitinae were proportionally under-represented in the African (Cameroon) and Asian (DVCA) assemblages respectively (Jones & Eggleton, 2000). The low encounter rate of hypogean nesting FGIV Apicotermitinae (Table 3.2) implies that these are genuinely rare and patchily distributed in the African systems,

and that they were collected here due to the large sampling area of the plot. The least abundant genera in Danum were mostly from the Nasutitermitinae family; either hypogeal nesting FGIII or non-soil-dwelling FGII genera (Table 3.1). Again the increased area, although pit-only sampling, has captured what may typically be less abundant or more patchy members of termite assemblages, and therefore may tend to be under-represented using the transect method.

The genus-level identification means that the very high species richness of *Anoplotermes*-group FGIII genera (Apicotermitinae) in African assemblages was not described here. These species can comprise 30% of an assemblage, and 77% of FGIII species (Deblauwe *et al.*, 2008). The most abundant genus in Ivindo, *Astalotermes*, is particularly species rich, and was found in 37% of pits, which remarkably is almost equivalent to the occupancy rate of the entire termite assemblage in Danum.

3.5.2 Occupancy and co-occurrence patterns of NSF and SF termite

One of the few similarities between the Ivindo and Danum termite assemblages is the occupancy rates of non-soil-feeding termites (NSF). The pit-only sampling protocol is likely to have resulted in low abundances and/or an under-representation of wood and arboreal nesting termites. For instance termites in the Kalotermitidae family were absent from both sites as they nest in and feed on arboreal dead wood material and therefore are unlikely to be encountered within the soil profile. One hypogeal-nesting genus dominates the respective NSF assemblages; *Globitermes* in Danum, and *Microtermes* in Ivindo. These therefore have a large influence on the overall NSF occupancy patterns.

It is clear that the soil-feeding (SF) assemblage in Ivindo is densely packed into the soil profile, occupying most of the surveyed space, and with genera consistently co-occurring at very fine scales (i.e. the pit). Contrary to expecting lower encounter rates if packing in the soil is intense, several genera are very abundant. Thirteen, including *Astalotermes*, were encountered in >100 of pits, compared with three genera with an encounter of >100 pits in Danum. The low predominantly single-genus occupancy in Danum demonstrates the comparatively low termite packing here, with substantially more vacant space in the soil profile. In Chapter 2 soil moisture and infiltration rates were identified as the environmental conditions that differ the most between the two plots. Whether the low occupancy in Danum can be attributed to spatial heterogeneity in this environment condition, and/or whether termites simply spread themselves more sparsely through the soil space, will be considered in Chapter 5.

The differences in the co-occurrence patterns of NSF and SF termites (Figure 3.9), may simply be due to the lower occupancy rates of each group in Danum, and therefore reduced co-occurrence opportunities at the pit scale. The lack of any spatial referencing clearly limits any interpretation at this stage. How these co-occurrence events are spatially distributed will shed light on whether inter-feeding-group relationships e.g. a hypothesized food-mediated facilitation, are different between Danum and Ivindo, and whether packing in the soil profile relate to this (Chapter 5).

3.5.3 Occupancy and co-occurrence patterns of termites and ants

A similar latitudinal gradient is seen in ant and termite diversity; in termites this has been attributed to stable closed-canopy forests in the tropics (Eggleton,

1994), while global ant diversity patterns are correlated with temperature and climate-driven extinction events (Dunn *et al.*, 2009). Termites, however, show a remarkable longitudinal difference in taxonomic and functional richness not matched by ants. Rather in the ants, many of the same genera were collected in Danum and Ivindo (Table 3.3 and Table 3.4). This taxonomic similarity appears to translate to similar occupancy patterns (in terms of pit occupancy and the frequency of poly-generic pits), despite the lower generic richness in Ivindo. This pattern of taxonomic overlap and similar occupancy rates is robust for predatory ants. In Ivindo, however, the ants may be taking advantage of the density of termites as a readily available food source, and therefore may be more abundant despite the lower predatory-ant taxon richness. Chapter 5 also examines in detail the nature of the spatial relationships between the predatory ant and termite assemblages.

Soil communities are structured by several ecological interactions that operate at a series of nested scales (Ettema & Wardle, 2002). The advantage of a spatially-explicit analytical approach is additional information concerning the scale of these interactions. In the following chapters I therefore take a spatial approach to examining ecological patterns in the termite assemblages. In Chapter 5 I examine three ecological interactions: 1) environmental relationships, 2) a within-assemblage food-mediated facilitation, and 3) a predator-prey interaction between termites and ants. In Chapter 6, earlier findings are used to interpret genus-level co-occurrence patterns described at multiple scales, and to construct assembly rules for termite assemblages at the one hectare scale. In these Chapters I compare the spatial structures of the *termite assemblages, the ecological relationships and the assembly rules, from the two sites.* The rationale behind this approach is that this allows us to begin

to understand the mechanisms that organise and pack rain forest termites into the soil profile, and whether biogeographic history, manifested as the taxonomic and functional differences described here, outweighs the role of proximate ecological differences.

4 Colony extent and inter-specific interactions in mound-building rain forest termites (*Cubitermes*-group: Termitidae)

4.1 Summary

True soil-feeding termites are particularly diverse in tropical rain forest soil systems, yet we know very little about their spatial structure, population processes, or inter-specific interactions. In this chapter species in the *Cubitermes*-group (Termitinae) confined to the Afrotropics, were examined, with termites sampled from their conspicuous epigeal mounds, and from the regularly spaced soil pits (2m x 2m) within the Ivindo plot. For *Cubitermes severus*, microsatellite markers were employed to assign 'offspring' termites collected from soil pits to 'parental genotypes' from within mounds. For two species within the genus-group, *C. severus* and *Thoracotermes macrothorax*, point pattern spatial analyses (Omega relative neighbourhood density) were used to determine the spatial extent of colonies, and spatial orientation of mounds. Soil pits occupied by these two species were strongly aggregated to 8m and 12m respectively, which was interpreted as representing the colony extent. This corresponded well with the more robust microsatellite 'offspring-to-mound' assignments at distances of <10m for *C. severus*. Mounds were also spatially structured at various scales. The mounds are spatially dispersed up to 12m, which as this is the same scale as the putative colony extents, suggests both territoriality and inter-specific dispersion at the colony level and competition. The mounds are aggregated at mid-scales possibly due to limited dispersal by alates, and at larger scales within the one hectare plot mounds are dispersed. As soil C_{tot} concentrations were not found to be higher where mounds were located, biotic interactions rather than heterogeneity in the

energetic quality of their diet (indicated by soil C_{tot}), appear to be important in structuring mound positioning at the one hectare scale.

4.2 Introduction

Population processes such as foraging, competition, dispersal and predation influence the spatial distribution of organisms (Tilman & Kareiva, 1997). For colonial organisms, social interactions, defence and foraging strategies influence the colony's cohesion and spatial extent (e.g. Bulmer & Traniello, 2002; Jouquet *et al.*, 2002; Depickere *et al.*, 2008), and the colony is therefore the finest scale of aggregation. Territory size is an economic outcome based on the costs and benefits of foraging and defence, and in social species is heavily influenced by competitive ability (e.g. Adams & Levings, 1987; Adams, 2003).

Intra-specific competition and density-dependent mortality generate spatial dispersion, and are important processes in density-dependent population regulation (e.g. Kammenga *et al.*, 2003; Lopez-Sepulcre & Kokko, 2005; Banda & Blanco, 2009). At the community level, mechanisms that promote the spatial separation of ecologically similar species reduce competitive interactions, thereby allowing co-existence. Population processes that lead to intra-specific aggregation, and spatial habitat heterogeneity facilitate this spatial separation (e.g. Wertheim *et al.*, 2000; Hanski, 2008). There are relatively few spatially explicit studies of soil biota, and therefore our understanding of the ecological processes structuring soil communities is limited (Ettema & Wardle, 2002).

Termites are often an abundant and diverse component of tropical region soil communities (e.g. Eggleton *et al.*, 1996; Eggleton *et al.*, 2002b), where they influence numerous soil processes, and therefore are therefore considered

'ecosystem engineers' (Lavelle *et al.*, 1997). In particular the physical, chemical and biological properties of termite mound material have frequently been examined in relation to upper profile soil material adjacent to mounds (e.g. Garniersillam & Harry, 1995; Lopez-Hernandez, 2001; Donovan *et al.*, 2001b; Ndiaye *et al.*, 2004). As mounds persist in the environment following colony death, these mound conditions will be contributing to the heterogeneity of soil properties and biota. Spatially-dependent ecological processes are likely to be determining the spatial distribution of termites and by extension will determine the scale at which termites contribute to ecosystem services.

Although it is possible to locate the colony centre in mound building termites, estimating the colony boundaries presents a challenge for subterranean species. Inter-colonial competition and territoriality is generally assumed to occur in termites based on agonistic behaviour, the spatial distribution of colonies identified by genetic structure, and observations of foraging parties (Levings & Adams, 1984; Thorne & Haverty, 1991; Bulmer & Traniello, 2002; DeHeer & Vargo, 2004). Colony fusion and overlapping foraging that lead to complex family structures do occur, but appear to be the exception rather than the rule (DeHeer & Vargo, 2004). Most of these studies are based on wood-feeding species and in particular *Reticulitermes* species. It cannot therefore be assumed that similar processes will be operating in soil-feeding termites where feeding resource availability, i.e. soil, differs greatly from that of wood (Brauman *et al.*, 2000).

Previous studies on the spatial extent of termite colonies have also mostly concentrated on rather atypical wood-feeding species. *Mastotermes darwiniensis* is a phylogenetically basal species with non-discrete nests and

territories that extend across 15,000m², estimated using genetic techniques (Goodisman & Crozier, 2002). *Reticulitermes* species are subterranean nesting termites that forage on dead wood at the soil surface, and have frequently been examined using genetic tools for colony identification. Generally foraging distances are short (mean of 5.6m in Deheer and Vargo (2004)), however extensive foraging areas of 1,200m² have been recorded (e.g. Bulmer & Traniello, 2002). *Nasutitermes* spp. construct conspicuous arboreal mounds, and, using direct observation of foraging parties, have been found to have highly variable foraging areas (range of 1–1750m² in Adams and Levings (1987)) determined by habitat structure and nest volume. Using baited traps and mark-recapture techniques, colony extents of up to 60m² have been recorded for *Globitermes sulphureus*, that consume decaying wood material (Ngee & Lee, 2002).

Termites consume dead plant material at different stages of decomposition referred to as the humification gradient (Donovan *et al.*, 2001a). The energetic quality and availability of the food differ along this gradient. Indeed termite colony organization, including nesting and foraging strategies, is inextricably linked with their nutritional ecology (Eggleton & Tayasu, 2001). Soil is energetically poor yet abundant and continuously distributed (Brauman *et al.*, 2000). Soil-feeding termites that consume mineral soil are considered to exist on an energetic knife-edge (Eggleton & Tayasu, 2001), which likely places an economic limit on foraging and colony defence. The evolution of large body size, composed mostly of a gut in some soil-feeding clades (e.g. *Apicotermes*-group and *Cubitermes*-group) appears to be a response to these energetic limitations, allowing a high through-put of soil material (Eggleton *et al.*, 1998).

Interestingly it is the soil-feeding termites that are the most diverse component of termite communities in tropical rain forests (Davies *et al.*, 2003a). As yet there is no knowledge of the spatial extent of soil-feeding termite colonies, or either, the inter-specific interactions between ecologically similar species, which would offer an insight into the mechanisms that maintain this diversity.

In order to address this I have selected *Cubitermes* species and *Thoracotermes macrothorax* within the *Cubitermes* genus-group (Termitinae) as the focus of this study. These species construct conspicuous epigeal mounds, from which the colony centres can be easily located. To determine the spatial extent of termite colonies, molecular techniques were used to assign foraging workers to colony centres, supported with spatial analyses to ascertain the finest scale of aggregation, which may reflect colony extent. The spatial position of termite mounds, combined with the measure of colony extent, was used to consider intra- and inter-specific interactions. In addition to biotic interactions influencing the spatial position of mounds, patches of organic rich soil material may also be important, if this increases the marginal energetic gains necessary to support the termite colony. To consider this factor, I compared soil C_{tot} concentrations between soil adjacent to mounds and from the remainder of the Ivindo survey plot.

4.3 Methods

4.3.1 Data collection

The soil-dwelling termite assemblage was sampled in Ivindo; termites were collected from soil pits positioned every 2m x 2m (2304 soil pits), from the 96m x 96m plot, and from all epigeal mounds encountered (full details in Chapter 2).

From this collection *Cubitermes* species and *Thoracotermes macrothorax* individuals were identified, using soldier morphology and enteric valve armature of the worker guts (Sands, 1998), and collections from the Natural History Museum, London. Samples of soil from each soil pit and *Cubitermes* spp. mound material was collected and air dried. Later these were analyzed for C_{tot} concentration using a Thermo Finnigan Flash EA1112 Elemental Analyzer, at the Natural History Museum, London.

4.3.2 Microsatellite genotyping

Microsatellite markers have previously been isolated from *Cubitermes* sp. *affinis subarquatus*, collected from gallery forest and savanna in Lope National Park in Gabon (Harry *et al.*, 2001). This species was not present within the study plot however reliable PCR products were obtained with a combination of these loci in several other species within the *Cubitermes*-group (Harry *et al.*, 2001). The most abundant *Cubitermes* species, was therefore selected for genotyping in this study; this was identified as *C. severus* based on the enteric valve (EV) structure in worker guts, according to Sands (1998), however this species name is likely to represent several species. Pit samples typically consisted of between 1 and 5 worker individuals. Up to 10 workers were collected from every *Cubitermes* mound within the plot. *Cubitermes* spp. mounds were also sampled from outside the plot at a distance of greater than 1km away, with the intention of characterising patterns of within-plot and between-site genetic structure. *C. severus* individuals from two of these mounds were included for genotyping.

DNA was isolated from the head and body tissue material of all workers using the DNeasy® Qiagen kit and manufacturer's instructions. Initial tests were made on the polymerase chain reaction (PCR) amplification success of the seven

microsatellite loci (P7, P14, P19, P32, P34, P36, P41), using the amplification conditions described in Harry et al. (2001). PCR products were not successfully amplified for P14. Worker DNA was amplified for the remaining six loci using VIC-, FAM-, NED- or PET fluorescently labelled forward primers. PCR products were resolved on an ABI 3130 Genetic Analyzer (Applied Biosystems) with internal size standard GeneScan 500LIZ (Applied Biosystems). Microsatellite allele sizes were scored using GENE MAPPER software (Applied Biosystems). When scores were missing or ambiguous at certain loci, the original DNA sample was re-amplified and scored. Due to the low heterozygosity observed in individuals at these six loci, further treatment of the genotype data is explained in the results section (Section 4.4.1).

4.3.3 Spatial analysis of mound and pit samples

Spatial structure of the 'mound' and 'occupied-pit' samples was measured using the Omega (Ω) relative neighbourhood density method (Condit *et al.*, 2000). As a point pattern analysis method, it measures whether the location of individual events are clustered, randomly or regularly distributed. Specifically, Omega measures the density of individuals (i.e. pit or mound) in the neighbourhood for each individual in a sample. The number of individual neighbours N_x and the area A_x in each distance annulus at distance x are summed over all individuals within the sample. $D_x = \sum N_x / \sum A_x$ gives the density of individuals as a function of distance from the average individual. The relative neighbourhood statistic (Ω_x) is a product of D_x divided by the mean density across the plot, and is therefore sample size independent. For randomly distributed samples $\Omega_x=1$ at all distances, $\Omega_x>1$ at short distances for aggregated samples, and $\Omega_x<1$ at short distances for hyper-dispersed samples. Plotting Ω_x at the distance classes

indicates the intensity and scale at which samples are spatially structured across the plot.

Statistical significance of Ω_x was ascertained using the bootstrap method outlined in Condit et al (2000). Confidence limits for Ω_x were estimated by randomly drawing half of the sample 15 times, and for each sub-sample Ω_x was calculated at each distance class. Variance and 95% confidence limits were calculated at each distance class based on a one-sample *t* test. The limits were divided by $(2)^{1/2}$ as the sample was halved, and then applied to the entire sample. Samples were considered significantly aggregated or over-dispersed at a given distance class, if the confidence limits did not include 1. Four sample-sets were analyzed using this method, 1) the pit sample containing *C. severus*, 2) the pit sample containing *Thoracotermes macrothorax*, 3) and a pooled sample of *C. severus* and *T. macrothorax* pits, to ascertain the spatial extent of colonies, and 4) mounds occupied by *Cubitermes* spp. and/or *Thoracotermes*, to ascertain the spatial scale at which colony centres are orientated. The 'mound' sample pools the mounds from >1 species in order to achieve a sample size of approximately 50, as below this sample size $\Omega_{0.10}$ tends towards 0 (dispersed) even when the sample is randomly structured (Condit et al., 2000).

4.4 Results

4.4.1 Genetic markers and parental genotypes

Three of the microsatellite (MS) loci (P7, P32 and P41) were monomorphic, or polymorphic but all individuals scored were homozygous. Individuals were heterozygous at the remaining three loci (P19, P34 and P36). In subsequent analyses only individuals with scores for all of these three loci were retained,

and therefore the number of sample points and individuals available for analysis was reduced (Table 4.1). For some of the pit and mound samples, none of the termites yielded MS scores at these three loci, and therefore represent missing data (see Figure 4.2: represented as red circles for mounds). This occurred in six of the 27 mounds, and eight of the 47 soil pit samples.

Table 4.1 Summary of the number of samples points (and individual workers in brackets) with DNA extracts, with PCR products at loci 19, 34 and 36, and of these the average # workers per sample point.

	DNA extracts	PCR products	# individuals per sample
Mounds	27 (133)	21 (97)	5.1
Soil pits	47 (146)	27 (68)	2.5

As genotypes from separate mounds were considered likely to be independent, while genotypes within mounds were not independent due to close family ties between colony members, tests of Hardy-Weinberg (H-W) equilibrium of the genotypes was analyzed on 10 sub-samples, consisting of a single worker randomly sampled from each mound (e.g. Nobre *et al.*, 2008). Significance was tested by the Markov chain method with 1000 iterations per batch and 100 batches in GENEPOP V1.2 (Raymond & Rousset, 1995). Loci P36 (6 alleles) and P19 (7 alleles) were consistently found to deviate from H-W equilibrium, while P34 (11 alleles) was in H-W equilibrium in seven of the ten tests.

Due to the low loci number and deviation from the H-W equilibrium within these, it was not possible to confidently assign individuals to colony units using likelihood tests (e.g. implemented in COLONY (Jones & Wang, 2009)). For each mound the allele combinations of all the associated worker genotypes (between 3 to 8 workers), was used to construct the possible 'parental

genotypes'. When no more than two diploid allele combinations at each loci were necessary to generate the worker genotypes, these were considered to have a possible monogamous family structure. This was achieved in 19 of the 21 mounds. For the remaining two, up to four allele combinations at any one of the loci was necessary to generate the worker genotypes. On repeating the H-W equilibrium test on the constructed mound 'parental genotypes', P34 was found to be in equilibrium and P36 and P19 to be heterozygote deficient.

4.4.2 Microsatellite assignment of pit samples to mounds

Termites collected from soil pits were assumed to be potential offspring from any one of the mounds, and based on their three loci genotypes, assigned to the constructed mound 'parental genotypes'. Twenty-seven pits contained termites with full microsatellite data, 19 of which contained termites that matched as offspring to the mound parental genotypes. Twenty-two offspring could be assigned to a single mound, 15 offspring could be assigned to >1 mound, and 28 termites could not be assigned to any mound. These assignment results have three non-exclusive explanations: 1) the assignments represent true occurrences and therefore colonies over-lap in soil pits, 2) missing data from mounds due to poor amplification or the parental mound being located out-side the plot, and 3) data weakness, both due to the lack of polymorphic markers resulting in multiple assignments, and/or scoring errors that result in false/absent assignment. In order to draw some conclusions from the offspring – mound assignments, the more robust and frequent assignment patterns were considered most likely to reflect real occurrences. The distance in meters between offspring and assigned mounds was calculated.

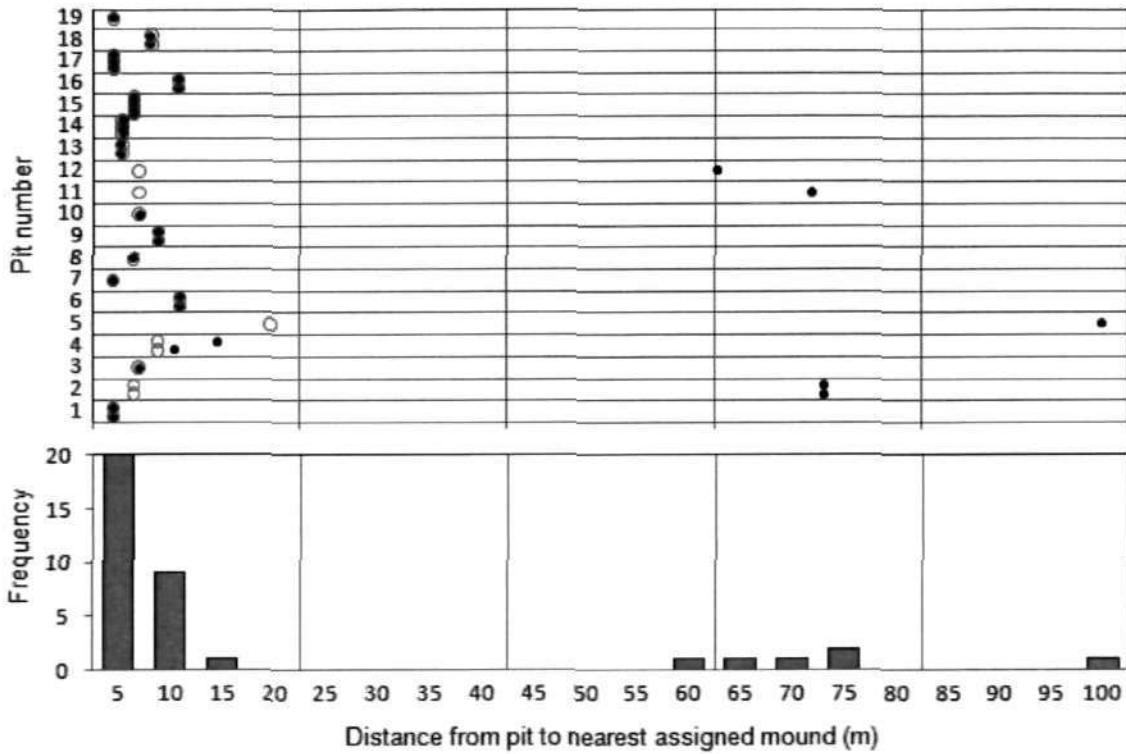


Figure 4.1 Upper section: Each row represents one of the 19 soil pits with full MS data. The distance to the nearest assigned mound (parental genotype) is represented along the x axis and indicated by the black circle. Green circles represent the distance from the soil pit to the nearest mound, e.g. pit #2, contained two offspring with full MS data which assigned to mounds ~70m away, while the mound closest to the pit was <5m away. In most cases offspring were assigned to their closest mound. Lower section: Frequency distribution of the distance between pit offspring and their nearest assigned mounds in 5m distance classes, e.g. 20 offspring were assigned to mounds 0 - 5m away.

