



## Original article

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



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## ABSTRACT

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

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## 1. Introduction

## 1.1. Allometric scaling laws

Body mass is one of the most studied physiological traits in ecology as, among other things, it influences metabolic rate,

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

$$\dot{B} = \bar{M}^b \quad (1)$$

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

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

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

$$\hat{B}_{tot} = \hat{B} \cdot N \quad (2)$$

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

## 1.2. Allometry in termites

Termites are one of the most important invertebrate decomposers, particularly in the tropics where their abundance and range of feeding-groups are high (Bignell and Eggleton, 2000; Donovan et al., 2001a; Eggleton et al., 1999, 1996) partly due to their symbiotic relationship with gut biota (Hongoh, 2010). The termite gut is a specialised habitat for bacteria, archaea, and protists which, along with termites' specialised guts and mandibles (wood-feeders), make them highly efficient decomposers (Eggleton, 2011; Hongoh, 2010). Termites have been categorised into five feeding-groups depending on the humification (decomposition) of the material they feed on (Donovan et al. 2001a,b). These feeding-groups range from wood-feeding termites, which feed on sound dead wood, to true soil-feeding termites, which feed on soil organic matter in mineral soil with no visible plant remains (Table 1). The difference in particle size of the diets of humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites, although no difference in isotope composition has been found (see Bourguignon et al. (2011) for C and N stable isotope ratios), may mean that the two feeding-groups metabolise their substrates in different ways. It is known, for example, that FGIV feeders have a more complex gut than FGIII feeding termites to allow the

decomposition of nutritionally poorer soil (Ji and Brune, 2005). Species of *Cubitermes* (FGIV soil-feeding termites) have been shown to stabilise nitrogen in a form which plants can utilise by increasing soil ammonia content (Ngugi et al., 2011; Ngugi and Brune, 2012). Through decomposition of organic matter and the construction of tunnels, runways and nesting structures (e.g. mounds) termites influence nutrient availability and distribution which affects water and air movement through the soil and promote plant growth (Jouquet et al., 2011, 2006). These activities make termites important ecosystem engineers as they contribute to the structural and chemical composition of their habitat (Brussaard et al., 1997; Jones et al., 1994).

Eggleton et al. (1998) investigated the relationship between total metabolic rate and body mass in two termite feeding-group assemblages (wood-feeding and soil-feeding termites) in Cameroon. Their analysis showed that small to medium-bodied wood-feeding termites had higher metabolic rates ( $O_2$  consumption per unit weight combined with population density to give energy use per unit area) than large-bodied species while large-bodied soil-feeding species had the highest metabolic rates. The latter indicates that the larger-bodied soil-feeding termites in Cameroon have a larger energy throughput (Damuth, 1981) than species of other mass classes due to their proportionally higher metabolic rate. Recent biomass estimates across the three study sites (Dahlsjö et al., 2014) show that termite biomass varies among regions with highest biomass per unit ground area being found for large-bodied soil-feeding termites (*Cubitermes*-group & *Apicotermes*-group) in Cameroon. These very large soil-feeding termites are absent from Asia and South America.

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

In this study we (a) treat Damuth's law as a null hypothesis (Isaac et al., 2013), by testing the observed slope values for population density and body mass against the predicted value ( $-0.75$ ) of Damuth's law, for three feeding-groups (true soil-feeding termites FGIV, humus-feeding termites FGIII and wood-feeding termites FGI, FGII and FGIIIF) across three regions (Cameroon, Peru and Malaysia) and (b) discuss the causes of the observed patterns (biogeography and evolution) and the potential implications on ecosystem processes. We predict that the dominance of large-bodied true soil-feeding (group IV) termites in Cameroon will greatly impact on the population density – body mass relationships and is, therefore, expected to diverge from Damuth's law. The population density – body mass relationships in all other feeding-groups are expected to follow Damuth's law.

