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The combined effect of termite bioturbation and water erosion on soil nutrient stocks along a tropical forest *catena* in Ghana

Jeppe Aagaard Kristensen[a,*], Susan Helene Boëtius[b], Mark Abekoe[c], Theodore W. Awadzi[c], Henrik Breuning-Madsen[b,1]

[a] Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, 223 62 Lund, Sweden
[b] Department of Geoscience and Natural Resource Management, Faculty of Science, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K., Denmark
[c] Department of Soil Science, University of Ghana, Legon, P.O. Box LG59, Accra, Ghana

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ABSTRACT

In the tropical moist semi-deciduous forests of West Africa, soil catenas with extremely gravel-rich soil horizons at the summits and upper slopes and largely gravel-free profiles at the lower slope are common. Previous investigations have suggested that these gravel layers are the result of macro-invertebrates mining of fine-grained soil material from the subsoil leaving behind the gravel, to build galleries at the surface subsequently exposing it to water erosion transport downslope. We examined the indirect effect of this process on the distribution along a soil *catena* of crucial base cations (Ca^{2+}, Mg^{2+}, K^{+}) and plant available phosphorous (P), which is often growth-limiting in these tropical ecosystems. We found that the export of fine-grained soil material at the top of the *catena* reduces the soil stocks (to 1 m) of these elements by up to 60%, while the soil fertility downslope did not change significantly. This important long-term (100–1000 yr scale) reduction in soil fertility at the top of slopes resulting from bioturbation and water erosion is overlooked in contemporary literature, which primarily focus on the beneficial impact termites and ants have on ecosystem functioning in more level savannah landscapes. As the type of *catena* studied is widespread across tropical environments, this effect is likely ecologically substantial. Future research should aim at understanding such long-term consequences of bioturbation on landscape ecology as well as soil heterogeneity and fertility, so we do not overlook potential negative ecosystem effects.

1. Introduction

In tropical West Africa, gravelly soil horizons are common at the summits and upper slopes of the landscape, while the soils at the lower part of the slope and at the bottom are almost gravel free throughout the profile (Nye, 1954; Dijkerman and Miedema, 1988; Adu, 1992). The gravelly layers are exposed at the surface or covered by a shallow gravel-free soil layer. They are typically 0.5–1 m thick and rarely > 1.5 m (Dijkerman and Miedema, 1988; Adu, 1992; Awadzi et al., 2004). The gravel consists of primarily iron nodules (pisolites) mixed with rock fragments, mainly quartz (Breuning-Madsen et al., 2007; Elberling et al., 2013).

The genesis of the gravelly layers is a matter of scientific dispute. A group of geological/geochemical models repeatedly emphasise the importance of great age, climatic changes and tectonic activity for formation and composition of continuous and discontinuous ironstone layers (e.g. Alexander et al., 1956; Nahon, 1986; Thomas, 1994; Fritsch et al., 2002). However, other authors have in parallel suggested that long periods of soil faunal activity, especially that of termites and ants, drive a relative accumulation of coarse fragments at a certain depth in the soil solum, because of selectively mining of bulk soil matrix finer than 1–2 mm at this depth for building structures at the surface (Nye, 1955; Fritsch et al., 2002). Thus, in areas with more upward transport of fine-grained particles than removal from the surface (e.g. by erosion), a gravel free soil layer might develop superimposing a gravel rich layer.

Our own studies in Ghana support the faunal theory (Awadzi et al., 2004; Breuning-Madsen et al., 2004, 2007, 2017; Kristensen et al., 2015). Based on sediment deposition dating (OSL), we suggested that on timescales of 1–5 ka, termites can cause redistribution of soil material finer than 2 mm that is relevant for soil and landscape formation (Breuning-Madsen et al., 2017; Kristensen et al., 2015). This conclusion is in line with several reviews (e.g. Lobry de Bruyn and Conacher, 1990; Wilkinson et al., 2009; Jouquet et al., 2016), and recent methodological

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[*] Corresponding author.
E-mail address: jeppe.aa.kristensen@gmail.com (J.A. Kristensen).
[1] Deceased.

