Insect. Soc.
DOI 10.1007/s00040-014-0385-z

Insectes Sociaux

RESEARCH ARTICLE

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

C. A. L. Dahlsjö · C. L. Parr · Y. Malhi · P. Meir · P. Eggleton

Received: 23 June 2014 / Revised: 15 December 2014 / Accepted: 16 December 2014

Abstract Termites are frequently dominant invertebrate decomposers and bioturbators in lowland tropical forests and therefore strongly influence ecosystem processes favouring soil stability, porosity and nutrient retention. In this study, we provide the first spatially replicated dataset on termite assemblage composition, abundance and biomass in a Peruvian rainforest by sampling six separate plots. In addition, two alternative sampling methods (transect method-TM and quadrat method-QM), providing termite species density data, were compared among the plots. The relationships between a range of environmental and spatial variables and species composition were examined using canonical correspondence analysis variation partitioning. We found that the TM captured a higher proportion of the known species in the site (82 %) compared with the QM (66 %). In addition, 56 % of the species sampled by TM were common between the plots while only 18 % of species overlapped using the QM. The QM may therefore potentially have undersampled the species pool. Environmental variables were shown to explain a larger proportion of the species patterns than the spatial variables with elevation, soil temperature and distance to the river being the most important. We discuss the impacts of the environmental and spatial variables on termite species composition.

Keywords Environmental variables · Quadrat method · Species composition · Spatial variables · Termitoidae · Transect method

Electronic supplementary material The online version of this article (doi:10.1007/s00040-014-0385-z) contains supplementary material, which is available to authorized users.

C. A. L. Dahlsjö (✉) · Y. Malhi
Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK
e-mail: cecilia.dahlsjo@ouce.ox.ac.uk; c.dahlsjo@gmail.com

C. A. L. Dahlsjö · P. Eggleton
Soil Biodiversity Group, Department of Entomology, The Natural History Museum, London SW7 5BD, UK

C. L. Parr
Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK

P. Meir
School of Geosciences, University of Edinburgh, Edinburgh, UK

P. Meir
Research School of Biology, Australian National University, Canberra, ACT 0200, Australia

C. A. L. Dahlsjö
Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

Introduction

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

Termites inhabit subtropical and tropical regions and are particularly abundant in lowland tropical rain forests (Bignell and Eggleton 2000). They exhibit a wide range of feeding habits, from single-piece wood-feeding to true soil-feeding, that are often classified into five feeding-groups

Published online: 27 December 2014

(the Donovan et al. (2001) and Inward et al. (2007) systems, see Table 1). Although, other feeding-group classifications are available, based on nesting habits (Abe 1987) or $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios (Bourguignon et al. 2011b), the Donovan/Inward system takes account of both gut morphology and gut contents and thus reflects the digestive process as well as the substrate ingested. Termites are ecosystem engineers (Jones et al. 1994), acting as bioturbation agents and affecting soil nutrient availability and turnover (Jouquet et al. 2011); additionally, the range of feeding-groups and the abundance of termites in lowland tropical forests make them one of the most important decomposer organisms in those habitats (Bignell and Eggleton 2000). Termite compositional and diversity data are therefore important for a better understanding of the role termites play in ecosystem processes, such as nutrient availability and distribution and physical alterations of the habitat, and for the understanding of the functioning of the ecosystem as a whole.

Despite their importance to ecosystem function, data on termite species and feeding-group diversity from tropical forests are restricted (Eggleton et al. 1996, 1999), particularly for South America (Martius 1992; Martius and Ribeiro 1996; Apolinário and Martius 2004; Bourguignon et al. 2011a; Cancello et al. 2014), and existing studies tend to examine single plots within different regions or land uses, with limited temporal or spatial replication (Jones 2000; Davies et al. 2003a; Huising et al. 2008; Palin et al. 2010; Dahlsjö et al. 2014).

