

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

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

Key Words: abundance, biomass, Cameroon, comparative study, density, diversity anomaly, equatorial regions, Malaysia, Peru, Termitoidea

INTRODUCTION

Termites (Blattodea: Termitoidea) are dominant invertebrate decomposers of dead organic matter in tropical and subtropical terrestrial regions (Bignell & Eggleton 2000). They are important ecosystem engineers that affect physical and chemical composition of soil through the breakdown and fixation of carbon and nitrogen, as well as the translocation of soil via the construction of mounds, tunnels and runways (Brussaard 1997, Jones *et al.* 1994, Jouquet *et al.* 2006, 2011). Termites feed on a range of dead organic plant-derived matter and have

been classified into five functional groups depending on the humification (decomposition) of the substrate that they feed on (Donovan *et al.* 2001a, Inward *et al.* 2007) (Table 1).

At present we have a relatively good understanding of tropical termite diversity patterns through sampling of termite species density using a standardized transect protocol (Davies *et al.* 2003, Eggleton *et al.* 1999, Palin *et al.* 2010). Studies have shown that there is a clear difference in termite functional diversity among the main tropical rain-forest regions: for example, large-bodied soil-feeding termite lineages dominate in Africa (Davies *et al.* 2003, Eggleton *et al.* 1994), and Macrotermitinae (fungus-growing termites) are completely absent from South America (Aanen & Eggleton 2005, Davies *et al.*

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

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

2003, Eggleton *et al.* 1994, Jones & Eggleton 2011). These functional differences have been referred to as the ‘termite functional diversity anomaly’ (Davies *et al.* 2003). The functional diversity anomaly has been shown to exist even when different types of land (cleared and lacking canopy to old-growth forests) have been compared (Davies *et al.* 2003, Eggleton *et al.* 1994).

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

We compare biomass and abundance estimates across three equatorial tropical forest regions (Africa (Cameroon), south-east Asia (Malaysian Borneo), South America (Peru)) to investigate whether the functional diversity anomaly exists for biomass and abundance data within functional groups. We aimed to (1) compare species density data for functional groups from the three study sites to confirm the existence of the functional diversity anomaly across our study areas, (2) compare biomass and abundance data for termite functional groups across the three sites, (3) explore the potential causes (termite evolutionary history or present-day climate) of the uncovered differences, and (4) discuss the implications of these differences for ecosystem processes across the main tropical forest blocks.

METHODS

Compilation of data

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

Study sites

Sampling was conducted in relatively undisturbed tropical rain-forest sites in Cameroon, Malaysia (Sabah, Borneo), and Peru. Full site details are provided in Table 2.

Sampling

In each site species density measurements (the number of species per square metre) were sampled using a standardized belt transect (100 × 2 m) (Eggleton *et al.* 1995, Jones & Eggleton 2000). Each transect was divided into 20 sections (5 × 2-m) in which termites from 12 soil pits (12 × 12 × 5 cm) and from all dead wood, nests and runways were collected for one person-hour. Four transects were sampled in Malaysia (Eggleton *et al.* 1999) and Cameroon (Eggleton *et al.* 1995) while six transects were sampled in Peru by CALD.

Sampling for biomass and abundance took place in four plots in Cameroon (two old-growth forest plots and two old regenerating forest plots), and six plots each in Malaysia (three old-growth forest plots and three regenerating forest plots) and Peru (six old-growth forest plots). Non-old-growth forest plots were chosen to be as comparable as possible to old-growth forests. At all sites plots were chosen to represent the main forest type and to take into account the natural variability of vegetation structure. A standardized quantitative sampling protocol based on 2 × 2-m quadrats was used in all three study sites following Eggleton *et al.* (1996). Broadly, the same method was used across all sites with slight variation in soil pit volume, and size and number of quadrats (Table 2). The effect of the differences in sampling effort on species encounters were examined by species rarefaction curves. The rarefaction curves clearly showed that Cameroon had the highest species richness while Malaysia had the lowest species richness despite the low sampling effort in Cameroon and the high sampling effort in Malaysia (Figure 1). As these results did not affect the outcome of this study, all values were made comparable by scaling them to unit area (m²). As this is the first time data from the Peruvian site has been published, a detailed account of the sampling methods is given below.