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developments have allowed scientists to quantify horizontal (e.g. remote sensing and geostatistics; Funch, 2015; Mujinya et al., 2014; Obi and Ogunkunle, 2009), and vertical redistribution of matter (e.g. sediment dating; Kristensen et al., 2015; Jouquet et al., 2017).

Recently, authors have applied the concept of ecosystem services to evaluate the importance of termites for humans (Jouquet et al., 2011; Kaiser et al., 2017). Yet, most research has hitherto focused on the improvement of soil conditions, due to the direct accumulation of soil organic matter (SOM) and nutrients in the faunal structures at or near the surface (mounds, nests, fungus combs) (e.g. Lobry de Bruyn and Conacher, 1990; Sarcinelli et al., 2009, 2013), and erosion control resulting from the creation of soil macropores in relatively level savannah landscapes. In contrast, the indirect long-term (100–1000 year) effects on the soil fertility due to termite mediated sorting of soil particle sizes – vertically in the soil profile, and horizontally across the landscape – have received less attention, although the vast majority of the desirable soil properties are related to the fine particles (< 0.2 mm), e.g. water and nutrient retention. Hence, the indirect termite impact on soil quality also varies substantially across the landscape. Here we asked the question: What is the effect of the faunal and water mediated downslope transport of fine-grained material on the soil stocks of the important nutrients phosphorus (P), calcium (Ca), potassium (K) and magnesium (Mg) along a typical West African forest *catena*?

2. Materials and methods

2.1. The study site

The study site is at the University of Ghana's research station in Kade (6.10°N 0.84°W, Fig. 1). The climate is humid tropical with an average annual rainfall of about 1400 mm, mainly falling from March to mid-July, and secondarily from September to November. There is typically a dry period from December to February. The annual potential evapotranspiration is about 1400 mm, while the annual actual evapotranspiration is about 1200 mm (Christensen and Awadzi, 2000). Christensen and Awadzi (2000) estimated the surface run off to be about 15% of the precipitation during the rainy season posing a risk of surface soil erosion, which resulted in small scale fluvial patterns in surface sediments along the *catena* (e.g. micro-scale alluvial fans and braided sediments). The mean annual temperature is about 27–28 °C with little seasonal variation (Christensen and Awadzi, 2000).

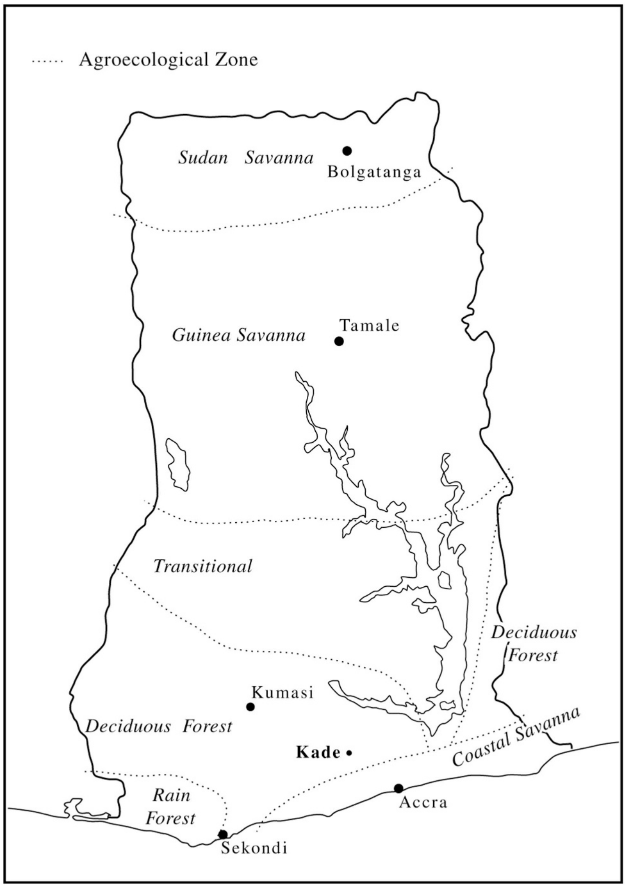

Fig. 1. The location of Kade in Ghana and the associated agroecological zones.