Two standardised sampling protocols have been widely used by the Natural History Museum (NHM) Soil Biodiversity Group, London, for termites in humid tropical forests (Bignell 2009), the transect method (TM) (Jones and Eggleton 2000) and the quadrat method (QM) (Eggleton et al. 1996). The TM is based on representative sampling in sequential adjacent sections, limited by time (1 person-hour per section, 20 h per transect). Thus different sites are addressed by a sampling exercise which is equal in effort as well as being logistically efficient (Jones and Eggleton 2000; Bignell 2009). This method is not exhaustive, but provides encounter data, which may be used to estimate termite species density (species richness per transect). In contrast, data from the QM are based on a higher point-scale sampling effort in a number of small separated quadrats, where all individuals are collected to provide absolute termite abundance (individuals m^{-2}), which may then be used to estimate biomass. However, the requirement to show confidence intervals for estimates of absolute abundance and biomass may mean that a large number of quadrats are sampled, and the logistical investment per site is generally greater (Eggleton et al. 1996; Bignell 2009). The TM has been used extensively to provide better understanding of termite species diversity both regionally (Eggleton et al. 1995, 2002; Jones 2000; Jones and Eggleton 2000; Jones et al. 2003) and globally (Davies et al. 2003a); while the QM, although less often deployed (Eggleton et al. 1996, 1999; Dahlsjö et al. 2014), has provided important insights into termite abundance and biomass for better understanding of their impact on ecosystem processes (Dahlsjö et al. 2014). Based on work in the humid forests of Malaysia and Cameroon, Jones and Eggleton (2000) showed that the TM could compile a comparable number of species to the QM in about one tenth of the field time; however, comparable studies have not been carried out in South America. A further complication arises from the lack of genuine replication in many previous studies, that is the restriction of sampling to a single plot within a defined land use within a gradient of land uses, rather than separate replicated plots within the same land use and site. Thus there is limited understanding of how species composition differs among plots within the same land use, or across a single site in relation to topographical or other environmental factors. In this study, the diversity and compositional patterns of termites within a Neotropical lowland rain forest in Peru were examined using two sampling methods, the TM and the QM. The results demonstrate the degree to which the two methods reveal similar patterns, and permit an evaluation of the strengths and weaknesses of each method. Environmental and spatial drivers behind the observed compositional patterns are also considered.

Table 1 Classification of termite feeding-groups and respective feeding substrates within tropical rain forests. Modified from Donovan et al. (2001) and Inward et al. (2007)

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

Methods

Study site

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

Sampling

Plots and sampling methods

Sampling took place in six replicated rectangular plots (50 m × 70 m) spaced approximately 300 m apart (Fig. S1). Each plot was divided into seven parallel (50 m × 10 m) sections, in four of which two standard sampling protocols were conducted: the transect method (TM) and the quadrat method (QM). Each sampling method was conducted in two sub-plot sections spaced 30 m apart (Fig. S1).

The transect method (TM) was used to estimate termite species density (species richness per transect), using two half-standardised belt transects (100 m × 2 m) (Jones and Eggleton 2000; Davies et al. 2003b) located 30 m apart in each plot. Each transect was divided into twenty 5 m × 2 m sections in which active searching for termites took place for one person-hour (sampling by one person for an hour), using twelve scrapes (12 cm × 12 cm × 5 cm soil pits) and by inspection of all dead wood, nests and runways. The total number of encounters for each species (the presence of a species in any given microhabitat, i.e. soil pit, log or branch in each 10 m^2 section) was recorded as a measure of relative abundance (as specified in Jones and Eggleton (2000)). Using the TM, a total of 6 transects and 1,200 m^2 were sampled over a total period of 120 h. Species density, absolute abundance and biomass were estimated using a standardised quadrat sampling protocol (QM) (Eggleton et al. 1996; Dahlsjö et al. 2014). These estimates are based on sampling of termites in ten 2 m × 2 m systematically placed quadrats per plot (5 quadrats in each sub-section with each quadrat 5 m apart). All worker termites that were encountered in dead wood (>20 mm diameter) were collected. Small branches were broken open, while larger logs were sampled with a saw before being split open to extract all, or a subsample of all, termites. Large logs (>20 cm diameter and >150 cm long) were sub-sampled by only collecting termites in 50 % of the log, or in 25 % of larger logs or trees. This may have underestimated the abundance of termites in some logs while it may have overestimated the abundance in others. In addition, all termites in one 25 cm × 25 cm × 10 cm depth soil pit in the centre of each quadrat were collected. A total of 60 quadrats and 240 m^2 were sampled using the QM.

Environmental variables

Soil temperature and moisture were measured using a probe thermometer and a Delta-T theta probe type ML2x, Delta-T Inc., Cambridge, UK, respectively, at a depth of 5 cm once in each quadrat. One soil sample was collected from each quadrat (60 sampled in total), at a depth of 5 cm, for chemical analysis of carbon (C) and nitrogen (N). Total soil C and N content were analysed using a Thermo Finnigan Flash Elemental Analyser 1,112 at the Imaging and Analysis Centre at the NHM in London. The plot coordinates (latitude and longitude) were estimated with a GPS in the field and used to collect plot-specific elevation data from Google Earth. The distance from each plot to the main river and the distance to the lake in the study area were measured using the 'ruler' tool in Google Earth.

Spatial variables

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

Identification

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

present within the species), these were identified by comparing enteric valve structures and head widths.