Table 2. Site descriptions and data sources. Many of the tropical rain forests in Africa are at a higher elevation than lowland forests on other continents as they are located on the central continental plateau (see Davies *et al.* 2003 and Eggleton *et al.* 2002 for examples of African forest site altitudes). It can therefore be argued that most African forests at an altitude similar to the one in Cameroon are considered lowland forests and therefore justifies the comparison of Cameroon with Malaysia and Peru.

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

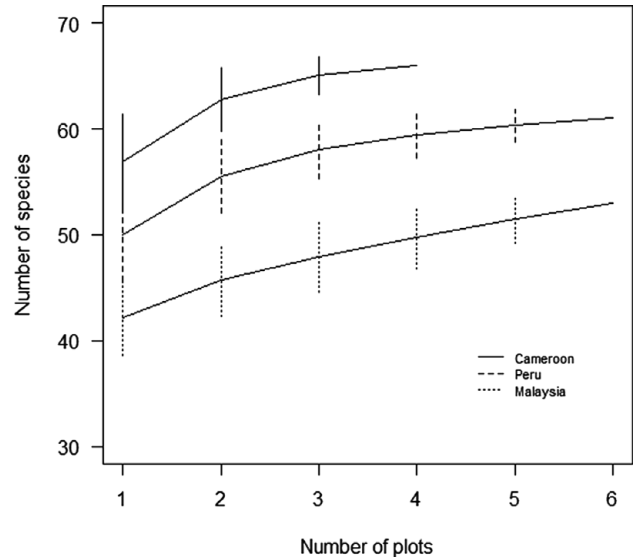


Figure 1. Species rarefaction curves (\pm SD) from Cameroon, Peru and Malaysia. Species richness data were collected in quadrats (2 \times 2 m). Although Cameroon had the lowest number of plots it had the highest number of species. Malaysia with six plots and the highest number of quadrats (20 per plot) had the lowest number of species suggesting that Cameroon may have increased its dominance over Malaysia and Peru had the sampling effort been equal.

In Cameroon, four 30 \times 20-m plots were created in old-growth and old regenerating forest. Termites from all dead wood in 10 quadrats per plot were sampled as well as all termites in 20 \times 20 \times 50-cm soil pit in the centre of each quadrat.

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

In Peru, six 60 \times 50-m plots were set-up at least 300 m apart. Each plot was divided into six subplots (10 \times 50-m each) of which two in each plot were used for the surveys reported in this paper. Those were spaced 30 m apart. Ten 2 \times 2-m quadrats, spaced 5 m apart, were placed in each plot and split between the two subplots, five quadrats in each. Within each quadrat, the total number of worker termites in all dead wood greater than 20 mm diameter were subsampled and extrapolated. Small branches were broken open while larger logs were subsampled with a saw before being split open to extract the termites. In addition, all termites were manually extracted from one soil pit (25 \times 25 \times 10-cm depth) in the centre of each quadrat. Termites were preserved in 70% alcohol and processed

and identified at the Natural History Museum in London (NHM).

Identification

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

Functional group classification

Termites can be classified into five feeding groups by the level of 'humification' (decomposition) of the organic matter upon which they feed (Donovan *et al.* 2001a, Eggleton & Tayasu 2001). The groups range from wood-feeding to soil-feeding termites (Table 1). Wood-feeding termites in FGI feed at the top of the humification gradient and include all wood-feeding termites outside the Termitidae. All other feeding groups, including wood-feeding termites in FGII, fungus-growing termites in FGIIIF, humus-feeding termites in FGIII and true soil-feeding termites in FGIV (Donovan *et al.* 2001a, Inward *et al.* 2007), are in the Termitidae. Only FGIIIF use external fungi (*Termitomyces*: Basidiomycotina) for decomposition of organic matter. They also have, along with all other termites, a complex community of symbiotic gut bacteria, Archaea and protists (Hongoh 2010) which vary in composition and abundance with the degree of humification of the feeding substrate (Brauman *et al.* 2001).

Analysis

Biomass and abundance data were estimated for worker termites only as soldiers represented a small proportion of the total number of individuals. In the majority of the termite species in this study soldiers represented less than 5% of the individuals while 30–40% of the species did not include soldiers at all (*Anoplotermes*-group). *Nasutitermes* (and other *Nasutitermitinae*) is the exception with approximately 25% of all individuals being

soldiers (Vasconcellos & Moura 2010). The biomass and abundance measurements for *Nasutitermes* may therefore have been underestimated, however, this was favoured over the potential error caused by comparing species which did not have soldiers to species with soldiers.