The landscape is gently rolling and the soils on the slopes form one of the most common catenas in the tropical moist semi-deciduous forest zone in Ghana, which is the Bekwai/Nzima-Oda association (Fig. 2) according to the Ghanaian soil classification system (Ahn, 1970; Owusu-Bennoah et al., 2000). The soil parent materials are almost exclusively Pre-Cambrian rocks, predominantly consisting of phyllites and schists (Adu, 1992). The *catena* is about 500 m long with an average slope of approximately 5%. The soils at the upper part of the slope, called Bekwai and Nzima soil series, are red-brown or brown, concretionary, acid, well-drained kaolinitic clay soils formed in phyllites with intrusions of quartz as the main constituents (Wills, 1962; Owusu-Bennoah et al., 2000). The soils are well drained, yet weathered rock is found at a depth of 150 to 200 cm, which occasionally impede the drainage in the wet season, resulting in the formation of temporary groundwaters producing pseudogley features near the base of the solum. According to the World Reference Base they are mainly classified as Acrisols (IUSS Working Group WRB, 2006). At the middle and lower slope, the Kokofu soil series are slightly-to-very acid, yellowish-brown clay loams developed in gravel-free colluvium deposited as a result of soil erosion upslope. The uppermost meter of the soil was deposited during the last 4–5 ka (Breuning-Madsen et al., 2017). The soils at the middle slope are mainly Acrisols. At the *catena* bottom, the soils are imperfectly drained greyish clay loams to sandy loams typical for the Oda soil series, which are usually flooded in the peak rainy season. The parent material is in situ weathered rock. They are classified as Gleysols (IUSS Working Group WRB, 2006). Due to the interference between nutrients coming from these seasonal floodings and the groundwater in general, the lowest catena member (Oda) is not used to infer any conclusions on the effects of upslope processes on soil nutrient stocks. At the lower end of the catena a small tributary channel called the Kadepon stream ('stream' in Fig. 2) is situated, which is only active in the main rainy season when the bottom is flooded (Christensen and Awadzi, 2000).

The study was conducted in a uniform and undisturbed (i.e. no dead wood has been removed since it was protected in the 1940s) semi-deciduous moist tropical forest. The dense vegetation belongs to the *Antiaris-Chlorophora* association (Lawson et al., 1970). Termites of the families Kalotermitidae (*Cryptotermes* sp.), Rhinotermitidae (*Coptotermes intermedius* and *Coptotermes* sp.) and Termitidae (*Microtermes subhyalinus*) dominate the macro-invertebrate community (Awadzi et al., 2004). These tree-eating termites do not build mounds like the savannah termites (primarily *Macrotermes*), but build galleries of soil material in dead logs and trees (see pictures of soil filled logs in supplementary information of Breuning-Madsen et al. (2017)). When the logs decompose, the gallery material forms a gravel-free horizon on top of the existing soil surface. When the dead trees collapse, the soil material in these can form passive dome-shaped heaps of considerable dimensions, which is subsequently levelled by erosion adding a fine-grained soil layer to the surroundings. Awadzi et al. (2004) estimated one of the larger mounds to be 1.6 m high with a diameter of 8 m yielding an approximate volume of 50 m^3 and weight of about 75 Mg, and they concluded that the soil was primarily mined from the subsoil below the A-horizon. Such heaps are visible on approximately the upper half of the *catena*. For a more thorough description of these processes and properties of the soil material in logs and heaps, we refer to Awadzi et al. (2004) and Breuning-Madsen et al. (2007). We cannot exclude the