In eight pit samples all offspring were assigned to a single mound (Figure 4.1: Pit # 1, 7, 13 to 17, and 19). In all cases the assignment was to the most closely positioned mound <10m away. Offspring from six pit samples could be assigned to several mounds, which included the mound closest to the pit (Figure 4.1: Pit # 3, 6, 8 to 10, and 18). Considering then that offspring tend to be assigned to their closest mound and these are most likely to represent real assignments, the frequency distribution of these closest-assignment distances, show that the

distance of these assignments are mostly <10m (Figure 4.1: lower section). Offspring from 5 pits could not be assigned to their closest mound (Figure 4.1: Pit # 2, 4, 5, 11 and 12). For each of these pits the parental genotype information is missing from their closest mound (Figure 4.2, red circles), or the pit is close to the edge of the sampling area, and therefore represent missing mound genotype data.

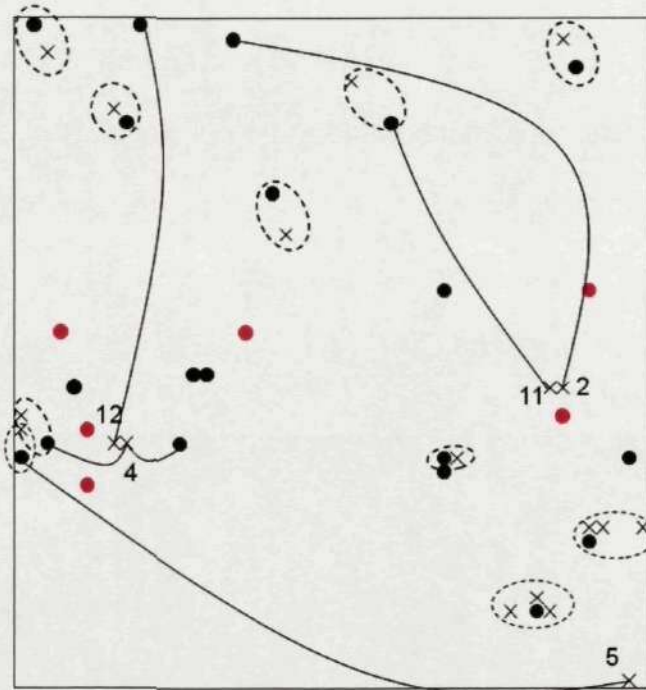


Figure 4.2 Location of *C. severus*. Black cross, pit offspring that were assigned to a mound parental genotype; black circles, mounds with MS data; red circles, mounds lacking full MS data. Connecting lines are between offspring that do not assign to their closest mound, with the numbering corresponding to the pit # in Figure 4.1 and lack mound parental genotypes from their closest mound, or putative closest mound outside the plot. Dashed circles indicate offspring assignments to their closest mounds.

4.4.3 Community description and spatial structure

Three *Cubitermes* spp. were identified from the pit and mound samples. *Cubitermes severus* was the most abundant, collected from 47 soil pits and 25 mounds (positions in Figure 4.4: insert left), *C. sulcifrons* from 8 pits and 7 mounds, and *C. bilobus* from one soil pit. Two types of mound architecture were described, "free-standing" and "against-tree" (see Figure 4.3 for photographs). *C. severus* were found in all 4 "free-standing" mounds, and occupied 21 "against-tree" mounds. *C. sulcifrons* were found to only occupy "against-tree" mounds. For "against-tree" mounds there did not appear to be an association with trees of a particular size. *Thoracotermes macrothorax* termites have very distinct mound architecture and were collected from 46 pits and 17 mounds (positions in Figure 4.4, insert right).



Figure 4.3 left to right. *Cubitermes* mound "against-tree", *Cubitermes* mound "free-standing", *T. macrothorax* mound.

By examining the location of mounds and the pits where *C. severus* and *T. macrothorax* termites were collected, the locations of occupied pits appear to mostly cluster around their respective mounds (Figure 4.4, inserts). In the

Omega analyses of soil pit locations, at short distances *C. severus* pits are significantly aggregated up to 8m ($\Omega_8 > 1$), while *T. macrothorax* is significantly aggregated up to 12m (Figure 4.4). A pooled sample of *C. severus* and *T. macrothorax* from pits was significantly aggregated up to 8m (Figure 4.5). In all of these three pit samples (*C. severus*, *T. macrothorax*, and the two species pooled), the degree of aggregation tends to decrease with distance. At greater distances the pit samples were generally hyper-dispersed or otherwise randomly distributed ($\Omega_{>12} < 1$, or ≈ 1).

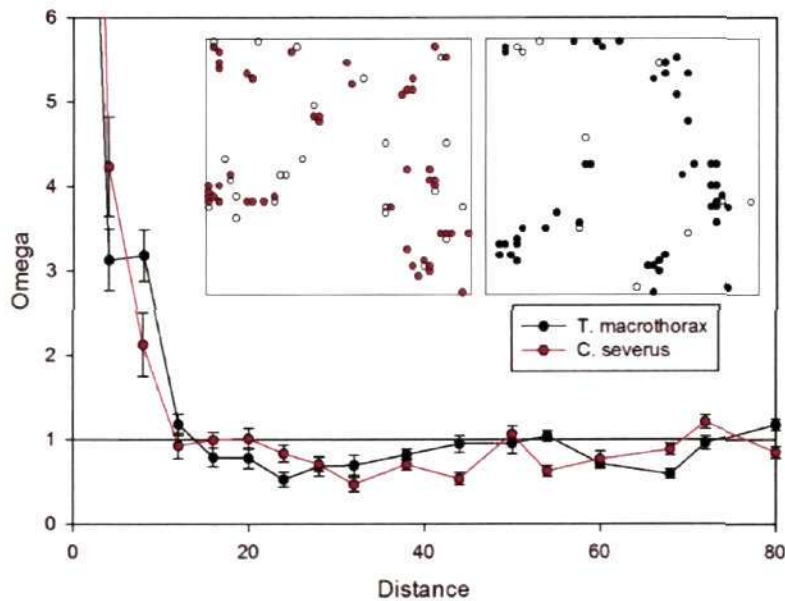


Figure 4.4 Relative neighbourhood density (Omega) by distance of *C. severus* pit sample, and *T. macrothorax* pit sample. $\Omega_x = 1$ for random distribution, $\Omega_x > 1$ for aggregated distributions, $\Omega_x < 1$ for dispersed distributions. Tails represent 95% confidence limits. Insert left: position of *C. severus* pits (red circles) and mounds (open circles). Insert right: position of *T. macrothorax* pits (black circles) and mounds (open circles).

In the Omega analysis of mound location (a pooled sample of all three species), the spatial position of mounds was found to fluctuate more (Figure 4.5). They were aggregated at the shortest distance, dispersed between 4m to 8m, and

aggregated at 12m (Figure 4.5). At greater distances the mounds tend to be dispersed or randomly distributed. Figure 4.5 illustrates that at short distances, the scale at which termites in the soil are aggregated (= putative colony) is the same scale at which mounds are dispersed.

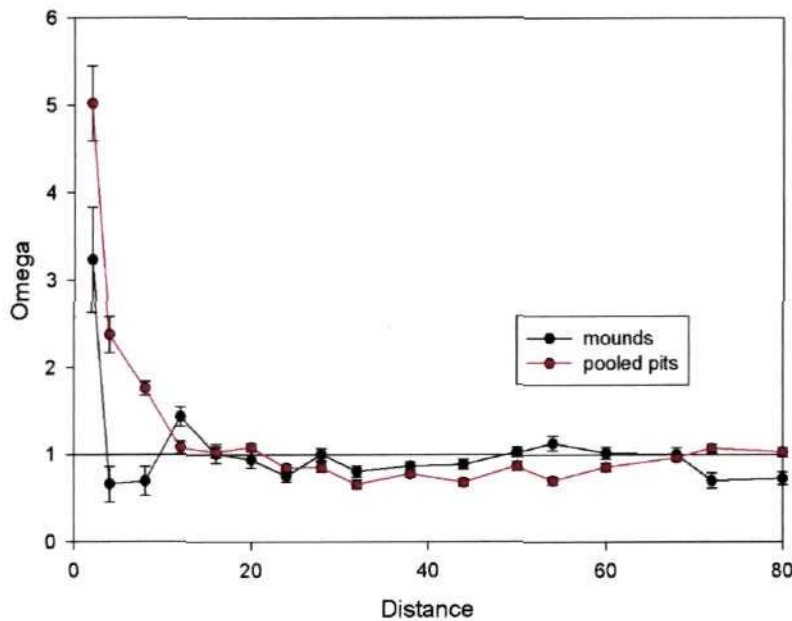


Figure 4.5 Relative neighbourhood density (Omega) by distance of all mounds, and a pooled sample of *C. severus* and *T. macrothorax* pits. $\Omega_x=1$ for random distribution, $\Omega_x>1$ for aggregated distributions, $\Omega_x<1$ for dispersed distributions. Tails represent 95% confidence limits.

4.4.4 Carbon concentrations

The C_{tot} concentration distributions from three groups of soil samples, 'mound' (active *Cubitermes* spp. mounds) (n=32), 'pit by mound' (the soil pit, whether occupied by *Cubitermes* spp. or not, adjacent to active mounds) (n=32) and 'pit' (all remaining soil pits not directly adjacent to a *Cubitermes* spp. mound, n=2272) are presented in Figure 4.6. C_{tot} concentrations in these sample groups were significantly different (Kruskal-Wallis Test; $H=26.74$, $df=2$, $p=0.000$; median = 3.83, 4.16 and 4.82 for 'pit', 'pit by mound' and 'mound' samples

respectively). The 'pit by mound' sample was not significantly different to the 'pit' sample (Mann-Whitney U test; $W=31143.5$, $p>0.05$). The paired differences between the C_{tot} of the 'mound' and 'pit by mound' samples were normally distributed (Shapiro-Wilk normality test, $p=0.325$). A paired T-test was therefore applied, which found these groups to have significantly different means, 5.07 and 4.20 respectively (Paired T-test: $T=4.76$, $p<0.001$).

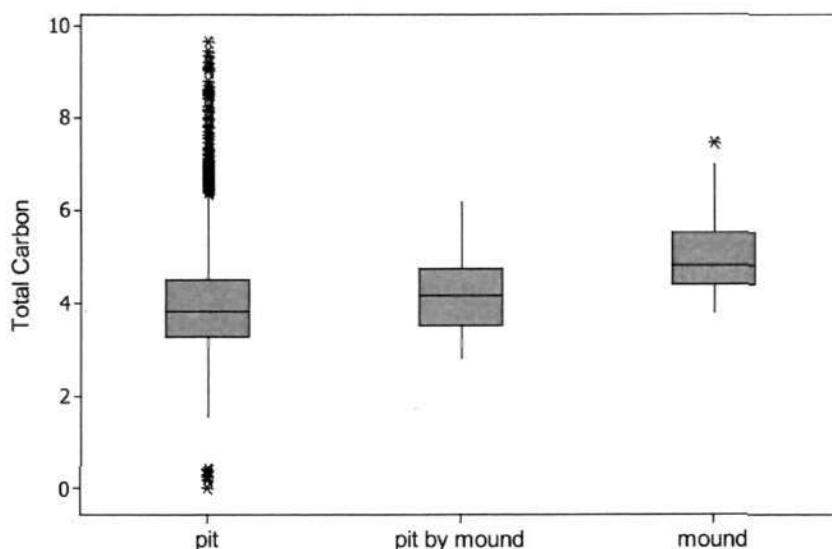


Figure 4.6 C_{tot} concentrations for soil samples from 'pits', soil pits not adjacent to a mound; 'pit by mound', soil pits adjacent to a mound; and 'mound', samples from *Cubitermes* spp. mounds. Boxes indicate the interquartile range, horizontal lines within boxes indicate the medians, whiskers include all points to 1.5 times the interquartile range, asterisks indicate outlying values.

4.5 Discussion

4.5.1 Foraging distances and mound dispersion

The significant aggregation of *C. severus* and *T. macrothorax* from soil pits at shorter distances, is taken to reflect typical colony foraging extent, i.e. ca. 8m and ca. 12m respectively (Figure 4.4). This appears reasonable as offspring assignment of *C. severus* was more frequently to the closest mound at less than 10m (Figure 4.1). At greater distances the distribution of termites are

mostly dispersed, or otherwise random. Where offspring were assigned to multiple or distant mounds this is likely to be due to a lack of resolution in the microsatellite markers, and incomplete representation of all mound genotypes respectively, rather than real events.

A colony extent of approximately 10m still appears large given the low energetic quality of soil, which might limit the marginal energetic benefits of foraging at a distance. Despite the low energetic quality of soil, there is no evidence for a tendency for colonies to be located on patches of higher organic quality soil (Figure 4.6). Perhaps then because of this, worker foraging over substantial distances is required, in order to maintain the colony's energetic needs, facilitated by the large body-size, and therefore consumption capacity of workers in these species (Eggleton *et al.*, 1998). This estimated foraging distance is comparable with some wood-feeding termite species, although they often have highly variable and more extensive foraging areas (Adams & Levings, 1987; Ngee & Lee, 2002; DeHeer & Vargo, 2004). A colony extent of approximately 10m may therefore represent their average colony extent, with variation around that depending on competitive interactions and microhabitat conditions (e.g. Adams & Levings, 1987).

Inter-colonial agonism has frequently been used to define colony boundaries (e.g. Cornelius & Osbrink, 2003; Nobre *et al.*, 2007) and provides evidence for territoriality in termites (e.g. Levings & Adams, 1984). The spatial signature of territoriality is spacing between individuals or colonies, observed as over-dispersion (Levings & Traniello, 1981; Korb & Linsenmair, 2001). As the mounds of *C. severus* and *T. macrothorax* were spatially dispersed to the same scale that individuals in the soil pits were aggregated (Figure 4.5), it appears

that the entire colonies tend to be spatially separated rather than overlapping, suggesting both territoriality and inter-specific competition at the colony level.

The substantial through-put of soil material afforded by large body-size in the *Cubitermes* spp. and *Thoracotermes macrothorax* (Eggleton *et al.*, 1998), must provide sufficient marginal energy to maintain colony defence strategies, including the soldier caste and mound construction. In addition, it is hypothesized that large body-size conforms to generalist feeding (Cammen, 1980), and if this applies also to large-bodied soil-feeding termites, there may be little resource partitioning for organic soil material. Despite its abundance, there may actually be a high intra- and inter-specific competitive pressure on soil for food and nesting spaces due to: 1) high consumption rates by colonies, 2) dense occupancy within the soil profile by large arid static colonies and 3) limited resource partitioning. A comparison between territories and overlapping home ranges in foraging crabs, shows that energy yields from defended territories are generally higher (Pereira *et al.*, 2003). Therefore if soil is a limiting resource for colony space and the energetic gains to sustain the colony, intra- and inter-specific competitive interactions may be driving territoriality and spatial dispersion at the colony scale in these species.

The mechanisms for establishing and maintaining territories have been more extensively studied in ants. However given the similar eusocial structure of these abundant insect groups, comparable mechanisms are likely to be operating. As colony formation by dispersing alates is typical in termites, the expulsion of founding queens and kings within a pre-established territory is likely to be an important mechanism, as demonstrated in ants (Levings & Franks, 1982). In ants, large colonies out-compete small colonies (Gordon &

Kulig, 1996), while colony boundaries change during investment in alate production (Adams, 2003). The observation that *C. severus* occupied the two mound architectures identified, does raise questions about the nature of any competitive interactions. As the most abundant of the *Cubitermes* spp., it may be competitively superior, such that *C. severus* colonies expel resident colonies of sympatric *Cubitermes* spp and occupy pre-existing mounds *Cubitermes fungifaber* colonies have been observed to make subterranean migrations when mounds are disturbed (Noirot *et al.*, 1986), a behaviour which may provide a means for one colony to oust a resident colony. Occupancy in termite mounds by secondary species has previously been examined; secondary occupancy rates in *Cubitermes* spp. mounds was found to be high (~50%), and included occupancy by closely related species e.g *Apilitermes* sp. and *Crenetermes* sp , but not different *Cubitermes* spp. (Eggleton & Bignell, 1997) These secondary occupants are likely to be making use of the mounds in a similar way to the primary hosts, and therefore the economic benefit of acquiring rather than constructing a mound may drive an usurper strategy, where species enter and eject the host

4.5.2 Mound aggregation

The lack of a significant difference in the mean of soil C_{tot} between soil pits adjacent to mounds and the remaining soil pits in the plot, suggests mound location is not being determined by soil quality, using carbon concentration as an indicator of soil organic material availability (Figure 4.6). By distinguishing between the age of *Macrotermes bellicosus* mounds, Korb and Linsenmair (2001) were able to show that younger mounds were aggregated according to micro-climatic conditions, while mature mounds were dispersed due to

competition. Although mound age classes were not measured in this study, similar age dependent microhabitat processes may be operating, and potentially explain the aggregation of termite mounds at the finest scale (Figure 4.5). Mound aggregation at the 12m scale may reflect the dispersal limitations of alates (Roy *et al.*, 2010).

4.5.3 Population processes and species co-existence

Termite diversity is greatest in equatorial rain forests, in particular in Africa where the regional species pool is dominated by soil-feeding species (Eggleton, 2000a). Here, average total species and soil-feeding richness from the standardised 100m transect method (Jones & Eggleton, 2000) is 53 and 40 respectively (Davies *et al.*, 2003a), raising interesting questions on just how this richness is maintained. If soil-feeding termites consume soil material at marginally different stages of decomposition, this resource partitioning offers a compelling explanation. The single study by Bourguignon *et al.* (2009) that suggest this using stable isotope ratios, suffers from weak sample replication for firm conclusions to be made.

In order to better understand diversity maintenance mechanisms, increasing emphasis has been placed on taking a spatially explicit view on co-existence (Cadotte, 2007). According to He and Legendre (2002), high assemblage diversity is promoted by ecological mechanisms that generate even species abundances and regular (or less aggregated) spatial distributions. Territoriality and density-dependent mortality contribute to population density-regulation (Lopez-Sepulcre & Kokko, 2005; Banda & Blanco, 2009). It is possible the dispersion patterns detected at various distances in the mound and pit samples reflect the different spatial scales at which these processes operate. In this

study one can only speculate at this. For instance competitive interactions are operating at the colony level generating spatial dispersion, which, combined with economic limitations of foraging define the colony boundaries and extent. The mound dispersion at broader scales (Figure 4.5) may be due to: 1) broader inter-specific competition with other mound-building species, and 2) predation pressure from ants, whereby ants respond to areas of high termite abundances. The outcomes from these hypothesized processes (intra- and inter-specific competition and ant predation) of both checking population densities of abundant species, and promoting spatial dispersion, may be important in promoting co-existence

4.5.4 Scale of ecosystem services

This study demonstrated that, at the one hectare scale, the density of active mounds is probably limited by intra and inter-specific interactions. Abandoned mounds are more abundant than active mounds, with 33 dead to 16 active *T. macrothorax* mounds, and approximately 90 dead to 32 active *Cubitermes* spp mounds. Once the termitaries have died, the organic material is again available to the soil biota, and the mounds in this study had an elevated carbon concentration. The abiotic conditions of mound material in relation to the surrounding soil material have previously been examined in detail for *Cubitermes* spp and *Thoracotermes macrothorax* (e.g. Garnier-Sillam & Toutain, 1995; Fall *et al.*, 2001; Donovan *et al.*, 2001b; Roose-Amsaleg *et al.*, 2005). The soil C values reported here (Figure 4.6), support the general findings that their mounds have increased levels of organic matter and high structural stability, thereby contributing to soil conservation and fertility (Garnier-Sillam & Harry, 1995; Ji & Brune, 2006). Due to the stability of mound material they may

persist for some time, and provide fine-scale high nutrient patches available to plant communities and indeed other termite species. The density at which these termitaries are creating fine-scale heterogeneity in soil properties is then a combination of population interactions, rates of colony turn-over and the decomposition rates of abandoned mounds.

4.5.5 Microsatellite markers

The markers employed here were designed for a population of *Cubitermes*. sp. *affinis subarquatus* sampled over a 30km scale (Harry *et al.*, 2001). The microsatellite divergence patterns of this population were used to suggest the presence of morphologically non-distinct cryptic species (Roy *et al.*, 2006). It appears highly unlikely that *C. severus* samples collected here would be composed of cryptic species, given the spatial extent of the study (<1 hectare), and identification of three *Cubitermes* spp. within this, using characters of the worker gut (Sands, 1998). Therefore the possible presence of cryptic species in the sample is an unlikely explanation for homozygosity in the microsatellite data. Of the seven primers isolated for *C. sp. affinis subarquatus*, six amplified reliable PCR products of the *C. severus* population sampled here. The *C. severus* population was found to be heterozygous at only three loci, with one marker confidently within the H-W equilibrium. Homozygosity and deviation from the H-W equilibrium in this sample may be due to in-breeding depression (non-random mating) and null alleles.

Null alleles arise when variation in the flanking region of microsatellite alleles prevents annealing of primers to template DNA during PCR amplification. They are more frequent in populations with a large effective size, and where mutation rates are particularly high in the flanking region (Chapuis & Estoup, 2007). Due

to the increase of null alleles with genetic divergence, microsatellite markers are typically employed in population-level studies, but are not exclusively species-specific (Jarne & Lagoda, 1996) When employed in poly-specific studies, their application may be limited to population-level studies of species derived from the species in which the loci were characterised, where sequence divergence in the flanking region would be limited (e.g. Eggert *et al.*, 2009) Null alleles at some loci in *C. severus* may therefore be inevitable if *C. severus* is not derived from a common ancestor with *C. sp. affinis subarquatus*.

Monogamy appears to be the predominant reproductive strategy in termites (e.g. DeHeer *et al.*, 2005; Dupont *et al.*, 2009), with morphological adaptations associated with reduced sperm competition during termite evolution (Baccetti *et al.*, 1981; Klass *et al.*, 2000). A predominantly monogamous mating system in *Cubitermes* spp. has recently been confirmed using genetic techniques (Roy *et al.*, 2010), which is supported by the frequent observation of a single queen and king in excavated *Cubitermes* sp. mounds (P. Eggleton personal communication) The parental genotypes constructed here also provide some evidence for a monogamous mating system in the sampled *C. severus* population. *Cubitermes* species are therefore likely to disperse and reproduce by swarming alates that found new colonies. If indeed colony foundation is mostly by dispersing alates rather than by colony budding and colonies remain monogamous, the high incidence of homozygous individuals in this population of *C. severus* cannot be explained by inbreeding

4.6 Conclusions

At the fine scale, biotic processes appear to be more important in determining the location and spatial orientation of termite colonies, than the selection of

organic rich patches in the soil profile (indicated by soil C_{tot} concentrations). An estimated foraging distance of 10m appears substantial, and possibly necessary to maintain the energetic requirements of large static colonies. Although this study is the first to provide data for a soil-feeding species in rain forests, much of the soil-feeding component of termite assemblages do not construct mounds. In addition there is substantial variation in body-size across the soil-feeding species (Eggleton *et al.*, 1998), with *Cubitermes* spp. and *Thoracotermes macrothorax* representing some of the larger bodied species. Therefore one should be cautious in assuming that these foraging distances are typical of rain forest or soil-feeding termites. On the other hand, *Cubitermes* spp. are a prominent feature of both forest and savanna systems in Africa, and therefore ecological information on these species is relevant across several habitat types in this region.