Data analyses

Data from the quadrats within each plot (QM only) were analysed using a split-plot design and pooled to make them directly comparable with the TM. The proportion of known species captured with the TM and QM in Peru compared with data from Malaysia (Eggleton et al. 1999) and Cameroon (Eggleton et al. 1996) was examined using ANOVA and post hoc Tukey HSD tests (R, version 2.15.3). Species turnover was calculated among plots for data collected with both the TM and the QM using Bray–Curtis similarity (BCS), calculated by subtracting the Bray–Curtis dissimilarity (BCD) measure from one (1−BCD = BCS). The BCS was used instead of BCD as it is an easier index to interpret: 0 (zero) means that the plots do not share any common species while 1 (one) means that the plots have the same species composition. Analyses were conducted using the *bray* method in the *vegdist* command in R (version 2.15.3). The *rarefaction* method in the *specaccum* command (vegan) in R was used to generate species accumulation and standard deviation values. The values were used to visualise the effectiveness of estimating species diversity with the two sampling methods (TM and QM) across plots (area) and over time (person-hours).

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

Variation partitioning analyses (Lepš and Šmilauer 2003) were conducted using species composition in wood and soil and the significant environmental and spatial variables identified with the Monte Carlo analyses of the QM data. The proportion of the variance that each environmental and spatial variable explained were examined using a split-plot CCA analysis (a constrained, unimodal ordination method) with log-transformed response variables and hierarchical permutation parameters for species composition in wood and soil separately (CANOCO, version 5). The effect of elevation and soil carbon content in each plot on species diversity was examined using ANOVA (R, version 2.15.3) and analysed at the plot level.

Results

Comparison of sampling regimes

In total, 94 species were found in the Peruvian lowland rain forest site using both the TM and QM (Table S1). Neither of the sampling methods yielded all species found in the site, although the addition of previously unsampled species by the TM was greatly reduced at the end of the study (Fig. 1). The efficiency of the two sampling methods differed with the TM capturing ~82 % of the total number of species collected while the QM captured ~66 % (see Table S1 for the total number of species collected with the TM and QM). The efficiency of the TM in this study was significantly higher than the efficiency of the TM in a methodologically similar study in Malaysia (Tukey HSD post hoc, $P = 0.03$) but was not significantly higher than the efficiency of the TM in Cameroon (Tukey HSD post hoc, $P > 0.05$). The proportion of species captured using the QM in Peru did not differ significantly among regions (ANOVA, $P > 0.05$) (see Table 2 for the proportion of species captured in each regions using the two sampling methods).

In Peru, species diversity within each of the feeding-groups was similar using the TM and QM for all groups except for humus-feeding (FGIII) termites (refer to Table 1 for feeding-group terminology) with the number of species collected using the TM being FGI = 4, FGII = 16, FGIII = 43, FGIV = 14 and with the QM being FGI = 1, FGII = 15, FGIII = 32, FGIV = 14. Eleven additional species of humus-feeding termites were encountered using the TM compared with the QM. A total of 77 species and 16 genera were collected with the TM over 120 person-hours (20 person-hours per plot) (Fig. 1) with mean (±SE) termite species richness per transect of 43 ± 1.7 spp. The mean species similarity index among plots was BCS = 0.56 ± 0.017, where 1 is complete similarity (Table 3).

Using the QM, a total of 62 species and 15 genera were collected over 360 person-hours (~60 person-hours per plot) (Fig. 1). The mean (±SE) termite species richness per plot (10 quadrats) was 24.7 ± 2.7 species, while termite abundance and biomass collected with the QM were 130 ± 39 individuals m^{-2} and 0.35 ± 0.10 g m^{-2}, respectively. The species similarity indices in soil and wood among quadrats (within plots) were very low with mean similarity in soil being BCS = 0.02 ± 0.01 and in wood BCS = 0.02 ± 0.008. These low similarity values suggest that termites are very patchily distributed at the quadrat level. At the plot level, the mean similarity of species composition among plots was higher with BCS 0.18 ± 0.025 (Table 3), although still much lower than the similarity found in the TM data.