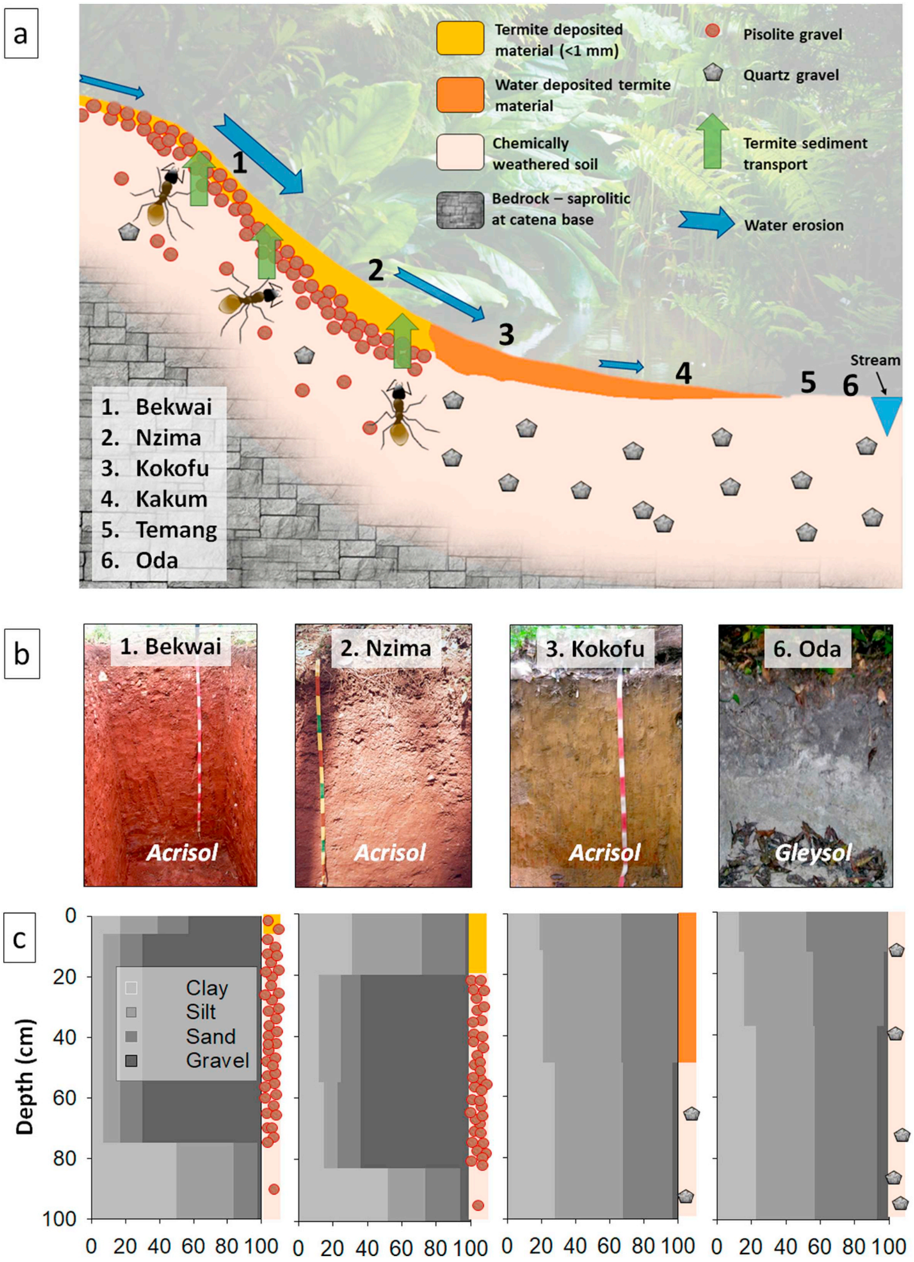

Fig. 2. Model of the genesis of the catena (a), pictures of the four soil profiles studied (b), and their particle size distributions (c).

possibility that some of the soil transport could be due to other animals or processes, but judging from our numerous visits at the site and previous studies mentioned above, we deem it is most likely that termites are the main upward soil transporting agents, while water erosion is the main downslope transport agent.