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

RESULTS

Species richness (\pm SD), from quadrats, was highest in Cameroon, when sampling effort was accounted for, followed by Peru and then Malaysia despite Cameroon having the smallest sampling area (Figure 1). The highest termites species richness overall and mean (\pm SE) species density were found in Cameroon with a total of 67 species and $10.3 \pm 1.6 \text{ spp. m}^{-2}$, respectively; followed by Peru with a total of 67 species and species density of $8.4 \pm 1.8 \text{ spp. m}^{-2}$ and then Malaysia with 52 species and species density of $5.8 \pm 0.8 \text{ spp. m}^{-2}$ (Figure 2). Cameroon had the highest mean (\pm SE) biomass and abundance with $14.5 \pm 7.90 \text{ g m}^{-2}$ and $1234 \pm 437 \text{ ind. m}^{-2}$, respectively, followed by Malaysia with $0.719 \pm 0.193 \text{ g m}^{-2}$ and $327 \pm 72 \text{ ind. m}^{-2}$ and then Peru with $0.345 \pm 0.103 \text{ g m}^{-2}$ and $130 \pm 39 \text{ ind. m}^{-2}$.

Soil-feeding termites (FGIII & FGIV) had their highest biomass density in Cameroon while 'wood-feeding' termites (FGI, FGII and FGIIIF) had their highest biomass in Malaysia (Figure 3a). Regionally, FGIV dominated in Cameroon while within Malaysia and Peru FGII and FGIII had the highest biomasses, respectively (Figure 3a). Abundances of all functional groups, with the exception of FGI, were by far the highest in Cameroon (Figure 3b).

Table 3. Results from one-way ANOVA comparing termite biomass and abundance for each functional group across Cameroon, Malaysia and Peru. *P < 0.05, **P < 0.01, ***P < 0.001.

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

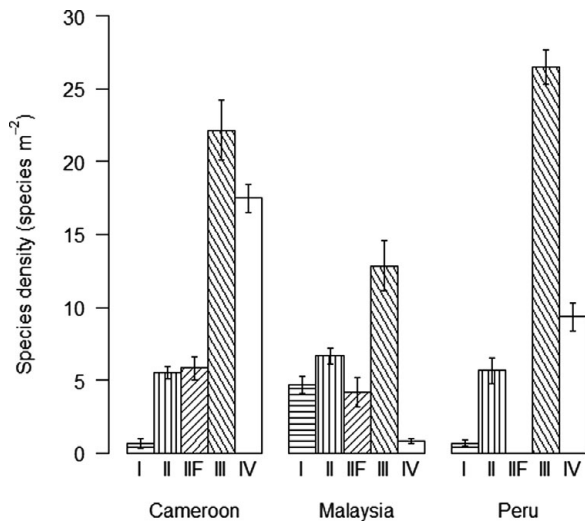


Figure 2. Termite species density (mean ± SE) for functional groups FGI and FGII wood-feeders, FGIIF fungus-growers, FGIII humus-feeders and FGIV true soil-feeders across the three sites, Cameroon, Malaysia and Peru, as estimated by standardized transects (data from Eggleton *et al.* (1996, 1999) and from the Peruvian site).

The high biomasses of wood-feeding termites in both Malaysia and Peru when compared with their relatively low abundances were due to the large body-size of a few wood-feeding termites in those sites (Figure 4). Wood-feeding termites were small-bodied in Cameroon while large-bodied in Malaysia and Peru, while soil-feeding termites were large-bodied in Cameroon and small-bodied in Malaysia and Peru (Figure 4). Regionally, the functional group with highest abundance matched the biomass patterns, except for the high abundance of one species of FGIV in some plots in Malaysia (Figure 3b). The biomass for all functional groups was significantly different across the three continents (Table 3). The same pattern was shown for termite abundance across all functional groups with the exception of wood-feeding termites (FGI) which did not differ among continents (Table 3).