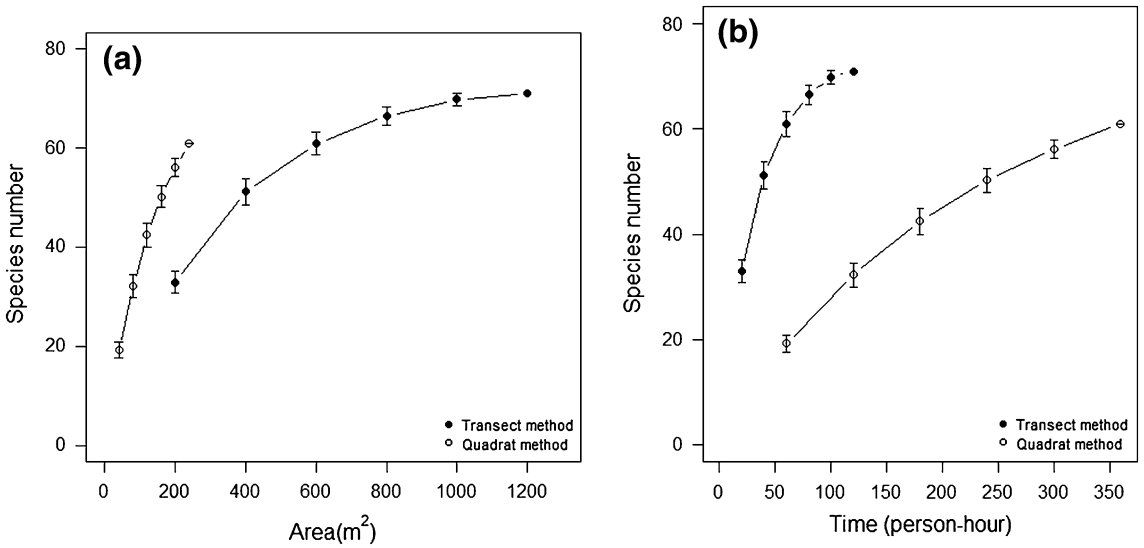

Fig. 1 Rarefraction curves for species accumulation (±SD) **a** across area (m^2) and **b** over time comparing the number of species collected with the transect and quadrat methods. Time is expressed in person-hours, i.e. sampling by one person for an hour

Table 2 Species richness sampled with the TM and the QM from three forest sites in Peru, Malaysia and Cameroon

Sampling method	Species sampled	Total known species	Proportion of total fauna (%)
Transect method			
Tambopata, Peru (transect 1)	47	94*	50.0
Tambopata, Peru (transect 2)	44	94*	46.8
Tambopata, Peru (transect 3)	46	94*	48.9
Tambopata, Peru (transect 4)	35	94*	37.2
Tambopata, Peru (transect 5)	43	94*	45.7
Tambopata, Peru (transect 6)	43	94*	45.7
Danum Valley, Malaysia (transect 1)	31	93#	34.4
Danum Valley, Malaysia (transect 2)	33	93#	35.5
Mbalmayo, Cameroon (transect 1)	46	136×	33.8
Mbalmayo, Cameroon (transect 2)	53	136×	39.0
Quadrat method			
Tambopata, Peru (plot 1, 10 quadrats)	24	94*	26.7
Tambopata, Peru (plot 2, 10 quadrats)	19	94*	21.1
Tambopata, Peru (plot 3, 10 quadrats)	20	94*	22.2
Tambopata, Peru (plot 4, 10 quadrats)	21	94*	23.3
Tambopata, Peru (plot 5, 10 quadrats)	37	94*	41.1
Tambopata, Peru (plot 6, 10 quadrats)	27	94*	30.0
Danum Valley, Malaysia (plot 1, 20 quadrats)	29	93#	30.2
Danum Valley, Malaysia (plot 2, 20 quadrats)	28	93#	30.1
Mbalmayo, Cameroon (plot 1, 10 quadrats)	30	136×	22.1
Mbalmayo, Cameroon (plot 2, 10 quadrats)	36	136×	26.5

The proportion of the total fauna sampled with the two sampling regimes is based on the total number of known species from available records (Cameroon and Malaysia) and field sampling as described in this study (Peru)

* This study, see Table S1

Eggleton et al. (1997, 1999)

× Eggleton et al. (1995, 1996); Jones and Eggleton (2000)

Table 3 Bray–Curtis similarity results for species composition collected with the quadrat method (bold) and the transect method

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

0 (zero) means that the plots (A–F) do not share any common species while 1 (one) means that the plots have the same species composition