2.2. Soil sampling

Four soil profile pits were inspected to represent the four dominant soil series along the slope: Bekwai and Nzima at the upper slope, Kokofu from the mid-lower slope and Oda from the bottom of the catena (Fig. 2). We do not have samples from replicated soil pits, but from three decades of research along the catena and excavation of several soil pits at all segments, we carefully selected these four pits as good representatives of the four dominant soil types. The soils were described in the field according to the FAO guidelines (FAO, 1990) and the colour according to Munsell Soil Colour Chart. From the soils without gravelly horizons, undisturbed soil samples for bulk density determinations were taken in triplicate from three depths within the uppermost meter. A horizontal surface was excavated at the chosen depth and three 100 cm^3 soil sampling steel rings were gently hammered vertically into each soil layer of interest, to avoid soil compaction. The soil samples were cut to fit the volume of the ring, before covering the top and bottom with plastic lids. In the two soil pits at the top of the slope, soil samples were taken from 4 depths. The procedure was the same as for the two profiles downslope, except for the gravelly horizons, where it was not possible to hammer the rings into the soil. Instead, the procedure described by Grossman and Reinsch (2002) was used in triplicates. Similar to the other horizons, a horizontal surface was excavated into the profile wall at the layer of interest. The gravel-rich soil sample was carefully taken from the surface by hand to create a hole without disturbing the surrounding soil. The volume of the removed soil was measured by carefully lining the whole with a plastic bag and filling it with water until the water surface was at same level as the exposed horizontal soil surface. The weight of water in the bag was converted to volume of soil (g water = cm^3 soil). Additionally, disturbed bulk soil samples from all horizons were collected for chemical analyses. Composite samples of minimum three subsamples were used to get a good representation of average soil conditions in each horizon.

2.3. Laboratory analyses

We dried the soil samples for determination of bulk density at 105 °C for 24 h. Based on the weight of dry soil and the volume of sample, the bulk density was calculated. The aggregates in the disturbed soil samples were crushed and sieved through a 2 mm mesh. The weight of particles (gravel) > 2 mm was determined. The particles finer than 2 mm was used for chemical and physical properties as follows:

The texture was determined by the hydrometer method for the silt and clay fractions (Day, 1965), and dry sieving of the sand and gravel fractions. Soil pH was determined potentiometrically in a suspension of soil and 0.01 M $CaCl_2$ at a soil-liquid ratio of 1:2.5 (Thomas, 1996).

Total organic carbon (TOC) was analyzed using the dry combustion method at 1.250 °C in oxygen on an Eltra SC-500 analyzer, with an accuracy of ± 0.2% (ELTRA, 1995). As no carbonates were present in the samples, the total carbon content is equivalent to the total organic carbon content.

The exchangeable Ca^{2+}, Mg^{2+} and K^{+} ions were extracted with 1 M ammonium acetate ($NH_4C_2H_3O_2$) at pH 7 (Chapman, 1965) and the concentrations were determined by Atom Absorption Spectrophotometry (AAS) using a Perkin Elmer Analyst 400 (Perkin Elmer, Waltham, MA, US). Plant available P (P_{Olsen}) was extracted with 0.5 M sodium bicarbonate. After extraction, the phosphorus content was determined spectrophotometrically by the molybdenum-blue method (Murphy and Riley, 1962). The exchangeable cations and P were analyzed in laboratory triplicates. Therefore, variation in Table 2 represent analysis variation.

2.4. Stock calculations

The nutrient stock (kg/ha) was calculated to the depth of 1 m using the formula:

$$Nutrient\ content_{100} = \sum_{i=100} (Th_i * 10000 * BD_i * C_i)$$

Th: thickness of the soil layer (m)
BD: bulk density (kg/m^3)
C: content of nutrient in %/100

3. Results

3.1. Soil physical and chemical characteristics

Gravelly horizons dominate the two profiles at the upper slope, especially at the top of the solum (Table 1; Fig. 2c). In the reddish-brown Bekwai, the gravelly layer began at the surface, while a 20 cm thick gravel-free layer superimposed the gravelly horizons in the yellowish-brown Nzima. The Kokofu soil was acid, gravel-free, yet less clayey than the termite deposited material on top of the Nzima. The soil at the *catena* bottom was poorly drained and only slightly acid at the top solum. Despite the wetness, the carbon content was low compared to the soils upslope. An auger boring to 5 m depth showed soft rock (saprolite) with quartz veins, and the 7% gravel below 37 cm depth exclusively consisted of quartz.