**Table 1**

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

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

## 2. Methods

### 2.1. Study site

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

### 2.2. Sampling

Broadly, the same method was adopted in all the three sites with slight variations in quadrat size and number (Table 2). This variation in sampling approach was overcome by scaling the data in each case to unit area (m<sup>2</sup>). Data from Cameroon and Malaysia were compiled from Eggleton et al. (1996) and (1999), respectively, while data from Peru were collected by the first author (CALD). In Peru, six 70 m × 50 m plots were set-up at least 300 m apart. Each plot was divided into six sub-plots (10 m × 50 m each) of which two in each plot were used for the surveys reported in this paper. Those were spaced 30 m apart. Ten 2 m × 2 m quadrats, spaced five metres apart, were placed in each plot and split between the two sub-plots, five quadrats in each. Within each quadrat, the number of termites in all dead wood greater than 20 mm diameter were sub-sampled and extrapolated. Small branches were broken open while larger logs were sub-sampled with a saw before being split open to extract the termites. In addition, all termites were manually extracted from one soil pit (25 cm × 25 cm × 10 cm depth) in the centre of each quadrat. Termites were preserved in 70% alcohol and identified by CALD at the Natural History Museum (NHM) in London.

### 2.3. Feeding-groups

Termites were classified into five feeding-groups by the level of humification (decomposition) of the organic matter they feed on (Donovan et al. 2001a,b). The feeding substrates of the feeding-groups range from wood at the top of the humification gradient and soil at the bottom of the humification gradient. FGI feed on wet and dry wood and include all termite families except the Termitidae. FGII and FGIIIF feed on wood and leaf litter, but only FGIIIF, the fungus-growing subfamily Macrotermitinae, use external symbiotic fungi (*Termitomyces*: Basidiomycotina) for decomposition (Table 1) (Aanen and Eggleton, 2005; Nobre et al., 2011). FGIII feed on soil with microscopically visible plant material while FGIV (true soil-feeding termites) feed at the bottom of the humification gradient on low quality soil with high mineral content.

**Table 2**  
Summary of the differences in sampling methods across the study sites.

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

### 2.4. Data analyses

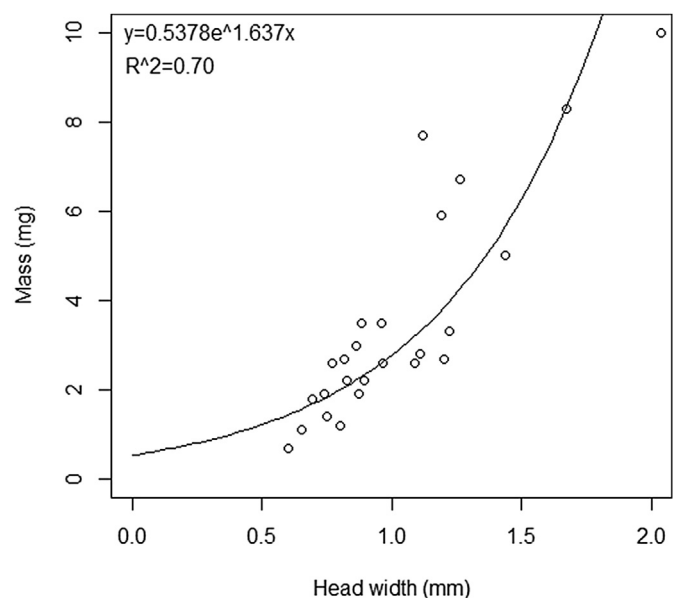
A total of 186 species of termites were used in this study representing all five feeding-groups. FGI, FGII and FGIIIF (Table 1) were grouped as wood-feeders due to the relatively low number of representatives in each feeding-group particularly in Peru and to an extent in Cameroon. In Peru, only FGI and FGII were pooled as fungus growing (FGIIIF) termites are absent from Peru, and from the whole of South America (Aanen and Eggleton, 2005). Humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites were analysed separately (note that there are very few FGIV termites in Malaysia). Here, the population density represents the average number of individual termites of a feeding-group found per square metre.

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

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

$$M = 0.5378e^{1.637w} \quad (3)$$

where  $M$  is the mass in mg and  $w$  is the head width in mm (Fig. 1). Equation (3) was used to calculate the average mass of each species found in the plot in Peru (see Eggleton et al. (1999 and 1996) for mass estimates in Malaysia and Cameroon). The head widths of at least ten individuals from each species were used to create the average mass estimates.



**Fig. 1.** Termite worker head width and body mass data from Malaysia. The worker termite head width – body mass regression was used to calculate the mass of worker termites in the sites in Peru.

