



Short communication

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



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ABSTRACT

We present results from one of the first *in situ* soil termite exclusion experiments using translocated soil that was not colonised by termites prior to the experiment. Macrofauna were excluded or included using fine (0.3 mm) and coarse (5 mm) mesh, respectively. We found that termites were the most dominant macrofauna in the macrofauna-included samples throughout the sampling period. Additionally, C and N depletion rates were consistently higher in samples with macrofauna than without macrofauna despite the seasonal decline of termites at the start of the wet season. This suggests that the presence of termites in soil promotes C and N depletion that may be linked to the passage of soil through the termite gut and the affect termites have on bioturbation and nutrient distribution.

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Soils are complex, heterogeneous and highly speciose environments which are vital components of most terrestrial habitats (Wolters, 2001; Decaëns et al., 2006; Lavelle et al., 2006). Soil biota are essential for soil functioning (Ekschmitt and Grif, 1998; Wolters, 2001) as they create soil bioturbation and contribute to decomposition of organic matter (Jouquet et al., 2006, 2011). The soil macrofauna in the tropics, particularly in lowland rain forests, is usually dominated by termites, which are often present at high densities (see e.g. Eggleton et al., 1996, 1999; Bignell and Eggleton, 2000).

Although numerous studies have investigated the importance of termites in carbon (C) and nitrogen (N) cycling (Yamada et al., 2006; Ackerman et al., 2007; Ngugi et al., 2011; Ngugi and Brune, 2012), few studies consider how termites and other macrofauna directly affect C and N availability in soils when compared with the

actions of microbes alone (Ngugi and Brune, 2012). Most studies have measured C and N fluxes, either in laboratory environments (Ngugi et al., 2011) or from mounds directly (Holt, 1987; Khalil et al., 1990; Donovan et al., 2001; Ackerman et al., 2007). These methods may have limitations: (i) laboratory experiments do not fully represent the natural occurring processes in the ecosystem, (ii) C and N emissions represent the emitted or fixed elements but not the availability of C and N to plants, and (iii) many soil-feeding termites have diffuse nests within the soil which complicate measurements of emissions from the nest of soil-feeding termites directly.

In this study, we collected soil (histic lithosol, inceptisols, USDA soil taxonomy, Malhi et al., 2011) with deep O-horizon (~30 cm) and soil C content of $14.99\% \pm 0.28\%$ from a montane tropical forest (Wayqecha, $13^{\circ}11'24\text{S}$, $71^{\circ}35'13\text{W}$) in Peru at an altitude of 3000 m asl. No termites were present at this elevation (Palin et al., 2010). The soil was translocated into a termite-inhabited soil (cambic horizon, inceptisols, USDA soil taxonomy, Aragão et al., 2009) with soil C content of $2.72\% \pm 0.15\%$ and a very shallow O-horizon (<3 cm) in a lowland tropical rain forest site (Tambopata, $12^{\circ}49.434\text{S}$, $069^{\circ}15.791\text{W}$). Using the translocated soil we conducted a macrofauna exclusion experiment with fine mesh

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(0.3 mm) and coarse mesh (5 mm) to exclude and include macrofauna, respectively. The aims were to examine (a) the effect of (i) microbes, smaller fauna and macrofauna combined and (ii) microbes and smaller fauna alone on soil C and N content, and (b) the possible contribution of termites to C and N depletion.

The experiment was conducted in Tambopata National Park, Peru, at 190 m asl and with mean annual rainfall and temperature of 1900 mm year⁻¹ and 24.4 °C, respectively (Malhi et al., 2013). The site has a dry and wet season and, due to the duration of the experiment, sampling spanned both seasons (day 7, 14 and 28 in the dry season and day 56 and 112 in the wet season). Six plots (50 m × 70 m) were established in the site with two sub-plots (10 × 50 m) each (see Fig. S1). Fifteen samples each of coarse mesh and fine mesh were paired in every one of the plots, with each pair placed randomly at least five metres apart (Fig. S1). At each sampling occasion three pairs were collected without replacement.

The C and N content in soil were analysed with a Thermo Finnigan Flash Elemental Analyser 1112 at the Imaging and Analysis Centre (IAC) at the NHM, London. Nonparametric ANCOVA was used to test the equality (difference in C and N content) and parallelism (difference in the shape of the curves) of the soil C and N content in samples with and without macrofauna over time. For nonparametric ANCOVA analyses the *sm* package in R (version 2.15.3) was used (Young and Bowman, 1995; Bowman and Azzalini, 2003), with cross-validation used to estimate bandwidths (*h*) for each ANCOVA. Analyses were conducted on logit (log($y/[1 - y]$)) transformed data (as recommended in Warton and Hui (2011) for

proportional data) but, as the results of these analyses are essentially identical to the untransformed data, we present the plots with the C and N data in their untransformed forms (%) as these are easier to interpret.

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

$$\mathcal{T} = -1/k \cdot \ln(1/2)$$

where \mathcal{T} is the half life in days and *k* is the decay constant. We used a relationship between worker termite head width and body mass to calculate the mean mass of individual termite species (see Dahlsjö et al., 2014 for further information). Nonparametric Mann–Whitney–*U* tests were used to examine the correlation between termite biomass, abundance and time with C and N depletion rates.