3.2. Nutrient concentrations

For all four studied nutrients (Ca, Mg, K, P), the concentrations decreased with depth (Table 2). At the top of the *catena*, Nzima had higher concentrations of Ca and Mg than Bekwai, while it was almost equal for K and P. Kokofu at the colluvium generally showed lower concentrations than Nzima but higher than Bekwai. The Oda soil at the bottom close to the stream showed relatively high nutrient concentrations. Overall, plant available P concentrations were very low along the catena; the ratios to the other nutrients were approximately 1:8 for K, 1:20 for Mg and 1:70 for Ca except for the valley bottom, where the concentrations of Ca and Mg were relatively high.

3.3. Nutrient stocks

Considering only the fine-earth fraction (< 2 mm), Nzima was more nutrient rich than the Bekwai, especially according to Ca and Mg (Table 3). Kokofu showed intermediate stocks of Ca, Mg and P compared to Nzima and Bekwai. The Oda soil at the valley bottom had a relatively high content of Ca and Mg compared to the other soils. Including the gravel changed the nutrient stock substantially. The nutrient stock increased downslope from the Bekwai at the top to the Oda soil at the bottom of the catena. The nutrient stock in the highly eroded Bekwai was reduced by 60% of a similar soil without gravel, while the reduction in nutrient stocks in the Nzima was only about 45%, due to the 20 cm thick termite soil layer upon the gravelly horizon. At the colluvium, the reduction in nutrient stocks due to gravel inclusion was negligible. Similarly, the Oda soil at the valley bottom showed very little difference between including/excluding gravel.

4. Discussion

4.1. The distribution of nutrients along the catena

The soil at the top of the catena showed a 45–60% reduction in soil nutrient stocks due to the upward termite transport of fine material and the subsequent downslope transport, which led to a relative increase in chemically inert pisolite gravel in the solum. We believe that the difference between the two upper-slope soil members in terms of nutrient stocks was primarily due to varying degrees of erosion. This is inferred from the following two assumptions: 1) the thicknesses of the gravel layer is proportional to the upward movement of the fine-grained soil matrix between the gravel, and 2) if the upward transport is similar, then the thickness of the gravel-free termite deposited layer on top of the gravel horizon indicates whether down-slope removal of soil exceeds the upward transport by termites. The thickness of the gravel layers (Table 1) suggests that the upward movement of soil is similar or slightly higher at the Bekwai (~75 cm) compared to the Nzima (~65 cm). Hence, the different thicknesses of the termite deposited layers (largely absent at Bekwai, ~20 cm at Nzima), suggests that the down-slope removal of soil is higher than the upward transport at the Bekwai compared to the Nzima, where a gravel-free and relatively fertile (based on cations) layer has accumulated on top of the gravel horizon. The Nzima also had higher stocks of Ca and Mg than Bekwai in the fine-earth fraction (< 2 mm, Table 3), while it was almost equal for K and P. This suggests that the Bekwai is also slightly stronger weathered than Nzima, which is consistent with previous studies (Owusu-Bennoah et al., 2000).

The Kokofu soil on the colluvial middle part of the slope was gravel-free as suggested by the conceptual model (Fig. 2). Yet, it was less clayey than the termite sediment at the top of the Nzima (Table 1). We speculate that this is because the finer material containing most of the nutrients was transported all the way to the stream at the bottom of the *catena* during the rainy season, when most of the surface erosion occurs. Quantifying the erosion over the year would be needed to check this assumption. The Kokofu soil had intermediate contents of Ca, Mg and P in the fine-earth fraction compared to Nzima and Bekwai, which might be expected, as it is formed by mixed material from these two upslope members. Thus, although the nutrient stocks including gravel was larger in the Kokofu than in the upslope soils, this was primarily caused by the reduction in stocks due to termite activity and erosion upslope rather than a positive impact downslope.

Table 1
Textures, organic matter contents, pH (H_2O) and bulk densities for all horizons.