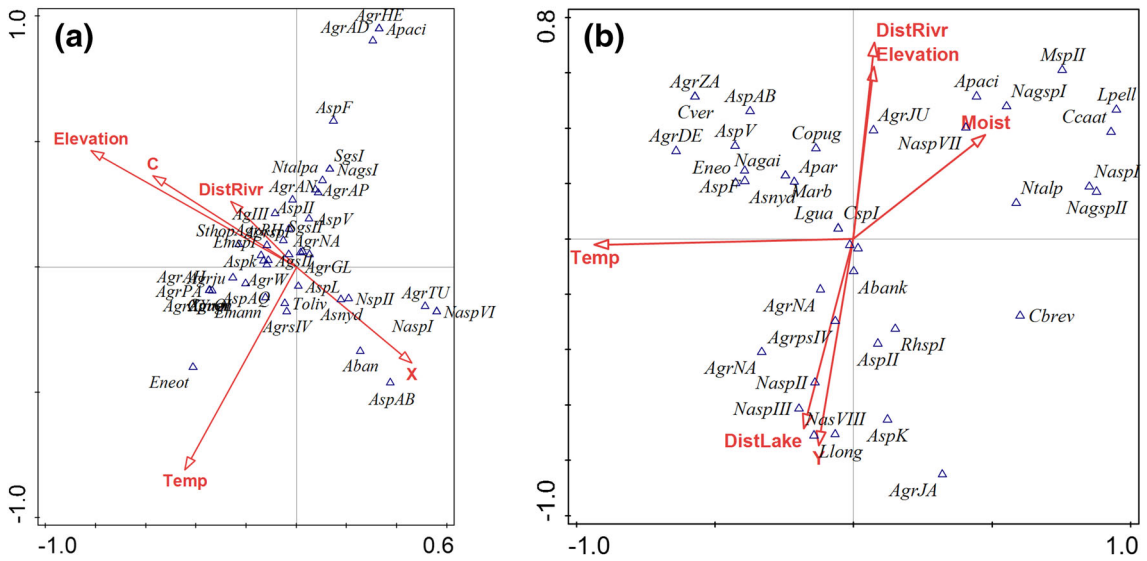

Fig. 2 Canonical correspondence analyses (CCA) ordination plots for species composition in **a** soil and **b** wood and the environmental and spatial variables with a significant effect on the species composition. *DistRivr* distance from the plot to the Madre de Dios River, *DistLake* distance from the plot to the Cococha lake, *Elevation* the elevation of the plot, *Moist* soil moisture, *Temp* soil temperature, C = soil carbon content (%), X = latitude, Y = longitude. Please, refer to Table S1 for complete species names

Environmental variables

Species composition in soil was significantly associated with soil temperature, soil carbon content, elevation and the distance to the main river (Fig. 2; Table 4). Temperature had a significantly positive association with *Anoplotermes*-group sp. AD, *Anoplotermes pacificus* and *Anoplotermes*-group sp. HE while it had a negative association with *Embiratermes neotenicus*. *Longustitermes manni* and *Anoplotermes* sp. V had a significantly negative association with the distance from the river. Elevation and soil carbon content were not significantly associated with particular species; however, the number of species was significantly higher (ANOVA, $F = 9.1$, $P = 0.04$) in the soil in plots with higher carbon which may have had an effect on species composition.

In wood, species composition was significantly associated with soil temperature, soil moisture, elevation, distance to the main river and distance to the lake (Fig. 2; Table 4). *Cylindrotermes brevipilosus, Cylindrotermes caata, Labiotermes pelliceus, Neocapritermes talpa* and *Nasutitermes* sp. I had a significantly negative association with temperature while the association with temperature was significantly positive for *Embiratermes neotenicus*. Both *Cylindrotermes caata* and *Labiotermes pelliceus* had a significantly positive association with moisture and *Nasutitermes* sp. III had a significantly negative association with elevation. *Atlantitermes snyderi* and *Anoplotermes* sp. F had a positive association with the distance from the river while Anoplotermes-*group* sp. AD, *Labiotermes longilabius, Nasutitermes* sp. II, *Nasutitermes* sp. III *and Nasutitermes* sp. VIII had a positive association with the distance from the lake.

Among the spatial variables, x (latitude) was the only variable significantly associated with species composition in soil while y (longitude) was associated with species compo-

Table 4 Canonical Correspondence Analysis (CCA) permutation test results examining the association between species composition in soil and wood with environmental and spatial variables

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

Data were collected using the quadrat method

* Variables that were highly significant (i.e. $\leq$0.01) and used in the partitioning of variation analyses

Table 5 Canonical correspondence analysis (CCA) variation partitioning of environmental and spatial data and the interaction between the two factors for termite species composition in wood (W) and soil (S)

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

Data were collected using the quadrat method

sition in wood (Fig. 2; Table 4). Variation partitioning showed that all environmental variables put together explained a larger proportion of the termite species community patterns in both soil and wood than the spatial variables (Table 5).

Discussion

Comparison and effectiveness of the transect and quadrat methods

While casual sampling was conducted in Cameroon (Eggleton et al. 1996) and Malaysia (Eggleton et al. 1999) it was not undertaken in Peru which may have contributed to the significantly higher proportion of species encountered with the TM in Peru compared with Malaysia. The total number of species (i.e. the site pool) may therefore have been underestimated for the Peruvian site. However, in the Peruvian work, the equivalent of one standard transect (two spatially separated half-transects) was run per plot, and this may have mitigated the autocorrelation effects known to be a disadvantage of transect methods (Bignell 2009). In addition, as sampling in Peru was restricted to breast height, microhabitats such as suspended dead wood were not sampled which may have reduced the potential of finding some species (e.g. Kalotermitidae) known to be associated with this microhabitat. The significant difference in the proportion of known species captured with the TM among the three globally separated sites may therefore be due to undersampling of the total species pool. This suggests that the efficiency of the TM and QM are similar among sites and that the two sampling protocols, therefore, provide robust methods for estimating termite species diversity.

In Peru, the similarity of the species composition among the plots was much higher when using the TM (56 %) compared with the QM (18 %), although presumably the same species pool was sampled. The humus-feeding termites, that were the most abundant in the site, were particularly better represented by the TM. This may be due

to the presence of humus-feeding termites in specialised microhabitats, such as the suspended soil in understory palms (Davies et al. 2003b), that may be better represented with the TM as it covers a greater area and a larger number of points (12 scrapes per section) per plot.