Cameroon had the highest presence of lineages with high biomass concentrated in particularly two lineages, the *Cubitermes*-group and *Apicotermes*-group, while those lineages were not found in any of the other sites

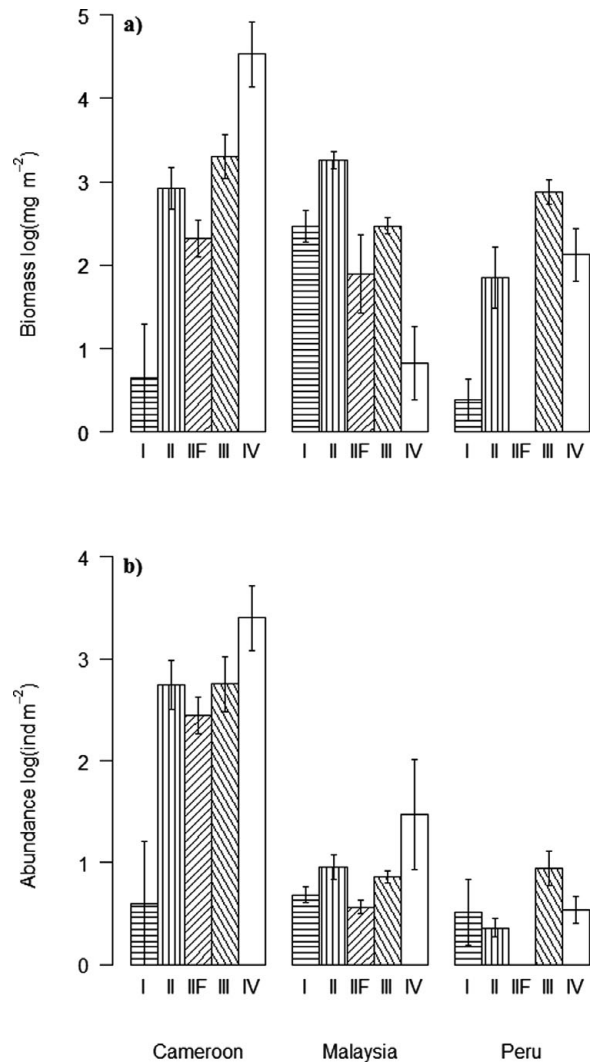


Figure 3. Termite biomass ($\text{mg m}^{-2} (\log(x+1))$) (a) and abundance ($\text{ind m}^{-2} (\log(x+1))$) (b) (mean ± SE) for functional groups FGI and FGII wood-feeders, FGIIF fungus-growers, FGIII humus-feeders and FGIV true soil-feeders across the three sites, Cameroon, Malaysia and Peru.

(Figure 5). The biomass of litter-feeding termites (FGII) in Malaysia was high and concentrated particularly in the *Nasutitermes*-group (Figure 5). The number of lineages in the Peruvian site was relatively low, with a highest biomass of humus-feeding (FGIII) termites, particularly those in the *Anoplotermes*-group and *Amitermes*-group (Figure 5).

DISCUSSION

Comparison of termite assemblage patterns

The main objective of this study was to investigate the existence of the functional diversity anomaly for biomass

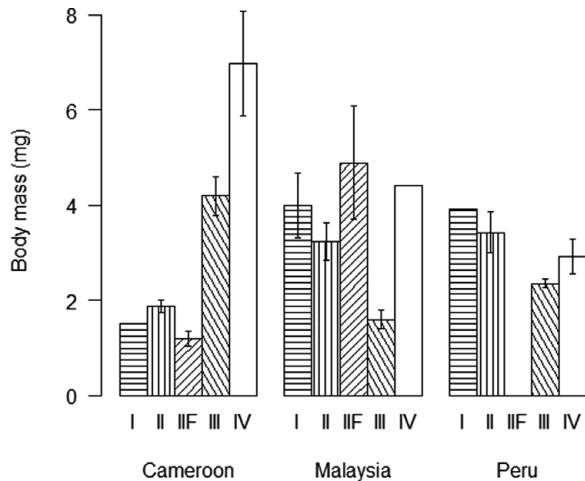


Figure 4. Individual termite body mass (mg) (mean ± SE) in each of the five functional groups, FGI and FGII wood-feeders, FGIII fungus-growers, FGIII humus-feeders and FGIV true soil-feeders, across the three sites, Cameroon, Malaysia and Peru.