5 Spatial patterns in rain forest termite assemblages; an examination of abiotic and biotic interactions

5.1 Summary

Very little is known about the spatial structure of termite assemblages or their ecological interactions in rain forest systems. In this chapter the spatial structures of the Danum (SE Asia) and Ivindo (C Africa) termite assemblages sampled from one hectare plots, were quantified at the assemblage and functional (feeding-group) level. Patterns were analysed in a spatially-explicit manner, with three categories of ecological interactions considered: 1) environmental relationships, 2) an inter-feeding-group food-mediated facilitation, and 3) a predator-prey interaction with ants.

The differences in the relationships between environmental variables and the termite assemblages between the two sites (as measured in pair-wise association tests of SADIE spatial descriptions) corresponded with region-specific factors e.g. climatic conditions and taxonomic representation. Despite these different environmental associations, the wood-feeding (FGII) and humus-feeding (FGIII) termites were similarly spatially structured in both sites; patchily and homogeneously respectively. This is likely to be due, in part, to the patchy and continuous nature of their respective food material. The true soil-feeding termites (FGIV), only present in Ivindo, were however heterogeneously structured at broad scales despite, as the FGIIIs, consuming and nesting in soil. Biotic factors must therefore also be important in determining the spatial patterns. Contrary to the expected inter-feeding-group facilitative interaction, the termite feeding-groups were spatially disassociated. Humus-feeding termites were absent from wood-feeding termite patches, which is suggested to result

from competitive exclusion by wood-feeding termites for nesting space in the soil profile, due to the high value of their limited food resource. Spatial disassociation between the soil-feeding-groups (FGIII and FGIV), may be due to competitive exclusion between intra-feeding-group aggregations for space in the soil profile, and/or opposing environmental relationships at broad scales. The spatial patterns between the predatory ant community and termites suggest that a generalist and specialist predation strategy may be operating at fine scales in the Danum plot, and at medium scales in the plot Ivindo respectively. It appears that: 1) the spatial patterns of wood- and humus-feeding termites are robust across regions and time-scales, while the additional true soil-feeding termite pattern is unique to Africa, 2) competition for nesting space in the soil profile may be important and 3) a predator-prey interaction exists between termites and ants.

5.2 Introduction

Termites are a dominant component of soil communities in tropical rain forests (Watt *et al.*, 1997). There they provide several ecosystem services including carbon mineralization, and influence soil structure and microbial communities (e.g. Holt & Lepage, 2000; Sugimoto *et al.*, 2000; Donovan *et al.*, 2001b; Yamada *et al.*, 2005), although this has yet to be studied in any great detail in tropical rain forests where they are most abundant. The scale at which termites provide these services is in part determined by their spatial distributions, e.g. the spatial distribution of mounds, or the scale of multi-species aggregations, however little information is currently available on termites. In the only published spatially explicit study on rain forest assemblages, termites that feed further up the humification gradient (i.e. wood-feeding) were heterogeneously structured,

while soil-feeding termites were homogenously structured at fine scales (<1 hectare) (Donovan *et al.*, 2007). It is uncertain, however, whether these patterns arise due to environmental responses such as food availability, or to biotic processes, such as competition or predation, all of which will be operating at various spatio-temporal scales (Ettema & Wardle, 2002)

To date there is no study that simultaneously examines a number of key ecological patterns at the assemblage level in termites, thereby accounting for the inter-dependency of the ecological interactions, and their possible confounding relationships. Not only do we lack a robust understanding of the ecological interactions, but also the scales at which assemblages are structured, and so the scales at which they are contributing to ecosystem services. Biogeographical history accounts for the asymmetric distribution of species diversity and abundances seen across the equatorial rain forest systems (Eggleton, 2000a; Davies *et al.*, 2003a). As a result of these differences, one cannot simply extrapolate the spatial patterns documented in one region to another, without a better understanding of the ecological patterns that generate them

In this study, the spatial structures of the two termite assemblages sampled in Danum (SE Asia) and Ivindo (Africa) and described in Chapter 3, were quantified for the full assemblage, but also for each feeding-group. The Danum and Ivindo assemblages represent patterns typical of their regional differences, i.e. Ivindo had a higher generic richness and relative abundances compared with Danum. Three categories of ecological interactions were considered that represent abiotic, intra- and inter- taxonomic interactions: 1) environmental relationships, 2) a food-mediated facilitation between functional components of

ther termite assemblage, and 3) a predator-prey interaction between ants and termites. This was carried out using the spatial analysis SADIE (Spatial Analysis by Distance Indices), which first generates spatial descriptions of data, followed by pair-wise association tests that assess whether these are positively or negatively correlated (Perry *et al.*, 1996; Perry & Dixon, 2002).

5.2.1 Environmental relationships

The nature of the soil matrix and the energetic costs associated with foraging is likely to be a major ecological constraint on termites (Eggleton & Tayasu, 2001). Therefore it would be expected that successful colony establishment is tightly linked with the spatial heterogeneity in the availability and quality of their food material. Individual termite species consume dead plant material at different stages of decomposition (the 'humification gradient'), from dead wood and leaf-litter, to organic-rich upper layers of soil, and nutrient-depleted mineral soil (Donovan *et al.*, 2001a). Along this humification gradient there is a general trend in energetic quality and spatial availability of the consumed food material; poor quality food tends to be abundant, while high quality food is patchy and finite (Eggleton & Tayasu, 2001).

Soil is low in carbon, and the most humified material is extremely nutritionally poor (Brauman *et al.*, 2000) although it is abundant and continuously distributed. Patches of humus associated with floral communities has been shown to effect the structure of termite communities (Davies *et al.*, 2003b). Heavily decomposed wood may also leave an energetic legacy within the top-soil and create heterogeneity in soil organic matter concentrations at fine scales. In the Danum and Ivindo study plots, heterogeneity of soil C_{tot} and N appeared to correspond with small scale topography (Chapter 2). Therefore at

local scales, interactions between organic inputs into the soil system, combined with topographic influences on this, may affect the spatial structuring of termite assemblages. Conversely, dead wood such as logs, can represent an important food source that is energetically rich, but patchily distributed. These differences in food availability and quality may then determine how the functional components (feeding-groups) of the termite assemblages are spatially structured, as suggested by Donovan *et al.* (2007).

Numerous other abiotic factors apart from food availability may determine termite occupancy of the soil profile. Our understanding of the environmental conditions important to rain forest termites have largely been acquired from studies along habitat gradients, for instance along a disturbance gradient (e.g. Eggleton *et al.*, 2002a, Jones *et al.*, 2003). Assemblage composition has been shown to vary with environmental conditions and habitat heterogeneity (Davies *et al.*, 1999, Gillison *et al.*, 2003; Davies *et al.*, 2003b). These studies, generally at broad spatial scales, point to the importance of stable local climatic conditions (Dibog *et al.*, 1999), soil properties (e.g. pH, Jones & Prasetyo, 2002), and food availability (Davies *et al.*, 1999). It is worth noting, however, that each of these environmental factors will be structured at different spatial scales. Compositional changes in termite assemblages to habitat disturbance have been shown to be remarkably similar across regions (Eggleton *et al.*, 1999, Davies *et al.*, 2003a), suggesting the functional components of termite assemblages are responding to environmental cues in a similar fashion, at least at the broad scale.

The sampled plots from Ivindo and Danum are, to a large extent, habitat analogues, in terms of environmental heterogeneity (see Chapter 2). Therefore

if individual environmental conditions, such as the provision of dead wood or microhabitat conditions are important for termite communities, one might expect to detect similar environmental relationships in both plots. The main environmental differences relate to regional rainfall patterns, local soil texture, and region-specific plant diversity patterns (Chapter 2), which may then be found to have differential relationships with the termite assemblages.

Termites themselves influence the local heterogeneity of soil properties; for example organic matter and moisture were higher in termite-worked soil (Donovan *et al.*, 2001b), soil infiltration and moisture were higher where the termite assemblage is intact (Mando *et al.*, 1996), and termite mound material is composed of stabilised clay-rich soil (Jouquet *et al.*, 2004). Most studies that examine termite impacts on soil conditions concentrate on mound-building species, and therefore influences at the scale of individual colonies and mounds. There is little understanding of whether termites influence soil properties at the assemblage or feeding-group level (although see Mando *et al.*, 1996). Soil-feeding termites essentially saturated the soil profile in Ivindo, and were far more abundant (as measured by encounter rates in soil pits) than in Danum (Chapter 3). These abundance differences, which are consistent with patterns from African and Asian assemblages (Eggleton *et al.*, 1999), mean that the influence of soil-feeding termites on the environment (e.g. soil porosity rates), may be more detectable at the assemblage level in Ivindo. Consideration of the feed-back loops where termites might be influencing the environment, and possibly accentuated by the high termite abundances in Ivindo, is necessary to interpret spatial associations.

5.2.2 Inter-feeding-group facilitation

Intra-trophic interactions in soil communities include competition and facilitation, summarised in Wardle (2006). Competitive interactions are generally considered to be weak in soil communities (Decaens, 2010), and this may be particularly so between the termite feeding-groups, due to the consumption of different food material. There is some evidence for food-mediated facilitative interactions from fungal communities. Frankland (1969) demonstrated that early fungal colonizers of dead plant material break-down recalcitrant compounds, and provide the food substrates for sugar fungi.

As wood, leaf-litter, and soil is consumed by termites, modified and continuously worked through the soil profile as oral and faecal products, patches of nutrient-rich substrate are created in the 'termitosphere' (Brauman, 2000, Lopez-Hernandez, 2001; Jimenez *et al.*, 2006a). The provision of progressively more decomposed material to termites that feed further down the humification gradient may generate a similar cascading facilitative interaction between the feeding-groups. Indeed a positive spatial association has previously been reported between the soil-feeding and wood-feeding components of an assemblage sampled in Danum, suggesting an interaction of this nature (Donovan *et al.*, 2007). This was, however, in the absence of soil carbon measurements, as an indicator of food material passed from one feeding-group to another, which would help clarify the details of the hypothesized interaction.

The scale and intensity of the hypothesized facilitative interaction between the feeding-groups is likely to be influenced by the spatial structure and abundance of the providing group, i.e. the group positioned further up the humification gradient. The spatial patterns of the feeding-groups will be described in this

chapter, while data is already available on the abundances of the feeding-groups from the sampled plots, measured as encounter rates in soil pits (Chapter 3). The wood-feeding termites had similar occupancy patterns in Danum and Ivindo, and a single hypogeal-nesting genus dominated this component of the termite assemblage in both plots: *Globitermes globosus* in Danum, and *Microtermes* spp. in Ivindo (Chapter 3). The provision of food material between the wood-feeding and humus-feeding termites might then be at a similar rate in the two plots. Detecting a facilitative interaction between the two soil-feeding-groups, if this exists, is only possible in Ivindo, where the humus-feeding termites (FGIII) and true soil-feeding termites (FGIV) are particularly abundant (Chapter 3). In Danum, FGIV termites were completely absent, and generally FGIV termites are rare in Asian forests (Davies *et al.*, 2003a), therefore if a facilitation occurs this would be at very fine scales.

5.2.3 Predator-prey interactions

Termites are particularly abundant in forest soils, and therefore potentially a readily available source of food. Top-down processes of predation may exert an influence on termite communities (DeSouza *et al.*, 2009), although the nature and intensity of this is largely unknown. Evidence of predation is largely based on observations of foraging behaviour by individual species, for instance ants (e.g. Jaffe *et al.*, 1995; Pie, 2004), but also apes (Deblauwe & Janssens, 2008), and reptiles (Vitt *et al.*, 2005), with these operating at various scales and intensity.

Collectively termites and ants constitute a large proportion of the tropical forest faunal biomass (Wilson, 1993; Watt *et al.*, 1997), and predatory ants and termites are likely to be a significant predator-prey interaction in tropical rain

forest systems. Indeed Noirot and Darlington (2000) suggested that an evolutionary arms race between ant predator and termite defence strategies has played out over the last 50 million years. Species-specific studies illustrate the varied and complex nature of ant-termite interactions. For instance, co-habitation of raiding termitophagous ants in active termite mounds has no negative effect on termite colony fecundity (Dejean & Feneron, 1999; Bayliss & Fielding, 2002), and therefore one might expect spatial aggregation between ants and termites in these systems. Ant raids can also inhibit the establishment of termite nests and prevent colonization by dispersing alates (e.g. Leponce *et al.*, 1999), which one would expect to generate spatial disassociations.

5.2.4 General hypotheses

By comparing and contrasting the spatial relationships from the Danum and Ivindo assemblages, similarities may provide evidence for over-arching ecological processes influencing rain forest termite assemblages, while existing evidence suggests that any differences will relate to region-specific factors. The following hypotheses were tested, using the spatial relationships as preliminary evidence for these.

Environmental hypotheses:

- 1 The availability of food material is important for termites, resulting in spatial associations between termite feeding-groups and their food materials.
- 2 Termites show broadly similar responses to environmental heterogeneity, and therefore associations between termites (at the assemblage and

feeding-group level) and soil properties and vegetation structure, will be consistent between Ivindo and Danum.

3. Any differences between sites (Danum and Ivindo) in the associations between termites and the recorded environmental conditions can be explained by site-specific environmental conditions or differences in termite abundances between sites.

Inter-feeding-group facilitation hypothesis:

4. Termites that feed higher up the humification gradient provide food material to those lower down the gradient, and therefore feeding-groups will be positively associated.

Predatory ant hypotheses:

5. Predatory ants co-habit with termites, and therefore predatory ants and termites will be positively spatially associated.
6. Predation by ants influences the occupancy of termites in the soil by depleting colonies, and therefore predatory ants and termites will have negative spatial relationships.

5.3 Methods

Biotic and abiotic data were collected from a single plot of 96m x 96m in Danum (SE Asia) and Ivindo (C Africa), with contiguous sample points positioned every 2m x 2m. The sampling protocols for termites, ants and environmental variables are described in detail in Chapters 2 and 3.

5.3.1 Spatial and Statistical analysis

5.3.1.1 SADIE red-blue method

Spatial analysis by distance indices (SADIE), developed for ecological count data (Perry *et al.*, 1999), was employed to assess the spatial structure in the biotic and abiotic data. The SADIE red-blue method identifies areas of clustering in local neighbours of consistently large or small counts, referred to as "patches" and "gaps" respectively.

A cluster index is calculated for each sample point (I_{ij}), referring to whether it contributes to a patch or gap. Sample points that have a value greater or less than the sample mean are assigned a positive (I_i), or negative (I_j) cluster index respectively. An arrangement of random neighbouring counts are assigned $I_i < 1$ or $I_j > -1$. The cluster indices are then contoured by interpolation and mapped (Surfer v6.04; Golden Software Inc., Colorado, U.S.A.) Neighbourhoods where $I_i > 1.5$ are identified as patches and indicated in red in mapped figures, and those where $I_j < -1.5$ are gaps and indicated in blue (Perry *et al.*, 1999). A global index of aggregation I_a is calculated which indicates whether the overall spatial pattern is non-random ($I_a > 1$), accompanied by an overall gap (I_j) and patch (I_i) index. The significance of indices were tested by Monte Carlo procedures with 5965 randomizations (as the default number of randomisations in the SADIE executable) (Perry *et al.*, 1999).

Using the SADIE red-blue method, spatial structures in the termite assemblages were analysed and the red-blue plots of count data generated, where "counts" refer to the number of genera per pit. Analyses were performed on the following data sets:

- the full termite assemblage
- non-soil-feeding (or wood-feeding) termites (FGII). For simplicity this group has been termed FGII, despite the inclusion of FGI taxa. These feeding-groups are distinguished by taxonomic membership rather than a distinct difference in the food material consumed (Donovan *et al.*, 2001a)
- humus-feeding termites (FGIII)
- true soil-feeding termites (FGIV), which were only recorded in Ivindo
- predatory ants, as identified and described in Chapter 3.

The SADIE method has also been used to analyse environmental variables (Donovan *et al.*, 2007). As SADIE only accepts integers, all non-integer variables were rounded to whole numbers. Where the frequency distributions of continuously distributed variables were strongly skewed (Figure 3.5, soil C_{tot} , soil N and infiltration) the variable was log transformed to normalize the distribution, multiplied by a factor of 10 to maintain an acceptable range of values, and subsequently rounded to whole numbers.

The local cluster index values (I_{ij}) provide the spatial descriptions of data, which are used in subsequent association tests, to assess the spatial relationships between pairs of data.

5.3.1.2 Association tests

Pairs of variables may be positively associated, disassociated or occur at random with respect to each other (Perry, 1998). Local spatial association was measured using the index χ_k . This is based on the similarity, measured at the k th unit (sample point), between the local cluster index values (I_{ij}) generated in

the SADIE analysis, from any pair of variables (Perry & Dixon, 2002), denoted z_{k1} and z_{k2} for the pair of indices. Positive values of χ_k arise from coincidences of patches ($I_j > 0$) or of gaps ($I_j < 0$) in a pair-wise analysis, termed "positive association". Negative χ_k values arise from coinciding "patch-gap" or "gap-patch" cluster types, termed "disassociation". Overall spatial association, X , was calculated as the mean of local values, $X = \sum_k \chi_k / n$, equivalent to the simple correlation coefficient between z_{k1} and z_{k2} . The significance of X was tested by randomizations, with values of z_k reassigned among the units, after allowance for small-scale spatial autocorrelation in either set of z_k to provide a probability value p_D (Dutilleul, 1993).

Environmental relationships

To examine the spatial relationships between termites and environmental conditions, pair-wise association tests of the SADIE red-blue descriptions were carried out between the complete termite assemblage, and each feeding-group, with of all the environmental variables that were significantly spatially structured ($I_a > 1$, $p < 0.05$).

Biotic interactions

Positive spatial association may be due to some broad-scale indirect effect, such as an environmental variable selecting against the presence of both biotic groups, and therefore generating overlapping gaps (Shea *et al.*, 1993). To consider just the localized interaction between biotic groups, from the SADIE spatial descriptions, 'empty soil pit' sample points, i.e. where the soil pit was not occupied by at least one of the biotic groups in question, were removed (Perry & Dixon, 2002). The association test was then carried on these "occupied only" data sets. The following pair-wise analyses were performed

- FGII and FGIII (Danum and Ivindo)
- FGIII and FGIV (Ivindo only)
- Predatory ants and full termite assemblage (Danum and Ivindo)

To examine in greater detail the heterogeneity and magnitude of relationships, plots were constructed of the local spatial index χ_k (Winder *et al.*, 2005). These plots are the χ_k value contoured by interpolation and mapped (Surfer v6.04; Golden Software Inc., Colorado, U.S.A.), where positive association ($\chi_k > 0$) and disassociation ($\chi_k < 0$) are distinguished by colour categories (Table 5.1). Local positive association ($\chi_k > 0$) encompasses the co-occurrence of both patches and gaps. Similarly local disassociation ($\chi_k < 0$) encompasses the co-occurrence of "variable 1 gap" and "variable 2 patch", and the co-occurrence of "variable 1 patch" and "variable 2 gap". By examining the local cluster index values (I_{ij}) from the SADIE red-blue analysis, it is possible to distinguish between these. At the sample points where χ_k exceeded the lower and upper percentile limits adjusted for local spatial autocorrelation (i.e. significant local spatial associations), these four spatial relationships were identified and presented by various symbols within the contour plots (see Table 5.1).

Table 5.1 Local spatial relationships (χ_k): contour colours and symbols used in plots of association tests between biotic data.

Local cluster index Patch: $I > 0$, Gap: $I < 0$		Spatial relationship	Local spatial index and contour colour	Symbol where $\chi_k >$ upper or $<$ lower percentile limits
Variable I	Variable II			
Patch	Patch	Positive Association	$\chi_k > 0$ Light grey	●
Gap	Gap			+
Patch	Gap	Disassociation	$\chi_k < 0$ Dark grey	O
Gap	Patch			X

5.4 Results

5.4.1 SADIE red-blue structure

The SADIE summary statistics of global spatial structure are summarized in Table 5.2, and the red-blue plots for each analysis of the termite assemblages are presented in Figure 5.1. In Danum, the termite assemblage was significantly spatially structured, with areas of scattered patches and gaps. The higher global index calculated for FGII is due to large gaps in the plot, with a few scattered patches. FGIII however is more homogeneously structured, with a low but significant I_a , and a structure that is dominated neither by patches or gaps.

Table 5.2 SADIE red-blue analyses summary statistics

	Danum			Ivindo		
	I_a	I_j	I_i	I_a	I_j	I_i
All termites	1.606***	-1.596***	1.538***	1.777***	-1.724***	1.663***
FGII	1.706***	-1.792***	1.758***	1.617**	-1.619***	1.630***
FGIII	1.348*	-1.355**	1.351**	1.22	-1.233*	1.158
FGIV				2.022***	-2.050***	1.967***

p value *** ≤ 0.001 , ** ≤ 0.01 , * ≤ 0.05 , I_a , Global index aggregation; I_j , Gap cluster index; I_i , Patch cluster index. When $I_a > 1$ spatial pattern is non-random.