The TM and QM may be used to estimate termite abundance although the TM provides relative abundance (encounters of species) rather than absolute abundance (individuals m^{-2}) that the QM provides. Relative abundance may be useful when comparing transects and total encounters across different regions or gradients of land use intensity (Eggleton et al. 1995, 2002) or altitude (Palin et al. 2010) and may serve as a proxy for species abundance; however, absolute abundance, which requires exhaustive sampling of soil and woody materials, is still required to provide a fuller understanding of the role of termites in ecosystem functioning, since process rates are assumed to be proportional to biomass. The TM is logistically preferable (Eggleton and Bignell 1995; Lawton et al. 1998) and has therefore been much more widely deployed across the humid tropics (see Davies et al. 2003a for a summary), while the QM is less well represented in the literature (Eggleton et al. 1996, 1999; Dahlsjö et al. 2014). Among the advantages of the TM are a relatively rapid sampling time of 20 person-hours per transect, a larger sampling area (200 m^2 per transect) and greater efficiency at capturing a larger proportion of the termite population (Table 6). Against this, the QM provides absolute abundance and biomass data and reduces autocorrelation effects, although high variance at the point scale complicates the statistical presentation and treatment of results. Due to the smaller quadrat sampling area (10 quadrats = 40 m^2), the encounter of termite species with patchy distributions may be lower than transects that include a larger sampling area and explore a larger variety of microhabitats.

Environmental and spatial drivers of species composition patterns

Environmental variables

The total proportion of the termite species compositional patterns explained by individual environmental variables accounted for a larger proportion of the variance than when the environmental variables were analysed together with variation partitioning. The same was true for the spatial variables suggesting that some of the variables may have explained similar species patterns. Individually, the environmental variables shown to be most important for termite species composition in soil and wood were soil temperature, elevation and distance to the main river. Canopy structure may have had an effect on the quadrat soil temperature microclimate (Gehlhausen et al. 2000; Szarzynski and Anhuf 2001) as gaps in the canopy from natural tree falls may have increased the temperature and reduced the 'buffer' effect that the canopy provides (Chen et al. 1999; Davies et al. 2003b; Jones et al. 2003). In soil, the termite species abundances of four humus-feeding (FGIII) species were significantly associated with temperature with the majority of humus-feeders showing a positive trend. In contrast to the present results, studies of termite assemblage structure along disturbance gradients where temperature and canopy cover are key variables, show that soil-feeding termites decline in areas associated with higher soil temperature (Eggleton et al. 1999, 2002; Bignell and Eggleton 2000; Guil et al. 2008; Vasconcellos et al. 2010). Although a higher number of species were encountered in plots with the lowest temperatures, the difference between plots was not significant. As temperature was only sampled once in each of the quadrats the data may not be fully representative of the natural fluctuations within the plots.

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

Two species each in soil and wood (all FGIII) were shown to be significantly associated with the distance from the river. As seasonal inundation may destroy their nesting galleries, humus-feeding termites in the soil were expected to increase away from the river. However, species in soil were shown to have a negative relationship with the distance

Table 6 Comparison of the data collected with the transect method (TM) and quadrat method (QM)

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

from the river while the association was positive in wood. These results suggest that the four humus-feeding species may have been principally affected by other factors such as soil type, which showed high heterogeneity throughout the forest. Species composition in soil was also affected by soil C content that may be linked to the proportion of plant-derived matter in the soil. No particular species were associated with soil carbon content; however, the number of species in plots with high carbon was significantly higher than in plots with low carbon (ANOVA, $F = 9.1$, $P = 0.04$). The distance from the lake showed a positive association with particularly *Nasutitermes* (FGII) species which may be due to habitat heterogeneity. Plot heterogeneity may have affected nesting patterns due to spatial density and quality of dead organic tissues leading to higher site-level diversity of feeding-groups (Hasemann and Soltwedel 2011) and species (see Eggleton 2011).

Spatial variables

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

Conclusion

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

Acknowledgments This study was funded by Natural Environment and Research Council grant NE/G018278/1 to PM and YM. PM is also supported by ARC grant FT110100457. We are grateful to Professor D. Bignell who provided useful insights and comments on the manuscript. We thank Explorers' Inn Tambopata for hosting the research and Tambopata Research Centre, SERNANP and Ministerio de Agricultura for issuing the relevant permits. We are also grateful to our research assistants H. Siccos and H. Lopes. YM is supported by the Jackson Foundation.