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

Potential causes of the functional diversity anomaly

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

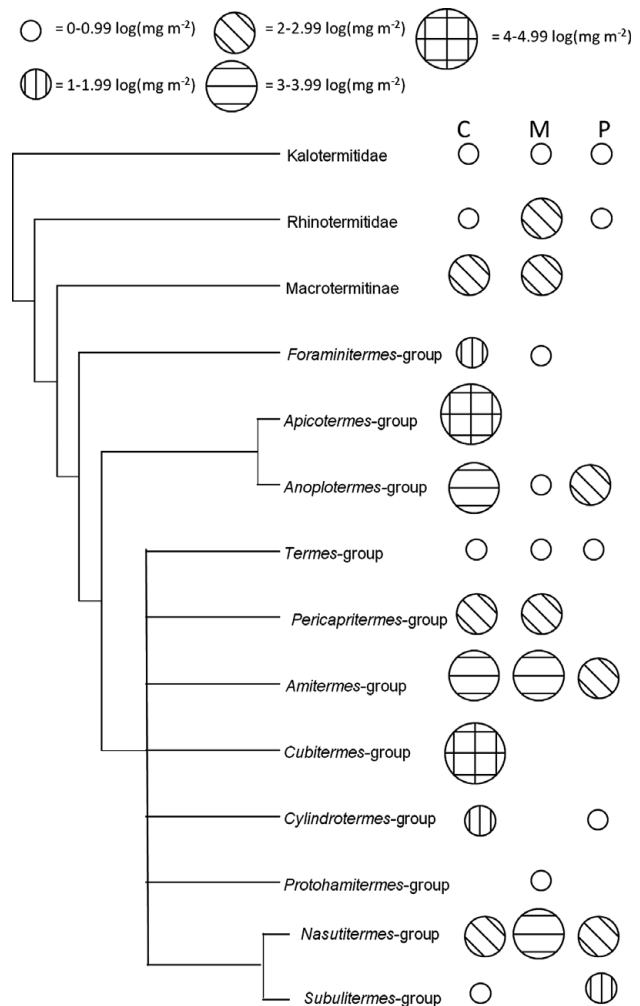


Figure 5. Phylogenetic tree including termite lineages from each site. The log transformed biomass (mg m^{-2}) of each lineage is represented by the size and hatched lines within the circles. No circle means that the lineage is absent from the region while lineages with white circles may be absent or have low biomass in the site. The three columns of circles represent each of the sites in Cameroon (C), Malaysia (M) and Peru (P).

bodied soil-feeding termites and relatively smaller-bodied wood-feeding termites compared with Malaysia and Peru. Size distribution across the functional groups is associated with the presence or absence of particular lineages. The high species density of the large-bodied species in the *Cubitermes*-group and *Apicotermes*-group (Jones & Eggleton 2011) contributed disproportionately to the high biomass of FGIV termites, and the biomass overall, at the Cameroonian site.

Fungus-growing termites are absent from the whole of South America (Aanen & Eggleton 2005), while humus-feeding and litter-feeding *Anoplotermes*-group and *Nasutitermes*-group termites (FGIII & FGII) had high biomasses in the Peruvian site. Additionally, FGIII were small-bodied but with high abundance

while FGII were large-bodied with low abundance. In Malaysia the presence of FGIV was low, with only one species recorded; while the dominance of wood-feeding termites in Malaysia was influenced by the presence of particularly Macrotermitinae and Rhinotermitinae. The dominance of the two large-bodied FGIV lineages in Cameroon, the absence of Macrotermitinae in Peru, and the low abundance of true soil-feeding termites (FGIV) in Malaysia strongly contributed to the different patterns of biomass and abundance across sites.

The presence or absence of certain termite lineages therefore appears to be an important correlate of biomass and abundance patterns, as some lineages are widely distributed (*Nasutitermes*-group and the *Amitermes*-group) while others are restricted to certain regions (*Cubitermes*-group, *Apicotermes*-group and Macrotermitinae). Our data therefore support earlier suggestions (Bignell & Eggleton 2000, Davies *et al.* 2003, Jones & Eggleton 2011) that present-day termite distributions are driven by the evolutionary history of termites and not present-day climate. Although temperature and moisture may influence regional termite assemblages (Eggleton *et al.* 1996, 1999; Palin *et al.* 2010), the distribution of feeding groups is more likely to be linked to termite evolutionary history through differential patterns of both dispersal and the regional diversification of functional groups within lineages (Aanen & Eggleton 2005, Eggleton *et al.* 1994, Jones & Eggleton 2011). In addition, the climatic similarity of the studied habitats, all lowland tropical rain forests, suggests that climate is not the most important factor in explaining the functional diversity anomaly. Moreover, climate can only act as a filter to allow or exclude species through their environmental tolerances. This filter can only act on the regional pool of species and that composition of that regional pool is dependent on historical factors that usually predate the onset of contemporary climates. In this case the regional pools are fundamentally distinct at the major lineage level and those lineages are dated to be several million years old (Eggleton, unpubl. data).