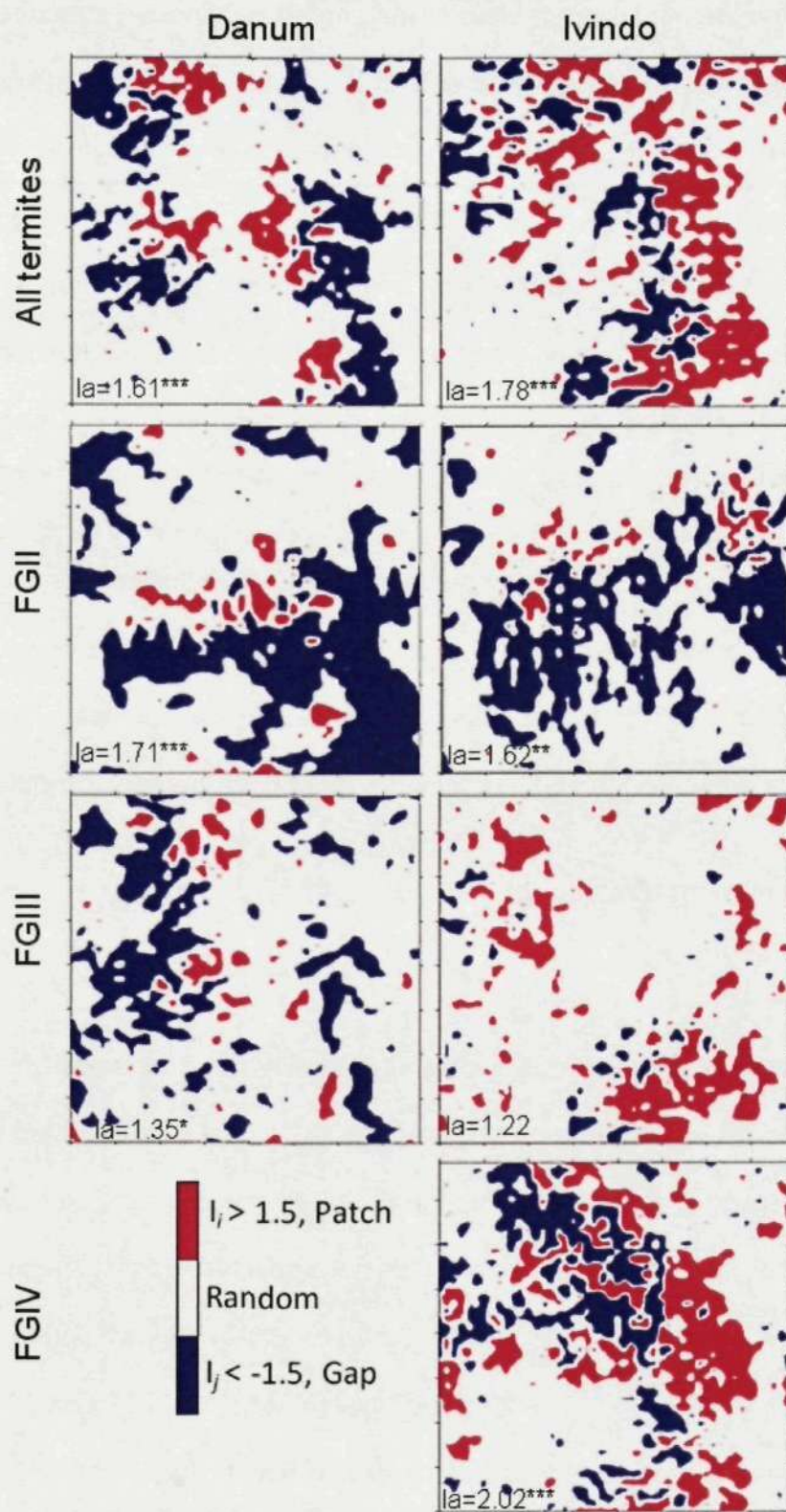


Figure 5.1 SADIE red-blue plots, from Danum and Ivindo, for the full assemblage, and by feeding-group. I_a , Global index aggregation (from Table 5.2) is included in each plot.

In Ivindo the termite assemblage was heterogeneously structured with significant patches and gaps (Figure 5.1 and Table 5.2). Although the FGII termites have a similar I_a value to the full assemblage, the significant spatial structure is dominated by several large gaps. The FGIII assemblage was globally not significantly structured, with non-significant patches broadly divided into two clusters, and small significant gaps. The FGIV assemblage was significantly aggregated, with patches largely concentrated in the east of the plot, and gaps in the north-west.

The feeding-group spatial patterns were similar in Danum and Ivindo; FGII is heterogeneously structured, and of the significant spatial structure large gaps dominated over small patches. FGIII termites show weaker spatial structure, and therefore compared to FGII termites are more homogeneously structured.

5.4.2 Environmental relationships

5.4.2.1 Danum

All of the environmental variables were significantly structured apart from trees (Table 5.3). The two feeding-groups were in most cases positively associated with their respective measures of food material. FGII was aggregated with dead wood material, i.e. logs and sticks, but was not significantly associated with leaf-litter depth. FGIII was aggregated with both soil C_{tot} and N, which strongly covary (C and N, $r=0.813^{***}$), and disassociated with the C/N ratio. Non-food material relationships were also detected. FGIII was significantly aggregated with leaf-litter. FGII was disassociated and positively associated with soil N, and the soil C/N ratio respectively, the direct opposite to relationships between FGIII and these soil measures (Table 5.3, Figure 5.2).

Table 5.3 Danum SADIE global index aggregation (I_a) for the environmental variables, and SADIE global association index (X) from association analyses between the environmental variables and the termite assemblage, FGII and FGIII.

Abiotic variables	SADIE I_a	All Termites		FGII		FGIII	
		X	p	X	p	X	p
Nitrogen	265.1***	-0.041	0.878	-0.130	1.000	0.122	<0.001
Carbon	5.574***	-0.027	0.761	-0.037	0.817	0.106	0.001
CN ratio	563.1***	0.016	0.324	0.294	0.000	-0.117	1.000
Logs	1.602***	0.073	0.047	0.118	0.006	0.054	0.091
Sticks	3.769**	0.045	0.091	0.087	0.024	-0.003	0.530
Leaf-litter	2.156**	0.068	0.068	0.068	0.090	0.091	0.012
pH	4.303***	-0.057	0.876	-0.072	0.912	-0.002	0.511
Infiltration rate	1.868***	-0.035	0.786	-0.147	0.999	0.107	0.005
Moisture	3.465***	-0.084	0.978	-0.978	0.990	-0.069	0.961
Trees	0.052	NA	NA	NA	NA	NA	NA
Stems	2.610***	-0.074	0.986	-0.060	0.941	-0.051	0.940
Ground vegetation	2.317**	-0.096	0.974	-0.060	0.949	-0.613	0.974

When $I_a > 1$ spatial pattern is non-random. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Global spatial association (X) Two-tailed significance threshold; positive association, $p < 0.025$ is highlighted in green, disassociation, $p > 0.975$ is highlighted in red.

FGII and FGIII also showed opposite associations with soil infiltration rate, negative (where soil is less porous) and positive (more porous soil) respectively. The termite assemblage is disassociated with soil moisture content and with two measures of understorey vegetation: the number of stems and ground vegetation cover (although here the p value was marginally short of the two-tailed threshold). Most of the spatial associations are weak ($-0.1 < X < 0.1$), apart from with soil C_{tot} and N.

5.4.2.2 Ivindo

Similar to the Danum SADIE red-blue analyses, all of the environmental variables apart from trees are significantly spatially structured (Table 5.4),

although the degree of spatial structure, indicated by the magnitude of I_a , typically varied between the sites. The association analyses between these and the termite assemblages are marked by a paucity of significant relationships, which are weak in overall magnitude. The only association with food material was between FGII termites and the abundance of small dead wood (sticks). FGII and FGIII were disassociated with the number of large dead wood (logs), while FGIV was positively associated with logs. Soil porosity (infiltration rate) was positively associated with FGIV termites, and pH negatively associated with FGIII. The termite community was positively associated with the number of small trees, arising from an association with FGII and FGIV, but not FGIII.

Table 5.4 Ivindo SADIE global index aggregation (I_a) for the environmental variables, and SADIE global association index (X) from association analyses between the environmental variables and the termite assemblage, FGII, FGIII and FGIV.

Abiotic variables	SADIE I_a	All Termites		FGII		FGIII		FGIV	
		X	p	X	p	X	p	X	p
Nitrogen	4.68***	-0.017	0.661	-0.061	0.932	-0.319	0.802	0.027	0.253
Carbon	2.55***	-0.014	0.635	-0.007	0.567	-0.047	0.902	-0.017	0.666
CN ratio	2.88***	0.002	0.486	-0.008	0.426	-0.028	0.799	0.005	0.451
Logs	2.90***	0.046	0.137	-0.087	0.978	-0.113	1.000	0.152	0.000
Sticks	4.31***	0.041	0.099	0.106	<0.001	0.048	0.052	0.004	0.542
Leaf-litter	2.90***	-0.056	0.929	-0.041	0.860	-0.009	0.612	-0.032	0.806
pH	2.26***	0.010	0.406	0.035	0.195	-0.088	0.997	0.020	0.302
Infiltration rate	254.29***	-0.004	0.550	-0.038	0.905	-0.040	0.925	0.060	0.020
Moisture	7.33***	0.055	0.081	0.074	0.037	0.034	0.152	-0.013	0.619
Trees	0.90	NA	NA	NA	NA	NA	NA	NA	NA
Stems	2.68***	0.075	0.002	0.057	0.010	0.009	0.358	0.054	0.018
Ground vegetation	3.60***	-0.009	0.604	-0.045	0.872	-0.059	0.958	0.018	0.313

When $I_a > 1$ spatial pattern is non-random. *p < 0.05, **p < 0.01, ***p < 0.001. Global spatial association (X) Two tailed significance threshold; positive association, p < 0.025 is highlighted in green, spatial disassociation, p > 0.975 is highlighted in red.

The significant spatial associations in Danum and Ivindo are summarized in Figure 5.2. The relationships unique to Danum are those with soil C_{tot} and N (and therefore by extension with the C/N ratio), a disassociation between the assemblage and soil moisture, and a positive association between FGIII termites and leaf-litter. The only relationship unique to Ivindo is a positive association between soil pH and FGIII termites. The termite assemblages show opposing associations in Danum and Ivindo with the number of stems, and between FGII termites and logs.

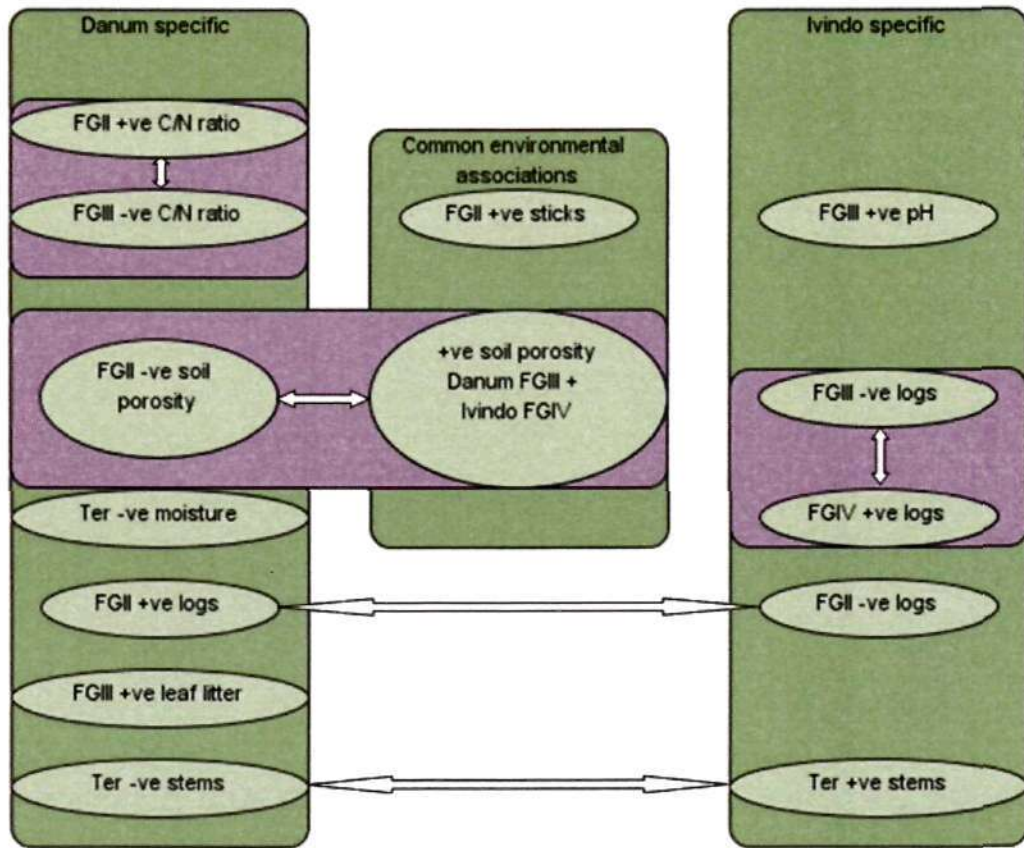


Figure 5.2 Site-specific and common significant SADIE spatial relationships between the termite assemblages and environmental variables. +ve, positive association; -ve, disassociation. Ter, full assemblage; FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding. Arrows highlight where associations were opposing, either between feeding-groups within sites (highlighted in purple), or between sites.

5.4.3 Inter-feeding-group relationships

5.4.3.1 Danum

Thirty-eight percent of sample points were retained for an association analysis between FGII and FGIII of the "occupied-only" samples (only includes the sample points where pits were occupied by at least one of the FGs). This yielded a strongly disassociated global relationship ($X=-0.467$, $p>0.999$). Disassociation dominates much of the plot as evidenced by the dark shading due to negative χ_k values (Figure 5.3a). Of the 19 sample points that negatively exceeded the a_i , most are coinciding "FGII patch - FGIII gap" points (open circles). These points are positioned in the FGII patches identified in the red-blue SADIE analysis (Figure 5.1). The global disassociation is therefore largely due to an absence of FGIII termites in FGII patches, and this is most apparent where FGII termites are significantly aggregated.

5.4.3.2 Ivindo

In the association analysis of the "occupied only" spatial structures (76% of the complete data set), the FGII and FGIII termite assemblages were globally disassociated ($X=-0.144$, $p>0.999$). This disassociation is distributed across the plot, and the sample points with the strongest dissociation (χ_k values exceed the a_i critical value) mostly comprise "FGII patch - FGIII gap" co-occurrences (Figure 5.3b). These sample points are located within clusters of high magnitude, which overlap with the FGII patches identified in the red-blue SADIE analysis (Figure 5.1). Therefore, as in Danum, the disassociation is largely due to an absence of FGIII termites in FGII aggregations.

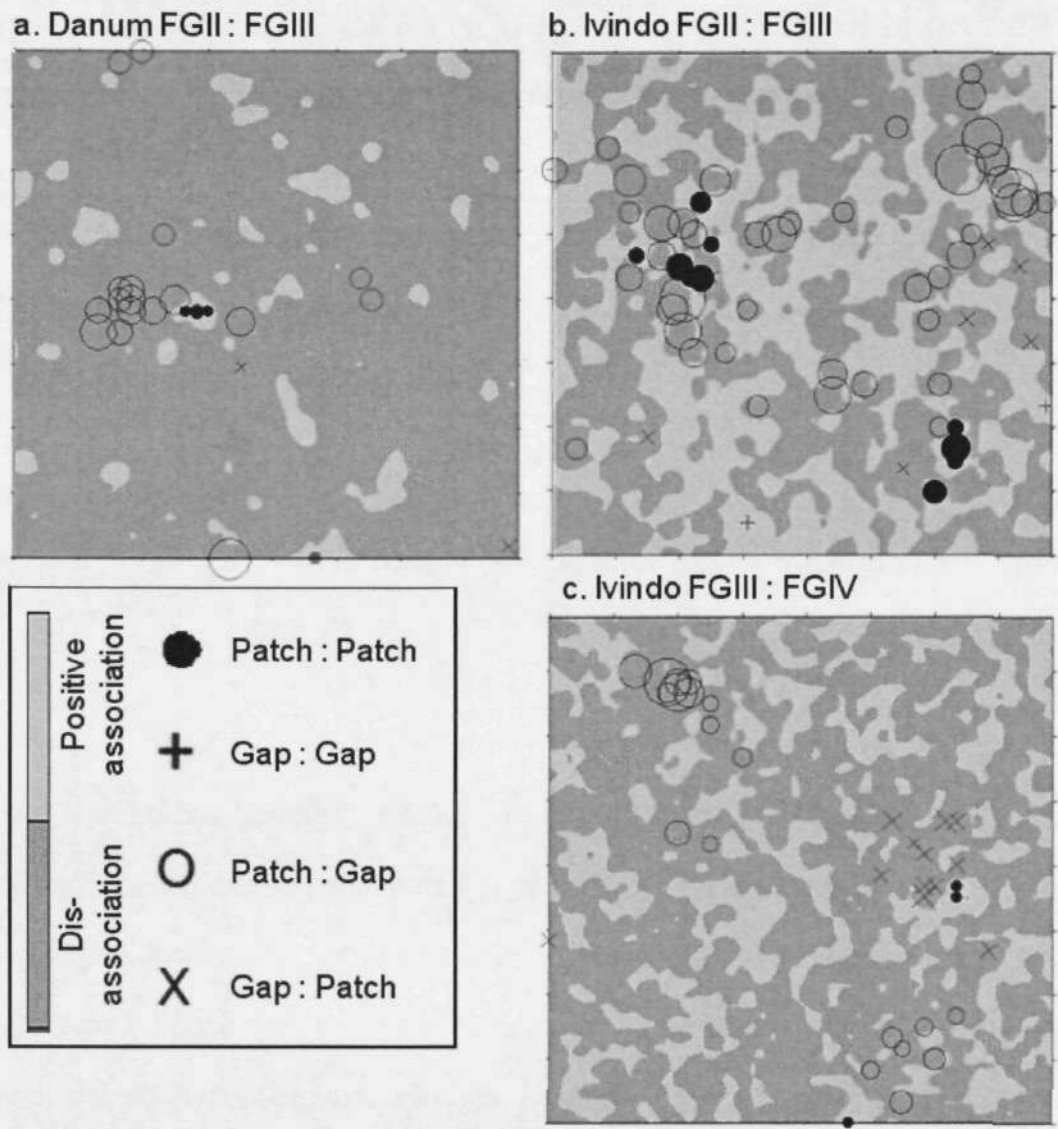


Figure 5.3 Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th a_u percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k . a) Danum FGII vs FGIII, $a_l=-2.73$, $a_u=2.71$. b) Ivindo FGII vs FGIII, $a_l=-2.800$, $a_u=2.841$. c) Ivindo FGIII vs FGIV, $a_l=-2.522$, $a_u=2.417$.

A global disassociation was also found between “occupied only” spatial structures of the FGIII and FGIV assemblages ($X=-0.256$, $p>0.999$) (88% of complete data set). Here the disassociation is due to two clusters of “FGIII patch – FGIV gap” co-occurrences (open circles), and one cluster of “FGIII gap

– FGIV patch” co-occurrences (crosses) (Figure 5.3c). These three clusters are positioned in the major patches identified in the red-blue SADIE analyses of FGIII and FGIV (Figure 5.1). In the previous FGII-FGIII feeding-group analyses in Danum and Ivindo, the soil-feeding-group (FGIII) was absent from the wood-feeding (FGII) patches. Between the two soil-feeding-groups, however, each group is equally dispersed away from patches (FGIII patches are not however significant, see Table 5.2) of the other group.

5.4.4 Predatory-ant/termite assemblage relationships

5.4.4.1 Danum

The Danum predatory ant assemblage (described in Chapter 3) is weakly spatially structured ($I_a=1.29$, $p<0.05$) with scattered patches, and gaps (Figure 5.4a, SADIE red-blue plot). Fifty percent of the sample points were retained for the “occupied only” association analysis of the predatory-ants/termite assemblage spatial patterns. The strong global disassociation ($X=-0.398$, $p>0.999$) is broadly distributed across the plot, as evidenced by the dark shading (Figure 5.4b). Of the sample points with χ_k values that exceed the a critical value, most are “ant patch - termite gap” co-occurrences, and these are scattered across the plot (Figure 5.4b, open circles). Therefore the disassociation reflects an absence of termites in predatory-ant patches, which are structured at fine scales within the plot.

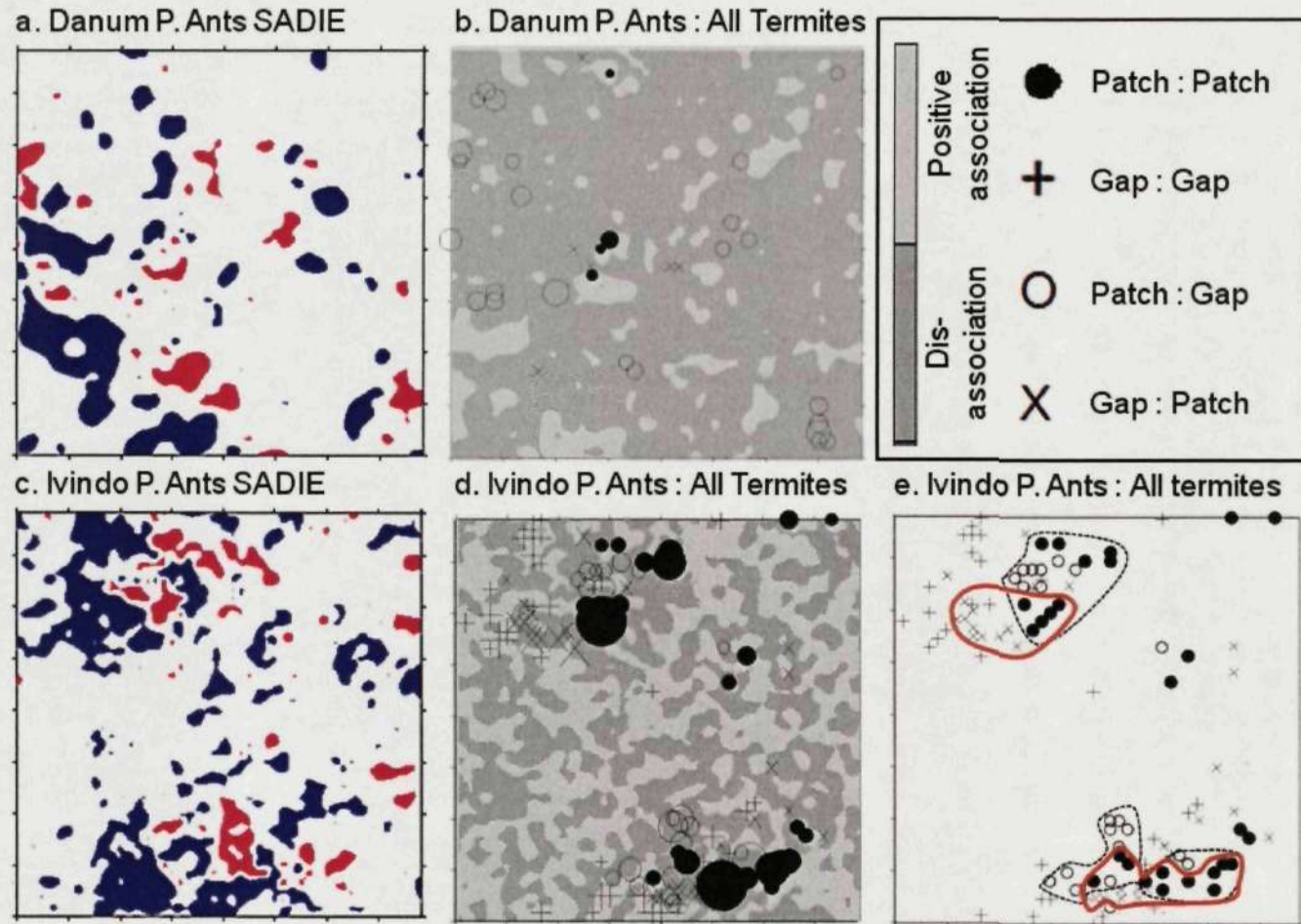


Figure 5.4 Association results of predatory ants (P. Ants) vs termite assemblage. a) and b) Danum. c), d) and e) Ivindo. a) and c) SADIE red-blue plot for predatory ants. b) and d) Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th (a_u) percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k . b) Danum, $a_l=-2.488$, $a_u=2.443$. d) Ivindo, $a_l=-2.560$, $a_u=2.146$. e) Additional plot taken from Ivindo (d) presenting only the significant local associations; black line envelopes ant patches (black dot and open circle); orange line envelopes termite patches (black dot and X).