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

### 3. Results

None of the termite feeding-groups had population density-body mass relationships where  $M^{-0.75}$  as proposed in Damuth's law (Fig. 2, Table 3). However, only population density-body mass relationships in large-bodied true soil-feeding (FGIV) termites in Cameroon (*slope.test*:  $M^{2.7}$ ,  $R^2 = 0.44$ ,  $P = 0.0007$ ) and large-bodied wood-feeding (FGI & FGII) termites in Peru (*slope.test*:  $M^{1.5}$ ,  $R^2 = 0.46$ ,  $P = 0.005$ ) were significantly different from the expected values given by Damuth's law (Fig. 2, Table 3). Population density and body mass showed weak correlations in the humus-feeding termites in all sites (Table 3) which is likely to be due to variations in population density with little variation in body mass (Fig. 2). The non-significant population density - body mass relationships in soil-feeding termites in Peru may be due to the small number of samples and the large scattering of data points around the mean (Fig. 2 and Table 3). True soil-feeding termites were rare in Malaysia with only one species encountered in the plot. The small data set for true soil-feeding termites in Malaysia did not contribute to the analyses and may have restricted the overall comparison of true soil-feeding termites across the three regions. Additionally, while the wood-feeding termites in all sites were well represented the large scattering of the data around the mean in Cameroon and Malaysia may have contributed to the non-significant results in those sites.

### 4. Discussion

Although none of the feeding-groups had the same scaling

**Table 3**

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

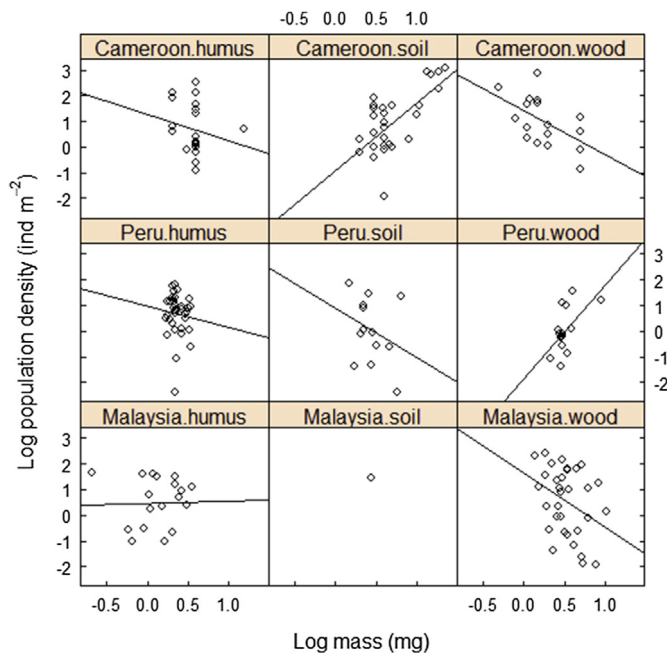
Geographic region	Functional group	n	R	R <sup>2</sup>	Slope (OLS)
Cameroon	humus	20	-0.19	0.038	-1.0
	soil	29	0.66	0.44	2.7***
	wood	18	-0.56	0.31	-1.7
Peru	humus	34	-0.06	0.003	-1.0
	soil	13	-0.10	0.01	-1.2
	wood	15	0.68	0.46	1.5**
Malaysia	humus	19	0.24	0.00061	0.1
	soil	1	NA	NA	NA
	wood	32	-0.23	0.12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

exponent as proposed by Damuth's law ( $M^{-0.75}$ ) our results suggest that the largest (significant) diversion from the expected value ( $-0.75$ ) was found in large-bodied true soil-feeding termites in Cameroon, with a slope of  $2.7 \pm 0.6$  SE, and large-bodied wood-feeding termites in Peru with a slope of  $1.5 \pm 0.7$  SE. These results suggest that the larger-bodied species of true soil-feeding termites in Cameroon and wood-feeding termites in Peru produce a larger number of individuals per unit area than expected by their body mass and so use more energy than expected by their body mass in a population with species of different sizes (Damuth, 1981).