References

Abe T. 1987. Evolution of life types in termites. In: *Evolution and Coadaptation in Biotic Communities* (Kawano S., Connell J.H. and Hidaka T., Eds), University of Tokyo Press, Tokyo, pp 125–148

Apolinário F. and Martius C. 2004. Ecological role of termites (Insecta, Isoptera) in tree trunks in central Amazonian rain forests. *For. Ecol. Manage.* **194**: 23–28

Bignell D.E. 2009. Towards a universal sampling protocol for soil biotas in the humid tropics. *Pesq. Agropec. Bras* **44**: 825–834

Bignell D.E. and Eggleton P. 2000. Termites in ecosystems. In: *Termites: Evolution, Sociality, Symbiosis, Ecology* (Abe T., Bignell D.E. and Higashi M., Eds), Kluwer Academic Publishers, Dordrecht, pp 363–387

Bourguignon T., Leponce M. and Roisin Y. 2011a. Beta-diversity of termite assemblages among primary French Guiana rain forests. *Biotropica* **43**: 473–479

Bourguignon T., Šobotník J., Lepoint G., Martin J.-M., Hardy O.J., Dejean A. and Roisin Y. 2011b. Feeding ecology and phylogenetic structure of a complex neotropical termite assemblage, revealed by nitrogen stable isotope ratios. *Ecol. Entomol.* **36**: 261–269

Cancello E., Silva R., Vasconcellos A., Reis Y.T. and Oliveira L.M. 2014. Latitudinal variation in termite species richness and abundance along the Brazilian atlantic forest hotspot. *Biotropica* **46**: 441–450

Chen J., Saunders S., Crow T., Naiman R., Brosofske K., Mroz G., Brookshire B. and Franklin J. 1999. Microclimate in forest ecosystem and landscape ecology variations in local climate can be used to monitor and compare the effects of different management. *Bioscience* **49**: 288–297

Constantino R. 1998. Catalog of the living termites of the new world (Insecta: Isoptera). In: *Arquivos de Zoologia* (Ferreira Brandão C.R. and Marques D.M., Eds), Arquivos de Zoologia, São Paulo, pp 135231

Constantino R. 2002. An illustrated key to Neotropical termite genera (Insecta: Isoptera) based primarily on soldiers. *Zootaxa* **67**: 1–40

Dahlsjö C.A.L., Parr C.L., Malhi Y., Rahman H., Meir P., Jones D.T. and Eggleton P. 2014. First comparison of quantitative estimates of termite biomass and abundance reveals strong intercontinental differences. *J. Trop. Ecol.* **30**: 143–152

Davies A.B., Levick S.R., Asner G.P., Robertson M.P. van Rensburg B.J. and Parr C.L. 2014. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography (Cop.)* **37**: 1–11

Davies R., Eggleton P., Jones D.T., Gathorne-Hardy F.J. and Hernandez L.M. 2003a. Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *J. Biogeogr.* **30**: 847–877

Davies R.G. 2002. Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. *Oecologia* **133**: 233–242

Davies R.G., Hernández L.M., Eggleton P., Didham R.K., Fagan L.L. and Winchester N.N. 2003b. Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. *J. Trop. Ecol.* **19**: 509–524

de Oliveira-Filho A.T. 1992. Floodplain 'murundus' of Central Brazil: evidence for the termite-origin hypothesis. *J. Trop. Ecol.* **8**: 1–19

Donovan S., Eggleton P. and Bignell D. 2001. Gut content analysis and a new feeding group classification of termites. *Ecol. Entomol.* **26**: 356–366

Eggleton P. 2011. An introduction to termites: biology taxonomy and functional morphology. In: *Biology of Termites: A Modern Synthesis* (Bignell D.E., Roisin Y. and Lo N., Eds), Springer Science + Business Media B.V, pp 1–26

Eggleton P., Bignell D., Hauser S., Dibog L., Norgrove L. and Madong B. 2002. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agric. Ecosyst. Environ.* **90**: 189–202

Eggleton P., Bignell D., Sands W., Waite B., Wood T.G. and Lawton J.H. 1995. The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *J. Trop. Ecol.* **11**: 85–98

Eggleton P. and Bignell D.E. 1995. Monitoring the response of tropical insects to changes in the environment: troubles with termites. In: *Insects in a Changing Environment* (Harrington R. and Stork N.E, Eds), Academic Press, London, pp 473–497

Eggleton P., Bignell D.E., Sands W.A., Mawdsley N.A., Lawton J.H., Wood T.G. and Bignell N.C. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.* **351**: 51–68

Eggleton P., Homathevi R., Jeeva D., Jones D., Davies R. and Maryati M. 1997. The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. *Ger. Soc. Trop. Ecol.* **3**: 119–128

Eggleton P., Homathevi R., Jones D.T., MacDonald J., Jeeva D., Bignell D.E., Davies R.G. and Maryati M. 1999. Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.* **354**: 1791–1802

Gehlhausen S., Schwartz M. and Augspurger C. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecol.* **147**: 21–35

Gessner M.O., Swan C.M., Dang C.K., McKie B.G., Bardgett R.D., Wall D.H. and Hättenschwiler S. 2010. Diversity meets decomposition. *Trends Ecol. Evol.* **25**: 372–380