5.4.4.2 Ivindo

The Ivindo predatory ant assemblage (described in Chapter 3) is heterogeneously structured ($I_a=1.57$, $p<0.001$), with two broad clusters in the north and south that include both patches and gaps (Figure 5.4c). The global index of the "occupied only" association test between the predatory ant and termite assemblage (91% of complete data set) was weak and non-significant ($X=0.004$, $p=0.439$). Inspection of the local association plot identifies two discrete clusters of significant local association values (χ_k values exceeding the a_l and a_u values). Each cluster consists of all four possible spatial associations, within which the predatory ant and termite patches overlap to various degrees (Figure 5.4d and for clarity see the additional plot Figure 5.4e). The lack of a significant global relationship is therefore due to both strong positive and negative interactions, positioned in two large clusters within the plot. Further to this, the location of these interactions broadly overlaps with the FGIII patches (although these are non-significant) identified in the FGIII red-blue analysis (Figure 5.1).

5.5 Discussion

5.5.1 Environmental relationships

The spatial relationships between the measures of food quality and availability, soil properties and understorey vegetation, with the termite feeding-groups were inconsistent between the two regions (summarized in Figure 5.2). The only similarities across the sites were between wood-feeding termites and one measure of their food source, and between soil-feeding termites and soil porosity. Several

associations were unique to each site, while with the other environmental variables the direction of associations (positive or negative), were in some cases opposing between sites.

5.5.1.1 Similarities

The positive association with small dead wood (sticks) in both regions with wood-feeding termites was not accompanied by similar associations with logs, or leaf-litter depth. A lack of a relationship with leaf-litter may be due to constantly shifting foraging patterns as this resource is continuously produced and rapidly depleted by foraging workers. It is likely that leaf-litter is in a greater state of flux, as the soil macro-faunal communities play a dominant role in the rates of litter decomposition (Didham, 1998; Kurzatkowski *et al.*, 2004), while woody material would be depleted at a slower rate. Differences in the spatial heterogeneity of leaf-litter and sticks is reflected in the global SADIE I_a values, that indicate the magnitude of heterogeneity, where leaf-litter is more homogeneously distributed than sticks in both regions (Table 5.2 and Table 5.3). Sticks may be depleted at a slower rate than leaf-litter, and therefore represent both a patchier and more stable food source, determining both foraging patterns and colony location.

Soil porosity was positively associated with soil-feeding-groups, FGIII in Danum and FGIV in Ivindo. This may be due to the production of micro-aggregates in termite-worked soil that improve the microstructure and porosity of the soil (Mando *et al.*, 1996; Junderius *et al.*, 1999). In Ivindo heterogeneity in soil porosity was structured at a broad scale in the plot, with a high possibility this was due to the large influence of compacted soil along an active elephant trail. Many FGIV

termites have large body sizes (Eggleton *et al.*, 1998) and heavily compacted soil may inhibit worker foraging dynamics. The spatial association may then result from both termite avoidance of compacted soil (or in an ability for colonies to establish), combined with elevated porosity from the subterranean tunnelling of these large termites (Holt & Lepage, 2000)

5.5.1.2 Relationships unique to Danum

In Chapter 2, microhabitats were identified as being characterized by combinations of environmental conditions, for instance high leaf-litter, lower soil moisture levels, and higher soil C and N, tended to correspond with flatter areas in the plots. It is in Danum that the termite assemblage has a series of spatial associations with this combination of conditions; a positive association of FGIII with leaf-litter, a disassociation with soil moisture, and a positive association of FGIII with soil C and N. This suggests that the soil-feeding assemblage in Danum in particular, may be influenced to some degree by topographic influences on environmental conditions, despite these being only shallow slopes (Chapter 2). The fact that the same pattern is not observed in Ivindo, may relate to the key regional climatic and local environmental differences. Although rainfall during the sampling periods were roughly the same at both sites, precipitation rates are far greater in SE Asian rain forests (Primack & Corlett, 2005). In Danum the soils were wetter and infiltration rates were lower (Chapter 2), possibly due to a more clay soil-texture (Foth, 1990).

In terms of food availability, the limiting factor for soil-feeding termites may be availability of highly stable peptides in humic substances in soil (Ji *et al.*, 2000), rather than N, as soil-feeding termites have, in fact, massive concentrations of

ammonia within their intestine tracts (Ji & Brune, 2006). As soil C_{tot} positively co-varies with soil N, and negatively co-varies with C/N ratio (Chapter 2), any selection of soil C by soil-feeding termites in Danum, would have also generated the positive relationship with N, and negative relationship with C/N ratio (Table 5.3). It is not possible to identify in this study whether, despite the similarity in C_{tot} variance and spatial structure in both sites (Chapter 2), there are indeed differences in the availability of suitable food material for soil-feeding termites, which could explain the relationship between termites and soil C in Danum, but an absence of this relationship in Ivindo. If however the C fractions in soil are similar between sites, the negative effect of other environmental factors, such as soil moisture in Danum, may restrict otherwise available patches of food material to the soil-feeding termites.

Alternatively the casual direction of the soil C and N association in Danum is in the reverse order, and reflect the feedback mechanisms of termites on soil properties (Holt & Lepage, 2000). One would assume that the broad-scale pattern of soil C, which corresponded with topographic influences (Chapter 2), is relatively stable, but also that heterogeneity is occurring at finer scales which may be in a greater state of flux. The association may result from the fine-scale influence of termites on soil quality, due to the concentration of organic matter in termite-worked soil material (e.g. Fall *et al.*, 2001; Donovan *et al.*, 2001b). Heterogeneity of soil C_{tot} resulting from the influence of earthworm communities, a comparably important decomposer group, has previously been reported (Decaëns & Rossi, 2001). If this were the case with termites, given the abundance of soil-feeding termites in Ivindo it is interesting that no association was detected there.

The maintenance of moisture regimes has been shown to be important for colony function (Green *et al.*, 2005), however in this study the Danum termite assemblage was negatively associated with soil moisture. The effect of rainfall and seasonal flooding on termite assemblage composition and abundance is inconsistent between studies from Africa and Asia (Dibog *et al.*, 1998; Sajap, 1999, Inoue *et al.*, 2001), which may reflect regional differences in precipitation rates and soil moisture regimes. Three spatial relationships unique to Danum suggests that the high regional precipitation rates, confounded by high water retention due to soil texture (Foth, 1990), necessitates certain adaptations at the assemblage level: 1) termite disassociation with soil moisture, 2) FGII disassociation with soil porosity and 3) FGII disassociation with soil C and N. These FGII relationships could relate to mound construction by genera that either select or generate a clay-rich upper-soil layer. *Globitermes globosus* constructs discrete subterranean nests and was the most abundant FGII species in Danum. The mound material of fungus-growing termites has been shown to contain little organic matter (Contour-Ansel *et al.*, 2000), with a high clay content that regulates moisture levels (Jouquet *et al.*, 2003). Most soil feeding termites do not, however, construct mounds, and soil that tends to be water-logged may inhibit colony establishment, in particular by species less tolerant to flooding.

5.5.1.3 Relationships unique to Ivindo

During digestion, soil material undergoes a dramatic increase in pH in the termite gut (Bignell & Eggleton, 1995; Donovan *et al.*, 2001b). At the assemblage level FGIV *Anoplotermes*-group species within the Apicotermittinae family were

associated with more alkaline humified soil, from a Neotropical forest assemblage (Davies *et al.*, 2003b). In Ivindo, genera from the *Anoplotermes*-group were the most abundant component of the FGIII assemblage (Chapter 3), and may then be at sufficient densities to influence the soil pH. A significant increase in the pH of termite-worked soil was at a very range narrow (Donovan *et al.*, 2001b), and if termites are indeed elevating soil pH in Ivindo, the narrow variance recorded there (4.1 ± 0.3), suggests this would also generate a very narrow change in pH. The lower occupancy levels of FGIV termites, compared with FGIII termites, may reduce their influence on soil pH heterogeneity at this scale.

5.5.1.4 Opposing relationships

The higher density of trees in Danum compared with Ivindo (Chapter 2), may result from the known higher regional plant species richness in SE Asian forests (Latham & Ricklefs, 1993). This difference may explain the opposing relationships detected between stems and the termite assemblages, as patches of stems in Danum would represent a higher magnitude of stem density compared with in Ivindo. The disassociation of the Danum assemblage with denser under-storey vegetation may reflect an avoidance of the associated root matt (Donovan *et al.* 2007). The lower tree densities in Ivindo may not generate such an exclusion zone in the soil profile for termites if the associated root densities are correspondingly lower. Rather the positive association in Ivindo, may be due to fine-scale elevated carbon associated with root biomass (Fisher *et al.*, 1994). Spatial heterogeneity in under-storey vegetation may also be an important contribution in generating micro-habitat

heterogeneity, which at broader scales has been related with increased termite species richness (Gillison *et al* , 2003)

In summary, termites that feed further up the humification gradient (i.e. FGII) were found to be consistently associated with small dead wood, as one measure of their food material. In Danum the soil-feeding assemblage may be responding to heterogeneity in soil C, however the opposite causal relationship cannot be excluded. Due to the ecosystem engineering properties of termites, it is difficult to confirm the causal direction of spatial associations between soil properties and the termite assemblage. Relationships specific to Danum appear to represent adaptations to high precipitation rates in this region, and those specific to Ivindo are more likely to be due to the abundance of soil-feeding termites. In none of these associations, however, are the spatial structures of the termites and environmental variables at corresponding scales. For instance, the FGII termites are structured in a series of small patches (Figure 5.1), while heterogeneity in stick density is at broad scales (Figure 2.8c & f). Similarly soil-feeding termites are homogeneously distributed, while soil C varies as a gradient across the plot in Danum (Figure 2.8b). Biotic interactions, either directly or mediated through environmental conditions, must then also play a significant role in structuring the functional components of the termite assemblages.

5.5.2 Inter-feeding-group relationships

Spatial disassociation was consistently detected between feeding-groups, suggesting that there is no facilitation at the inter-feeding-group level. Two possible hypotheses might explain the observed patterns: 1) spatial heterogeneity of

environmental conditions facilitates spatial separation and 2) competitive exclusion is occurring at the inter-feeding-group level due to some shared resource.

Habitat or environmental heterogeneity can generate spatial segregation in the absence of competition, as has been observed in earthworm communities (Valckx *et al.*, 2009). Where the environmental requirements between feeding-groups differ, as seen in Danum with soil porosity and soil C and N (Figure 5.2), one might expect to find reciprocated disassociation patterns, i.e. FGII absent from FGIII patches and vice versa. Here, however, the disassociation was driven only by an absence of soil-feeding termites from the wood-feeding termite patches, in both Danum and Ivindo. Resource availability for the wood-feeding groups is more restricted (Brauman *et al.*, 2000), therefore placing a high competitive value on its availability. Subsequently they may exclude soil-feeding termites that are themselves less restricted by resource availability, by altering the environmental conditions or occupying the available space. In a previous study on spatial relationships from an assemblage in Danum, an aggregation was detected between the wood- and soil-feeding groups (Donovan *et al.*, 2007). Therefore although here the patterns appear robust between sites, repeated surveys may be necessary to determine their consistency.

In Ivindo the soil-feeding-groups were 'equally' disassociated, with FGIII being absent from FGIV patches and vice versa. The only opposing environmental association was with logs, for which there is no obvious interpretation in the absence of other co-varying associations (Figure 5.2). The question then remains whether the disassociation is due to: 1) some unmeasured variable associated with

the presence or absence of logs that preferentially favours FGIII termites over FGIV termites, or 2) a spatial disassociation caused by 'symmetric' competitive interactions for space at a broad humification level.

Typically, reduced inter-specific competition that results from niche partitioning is considered to be an important ecological process determining co-existence and community composition (Schoener, 1974). Here, however, aggregations of feeding-groups (rather than species) differentiated by a major niche axis, diet, were found to be spatially separated. A shared and potentially limiting resource may be space for the colony. In soil root systems, competition for space inhibits growth even if other factors are not limiting (Schenk *et al* , 1999). The majority of termite abundance appears to be in the top 20cm of the soil profile (Inoue *et al.*, 2001), and therefore if vertical stratification in the soil is restricted, space in the upper soil profile may also be a limiting resource. There is some recent evidence that sympatric soil-feeding termite species may be feeding on soil material at different stages along the humification gradient, which provides a mechanism of co-existence (Bourguignon *et al.*, 2009). If these findings hold true across the major soil-feeding clades, the food-mediated facilitation may actually be operating at fine humification levels generating aggregations, for instance within FGIV termites in Ivindo. Such aggregations may then generate sufficient occupancy of the soil profile, such that competition for space is inevitable but at a broader humification and spatial scale.

5.5.3 Predator-prey relationships

The predator-prey interaction between ants and termites is likely to be highly complex, influenced by the population dynamics of generalist and specialist ant species, and the energetic value, availability and dynamics of termite species. Insect predator-prey systems of crop pests have been the subject of some spatially explicit analyses. Spatial associations in these systems have been found to be varied, and in some cases absent (e.g. Pearce & Zalucki, 2006; Birkhofer *et al.*, 2007). Between generalist carabid species and aphid populations, predatory activity continued when their distributions were both associated and disassociated (Winder *et al.*, 2005). The spatial relationships detected in Danum and Ivindo suggest an interaction at the assemblage level exists. Assuming these are not due to some habitat variable or competitive exclusion determining the spatial relationship, some conclusions can be made that warrant further investigation.

In Danum, termites are absent from the small isolated patches of predatory ants (Figure 5.4b) suggesting that termites are being predated at the fine-scale contact points between the ants and termites. It seems ant patches are not specifically targeted to termite patches, as in Ivindo (Figure 5.4c). They may then be predated termites as they are encountered in the soil profile, reflecting an opportunistic predation strategy, possibly necessary due to the relatively low densities of termites here (Chapter 3), and generally in SE Asian forest soil systems (Eggleton *et al.*, 1999). In Ivindo the spatial clustering of significant local associations (Figure 5.4c) with a graduated overlap of termite and ant patches and gaps, could indicate a specialist predation on termites at medium scales, where predatory ants are

specifically targeting termite patches within the plot. Interpreting these local association patterns can be made either as a temporally static or dynamic shifting system.

In a static mode, overall termite and ant distributions are stable in space. Co-habitation of termites and ants is occurring with a zone of spatial overlap representing the interface of predation that may not deplete the termite community. Alternatively the pattern seen here could represent a snap-shot in time. Termite distributions may then be constantly shifting by colonizing space not occupied by ants, followed by concentrated ant predation that locally reduces the termite population. For this pattern to be detected, predator induced population movements could only be occurring at time scales greater than the four month sampling period. The ant-termite interaction appears to be strongest with FGIII termites, which are densely (Chapter 3) and evenly distributed in space (Figure 5.1), and therefore an abundant potential food source.

In this study it is difficult to attain a detailed understanding of the predator-prey dynamics due to the complexity of interactions, and largely unknown termite and ant spatio-temporal population dynamics. We do know that the soil-feeding termite community is able to recover relatively rapidly following disturbance, once a closed canopy is formed and with a source population in close proximity for re-colonization (Gathorne-Hardy *et al.*, 2002). As an extension of this, soil-feeding termites could also be well adapted to rapid re-colonization at the local scale following predation.

A remarkable diversity of morphological and chemical adaptations for defence is seen in soldier termites (Prestwich, 1984). Adaptation to predation pressure

appears to have been continuous throughout their evolutionary history (Scholtz *et al.*, 2008), where the suspected major predator is ants. Collectively termites and ants constitute the majority of animal biomass in rain forest systems (Hölldobler & Wilson, 1990; Eggleton *et al.*, 1996), particularly in the soil (Watt *et al.*, 1997). The spatial patterns described here provide some evidence for ant predation on termite assemblages, which may be one of the most significant trophic interactions within tropical rain forest faunal communities, in terms of mediated energy flows.

5.5.4 Synthesis of spatial structure and ecological interactions

The limited niche availability of termites that feed further up the humification gradient (i.e. wood-feeders) may restrict their spatial distribution to the patchy availability of their food material. These taxa typically construct hypogeal nests or epigeal mounds rather than having the diffuse nests more commonly seen in soil-feeding termites. Termites are considered 'extended phenotype engineers' (Jouquet *et al.*, 2006), due to the construction of mounds that provides a regulated and protected environment for the colony (e.g. Jouquet *et al.*, 2002). Indeed wood-feeding termites are generally more resilient to habitat disturbance (Eggleton *et al.*, 1997; Eggleton *et al.*, 2002a). The higher colony investment required for mound construction may result in longer lived colonies where workers forage over broad distances to sustain the colony's energetic requirements (e.g. Ngee & Lee, 2002; Lee *et al.*, 2003). Discrete mounds can have a high localized impact on soil properties (e.g. Jouquet *et al.*, 2005), and their presence could also inhibit colonization or occupancy by termites further down the humification gradient at fine scales.

Further down the humification gradient the humus-feeding termites (FGIII) in both sites are homogenously distributed. This is despite 1) heterogeneity of soil quality at broad scales, 2) possible competitive exclusion (at fine scales with FGII in Danum, and at fine and medium scales with FGII and FGIV respectively in Ivindo), and 3) possible predation pressure (at fine scales in Danum, and medium scales in Ivindo). A larger survey extent that incorporates greater habitat variation may be necessary to ascertain the environmental cues that promote heterogeneity of humus-feeding termites. One hypothesis, given the existing evidence, is that their potentially rapid colonization ability would allow them to occupy micro-site patches made available through localized extinction that may follow predation or the depletion of food resources. The smaller species pool and notably the absence of the *Anoplotermes*-group in SE Asia, but a particularly species-rich clade in the Neotropics and Afrotropics, may limit the level of occupancy attainable by the humus-feeding group of termites.

Following the consistent relationship between resource availability and assemblage structure seen from wood-feeders to humus-feeders in both sites, it is interesting that those termites that feed furthest down the humification (i.e. FGIV) are heterogeneously structured. The interactions that appear to be influencing the broad-scale structure of the FGIV assemblage were a disassociation with the FGIII assemblage, and an association with dead wood. The energetic constraints on FGIV termites may impose a greater spatial affinity to important food properties that were not measured in this study, such as stable humic substances (Ji *et al.*, 2000). This may combine with reduced colonization abilities, possibly due to energetic constraints. Also worth noting is the lower occupancy level (54% of pits)

of the FGIV group, despite species richness of FGIV termites typically being greater than FGIII termites in Africa (Davies *et al.*, 2003a). This suggests that FGIV species are able to co-occur at very fine scales (i.e. within pits). If indeed resource partitioning along the humification level of soil is occurring within FGIV termites, current evidence for which is the described diverse enteric-valve architecture (Sands, 1998; Donovan, 2002), firstly co-existence will be promoted due to a reduction in inter-specific competition, and secondly a facilitative interaction may be occurring at a fine humification scale, promoting aggregation.

5.5.5 Biotic interactions in termite assemblages

As most assemblage-level studies of termites have concentrated on habitat disturbance gradients (e.g. Eggleton *et al.*, 1996; Eggleton *et al.*, 2002a; Jones *et al.*, 2003), this study provides the first insight into a range of environmental and biotic interactions operating within termite communities at a fine scale. Regional differences in species richness and abundance are due to biogeographical factors (Davies *et al.*, 2003a), while the high species richness observed in rain forest termite communities has been attributed to micro-habitat complexity (Deblauwe *et al.*, 2008). This study presents preliminary evidence, based on spatial relationships, on the potential role of biotic interactions in: 1) determining how the functional components of termite assemblages are spatially structured, and 2) maintaining local species richness.

The hypothesized processes that generate dispersion and aggregation e.g. competition and facilitation respectively, operate at various spatial and functional (feeding-group) scales. The nature of these are influenced by resource availability

along the humification gradient (Brauman *et al.*, 2000) Competitive exclusion between the wood-feeding and humus-feeding termites is potentially manifested through alterations to soil structure by wood-feeding termites, in both Danum and Ivindo. Conversely the soil provides a continuous nesting and food resource, yet 'symmetric' competitive exclusion between feeding-groups may be occurring due to processes that generate broad-scale aggregations, e.g. intra-feeding-group facilitation (FGIV) The scale and nature of inter-generic co-occurrence patterns are examined in Chapter 6, with the aim of understanding the ecological interactions influencing spatial patterns in termite assemblage composition.

The nature of the hypothesized ant predation strategies in Danum (generalist) and Ivindo (specialist), may result from the abundance of termites in African forest soil systems (Eggleton *et al.*, 1999). This is assuming, however, that in order to maintain these abundances despite a potentially intense predation pressure, colony establishment is rapid following predation Interestingly, density-dependent mortality, such as through predation, can promote species co-existence by influencing relative abundances and spatial distributions (He & Legendre, 2002), and therefore may be a factor in maintaining high species richness and ecosystem stability in African forests

6 Fine-scale assembly rules in rain forest termites; genus-level co-occurrence patterns are dependent on spatial scale and biogeographic history

6.1 Summary

The high diversity seen in soil communities is attributed to reduced competitive interactions resulting from micro-habitat heterogeneity. Here the Danum and Ivindo termite assemblages are examined with the aim of generating hypotheses on the local ecological processes that determine spatial organisation of genus-level composition. This is considered across a resource availability gradient between feeding-groups, and across the diversity anomaly between regions. By pooling data collected from the survey plots at a series of nested scales (cell size), null models were used to assess the scale at which co-occurrences patterns are evident. Soil-feeding genera are consistently dispersed at the finest scale (2m x 2m cell size). As cell size increases, co-occurrence tends towards being aggregated, and as this was very close to significant it was interpreted as genus aggregation (12m x 12m cell size for the full assemblage in Danum, and 8m x 8m cell size for true soil-feeding termites in Ivindo). Wood-feeding termite assemblage co-occurrence patterns were less consistent between sites; inter-generic aggregation was, however, detected in both at various cell sizes. The measured environmental variables were consistently found to have very weak relationships with assemblage composition at all cell sizes, and therefore could not explain spatial patterns in the assemblages detected at mid- to broad-scales in both sites. The hypothesized assembly rules are: competitive interactions may be occurring at the colony level for nesting space while at broad scales facilitative interactions occurs, whereby soil

food-material is transferred through the assemblage. The functional scale of the facilitation, and other hypothesized positive interactions such as co-operative defence against ant predation, are dependent on regional taxonomic pools (i.e., biogeographic influences). Scale-dependent shifts from competition to facilitation may be important in determining the spatial patterns of termite assemblages at fine scales.

6.2 Introduction

Intra-specific aggregation on patchy resources allows the spatial dispersion of ecologically similar species, and is therefore important for coexistence (Atkinson & Shorrocks, 1981) It is these two factors that are at the centre of explaining the particularly high biodiversity found in the soil systems. soil organisms generally have limited dispersal abilities and are therefore aggregated, and microhabitat heterogeneity in the soil environment is particularly high (Anderson, 1975, Ettema & Wardle, 2002). The resulting spatio-temporal resource partitioning reduces competitive interactions and ultimately exclusion, thereby promoting coexistence and high species diversity in these systems (Wardle, 2002, Decaens, 2010) Exceptions to this generality of low competitive interactions in soil communities can be found mostly in the macrofaunal groups, and include ants, earthworms, beetles and molluscs (summarised in Decaens, 2010). Lower species co-occurrences than expected by randomly assorting assemblages has provided evidence for competitive exclusion in earthworm and ant communities (Sanders *et al.*, 2007, Decaens *et al.*, 2008)

Termites are both extremely abundant and functionally important in rain forest soil systems (e.g. Eggleton *et al.*, 1996; Donovan *et al.*, 2001b; Yamada *et al.*, 2005), and can be considered approximate ecological analogies to earthworms. Termite diversity is highest in equatorial rain forests (Eggleton, 2000a), where as many as 61 species have been recorded from a single transect of 100m x 2m (Deblauwe *et al.*, 2008). The extreme differences of the species and functional diversity patterns across the tropics has been attributed to biogeographic history (Davies *et al.*, 2003a), while within regions, assemblage diversity and composition is influenced by habitat factors associated with, for instance, disturbance and altitudinal gradients (e.g. Eggleton *et al.*, 1997; Jones, 2000). Both of these scale-dependent processes contribute to constraining localised species pools; what we lack is an understanding of the ecological processes that determine how local assemblage diversity patterns are spatially structured.