#### 4.1. Biogeography and evolution: potential causes of the allometric patterns

The high energy throughput in large-bodied true soil-feeding termites in Cameroon may be due to the dominance of two large-bodied lineages (the *Cubitermes*- and *Apicotermes*-groups) endemic to Africa (Davies et al., 2003; Jones and Eggleton, 2011). The absence of these lineages from other biogeographical regions may be due to their inability to form colonies in dead wood, and so there is limited potential for dispersal (i.e. by rafting) to other regions (Davies et al., 2003). In addition, they require wet, relatively buffered climatic conditions and so are unlikely to disperse through the arid or semi-arid environments that might have provided land bridges in the past (e.g. between Africa and Asia) (Davies et al., 2003). The dispersal of many soil-feeding termites has been limited in termite evolutionary history and although in many cases humus-feeding (FGIII) termites have evolved from lineages of wood-feeding termites, true soil-feeding (IV) termites have evolved relatively rarely outside Africa (Davies et al., 2003; Jones and Eggleton, 2011). Evolution towards larger-bodied soil-feeding termites in Cameroon may have been due to the enhanced nutrient uptake related to longer retention time that increases with gut size (Illius and Gordon, 1992). This is particularly important in organisms feeding on a nutritionally poor substrates (Eggleton et al., 1998). The relatively small-bodied soil-feeding termites in Peru and Malaysia may be due to the presence of other evolutionary pressures such as the evolution of closed canopy forests that may have impacted on the development of true soil-feeding termites in those regions (Davies et al., 2003).

The diversity of wood-feeding termites is higher in Malaysia compared with Cameroon and Peru (Dahlsjö et al., 2014; Davies et al., 2003) and fungus-growing (FGIIF) termites are absent from Peru and the whole of South America (Aanen and Eggleton, 2005). While the majority of wood-feeding termites in Peru were small-bodied, a few large-bodied species (e.g., *Nasutitermes* sp. I and sp. VI), had very high population densities. The *Nasutitermes* genus commonly occurs in all the study regions (Jones and Eggleton, 2011), however, only in Peru did body mass have a significantly



**Fig. 2.** Allometric scaling relationships between log body mass (mg) and log population density for humus-feeding termites, true soil-feeding termites and wood-feeding termites in Cameroon, Peru and Malaysia.

positive relationship with population density. The low diversity of wood-feeding termites in Peru, influenced by the absence of fungus-growing termites, may have reduced the competition for woody substrates (see Table 1) and enabled this genus to thrive. Although, the effect of fungus-growing wood-feeding termites on non-fungus-growing wood-feeding termites has not yet been quantified the absence of this lineage may have affected the population density-body mass relationship for wood-feeding termites in Peru. However, this hypothesis must be tested through exclusion of fungus-growing termites before such a conclusion may be reached.

#### 4.2. Allometry in termites and the potential impacts on ecosystem processes

Termites contribute to the breakdown of organic matter, turnover of nutrients, fixation and mobilisation of elements which make them exceptionally important in tropical ecosystems (Jouquet et al., 2011, 2006; Yamada et al., 2006). As body mass may influence the efficiency of nutrient uptake and turnover in different trophic groups the dominance of the true soil-feeding termites in Cameroon and wood-feeding termites in Peru is likely to have an impact on ecosystem processes. Illius and Gordon (1992) argue that gut retention time is longer in large-bodied animals with large guts which enhances nutrient uptake. Longer retention time plays an important role in termites and other organisms feeding on nutritionally poor substrates and may therefore play a particularly important role for true soil-feeding termites. Wood-feeding termites benefit from being small-bodied as smaller mandibles may enable them to break wood into finer pieces and subsequently increase the surface-to-volume ratio that enhance nutrient uptake (Eggleton et al., 1998; Nalepa, 2011). However, wood is also a nutritionally poor substrate and large-bodied *Nasutitermes* may feed on more recalcitrant materials with high lignin content, although no empirical evidence exists, for which increased gut retention time would be advantageous.

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

In both Peru and Malaysia the wood-feeding termites have been shown to be larger-bodied than the true soil-feeding and humus-feeding termites while the opposite has been shown to be true for the different feeding-groups in Cameroon (Dahlsjö et al., 2014). It may therefore be suggested that wood-feeding termites in Malaysia and Peru, to a larger extent, benefit from being large-

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

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#### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2015.01.003>.

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