Guil N., Hortal J., Sánchez-Moreno S. and Machordom A. 2008. Effects of macro and micro-environmental factors on the species richness of terrestrial tardigrade assemblages in an Iberian mountain environment. *Landsc. Ecol.* **24**: 375–390

Hasemann C. and Soltwedel T. 2011. Small-scale heterogeneity in deep-sea nematode communities around biogenic structures. *PLoS One* **6**: 1–13

Huising J., Coe R., Cares J., Louzada R., Zanetti R., de Souza Moreira F.M. and Huang S.P. 2008. Sampling strategy and design to evaluate below-ground biodiversity. In: *A Handbook or Tropical Soil Biology* (Moreira F.M.S., Huising E.J. and Bignell D.E., Eds), pp. 17–42

Inward D., Vogler A. and Eggleton P. 2007. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Mol. Phylogenet. Evol.* **44**: 953–967

Jones C., Lawton J. and Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386

Jones D. 2000. Termite assemblages in two distinct montane forest types at 1000 m elevation in the Maliau Basin, Sabah. *J. Trop. Ecol.* **16**: 271–286

Jones D. and Eggleton P. 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *J. Appl. Ecol.* **37**: 191–203

Jones D., Susilo F., Bignell D.E., Hardiwinoto S., Gillison A.N. and Eggleton P. 2003. Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *J. Appl. Ecol.* **40**: 380–391

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

Krishna K. and Araujo R.L. 1968. A revision of the Neotropical termite genus *Neocapritermes* (Isoptera, Termitidae, Termitinae). *Bull. Am. Museum Nat. Hist.* **138**: 83–130

Lawton J.H., Bignell D.E., Bolton B., Bloemers G.F., Eggleton P., Hammond P.M., Hodda M., Holt R.D., Larsen T.B., Mawdsley N.A., Stork N.E., Srivastava D.S. and Watt A.D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**: 72–76

Legendre P. 1990. Quantitative methods and biogeographic analysis. In: *Evolutionary Biogeography of the Marine Algae of the North Atlantic* (Garbary D.J. and South G.R., Eds), Springer-Verlag, Berlin, pp 9–43

Lepš J. and Šmilauer P. (Eds) 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge

Malhi Y., Farfán Amézquita F., Doughty C.E., Silva-Espejo J.E., Girardin C. a. J., Metcalfe D.B., Aragão L.E.O.C., Huaraca-Quispe L.P., Alzamora-Taype I., Eguiluz-Mora L., Marthews T.R., Halladay K., Quesada C. a., Robertson A.L., Fisher J.B., Zaragoza-Castells J., Rojas-Villagra C.M., Pelaez-Tapia Y., Salinas N., Meir P. and Phillips O.L. 2014. The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecol. Divers.* **7**: 1–21

Martius C. 1992. Density, humidity, and nitrogen content of dominant wood species of floodplain forests (várzea) in Amazonia. *Holz als Roh-und Werkstoff.* **50**: 300–303

Martius C. 1994. Termite nests as structural elements of the Amazon floodplain forest. *Andrias* **13**: 137–150

Martius C., Hoefer H. and Verhaagh M. 1994. Terrestrial arthropods colonizing an abandoned termite nest in a floodplain forest of the Amazon River during the flood. *Andrias* **13**: 17–22

Martius C. and Ribeiro J. d'Arc 1996. Colony populations and biomass in nests of the Amazonian forest termite *Anoplotermes banksi* Emerson (Isoptera: Termitidae). *Stud. Neotrop. Fauna Environment* **31**: 82–86

Meltsov V., Poska A., Reitalu T., Sammul M. and Kull T. 2012. The role of landscape structure in determining palynological and floristic richness. *Veg. Hist. Archaeobot.* **22**: 39–49

Meyer V.W., Braack L.E.O., Biggs H.C. and Ebersohn C. 1999. Distribution and density of termite mounds in the northern Kruger National Park, with specific reference to those constructed by *Macrotermes* Holmgren (Isoptera: Termitidae). *African Entomol.* **7**: 123–130

Mill A.E. 1982. Populations of termites Insecta Isoptera in 4 habitats on the lower Rio Negro river Brazil. *Acta Amaz.* **12**: 53–60

Palin O., Eggleton P., Malhi Y., Girardin C., Rozas-Davila A. and Parr C.L. 2010. Termite diversity along an Amazon-Andes elevation gradient, Peru. *Biotropica* **43**: 100–107

Szarzynski J. and Anhuf D. 2001. Micrometeorological conditions and canopy energy exchanges of a neotropical rain forest. *Plant Ecol.* **153**: 231–239

Vasconcellos A., Bandeira A.G., Moura F.M.S., Araújo V.F.P., Gusmão M.A.B. and Constantino R. 2010. Termite assemblages in three habitats under different disturbance regimes in the semi-arid Caatinga of NE Brazil. *J. Arid Environ.* **74**: 298–302