Competitive interactions are known at the colonial level in rain forest termites. In arboreal nesting species, colonies were spatially dispersed and exhibited inter-colonial aggression (Levings & Adams, 1984). For the mound-building species *Cubitermes* spp. and *Thoracotermes macrothorax* in Gabon colonies were also spatially dispersed (Chapter 4). Mound-building and arboreal nesting species are, however, a minor component of rain forest termite assemblages, which typically are dominated by soil-feeding hypogeal-nesting species (e.g. Eggleton *et al.*, 1996; Eggleton *et al.*, 2002b). At the functional level, defined by the state of decay of consumed dead plant material (Donovan *et al.*, 2001a), feeding-group aggregations were spatially dispersed (Chapter 5), possibly due to competitive exclusion. The nature of this spatial dispersion, detected from one hectare plots,

was dependent on the position of the feeding-group along the 'humification gradient' (stage of decomposition of consumed material (Bignell & Eggleton, 1995, Tayasu *et al.*, 1997)) Soil-feeding termites were excluded from aggregations of wood-feeding termites, while the opposite exclusion was not observed. However multi-genera aggregations of the two soil-feeding-groups (humus-feeding, and true soil-feeding termites), were equally dispersed at broader scales within the plot. This suggests that competitive interactions between genera within feeding-groups (and therefore ecologically similar), would have to be sufficiently weak to support intra-feeding-group aggregations (seen in wood-feeding and true soil-feeding termites), and/or that inter-feeding-group spatial dispersions is due to active selection of particular environmental conditions.

This raises certain questions: 1) at what spatial- and functional- (defined as the feeding-group) scale do competitive interactions occur, and 2) are the feeding-group aggregations due to habitat heterogeneity, or biotic processes such as facilitation? With answers to these questions, one can begin to construct spatially-explicit assembly rules of termite assemblage composition at the plot scale. One can also raise the question of whether similar assembly rules apply to assemblages that differ in their biogeographic history, and exhibit vastly different contemporary patterns of abundance and diversity (Davies *et al.*, 2003a)

6.2.1 Resource availability gradient

It is strictly subterranean soil-feeding termites that do not construct discrete mounds that dominate rain forest assemblages (e.g. Eggleton *et al.*, 1999; Davies *et al.*, 2003a). Soil is an hyper-abundant and continuous food resource (Brauman

et al., 2000), albeit of poor energetic quality. It may then be a non-limiting resource where competitive interactions will be weak, therefore supporting the high diversity seen in soil-feeding termites. For termites that feed further up the humification gradient on food material such as wood and leaf-litter, food is a patchier resource, yet of higher energetic value. One might then expect competitive interactions to be more intense for this resource. The high competitive value of this food material for wood-feeders compared with soil for soil-feeders may explain the asymmetric dispersion seen at the feeding-group level (Chapter 5), where wood-feeding termites exclude other termites, possibly by securing nesting space near an available patch of food.

6.2.2 Biogeographic history

At global scales the differences in diversity and abundance across the equatorial rain forest blocks are due to evolutionary history in stable closed-canopy forest (Davies *et al.*, 2003a). African rain forests support an extremely high diversity, dominated by termites from the *Apicotermes*- and *Anoplotermes*-group (Apicotermitinae) and *Cubitermes*-group (Termitidae) that consume humified soil. Conversely SE Asian rain forest termite assemblages are relatively low in diversity and abundance. The major differences are in the soil-feeding rather than non-soil-feeding-groups, with the true soil-feeding termites being extremely rare in SE Asia (Eggleton *et al.*, 1999). Such differences in species packing in the soil profile may also potentially determine the importance of competition or facilitation, for instance the high abundance in Africa systems may generate stronger facilitative

interactions, but necessitates weaker competitive interactions to support co-existence.

6.2:3 Co-occurrence patterns

An ongoing endeavour in community ecology is to ascertain whether communities are structured by deterministic processes and therefore governed by assembly rules (Diamond, 1975, Drake, 1990; Ulrich, 2004). In response to this, null models of co-occurrence have been developed that test whether species co-occurrence levels are more or less than expected by a randomly assorting assemblage (Connor & Simberloff, 1979, Gotelli, 2000, Gotelli & Entsminger, 2001) The traditional interpretation of low co-occurrence is that ecologically similar species undergo competitive exclusion for a limiting resource (Diamond, 1975). Non-random co-occurrences in the absence of competitive exclusion can, however, occur when certain species are favoured along different parts of a habitat gradient (Peres-Neto *et al* , 2001, Gotelli & McCabe, 2002, Ellwood *et al.*, 2009, Ulrich *et al* , 2010) It has also been shown that non-random co-occurrence can arise through neutral dynamics (Ulrich, 2004), and predation pressure (Englund *et al.*, 2009). In addition co-occurrence patterns vary with the spatial scale of the study, due to spatial dependency of these various ecological processes (e.g. Gotelli & Ellison, 2002; Sanders *et al* , 2007). The numerous possible causes of the existence of non-random patterns means that additional information is necessary to fully interpret co-occurrence patterns, such as whether community composition can be explained by environmental heterogeneity (e.g. Ellwood *et al.*, 2009).

Spatial structure in communities can result from: 1) a response to environmental variables that are themselves spatially structured, and 2) biotic processes such as limited dispersal more typical at fine scales (Ettema & Wardle, 2002). If a spatially-structured habitat is acting as a filter on species distributions, species may be aggregated if certain groups of species with particular habitat preferences are selected according to the associated environmental conditions (Gotelli & Ellison, 2002). Partitioning community variance into that explained by (1) environmental and (2) spatial components allows one to consider the relative contribution of abiotic and biotic processes (Legendre *et al.*, 2009) and, by extension, to interpret co-occurrence patterns. Variance partitioning analysis uses constrained ordination analyses such as redundancy analysis (RDA) to separate the amount of community variance explained by pure environment ("PE"), spatially-structured environment components ("SSE"), and pure space ("PS") (Borcard *et al.*, 1992; Borcard *et al.*, 2004). The pure space can then be taken to represent spatially structured biotic processes, and the spatial scale of this examined. Variance partitioning analysis is performed using environmental data ("environment"), and vectors that describe spatial patterns in the orientation of the sampling points ("space").

In this study the fine-scale ecological patterns in soil-dwelling rain forest termites are examined. The aim is to generate hypotheses concerning ecological processes, that structure genus-level diversity across 1) a resource-availability gradient (wood and soil), and 2) a diversity anomaly (SE Asia and Africa), and to consider the scale at which the patterns are structured. First I ask whether there are any evidence for genus-level dispersion or aggregation, using co-occurrence

patterns generated by null model analyses on assemblages across the two 'gradients'. As scale has been shown to be important in detecting co-occurrence patterns (e.g. Zhang *et al.*, 2009), null model analyses are performed on sample data collected from a single 96m x 96m plot (Chapter 3), that was pooled at a series of nested cell sizes. Secondly variance partitioning analyses (VPA) were applied at each nested cell size, to consider whether significant co-occurrence could be attributed to environmental heterogeneity within the plot. For instance, if assemblages are aggregated due to the filtering effect of habitat structure within the plot, one would expect to detect a substantial spatially-structured environmental (SSE) component relating with assemblage composition. Thirdly to consider the scale at which the assemblages are spatially structured, a forward selection procedure was used during ordination analyses, from which the reduced set of significant spatial vectors could be examined in more detail. It will then be considered whether this spatial structure may be due to relationships with the measured environmental variables, or biotic processes such as limited dispersal or facilitative interactions causing aggregation.

6.3 Methods

Biotic and abiotic data were collected from a single plot. The sampling protocols for termites and environmental variables in Danum (SE Asia) and Ivindo (Africa) are described in detail in Chapters 2 and 3. Termite genus data and environmental data from the 2m x 2m sample points, were pooled to generate data matrices of the following cell sizes: 2m x 2m (n=2304 composed of a single pit), 4m x 4m (n=576 composed of 4 pooled pits), 8m x 8m (n=144 composed of 16 pooled pits),

and 12m x 12m (n=64 composed of 36 pooled pits). In addition to the full termite assemblage data matrices, feeding-group matrices were generated containing genera from the separate feeding-groups as identified by Donovan *et al* (2001a): (i) wood-feeding that included both FGI and FGII, (ii) humus feeding (FGIII), and (iii) true soil feeding (FGIV), which was only recorded from Ivindo.

6.3.1 Null model analysis

Patterns of genus-level co-occurrence for each termite matrix (full community, FGII, FGIII and FGIV at four cell sizes) were analyzed and compared using the checker-board C-score index in EcoSim (Gotelli & Entsminger, 2004). The checkerboard C-score (Stone and Roberts, 1990) is based on average co-occurrence (Gotelli, 2000) and measures the average number of "checker-board units", in this study between all genus pairs. In a community (pooled pits) with low co-occurrence, the C-score will be significantly greater than expected by chance.

At all cell sizes presence-absence matrices were used with fixed row, equiprobable column null models (SIM2), which has a low Type I error in both indices. It retains row (i.e. genera) abundances in the null model, while each column (i.e. sample points of pooled pits) is equally likely to be represented in the null model. This configuration is recommended for "sample data" at small spatial scales (Gotelli, 2000). The large sample size at some cell sizes can be prone to Type I error, and therefore a large number of random matrices were simulated (49,999) and tested against the observed matrix, to reduce this error potential (Fayle & Manica, 2010). The standardised effect size (SES) allows the comparison of

results from different analyses or studies, and was therefore used here to present the results at the four spatial scales

SES= (Observed index – Simulated index)/(Standard deviation of simulated indices)

The two-tailed 95% confidence interval for the SES is approximately -1.96 to 1.96, thus when genera are dispersed (low generic co-occurrence) the C-score SES value >1.96, while when genera are aggregated (high generic co-occurrence), C-score SES values will be <1.96.

6.3.2 Partitioning community variance into spatial and environmental components

6.3.2.1 Genus response matrices

As with the co-occurrence analyses, pooled-pit genus sample matrices were generated at each of the four cell sizes. At the 2m x 2m cell size, the matrix presents genus presence/absence rather than abundance data, as conspecifics within pits are highly likely to be colony siblings and therefore non-independent. As it is not possible to identify individual colonies, it was assumed that individuals within a genus from adjacent pits are less likely to be colony siblings, and therefore treated as independent. Therefore at all other cell sizes (4m x 4m, 8m x 8m and 12m x 12m) genera abundance matrices reflect the number of pits containing each genus within each pooled-sample point. A Hellinger transformation was applied to the matrices (Legendre & Gallagher, 2001), where abundances are square-root transformed proportionate abundances. This transformation down-weights very

abundant taxa, and reduces attraction of samples that have numerous rare response columns (Zuur *et al.*, 2007).

6.3.2.2 Spatial explanatory vectors

Principal coordinates of neighbour matrix (PCNM) variables are continuous spatial vectors (see Figure 6.1) that describe complex spatial patterns at all spatial scales encompassed in a survey area (Borcard & Legendre, 2002; Borcard *et al.*, 2004; Dray *et al.*, 2006). The PCNM spatial model method was selected over cubic-trend surface analysis, which is limited to describing broad spatial patterns, while PCNM models are better able to capture community variance (Borcard & Legendre, 2002; Jones *et al.*, 2008). For a full description of the PCNM method see Borcard and Legendre (2002), Borcard *et al.* (2004) and Dray *et al.* (2006). In brief, the PCNM variables are generated by first computing a matrix of the Euclidean distances between the x and y coordinates of the sample points. The distance matrix is truncated at a given distance; for regular sampling designs, the recommended truncation distance is the distance of first neighbours (Borcard *et al.*, 2004). A principal coordinates analysis (PCoA) of the truncated distance matrix is then calculated. The principal coordinates generated consist of orthogonal waves, whose wavelengths range across all scales encompassed in the survey area. Only those coordinates associated with positive eigenvalues are retained, as these vectors describe positive spatial autocorrelation in the survey area (Dray *et al.*, 2006).

The truncation distance in each cell size PCNM analysis was equal to the respective grid size: 2m, 4m, 8m and 12m (i.e. distance to first neighbours). The

number of PCNM vectors generated for each cell size PCNM matrix (2m, 4m, 8m, and 12m) were 1617, 403, 102 and 44 respectively, where at the progressively broader cell sizes, fine-scale spatial information can no longer be described (see Figure 6.1). Within each PCNM matrix, the eigenvectors with high associated eigenvalues represent broad-scale spatial patterns. The PCNM vectors are used as the "space" explanatory variables in subsequent ordination analyses.

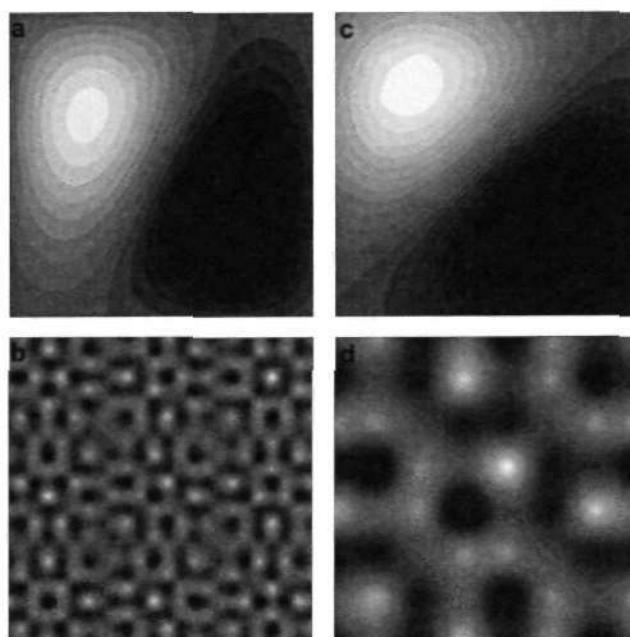


Figure 6.1 Contour plots of the broadest and finest spatial vectors from PCNM analysis at two scales (cell sizes). 4m x 4m cell size a) PCNM vector 1 b) PCNM vector 403. 12m x 12m cell size c) PCNM vector 1 and d) PCNM vector 44.

6.3.2.3 Environmental explanatory matrices

Treatment of the environmental data in the pooling of sample points for each cell size is summarised in Table 6.1. Where necessary the un-pooled and pooled

environmental variables were transformed in order to normalise their frequency distribution.

Table 6.1 Environmental data treatment during pooling of sample points. x, value recorded at sample point as described in Chapter 2; P/A, presence/absence data; Dan, Danum; lvi, lviindo.

Variable	2m x 2m	4m x 4m	8m x 8m	12m x 12m
Soil Carbon %	Removed due to high correlation with soil N.			
Soil Nitrogen %	$\log_{10}(x+1)$	$\log_{10}(\text{mean}(x)+1)$	$\log_{10}(\text{mean}(x)+1)$	$\text{mean}(x)$
Logs	P/A	$\text{sum}(x)$	Dan: $\text{sum}(x)$ lvi: $\log_{10}(\text{sum}(x))$	$\text{sum}(x)$
Sticks	x	$\log_{10}(\text{sum}(x)+1)$	$\log_{10}(\text{sum}(x)+1)$	$\log_{10}(\text{sum}(x))$
Leaf-litter depth	x	$\text{mean}(x)$	$\text{mean}(x)$	$\text{mean}(x)$
Soil pH	x	$\text{mean}(x)$	$\text{mean}(x)$	$\text{mean}(x)$
Soil Moisture	x	$\text{mean}(x)$	$\text{mean}(x)$	$\text{mean}(x)$
Trees	P/A	$\text{sum}(x)$	$\text{sum}(x)$	Dan: $\log_{10}(\text{sum}(x))$ lvi: $\text{sum}(x)$
Stems	x	$\log_{10}(\text{sum}(x)+1)$	$\log_{10}(\text{sum}(x)+1)$	$\log_{10}(\text{sum}(x))$
% Ground vegetation cover	x	$\text{mean}(x)$	$\text{mean}(x)$	$\text{mean}(x)$

6.3.2.4 Variance partitioning analysis

By partitioning out the spatial component of the environmental relationships with the response matrices, the proportion of assemblage composition variance explained by the pure environmental (PE), the spatially structured environmental variance (SSE), and the pure space (PS) is quantified during the VPAs (Borcard *et al.*, 1992). The linear Redundancy Analysis (RDA) and partial Redundancy Analysis was selected as an appropriate constrained ordination, due to the assumed short gradients between samples collected at this fine scale. The proportion of variance explained based on the adjusted R^2 value was considered,

which accounts for the number of sample points and explanatory variables in ordinations (Peres-Neto *et al.*, 2006).

The RDAs and partial RDAs were performed on each of the feeding-group matrices and full community matrix, against the respective spatial and environmental explanatory matrices, at each cell size. Only the significant spatial or environmental models in a permutation test (999 permutations) were retained for subsequent variance partitioning analysis.

6.3.3 Scale of spatial structure in community composition

The amount of assemblage variance explained by the PCNM spatial vectors was relatively high ($\text{adj}R^2 \approx 25\%$) at the 8m x 8m cell size in both Danum and Ivindo (see results, Table 6.3). To identify the scales of this spatial structure, a forward selection by permutation of residuals (999 permutations) of the PCNM vectors was performed at this cell size. Retained PCNM vectors were those that contributed an R^2 value of >0.001 at $p < 0.05$. The order of the PCNM vectors relates to the scale of the spatial pattern they describe (see Figure 6.1). Therefore low-value PCNM vectors describe broad structure, and high-value vectors describe fine spatial patterns. The PCNM vectors retained in the forward selection were divided into two groups, "broad-scale" (retained vectors 1 to 10) and "medium-scale" (retained vectors 11 to 102) PCNM matrices. Further RDAs of the medium and broad PCNM matrices on the termite assemblages were performed. The $\text{adj}R^2$ values of the broad and mid-scale analyses were compared to ascertain whether assemblage composition was mostly structured at broad or medium scales within the plots

The software 'R', and packages spacemakerR (Dray *et al.*, 2006), vegan, packfor and decostand were used to perform PCNM analysis, variance partitioning analysis, forward selection and matrix transformations respectively.

6.4 Results

6.4.1 Generic richness

Twenty-nine termite genera were sampled from 44% of the soil pits in Danum, in stark contrast with 43 genera from 91% of pits in Ivindo (full details in Chapter 3). Apart from at large cell sizes for FGII, genus frequency per sample, by feeding-group and for the full community, is always greater in Ivindo than in Danum (Table 6.2). This is exemplified in the full assemblage frequency at the 2m x 2m cell size, where the average number of genera is greater by a magnitude of four in Ivindo. Despite the similar genus richness of FGII and FGIII in Danum (13 and 16 respectively) and Ivindo (both 8), the average genus frequency per sample was higher for FGIII than FGII at all cell sizes (Table 6.2), which reflects the high occupancy of FGIII termites (Chapter 3). For FGIII in Ivindo, the high genus richness and low deviation at the 12m x 12 m cell size, combined with the high pit occupancy rate (70% of pits, Chapter 3), demonstrates that the FGIII genera are consistently distributed throughout the plot.

Table 6.2 Mean number and standard deviation of genera at each cell size sample. FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding; Comm, full assemblage.

	# genera	2m x 2m	4m x 4m	8m x 8m	12m x 12m	
FGII	Danum	13	0.16±0.38	0.48±0.61	2.11±1.27	3.47±1.71
	Ivindo	8	0.21±0.42	0.69±0.66	1.49±0.81	2.11±0.89
FGIII	Danum	16	0.28±0.49	0.98±0.90	2.97±1.37	5.06±1.79
	Ivindo	8	0.98±0.81	2.69±1.04	4.76±0.92	5.58±0.79
FGIV	Danum	0	-	-	-	-
	Ivindo	29	0.70±0.78	2.47±1.42	6.94±2.17	10.64±2.16
Comm	Danum	29	0.44±0.61	1.46±1.11	4.13±1.67	6.75±2.07
	Ivindo	43	1.88±1.16	5.86±1.91	13.19±2.46	18.33±2.50

6.4.2 Co-occurrence patterns

At the fine cell size the soil-feeding-groups (FGIII and FGIV) have consistently lower genus-level co-occurrence than expected, indicating genus-level exclusion in both sites (Figure 6.2a & b). The SES index is highest in the Danum FGIII assemblage (SES=5.040, $p < 0.001$), followed by the Ivindo FGIII assemblage (SES=4.225, $p < 0.001$), and then Ivindo FGIV assemblage (SES=1.980, $p = 0.021$). As cell size increases the soil-feeding co-occurrence patterns tend toward significant (two-tailed significance test) aggregation; in Danum SES=-1.671 ($p = 0.051$) at 12m x 12m for FGIII, and in Ivindo SES=-1.860 ($p = 0.037$) at 8m x 8m for FGIV. At the 12m x 12m cell size, however the full Danum assemblage is significantly aggregated (SES=-2.670, $p = 0.007$).

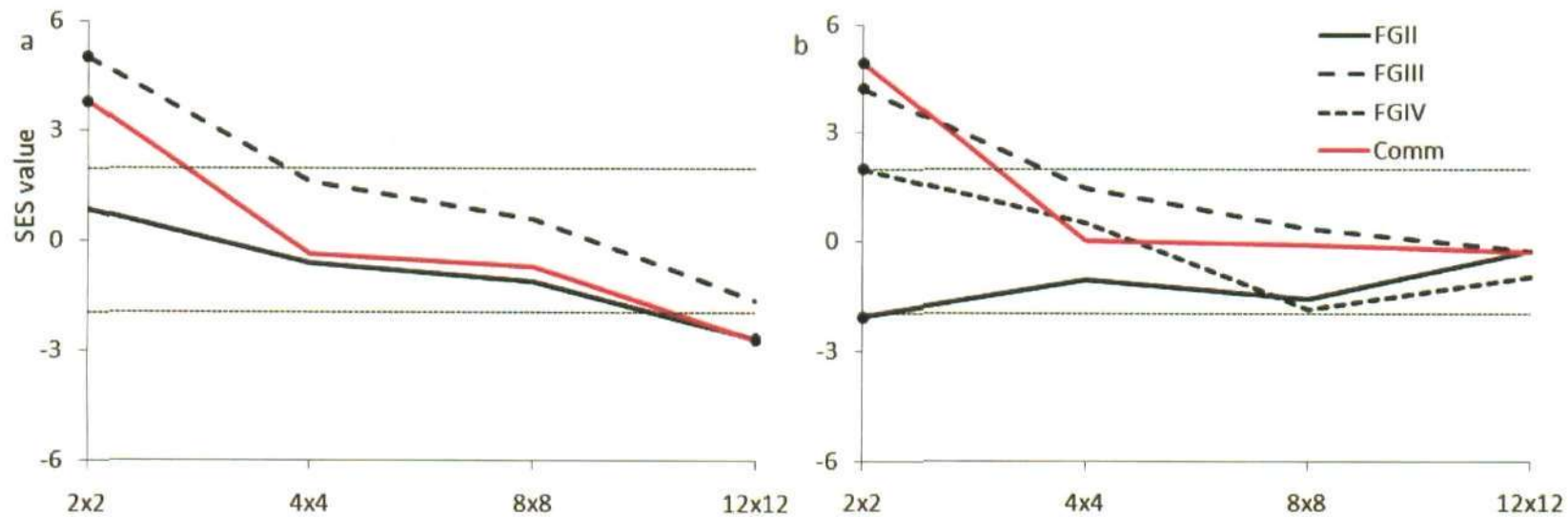


Figure 6.2 C-Score index co-occurrence SES values at four cell sizes. a) Danum, b) Ivindo. FGII, wood-feeding; FGIII, humus-feeding; FGIV; true soil-feeding; Comm, full assemblage. Significant results exceed the upper and lower SES limits ($SES > 1.96$, lower co-occurrence than random i.e. exclusion; $SES < -1.96$, higher co-occurrence than random i.e. aggregation) with the critical limits represented by the parallel black dotted lines, and specific statistically significant results indicated by a black dot.