The Termitidae (FGII–FGIV) probably evolved and dispersed from Africa with higher dispersal rates for wood-feeding termites compared with soil-feeding termites (Aanen & Eggleton 2005, Jones & Eggleton 2011). Soil-feeding termites such as the *Cubitermes*-group and the *Apicotermes*-group are probably more dependent on the buffered environment within tropical rain forest, which offer less fluctuation in temperature and moisture compared with non-forest habitats (Davies *et al.* 2003). Therefore, arid and semi-arid habitats such as woodland, savanna and desert would be more likely to be barriers to dispersal for those groups. Wood-feeding termites on the other hand (with the probable exception of fungus-

growing termites) are more likely to have been able to disperse across different types of barrier, including bodies of water, because of their rafting abilities (Gathorne-Hardy *et al.* 2000). These activities are probably dependent on their harder and thicker exoskeletons, which support their foraging behaviour (Nalepa 2011) and therefore the likelihood of allowing dispersal across suboptimal habitat types. The biogeographical patterns of wood-feeding termites may therefore have evolved through a wider range of dispersing types than soil-feeding termites, which may have had relatively low dispersal rates. However, it seems likely that soil-feeding (particularly FGIII) termites may have evolved independently from rafting wood-feeding termites on several occasions across the continents (Inward *et al.* 2007, Jones & Eggleton 2011) leading to the relatively depauperate humus- and soil-feeder assemblages of the non-African sites.

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

Possible implications of biomass and abundance patterns on ecosystem processes

The patterns of biomass and abundance uncovered here are likely to affect ecosystem processes across equatorial sites differentially because of the differential dominance of particular functional groups (Ji & Brune

2001, Jouquet *et al.* 2011, Schuurman 2005). While it was shown that true soil-feeding (group IV) termites dominated the Cameroonian site, litter-feeding and humus-feeding (group II and III) termites dominated the sites in Malaysia and Peru, respectively. This biomass and abundance anomaly may have an effect on the processes of soil and wood decomposition and in turn the turnover and availability of nutrients in the respective sites.

True soil-feeding termites (group IV) are not only physiologically distinct from wood-feeding termites but also have more complex guts than humus-feeding (group III) termites (Ji & Brune 2005). FGIV termites break down bacterial polysaccharides as a carbon energy source while stimulating the mineralization of soil cellulose and protein (Ji & Brune 2001, 2005). True soil-feeding (group IV) *Cubitermes* species have also been shown to influence soil pH, organic carbon content and water content (Donovan *et al.* 2001b). Further, group IV termites have been shown to stabilize nitrogen in a form which plants can use, releasing no more than 3% to the atmosphere compared with other macrofauna (e.g. earthworms) for which emission of N₂ gas is higher (Ngugi & Brune 2012). Tropical forest soils are however generally neither nitrogen nor carbon limited, so these termite effects may only be of local importance, for example, by enhancing soil heterogeneity (Donovan *et al.* 2001b). Phosphorus (P), on the other hand, is in short supply (Aragão *et al.* 2009) but seems to accumulate in termite mound and nest material (Chapuis-Lardy *et al.* 2011, Rückamp *et al.* 2010). Mound and nest erosions may increase soil P content through, for example, leaching (Chapuis-Lardy *et al.* 2011), although erosion rates have been shown to vary greatly both within and across species (Brossard *et al.* 2007). We therefore predict that the presence of true soil-feeding termites, particularly of the genus *Cubitermes*, may affect soils by influencing soil heterogeneity.