The loss of soil C and N was higher in samples with macrofauna (total loss of C = 35.4% and N = 30.6%) compared with samples with microbes and micro-/mesofauna (total loss of C = 27.2% and N = 22.1%). C and N depletion rates were significantly different, in both their gradients (rejecting equality, all $P < 0.01$) and the shape of the curves (rejecting parallelism, all $P < 0.01$), when samples including and excluding macrofauna were compared (Fig. 1 & Table S1). In samples with macrofauna the half life of C and N were 177.7 days and 212.7 days, respectively across the sampling period, while C and N had a half life of 244.6 days and 310.1 days, respectively, in samples without macrofauna. Highest mean termite abundance and biomass were found in the dry season at day 28

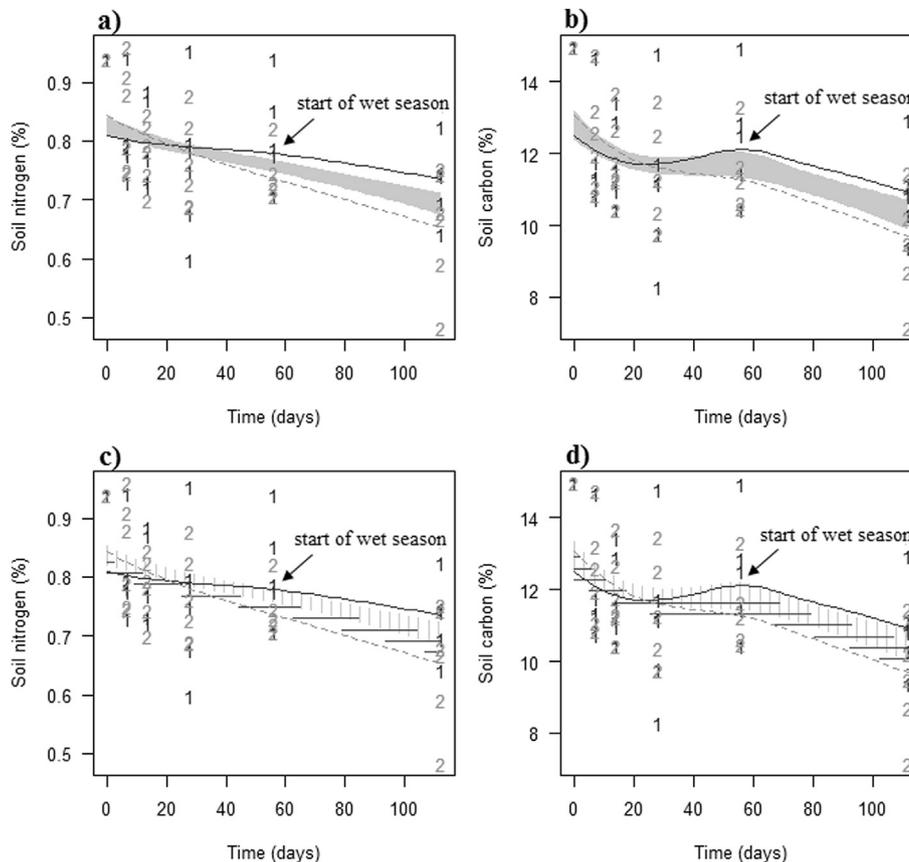


Fig. 1. Nonparametric ANCOVA results of equality (a–b) and parallelism (c–d) for N and C content comparing samples including (hatched line) and excluding (solid line) macrofauna. The numbers 1 (samples without macrofauna) and 2 (samples with macrofauna) display the range of the data. The equality analysis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

(658.7 indv/sample and 2.2 g/sample, respectively), while the lowest abundance and biomass were reached at the end of the experiment in the wet season at day 112 (116.7 indv/sample and 0.2 g/sample, respectively). However, the difference between the maximum and minimum abundance and biomass were not significantly different. The only other macrofauna encountered in the samples were pot worms (Enchytraeidae) which had low abundance and biomass with a maximum of 2.3 indv/sample and 0.0004 g/sample, respectively. Termite biomass and time (days after the start of the experiment) were significantly correlated with C and N depletion rates (Mann–Whitney *U* test, $P < 0.01$) while termite abundance did not show a significant correlation (Mann–Whitney *U* test, $P > 0.05$).

This study is one of the first *in situ* soil termite exclusion experiments examining the direct effect of termites and other macrofauna on soil C and N content. Depletion rates were highest at the start of the experiment, which may be due to the rapid breakdown of labile C and N pools, which then slowed as the proportion of stable elements became higher (Schwendenmann and Pendall, 2008). Soil that had not been inhabited by termites was shown to have lower depletion rates even in the wet season when microbial activity increases (Araújo et al., 2013). In contrast, the C and N depletion rates were continuously higher in samples including macrofauna even when termite activity decreased in the wet season. These trends suggest that the presence of termites in the soil may promote depletion of C and N compared with the presence of soil microbes and micro-/mesofauna alone. Termites have specialised mandibles that enable breakdown of the feeding substrate by increasing the surface to volume ratio (Eggleton, 2011) and their guts contain a high density of unique microbes (Hongoh, 2010) that enter the soil with the faeces. These traits may influence the microbial composition and activity in the soil samples with termites and subsequently affect C and N depletion. Although, soil microorganisms contributed to C and N depletion, the passage of soil through the termite gut and the role termites play as ecosystem engineers (e.g. by encouraging bioturbation (Jouquet et al., 2011)) may have resulted in higher depletion rates in samples with termites despite the increased microbial activity in the wet season.

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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.soilbio.2014.05.033>.

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