In contrast co-occurrence patterns for the FGII assemblages were dissimilar at the two sites (Figure 6 2a & b). In Danum FGII genera co-occurrence is random at all cell sizes, except at the 12m x 12m cell size where genera are significantly aggregated. In Ivindo FGII genera are aggregated at the 2m x 2m cell size and otherwise co-occurrence is random. The full assemblage co-occurrence patterns are largely intermediate between the patterns in the separate feeding-groups. Two exceptions are the higher SES value in Ivindo at the 2m x 2m cell size, and lower SES value in Danum at the 12m x 12m cell size, reflecting that respectively, genus-level exclusion and aggregation is also occurring between feeding-groups at these two sites.

6.4.3 Variance partitioning analysis

Irrespective of cell size, assemblage type (individual feeding-groups or full assemblage) or site, the variance explained by pure environment (PE) and spatially structured environment (SSE) is remarkably low (Table 6.3). Combined PE and SSE never exceed an adjR^2 of 5%. In the progressively broader cell size analyses, despite the loss of fine-scale spatial descriptors in the PCNM matrices (see methods), assemblage composition explained by spatial structure (PS+SSE) typically increases. Of the significant analyses, spatial structure in assemblage composition tends to be best captured in the 8m x 8m cell size analyses, e.g. $\text{adjR}^2 = 42\%$ in Danum FGII, and $\text{adjR}^2 = 37\%$ in Ivindo FGIII. This cell size was therefore selected to ascertain the scale at which the full assemblage was spatially structured in subsequent forward selection procedures (see below). Many of the explanatory matrices were found not to be significant in partial RDAs and therefore were not included in the VPA. This is

most apparent with the environmental matrices at the broader cell sizes, and in the Ivindo FGII and Ivindo FGIII assemblages.

Table 6.3 Adjusted R^2 values (as percentage) for the pure environment component (PE), spatially-structured environment component (SSE), and pure space component (PS) in the VPA on the full and feeding-group assemblages at four cell sizes.

FGII		2m x 2m	4m x 4m	8m x 8m	12m x 12m
Danum	PE	1***	-2**	2*	-
	SSE	<0.5	4	3	-
	PS	9***	17***	42***	-
Ivindo	PE	<0.5**	2*	-	-
	SSE	<0.5	-	-	-
	PS	8*	-	-	-
FGIII		2m x 2m	4m x 4m	8m x 8m	12m x 12m
Danum	PE	<0.5***	<0.5***	<0.5**	-
	SSE	<0.5	2	3	-
	PS	12**	11***	20***	30***
Ivindo	PE	-	-	-	-
	SSE	-	-	-	-
	PS	-	17***	37***	-
FGIV		2m x 2m	4m x 4m	8m x 8m	12m x 12m
Ivindo	PE	<0.5*	<0.5*	-	-
	SSE	<0.5	<0.5	-	-
	PS	6***	13***	22***	14*
Community		2m x 2m	4m x 4m	8m x 8m	12m x 12m
Danum	PE	1***	<0.5***	2***	-
	SSE	<0.5	2	2	-
	PS	11***	13***	24***	30***
Ivindo	PE	<0.5*	1**	-	-
	SSE	<0.5	1	-	-
	PS	3*	14***	26***	16**

Significance levels of each testable component (PE and PS) are indicated: $p < 0.001$ ***, $p < 0.01$ ** , $p < 0.05$ *. Non-significant explanatory matrices in partial RDAs are indicated as "-" (see methods), and the $adjR^2$ is derived from a RDA analysis of the remaining significant environment or PCNM matrix.

6.4.4 Scale of assemblage spatial structure

The PCNM vector 10 in the 8m x 8m cell size PCNM analysis describes spatial autocorrelation at approximately the 30m scale (see right contoured plot in Figure 6.3). Thus the "broad-scale" (vector range 1 to 10) PCNM vectors

retained in the forward selection of PCNM space matrix on the full community, describe spatial structure at a scale of >30m. The contoured plot for PCNM vector 47 is also presented as most of the remaining retained PCNM vectors in the forward selection procedure were <47 (Figure 6.3). As this vector is structured at a scale of approximately 10m, the "medium-scale" model describes spatial structure between 10 - 30m. As in both Danum and Ivindo, only one PCNM vector >47 is retained in forward selection, it appears that fine-scale (<10 m) spatial structure is negligible in both regions.

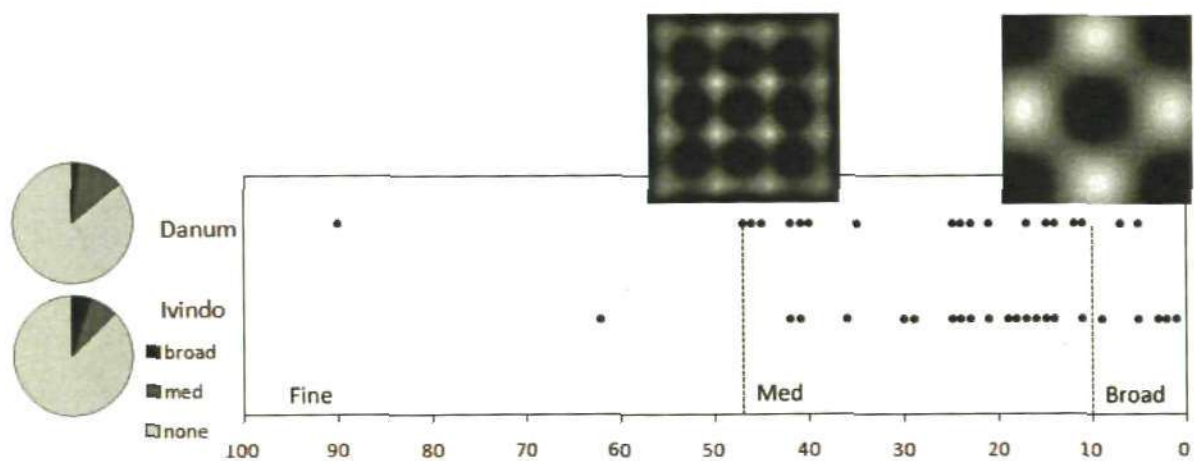


Figure 6.3 Plot of the PCNM vectors retained in a forward selection with the 8m x 8m full assemblage data, with dots representing retained vectors from the original matrix of 102 PCNM vectors. Low values represent broad spatial structure; retained vectors between 1 and 10 represent the broad spatial model, and retained vectors between 11 and 102 represent the medium spatial model. Contoured plots of PCNM vector 10 and 47 plots are positioned above their respective location. The pie charts present the adjR^2 values of the 'broad' scale and 'medium' scale models, as well as unexplained community variance 'none', in the RDA analyses.

The amount of community variance explained by the retained PCNM vectors was similar in both regions; $\text{adjR}^2=15.6\%$ in Danum and $\text{adjR}^2=14.1\%$ in Ivindo. In Danum 19 of the 102 PCNM vectors were retained, with the community

variance mostly explained by the medium-scale model (10 – 30 m scale) rather than broad-scale model (Figure 6.3, upper pie chart). In Ivindo 22 vectors were retained, and assemblage variance was composed of approximately equal amounts of broad- and medium- scale structure (Figure 6.3, lower pie chart).

6.5 Discussion

6.5.1 Resource availability gradient

Although competitor avoidance strategies and spatial niche partitioning is known in wood-feeding termites (Schuurman, 2006; Evans *et al.*, 2009), the co-occurrence patterns here provide no evidence of genus-level competitive exclusion at any scale (Figure 6.2). This lack of generic separation may be due to the sampling of soil pits where competitive interactions for food would not be operating, although one might still expect competition for nesting space in the soil profile at fine scales. As there are several nesting strategies, including arboreal nesting e.g. *Nasutitermes*, wood nesting e.g. *Schedorhinotermes*, epigeal (mounds that extend above the soil profile) e.g. *Macrotermes*, and hypogeal (nests exclusively in the soil profile) e.g. *Globitermes*, resource partitioning for nest site may reduce competitive interactions.

In contrast to evidence for competitive exclusion, the genus-level co-occurrence was greater than random at the fine cell size in Ivindo, and broad cell size in Danum (Figure 6.2). Spatial aggregation such as this is typically associated with habitat filters. Taxa with similar ecological requirements co-occur according to the provision of these ecological conditions (Gotelli & Ellison, 2002; Sanders *et al.*, 2007; Ulrich *et al.*, 2010). Here the scale being considered combined with a negligible environmental influence on FGII composition (Table 6.3) provides no

support for a strong effect of the measured environmental conditions selecting certain genera

In Ivindo this aggregation may represent the sharing of nesting material at very fine scales *Microtermes* spp (Macrotermitinae) was the most abundant FGII genus in Ivindo, and is found as a secondary occupant of epigeal mounds of soil-feeding species (Eggleton & Bignell, 1997) Incipient colonies or sub-colonies may be able to occupy marginal nesting sites, therefore also making use of shelter and a site for fungus-combs in the mounds of other Macrotermitinae termites

In Danum the most abundant genus was *Globitermes*, which consumes wood that is in an advanced state of decay Thus the aggregation may represent a facilitative interaction (as suggested by Donovan *et al.*, 2007), where the remaining FGII genera have contributed to initial wood decay, and therefore provide the material consumed by *Globitermes* This interaction may be detected across a broad area, due to the 'separate-piece' foraging strategy (Abe, 1987) of many FGII termites, which have a particularly high taxonomic representation in SE Asia (Eggleton & Tayasu, 2001). Due to the spatial separation of the food and nesting material, these arboreal nesting genera would not compete with *Globitermes* for nesting space, while worker foraging parties may cover a substantial area; as an example colony foraging areas were consistently >50m for Panamanian *Nasutitermes* spp (Levings & Adams, 1984).

Despite the abundance of soil as a food resource, the low co-occurrence of the soil-feeding-groups (FGIII and FGIV) at the single-pit scale (Figure 6 2) could be interpreted as competitive exclusion operating at fine (soil pit) scales among the

soil-feeding termite genera (Figure 6.2). The colonies of mound-building FGIV species were previously shown to be spatially dispersed in the Ivindo plot, where the colony extent was also far greater than 2m (Chapter 5). Little is known, however, about the nesting strategy and colony extent of most soil-feeding species. One would expect that colony extent is likely to be far less for genera where worker size is particularly small, or worker numbers per colony low. It is not possible to ascertain whether the inter-generic dispersion detected here is at the entire colony scale, as observed in ants (Albrecht & Gotelli, 2001), or that colony ranges overlap spatially while the foraging patterns of workers undergo small-scale shifts within this. The soil-feeding component of rain forest assemblages is phylogenetically diverse (Inward *et al.*, 2007b), and the resulting differences in size, life-history and nesting strategies may mean that both types of structures (complete colony dispersion, and overlapping colonies with foraging shifts) operate to varying degrees. Heterogeneity in the measured environmental variables does not account for the soil-feeding composition at the fine-, or any other cell size (Table 6.3). As genus-level dispersion is detected only at the fine scale, competition for colony space is a more plausible explanation for competitive exclusion than for food.

In this study, no conclusions can be made regarding the strength of competitive interactions within termites according to food resource availability within the feeding-groups. As wood on the surface of the soil was not also sampled, co-occurrence patterns in this feeding-group may reflect positive colony nesting interactions between genera. Unlike the wood-feeding genera, most soil-feeding termites are hypogean nesting, limiting the vertical stratification of nesting opportunities. Within the soil profile, the majority of termite abundance and biomass is found in the upper 20cm of the profile (Inoue *et al.*, 2001), and

therefore the dominant interactions at the finest scale may reflect colony-level interactions, for nesting space, and/or for food depending on the degree of resource partitioning of soil within the soil-feeding termites (discussed below)

6.5.2 Biogeographic history

Between Asia and Africa, termite species and biomass density increase by a magnitude of approximately 1.5 and 16.3 respectively (Eggleton *et al.*, 1999), with most of this difference deriving from soil-feeding-groups (Davies *et al.*, 2003a). As the low co-occurrence patterns in these groups were consistently only at the finest scale (Figure 6.2), this suggests that genus-level dispersion is at the colony rather than population level, and therefore remarkably these patterns were consistent across the sites. One might have expected small-scale exclusion to break-down in Danum given the greater available space in the soil profile to accommodate termite colonies (Chapter 3). Of the soil-feeding-groups, FGIV which is unique to Ivindo and extremely genus-rich, showed the weakest yet still significant exclusion at the 2m x 2m scale (Figure 6.2). If FGIV genera are partitioning food resources in the soil profile, competitive interactions may indeed be weaker at the colony level, and explain the high number of genera that are able to co-occur in individual pits (Table 6.2, and discussed below).

The SE Asian soil-feeding species pool is considered to be largely descended from African termite fauna that dispersed to the Indian plate, which subsequently collided with Asia during the Miocene (Davies *et al.*, 2003a). Despite the lower abundances, competitive interactions for nesting space in Asia may therefore be a legacy of those already occurring in the ancestral African assemblages

6.5.3 Interpreting the co-occurrence patterns

6.5.3.1 Competition for colony space

Competitive interactions for space in the soil profile have been described in the root matt of plant communities (Schenk *et al.*, 1999; Cahill & Casper, 2000), and may be a generality for larger soil organisms at the individual or colony level. For soil-dwelling termites, competition for nesting space may be important, in particular between the hypogeal nesting termites that are therefore limited to the soil profile. Indeed the increased SES value for the full assemblage at the 2m x 2m scale in Ivindo (Figure 6.2), compared with FGIII and FGIV, implies competitive interactions between termites that have differentiated feeding strategies, but frequently similar nesting requirements. Interestingly spatial dispersion was detected at the inter-feeding-group level in these assemblages: the soil-feeding termites were dispersed from fine-scale patches of wood-feeding termites, and broad-scale aggregations of humus- (FGIII) and true soil-feeding (FGIV) were spatially separated (see Chapter 5). Although in some cases the feeding-groups had opposing relationships with environmental variables that could then explain the spatial dispersion by environmental selection, the results from the environmental ordinations in this study (Table 6.3) suggest that environmental heterogeneity provides only a weak influence on the spatial structures of the assemblages at this fine scale. It may be, then, that at a broad scale competition for space in the soil profile is also occurring between multi-genus feeding-group aggregations.

6.5.3.2 Competition for food

Although soil is abundant, it is a low quality food material (Brauman *et al.*, 2000). One evolutionary adaptation to this energetic constraint is large worker

body-size in the *Apicotermes*- and *Cubitermes*-groups (Termitidae), that allows a high through-put of soil material (Eggleton *et al.*, 1998) In these termites, which are all FGIV, an anatomical character in the worker gut, the enteric valve, is important for the filtering and concentration of organic portions of the soil material during digestion. Its structure, however, is particularly varied (Sands, 1998, Donovan, 2002), possibly due to the filtering of specific components (e.g. of clays) of soil material. Such ecological specialisation, if it does occur, would reduce competitive interactions for the extracted components of consumed food material, and explain the rather low but still significant C-score value compared with the FGIII assemblage (Figure 6.2).

Stable isotope analysis has been applied to sympatrically occurring species within the *Anoplotermes*-group (sub-family Apicotermitinae) (Bourguignon *et al.*, 2009), which is an extremely species-rich clade in African and American rain forests. Delta¹⁵N isotope ratio reflects the decomposition or humification status of the consumed soil material. The reported inter-specific differences do provide some compelling evidence for resource partitioning within this species group along the humification gradient, which should be confirmed with more within-species replication. Presuming, however, that both FGIII and FGIV soil-feeding genera do not fully partition the food resource, or at least this varies within and between the soil-feeding clades, the resulting competitive interactions may generate the spatial dispersion seen at the single pit scale.

6.5.3.3 Ant Predation

Apart from competitive interactions, and habitat or environmental constraints on sample composition which here appears to have a weak influence, low co-occurrence patterns can result from random localised extinctions (Ulrich, 2004).

A possible cause of highly localised genus loss in this system is colony death or depletion from ant predation. There are several examples of predator-prey interactions between ants and termites (e.g. Dejean & Feneron, 1999; Leponce *et al.*, 1999), however, the nature (i.e. specialist or generalist) and strength of this interaction at the community level is essentially unknown. In previous analyses of the same termite assemblages, spatial relationships were detected between the predatory ant and termite assemblages (Chapter 5). In Danum this was apparent at fine scales where termites were absent from predatory ant patches, possibly due to the consumption or death of the termite colony due to ant predation. If ant predation could be responsible for the lower co-occurrences at fine scales, this would imply that this interaction was intense and operating at the fine scale in Danum. The spatial relationships between the ants and termites were, however, at broad scales in Ivindo (Chapter 5), and therefore are unlikely to explain the low co-occurrence patterns at fine scales.

The broad scale at which genera were aggregated in the co-occurrence analyses (Figure 6.2) corresponds with assemblage composition being spatially structured at medium to broad scales in each plot as revealed by the PCNM analysis (Figure 6.3). As this broader-scale inter-generic aggregation is not associated with environmental heterogeneity (Table 6.2), a facilitative interaction may be occurring. Termites demonstrate remarkable diversity in worker and soldier defensive strategies (Prestwich, 1984; Scholtz *et al.*, 2008). Soldiers typically guard and block core artery passages (P. Eggleton personal communication), thereby protecting the queen and brood, while foraging workers may be vulnerable to predation as they leave the colony centre. Security in numbers, and combining the defensive strategies of aggregated genera, may make it progressively more difficult for raiding ants to penetrate

into mixtures of termite colonies. Such mutualism in anti-predation may explain mixed-species foraging mammals on the African plains (Altmann & Altmann, 1970), and within flocks of birds (Barnard & Thompson, 1985), however in these groups co-operation improves predator avoidance through alarm calls, rather than improved defence.

In Ivindo the termite and predatory ant spatial patterns overlapped in a complex fashion at broad scales within the plot, which may reflect broad-scale cooperation (Chapter 5). Genus-level assemblage composition of the predatory ants was very similar in Danum and Ivindo, however, in Ivindo their occupancy in pits was greater despite a lower generic richness (Chapter 3). This does suggest that predatory ants are adapted to exploiting the high abundance of termites in this assemblage, while not resulting in a depletion of the termite population. This could be considered analogous to co-habitation of termitophagous ants and termites (e.g. Dejean & Feneron, 1999), but at the assemblage rather than individual colony level.

6.5.3.4 Food transfer facilitation

An alternative type of facilitation that could generate the aggregation patterns at broad scales is the provision of food material at different stages of decay. Donovan et al (2007) suggested a possible cascade of food material between the wood- and soil-feeding termites in an assemblage sampled in Danum. Contrary to this hypothesis, spatial dispersion between these feeding-groups was detected at fine scales (Chapter 5), where it was suggested the soil-feeding termites were excluded from the nesting space of wood-feeding genera. If however material deposited by wood-feeding termites is incorporated as diffuse

patches within the soil profile, a food-mediated facilitation may be occurring at a scale broader than the colony extent.

Evidence for food resource partitioning between soil-feeding termites is currently weak (poor replication in Bourguignon et al. (2009)). Soil-feeding genera within FGIV are however phylogenetically diverse (Inward *et al.*, 2007b), and there appears to be more eco-morphological differentiation in this group than in FGIII. As described above, the diversified enteric valve architecture in worker guts must relate to differing feeding strategies, but has yet to be investigated fully. If, then, these termites consume large quantities of soil, but genera specialise on specific components of organic material, first, competitive interactions may be reduced or weaker. Further to this, these termites, which as FGIVs are already at the extreme lower end of the humification gradient, will be excreting more humified material into the soil profile, which will then be available to other termites within this group. Such a facilitative interaction has been described in fungal communities, where material at different stages of decay is passed through a community (Frankland, 1969). Due to the low co-occurrence at fine scales, possibly reflecting colony-level dispersion, a termite-mediated transfer of soil material must be spatio-temporally dynamic; as soil is deposited into the soil profile by foraging workers, small-scale shifts in the colony or worker foraging parties would make this available to other genera, with these shifts occurring within broad aggregations of on average seven genera (Table 6.1).

6.5.4 Fine-scale assembly rules

The scale dependency of co-occurrence patterns has frequently been documented, with many of these studies comparing patterns from across

habitat gradients with those at the local scale (e.g. Albrecht & Gotelli, 2001, Gotelli & Ellison, 2002; Sanders *et al.*, 2007). These have been used to construct assembly rules that describe the ecological processes that structure and maintain assemblage diversity (Diamond, 1975). For instance, in earthworm communities, co-occurrence patterns at various scales demonstrated that both habitat and competition operate to constrain the species pool at regional and local scales respectively (Decaens *et al.*, 2009). The small spatial extent of the plot in this study would not have incorporated significant habitat or environmental gradients, particularly as topographic features were intentionally avoided during plot selection. This may explain the low influence of environmental variables in explaining the community composition (Table 6.2). Rather the co-occurrence patterns detected here reflect fine-scale biotic interactions that vary according to the spatial-scale being considered (i.e. nested cell size). The hypothesized scale-dependent interactions operating in termite assemblages are summarised in Table 6.4, and how this translates into the spatial structuring of the termite genera and feeding-groups, is presented in Figure 6.4.

Table 6.4 Summary of hypothesized ecological interactions, operating at various functional levels and spatial scales. Full, full assemblage, FGII, wood-feeding; FGIII, humus-feeding, FGIV, true soil-feeding, scale of interactions in parenthesis.