Macrotermitinae (fungus-growing termites) have been shown to be very important for the decomposition of wood. Results from African studies in savanna woodlands have shown that 90% of the termite wood decomposition was due to fungus-growing termites, and *Macrotermes* in particular (Buxton 1981, Schuurman 2005, Wood & Sands 1978). Both Cameroon and Malaysia had fungus-growing termites (Eggleton *et al.* 1996, 1999) while these were absent from Peru altogether. We suggest it is likely therefore that sites with Macrotermitinae may have higher wood decomposition rates than the sites without fungus-growing termites, holding all other factors constant. For example, annual consumption by species of Macrotermitinae was recorded as 35.5 g m⁻² and 669 kJ m⁻² compared with only 20.0 g m⁻² and 377 kJ m⁻² for other wood-feeding species (Wood & Sands 1978).

Conclusion

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

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LITERATURE CITED

- AANEN, D. & EGGLETON, P. 2005. Fungus-growing termites originated in African rain forest. *Current Biology* 15:851–855.
- ARAGÃO, L. E. O. C., MALHI, Y., METCALFE, D. B., SILVA ESPEJO, J. E., JIMENEZ, E., NAVARRETE, D., ALMEIDA, S., COSTA, A. C. L., SALINAS, N., PHILLIPS, O. L., ANDERSON, L. O., ALVAREZ, E., BAKER, T. R., GONCALVEZ, P. H., HUAMAN-OVALLE, J., MAMANI-SOLORZANO, M., MEIR, P., MONTEAGUDO, A., PATINO, P., PENUELA, M. C., PRIETO, A., QUESADA, C. A., ROZAS-DAVILA, A., RUDAS, A., SILVA, J. A. & VASQUEZ, R. 2009. Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* 6:2759–2778.
- BIGNELL, D. E. & EGGLETON, P. 2000. Termites in ecosystems. Pp. 363–387 in Abe, T., Bignell, D. E. & Higashi, M. (eds.). *Termites: evolution, sociality, symbiosis, ecology*. Kluwer Academic Publishers, Dordrecht.