Dispersion	Danum	Ivindo	Aggregation	Danum	Ivindo
Colony occupancy, competitive exclusion	FGIII (fine).	Full, FGIII & FGIV(fine)	Shared nesting material		FGII (fine)
Ant predation	Full (fine)		Food transfer	Full (broad)	FGIV (med)
			Improved defensive ability		FGIV (med)

In order to generate assembly rules for rain forest termite assemblages, these hypotheses have been assimilated with the inter-feeding-group spatial relationships described from the same assemblages in Chapter 5. At the finest scales, a likely causal explanation of spatial dispersion of termites, most consistently seen in the soil-feeding-groups, is competition for nesting space. In Ivindo, however, *Microtermes*, as an abundant and small termite, may be sharing nesting space with other FGII termites. Highly localised ant predation may also be depleting termite colonies or influencing their extent in the soil in Danum. At medium and broad scales the aggregations, seen in the soil-feeding group and full assemblage in Danum, and true soil-feeding-group in Ivindo (although not statistically significant), may be due to differentiation of food material that facilitates a transfer of food material within the assemblage. In Ivindo this pattern may also occur due to genus-level cooperation against ant predation. It is likely that nesting space is generally a limiting factor both at the individual colony scale of soil-feeding genera that have limited nesting resource partitioning, and between feeding-groups, depending on the scale at which intra-feeding-group aggregations occur (Chapter 5). It appears, then, that a scale-dependent trade-off between competitive and facilitative interactions may be important in structuring these termite assemblages. The precise nature of this depends on the region-specific representation and abundance of taxonomic groups.

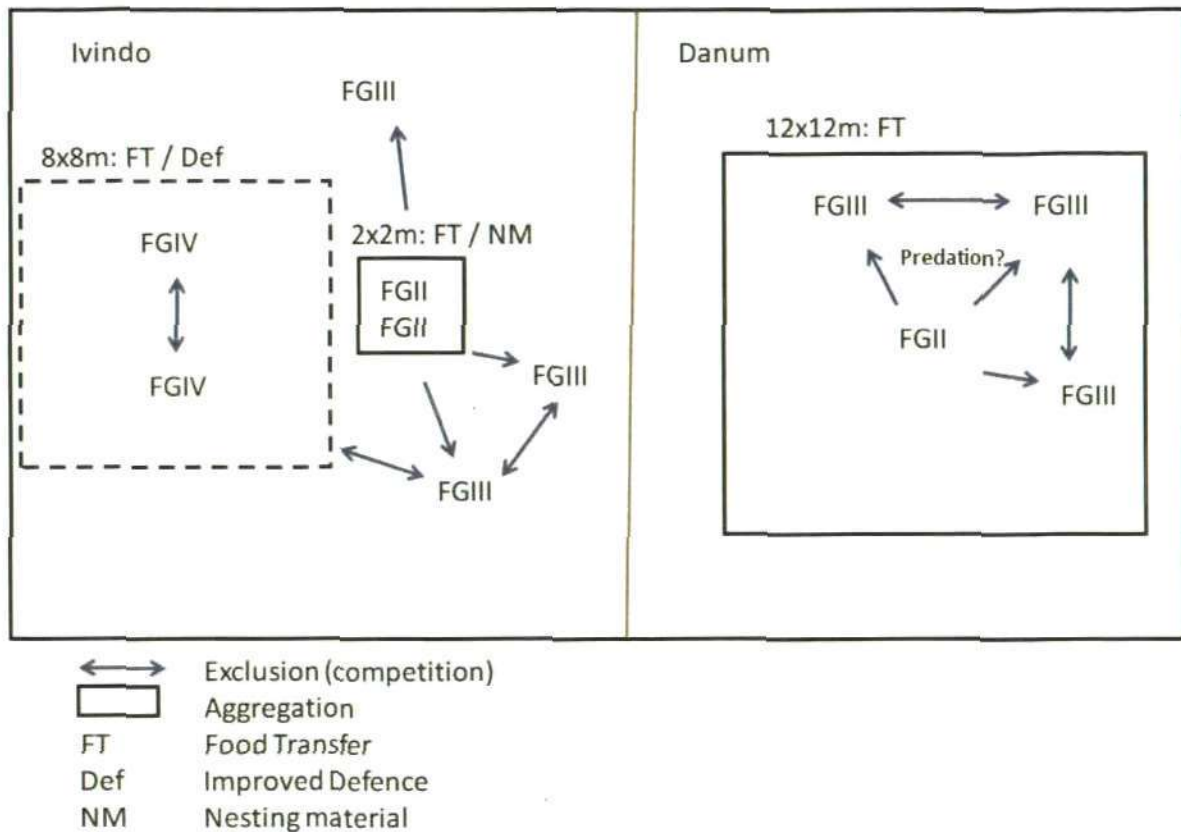


Figure 6.4 Schematic diagram of spatially structured processes occurring at various scales between feeding-groups (FGII, wood-feeding; FGIII, humus-feeding; FGIV, true soil-feeding) in Ivindo and Danum. Black outlines indicate inter-genus aggregation, dashed in Ivindo as two-tailed test was not significant (see Figure 6.2). Arrows for exclusion indicate direction of exclusion.

The suggested competitive interactions at the colony level are consistent with existing evidence provided in Chapter 4 of this thesis and by Levings and Adams (1984), of colony dispersion and territoriality in rain forest termites. Spatio-temporal niche partitioning at the colony level has been described in grassland ants (Albrecht & Gotelli, 2001), however here nesting space may be the limiting resource for termite colonies. Beyond the inter-colony dispersion hypothesized here at fine-scales, broader scale aggregation that is independent of environmental heterogeneity appears to supersede fine-scale competitive interactions. Weak competition is considered a generality for soil communities

due to micro-habitat heterogeneity (Ettema & Wardle, 2002; Wardle, 2006; Decaëns, 2010). Although micro-habitat heterogeneity is indeed likely to promote co-existence in termites as suggested by Deblauwe et al. (2008), positive interactions within the termite assemblage may be equally important in determining local diversity patterns and their spatial structure. At scales broader than this study, habitat filters may also be constraining local assemblages. An interesting avenue of further research would be to ascertain whether a scale-dependent shift from competition to facilitation occurs across wider decomposer communities.

7 Final discussion

7.1 Summary

In this chapter, I briefly re-address some of my key findings, outlining their broader relevance, and suggesting future research avenues. First I describe the fine-scale environmental structure, and the role of historical and local processes in influencing the observed patterns in tropical rain forests. The following subsections review the conclusions on the scale of positive and negative ecological interactions on the termite assemblages, from the colony to assemblage level, and how these shape the over-all spatial patterns in termite composition. I also touch on the importance of putative predatory-ant/termite interaction. Finally I suggest that the role of biotic interactions in shaping termite assemblage structure, and hence their provided ecosystem services, should also be considered, particularly under the anthropogenic stresses of habitat fragmentation and climate change.

7.2 Fine-scale rain forest structure

Tropical rain forests are characterised by tall evergreen trees, a closed upper-canopy, high rainfall, poor soils, and rapid decomposition of dead organic matter. As moist megathermal multistratal closed canopy forests were first widespread from the Paleocene, 60 Ma, after the Gondwanan break-up, 120 Ma, the characteristic rain forest structure evolved independently across the major forest blocks (Morley, 1999). Several biotic groups have undergone convergent evolution to fill similar ecological niches, generating similarities in the habitat structure and ecosystem dynamics (Corlett & Primack, 2006). Differences are generated by biogeographic effects, and region-specific climatic

conditions have left a legacy on ecological patterns such as species richness (e.g. Parmentier *et al.*, 2007). So while there are many similarities, differences arising from regional evolutionary and climatic histories will inevitably be apparent in the forest structure.

The examination of the environmental variables collected here demonstrated that in many respects environmental conditions and habitat structure in a single one hectare plot from an African and SE Asian primary rain forest were very similar (Chapter 2). The mean and standard deviations of soil C and N, and soil pH were remarkably similar, while the measurements of leaf-litter and dead wood were necessarily coarser, they had similar frequency distributions (Figure 2.5 and Figure 2.6). This particular combination of variables may indicate that net decomposition rates, which would influence the accumulation of above and below ground dead organic matter (e.g. Didham, 1998), are relatively consistent at these sites, which may extend to the regional scale. This is fascinating as, if decomposition rates are indeed similar, the decomposer communities that mediate decomposition are not (as indicated in termites, Davies *et al.*, 2003a; Yamada *et al.*, 2005). Therefore decomposer groups may be compensating for the presence or absence of each-other, have certain environmental tolerances, and so may be differentially directly and indirectly affected by anthropogenic pressures.

Variables that differed more clearly were measurements of soil moisture and infiltration, possibly due to site-specific differences in soil texture, and tree density, which may result, in part, from regional differences in tree species richness. Other site-specific factors may also be important, such as intense herbivory due to the high density of elephants in Ivindo (Maisels *et al.*, 2009),

while the southern end of Ivindo National Park has lower tree species richness compared with neighbouring rain forest sites (G Walters personal communication). Therefore the differences detected between sites may have arisen from site location within each region, in addition to region-specific factors. Returning to the frequently-cited point that ecological patterns and processes are scale-dependent, at broad scales rain forests in general provide similar structures and ecosystem services, however as one examines patterns at progressively finer scales or in a more detailed fashion, the differences between the major rain forests blocks are likely to be more apparent (Corlett & Primack, 2006). This scale-dependent effect appears to be reflected in the environmental PCA's (Figure 2.8 and Figure 2.9), where the general rain forest characteristics have a dominant influence over the environmental relationships. The axes that describe the greatest proportional variance (i.e. axes 1 and 2) mostly describe similar relationships in both sites. I suggested that these axes correlated with topographic effects, and associated water and solute transport and accumulation through the soil (axis 1 relationships), and tree-fall events and canopy gaps (axis 2 relationships). Those that describe proportionally less variance, although only marginally so (i.e. axes 3 and 4), describe relationships that are mostly unique to sites, which presumably are associated with site- or region-specific characteristics. One would then expect that observed biotic patterns are influenced both by factors common across regions, and by those that are unique to regions.

Understanding such global generalities, along with region- and site-specific patterns, are valuable in current efforts to quantify rain forest structure (e.g. to assess carbon stocks), and to understand diversity maintenance mechanisms

and the links between biodiversity and ecosystem services (e.g. carbon fluxes). From a management and conservation perspective, understanding the differences are as important as emphasizing the generalities.

7.3 Colony extent and intra- and inter-specific interactions in soil-feeding termites

Using a combination of molecular tools and spatial analyses, it was estimated that colony extent of mound-building species within the *Cubitermes*-group is ~10m (Chapter 4). This foraging distance is comparable to some wood-feeding termites (e.g. *Reticulitermes* spp. (DeHeer & Vargo, 2004)), which therefore appears to be substantial, as the energetic gains of their food material, which as soil is low, must be sufficient to compensate for the foraging effort over such distances. It is possible the large body-size of these species allows for this, due to the high through-put of soil material. Therefore small sized soil-feeding termites may have substantially more restricted colony extents.

As the mounds of *Cubitermes severus* and *Thoracotermes macrothorax* (*Cubitermes*-group; Termitinae) were over-dispersed to the same scale at which termites collected from regularly-spaced soil pits were aggregated (i.e. putative colony extent), this was interpreted as intra- and inter-specific spatial dispersion at the colony level (Chapter 4). It seems that 1) territoriality is operating, which is an important processes in density-dependent population regulation (Gordon, 1997; Lopez-Sepulcre & Kokko, 2005), and 2) inter-specific competition between these ecologically similar species occurs, which may be as much for colony nesting space as for food material.

The *Cubitermes*-group has high species densities in African systems, and many of the species do not construct mounds. It would be interesting to ascertain

whether these non-mound building species also demonstrate inter-specific dispersion due to competition; investment in constructing a mound is likely to place a higher value on defending a static colony. It may be that where colonies are not bound to a mound, inter-specific spatio-temporal resource partitioning is greater for instance through small-scale shifts by worker foraging parties due to highly localised food depletion. As has been observed in ants, such shifts at short time and spatial scales facilitate co-existence (Albrecht & Gotelli, 2001) and would help to explain the high diversity seen in this clade

Microsatellite markers can provide a powerful tool and arguably the only means to study the colony structure and extent of soil-feeding termites that do not construct mounds, and therefore lack an easily identifiable colony centre. It is recommended that future efforts to design genetic markers in rain forest termites, consider species within the *Anoplotermes*-group (Apicotermitinae). This clade is particularly species diverse, and their colony structure and reproduction are essentially unknown, although it is suspected that their colonies are small. The relevance of such information is to better understand termite colony spatio-temporal dynamics, and therefore the processes that maintain their high diversity.

7.4 Feeding-group spatial structures

7.4.1 Wood-feeding termites

In both Danum and Ivindo wood-feeding (FGII) genera were aggregated in small patches, with large gaps across the plot area (Figure 5.1). As FGII spatial structure was positively associated with that of dead wood, this may in part be explained by food availability (Table 5.3 and Table 5.4). This does not

necessarily explain the large gaps, unless foraging for dead wood is over substantial areas, as is apparent in some wood-feeding termites (up to 60m² *Globitermes sulphurous* (Ngee & Lee, 2002), and up to 1,200m² in *Reticulitermes flavipes* (Bulmer & Traniello, 2002), both of which are hypogean nesting), and therefore driving spatial dispersion at scales far greater than the colony centres in the soil.

7.4.2 Humus-feeding termites

Due to the continuous nature of their food and nesting material, humus-feeding genus richness (FGIII) is homogenously structured; in Ivindo to the extent that the spatial structure was non-significant with few gaps (Figure 5.1). This homogeneity across the plots implies that humus-feeding termites are not influenced by broader scale heterogeneity in the soil quality (as indicated by soil C_{tot}). Disassociation with wood-feeding termites at fine-scales (i.e. the spatial scale of the FGII termite aggregations) is presumably due to competitive exclusion by wood-feeding termites for nesting space (Figure 5.3). Further to this the spatial disassociation with true soil-feeding termites in Ivindo at broad scales (Figure 5.4), did not generate gaps in the humus-feeding spatial patterns. Therefore despite these spatial disassociations with the remaining feeding-groups, this does not affect the overall continuous distribution of the humus-feeding termites. The wood- and humus-feeding patterns correspond with those previously described from Danum Valley Conservation Area (Donovan *et al.*, 2007). These consistencies in time (Danum; 2006 and 2009) and space (Danum and Ivindo) strongly suggest that these patterns are typical for these two feeding-group components of rain forest termite assemblages.

7.4.3 True soil-feeding termites

The true soil-feeding termites (FGIV), only collected in Ivindo, were aggregated at broad scales (Figure 5.1). In the absence of any apparent association with environmental heterogeneity (Table 6.3) this multi-generic aggregation, supported also by the high FGIV genus-level co-occurrence patterns at a broad cell size (Figure 6.2) may rather be due to biotic interactions that promote aggregation. In Chapter 6 I speculated that the cause of this inter-generic aggregation was facilitative interactions. 1) genera extract specific elements of soil organic material from their consumed food, generating trophic transfer of soil material at different stages of decomposition between genera within this functional group, and/or 2) cooperative defence against ant predation whereby combined defence strategies between genera reduces the ability of raiding ants to penetrate into aggregations of colony centres. The former assumes that FGIV genera specialise on precise fractions of soil organic material, and therefore also implies resource partitioning. The use of stable isotope ratios may help to elucidate this (e.g. Bourguignon *et al.*, 2009), and if this holds true, such resource partitioning would help to explain the high species diversity seen in this feeding-group. The latter assumes that ant predation is intense, which is suggested by the strong spatial association observed with predatory ants, however seemingly more so with humus-feeding patches (Figure 5.4). Currently ant predation on termites sampled from Ivindo is being examined using DNA probing of the ant gut-contents (T. Fayle, personal communication), while removal of ants in field experiments would also indicate the trophic intensity of an ant-termite interaction. With an improved understanding of these biotic processes, one can go on to ask whether critical thresholds of local diversity (either within the termites, or of predatory ants) are necessary to maintain these

interactions, and hence the ecosystem services associated with the aggregations.

FGIV were spatially disassociated from FGIII (humus-feeding termites) at broad scales (Figure 5.3). Although opposing environmental relationships were detected between these two feeding-groups (Figure 5.2), spatial dispersion may also be due to competitive exclusion for nesting space. These findings of spatial disassociation between feeding-groups are contrary to the hypothesis of and previous findings by Donovan et al. (2007), that feeding-groups will be spatially associated due to the provision of dead plant material at different stages of decomposition. The role of competitive interactions beyond the colony scale and facilitative interactions in structuring termite assemblages therefore requires further investigation.

7.5 Scale-dependency of positive and negative interactions

This study provides preliminary evidence that both competitive and facilitative interactions may be operating at various spatial and functional scales in termite assemblages. These in turn determine the spatial patterns of termite assemblage composition at the one hectare scale. Inter-generic dispersion at fine scales in soil-feeding termites suggests that individual colonies are competing for nesting space (Figure 6.2). Broad-scale aggregations do not appear to be due to environmental heterogeneity, but rather facilitative interactions (in true soil-feeding termites in Ivindo, and across the full assemblage in Danum). Space in the soil profile appears to be a limiting resource between feeding-groups, as evidenced by their spatial dispersion, but this does not necessarily influence the overall spatial structure of the feeding-groups (Chapter 5).

Facilitation does appear to be important in termites, and its role may vary under anthropogenic stress. In an experimental study that examined the effect of forest clearance on termite assemblages in Cameroon (Davies *et al.*, 1999), recolonisation by wood-feeding termites was improved when substantial dead wood debris was left in cleared plots. Interestingly this also encouraged recolonisation by humus-feeding termites, possibly due to the provision of higher quality organic material by the wood-feeding termites. Therefore understanding the facilitative interactions has implications for land-management practices, and the restoration of forest biodiversity and ecosystem processes.

Temporal shifts from competitive to facilitative interactions have frequently been examined in systems that experience abiotic stress or environmental fluctuations (e.g. Callaway & Walker, 1997; Valiente-Banuet & Verdu, 2008). Facilitation is more intense under abiotic stress, while competitive interactions come to dominate as conditions become more stable. Following forest disturbance, facilitative interactions may be important in encouraging the re-establishment of termite functional diversity. As assemblages become increasingly established, and features such as a closed canopy are re-formed, a shift to competitive interactions for increasingly limited nesting space may ensue between colonies. Here I suggest that facilitation continues to operate in unstressed conditions, but a broader spatial scale to inter-colonial competition. This might therefore represent a scale-dependent (spatial extent) shift of facilitation during community recovery.

7.6 Predatory-ant/termite interactions

De Ruiter *et al.* (1995) noted that, in general, community structure in lower trophic groups (e.g. primary producers and consumers) is controlled more by

top-down effects of predation rather than bottom-up effects. In a field setting both top-down (ant predation) and bottom-up (N availability) trophic controls appeared to be operating in equal intensity (DeSouza *et al.*, 2009). The spatial relationships between the termites and predatory ants (Figure 5.4), suggest that this hypothesized trophic interaction is more intense in Iwindo (tight spatial overlap of termite and ant aggregations at broad scales) than in Danum (diffuse points of termite absences in ant patches). If indeed predation is generally an intense interaction in Africa, this has not resulted in a reduction in termite abundances there relative to Asia. Rather the intensity of this interaction might well be due to the high termite abundances. Termites may be well adapted to the predation pressure, through effective colony defence and/or high colony turn-over. This interaction is worthy of further investigation: 1) density-dependent predation may be important in maintaining termite assemblage composition and spatial patterns, and 2) due to their abundances in forest systems any uncoupling of this interaction following disturbance may have dramatic impacts on ecosystem energetic fluxes.

7.7 Ecosystem services

The feeding-group spatial patterns allude to the scale at which termites provide ecosystem services e.g. nitrogen and carbon mineralization (Ji *et al.*, 2000; Yamada *et al.*, 2005; Ji & Brune, 2006), soil heterogeneity (Donovan *et al.*, 2001b), and pedogenesis (Holt & Lepage, 2000). Wood-feeding termites appear to be operating at fine, low-density, scales in both Africa and Asia, however as wood debris was not also excavated, these patterns largely represent the wood-feeding termites that are hypogeal-nesting. While humus-feeding termites are distributed throughout the soil, the magnitude of provided services will be far

greater in Africa due to their abundances (Eggleton *et al.*, 1999) Although true soil-feeding (FGIV) termites are present in Asia, their complete absence from the Danum study plot, suggest that their functional contribution (e.g. nitrogen mineralisation and provision of ammonia (Ji & Brune, 2006)) there will be marginal compared with African forests

Soil-feeding abundances and species diversity is strongly negatively affected by habitat disturbance in both regions (e.g. Eggleton *et al.*, 1996; Eggleton *et al.*, 1997, Gathorne-Hardy *et al.*, 2002) Further to this it seems that under disturbance the continuous spatial structure in soil-feeding termites is heavily disrupted In a secondary forest plot surveyed in Danum Valley Conservation Area, the spatial distribution of the soil-feeding termites was characterised by a large gap, with small isolated aggregations (Donovan *et al.*, 2007). This complete break-down of the soil-feeding structure is likely to result from the lack of a closed canopy and stable micro-climatic conditions in the soil following logging.

Canopy loss has a large impact on rain forest termite assemblages, and in particular the soil-feeding component (Dibog *et al.*, 1999). This study suggests that the role of biotic interactions, in particular facilitation and ant predation, in structuring termite assemblages should also be investigated, under the possibly more subtle impacts of forest fragmentation and climate-induced effects on forest structure There is a growing awareness of the importance of soil biodiversity and provided ecosystem services, and changes to these under climate-induced stress (Antoninka *et al.*, 2009, Castro *et al.*, 2010) In controlled studies, climate-change effects on plant composition had a greater effect on soil properties that influenced ecosystem function (as indicated by microbial activity

and nematodes), than the direct climate-change effects on soil conditions (Kardol *et al.*, 2010). Ecosystem functional shifts in response to climate change are therefore likely to be complex, and the interactions between both indirect and direct effects need to be considered. It would be interesting to speculate as to the impacts of climate-change, e.g. accelerated tree mortality (Phillips *et al.*; 2008), on termite assemblages, which may then be manifested in above-ground effects as their provided services, such as decomposition, also change. In this regard the two key future research avenues would be to: 1) quantify the role of termite assemblages in decomposition processes, with consideration of the major biogeographic differences in these e.g. the absence of Macrotermitinae in S. American forests, and in relation to other decomposer groups, and 2) better understand the key biotic and abiotic drivers on assemblage composition under the various major disturbance regimes.

7.8 Final conclusions

This study demonstrated that one hectare plots in an African and Asia forest, selected according to a series of criteria to maximise comparability, are very similar in their over-all structure and environmental heterogeneity. The known differences in taxonomic and functional diversity and abundances from African and Asian forests were captured in the single study plots, with the soil profile in Ivindo saturated by termites. As an over-arching rule, it appears the distribution of food material is important in structuring the wood- and humus-feeding termite assemblages (i.e. patchy and continuous respectively). Humus-feeding termites are evenly spread through the soil profile and this homogenous distribution is seemingly not influenced by heterogeneity in soil C_{tot} (i.e. soil quality), dispersion from aggregations of wood-feeding termites, or indeed dispersion

from aggregations of true soil-feeding termites in Ivindo. The aggregation observed for the true soil-feeding termites was not explained by environmental heterogeneity, and may rather result from within-assemblage facilitative interactions, hypothesized to be the transfer of food material or co-operative defence. A similar aggregation in the full termite assemblage in Danum, may mean that a facilitative interaction (in the transfer of food material rather than for defence) may also be operating, and maintain assemblage composition. In this soil system, competitive interactions at the colony scale between soil-feeding termites appears to be the norm, while the functional scale at which facilitative interactions occur depends on the biogeographic influences on assemblage composition.

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