- BRAUMAN, A., DORÉ, J., EGGLETON, P., BIGNELL, D., BREZNAK, J. & KANE, M. 2001. Molecular phylogenetic profiling of prokaryotic communities in guts of termites with different feeding habits. *FEMS Microbiology Ecology* 35:27–36.
- BROSSARD, M., LÓPEZ-HERNÁNDEZ, D., LEPAGE, M. & LEPRUN, J.-C. 2007. Nutrient storage in soils and nests of mound-building *Trinervitermes* termites in Central Burkina Faso: consequences for soil fertility. *Biology and Fertility of Soils* 43:437–447.
- BRUSSAARD, L. 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 26:563–570.
- BUXTON, R. 1981. Termites and the turnover of dead wood in an arid tropical environment. *Oecologia* 51:379–384.
- CHAPUIS-LARDY, L., BAYON, R. C., BROSSARD, M., LOPEZ-HERNANDEZ, D. & BLANCHART, E. 2011. Role of soil macrofauna in phosphorus cycling. Pp. 199–214 in Brünemann, E. K., Oberson, A. & Frossard, E. (eds.). *Phosphorus in action*. Springer, Heidelberg.
- CONSTANTINO, R. 2002. An illustrated key to Neotropical termite genera (Insecta: Isoptera) based primarily on soldiers. *Zootaxa* 67:1–40.
- DAVIES, R., EGGLETON, P., JONES, D. T., GATHORNE-HARDY, F. J. & HERNANDEZ, L. M. 2003. Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *Journal of Biogeography* 30:847–877.
- DONOVAN, S., EGGLETON, P. & BIGNELL, D. 2001a. Gut content analysis and a new feeding group classification of termites. *Ecological Entomology* 26:356–366.
- DONOVAN, S., EGGLETON, P. & DUBBIN, W. 2001b. The effect of a soil-feeding termite, *Cubitermes fungifaber* (Isoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. *Pedobiologia* 11:1–11.
- EGGLETON, P. & TAYASU, I. 2001. Feeding groups, lifestyles and the global ecology of termites. *Ecological Research* 16:941–960.
- EGGLETON, P., WILLIAMS, P. & GASTON, K. 1994. Explaining global termite diversity: productivity or history? *Biodiversity and Conservation* 330:318–330.
- EGGLETON, P., BIGNELL, D. E., SANDS, W. A., WAITE, B., WOOD, T. G. & LAWTON, J. H. 1995. The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo forest reserve, southern Cameroon. *Journal of Tropical Ecology* 11:85–98.
- EGGLETON, P., BIGNELL, D. E., SANDS, W. A., MAWDSLEY, N. A., LAWTON, J. H., WOOD, T. G. & BIGNELL, N. C. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society: Biological Sciences* 351:51–68.
- EGGLETON, P., HOMATHEVI, R., JONES, D. T., MACDONALD, J., JEEVA, D., BIGNELL, D. E., DAVIES, R. G. & MARYATI, M. 1999. Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. *Philosophical Transactions of the Royal Society: Biological Sciences* 354:1791–1802.
- EGGLETON, P., BIGNELL, D. & HAUSER, S. 2002. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agriculture, Ecosystems and Environment* 90:189–202.
- GATHORNE-HARDY, F., JONES, D. T. & MAWDSLEY, N. A. 2000. The recolonization of the Krakatau islands by termites (Isoptera), and their biogeographical origins. *Biological Journal of the Linnean Society* 71:251–267.
- HONGO, Y. 2010. Diversity and genomes of uncultured microbial symbionts in the termite gut. *Bioscience, Biotechnology, and Biochemistry* 74:1145–1151.
- INWARD, D., VOGLER, A. & EGGLETON, P. 2007. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Molecular Phylogenetics and Evolution* 44:953–967.
- JI, R. & BRUNE, A. 2001. Transformation and mineralization of 14 C-labeled cellulose, peptidoglycan, and protein by the soil-feeding termite *Cubitermes orthognathus*. *Biology and Fertility of Soils* 33:166–174.
- JI, R. & BRUNE, A. 2005. Digestion of peptidic residues in humic substances by an alkali-stable and humic-acid-tolerant proteolytic activity in the gut of soil-feeding termites. *Soil Biology and Biochemistry* 37:1648–1655.
- JONES, C., LAWTON, J. & SHACHAK, M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- JONES, D. & EGGLETON, P. 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology* 37:191–203.
- JONES, D. T. & EGGLETON, P. 2011. Global biogeography of termites: a compilation of sources. Pp. 477–498 in Bignell, D. E., Roisin, Y. & Lo, N. (eds.). *Biology of termites: a modern synthesis*. Springer Science+Business Media B.V., Dordrecht.
- JOUQUET, P., DAUBER, J., LAGERLÖF, J., LAVELLE, P. & LEPAGE, M. 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* 32:153–164.
- JOUQUET, P., TRAORÉ, S., CHOOSAI, C., HARTMANN, C. & BIGNELL, D. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology* 47:215–222.
- LO, N. & EGGLETON, P. 2011. Termite phylogenetics and cladogenesis with symbionts. Pp. 27–50 in Bignell, D. E., Roisin, Y. & Lo, N. (eds.). *Biology of termites: a modern synthesis*. Springer Science+Business Media B.V., Dordrecht.
- NALEPA, C. A. 2011. Body size and termite evolution. *Evolutionary Biology* 38:243–257.
- NGUGI, D. K. & BRUNE, A. 2012. Nitrate reduction, nitrous oxide formation, and anaerobic ammonia oxidation to nitrite in the gut of soil-feeding termites (*Cubitermes* and *Ophiotermes* spp.). *Environmental Microbiology* 14:860–871.
- NOBRE, T., EGGLETON, P. & AANEN, D. K. 2010. Vertical transmission as the key to the colonization of Madagascar by fungus-growing termites? *Proceedings of the Royal Society: Biological Sciences* 277:359–365.
- PALIN, O., EGGLETON, P., MALHI, Y., GIRARDIN, C., ROZAS-DAVILA, A. & PARR, C. L. 2010. Termite diversity along an Amazon–Andes elevation gradient, Peru. *Biotropica* 43:100–107.

- RÜCKAMP, D., AMELUNG, W., THEISZ, N., BANDEIRA, A. G. & MARTIUS, C. 2010. Phosphorus forms in Brazilian termite nests and soils: relevance of feeding guild and ecosystems. *Geoderma* 155:269–279.
- SCHURMAN, G. 2005. Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology* 86:1236–1249.
- VASCONCELLOS, A. & MOURA, F. 2010. Wood litter consumption by three species of *Nasutitermes* termites in an area of the Atlantic Coastal Forest in northeastern Brazil. *Journal of Insect Science* 10:1–9.
- WOOD, T. G. & SANDS, W. A. 1978. The role of termites in ecosystems. Pp. 245–292 in Brian, M. V. (ed.). *Production ecology of ants and termites*. Cambridge University Press, Cambridge.