Profile	Horizon*	Depth cm	Clay < 2 μm	Silt 2–50 μm	Sand 50–2000 μm	Gravel > 2000 μm	Organic matter %	pH H_2O	Bulk density kg m^{-3}
Bekwai	Bτ(+A)	0–6	17	22	18	43	7.2	5.1	920
	Eτ1	6–40	7	9	14	70	1.4	5.3	1090
	Eτ2	40–75	7	10	13	70	1.3	5.2	890
	B + C	75–100	51	35	14	2	0.8	4.8	1390
Nzima	Bτ	0–20	31	41	25	3	2.9	5.8	1380
	A + Eτ	20–55	12	13	11	64	1.6	5.9	1410
	Eτ	55–83	15	8	13	64	1.1	5.8	1380
	B + C	83–100	52	22	20	6	1.1	5.5	1370
Kokofu	A	0–12	19	48	33	0	3.1	5.3	1400
	E + B	12–49	21	46	33	0	1.0	5.2	1570
	Bt	49–100	28	40	29	3	0.8	5.6	1660
Oda	A	0–13	13	39	47	1	2.3	6.3	1290
	Cg1	13–37	16	40	41	3	0.3	6.4	1680
	Cg2	37–100	23	34	36	7	0.2	7.1	1760

* According to Breuning-Madsen et al. (2004).

Table 2
Concentrations (‰) of calcium (Ca), magnesium (Mg), potassium (K) and phosphorus (P) for all horizons. AVG = average, SE = standard error on the analysis (n = 3).

Soil	Horizon	Chemical analyses, < 2000 μm							
		Ca, ‰		Mg, ‰		K, ‰		P, ‰	
		AVG	SE	AVG	SE	AVG	SE	AVG	SE
Bekwai	Bτ(+A)	1.634	0.049	0.401	0.002	0.108	0.028	0.015	0.001
	Eτ1	0.299	0.002	0.141	0.002	0.091	0.004	0.009	0.001
	Eτ2	0.290	0.040	0.118	0.009	0.094	0.005	0.009	0.001
	B + C	0.181	0.023	0.071	0.007	0.049	0.007	0.006	0.002
Nzima	Bτ	1.262	0.026	0.258	0.001	0.087	0.019	0.013	0.000
	A + Eτ	0.841	0.035	0.298	0.006	0.083	0.023	0.010	0.001
	Eτ	0.716	0.023	0.286	0.004	0.060	0.016	0.010	0.000
	B + C	0.690	0.009	0.306	0.003	0.051	0.008	0.009	0.001
Kokofu	A	0.920	0.017	0.187	0.001	0.073	0.009	0.014	0.001
	E + B	0.416	0.025	0.115	0.004	0.051	0.020	0.009	0.001
	Bt	0.668	0.018	0.172	0.002	0.055	0.012	0.009	0.000
Oda	A	1.336	0.026	0.349	0.002	0.042	0.007	0.021	–
	Cg1	0.725	0.018	0.408	0.008	0.055	0.005	0.024	–
	Cg2	1.094	0.062	0.972	0.015	0.083	0.013	0.014	–

Table 3
Nutrient stocks to the depth of 1 m. The left part shows the nutrient stocks excluding the gravel (> 2 mm), while the right part shows the nutrient stocks including the gravel.

	Excluding gravel				Including gravel			
	kg m^{-2}				kg m^{-2}			
	Ca	Mg	K	P	Ca	Mg	K	P
Bekwai Upper slope *Strongly eroded*	0.564	0.221	0.143	0.014	0.246	0.092	0.057	0.006
Nzima Upper slope *Slowly eroded*	1.539	0.525	0.131	0.019	0.867	0.276	0.069	0.010
Kokofu Mid-lower slope *Colluvium*	0.968	0.246	0.089	0.015	0.951	0.241	0.088	0.015
Oda Catena bottom In situ *weathering*	1.762	1.328	0.124	0.010	1.664	1.245	0.116	0.009

The Oda soil at the *catena* bottom seems to have received negligible amounts of particulate soil material from upslope. If this was the case, relative clay and SOM accumulation would be expected, which contradicts our results (Table 1). Instead, we think the most likely explanation for this net loss of fine material from the *catena* is that most of the fine-grained material from upslope washed all the way to the stream during the rainy season when the water erosion was highest and the valley floor flooded, i.e. was flushed directly out of the system. However, the higher content of nutrients in the Oda compared to upslope might be due to the addition of dissolved nutrients from upslope, but might also be due to nutrient enrichment during flooding.

4.2. Ecosystem consequences

The ecosystem consequences of termite and ant activity are increasingly recognised in contemporary literature. Most studies conclude that the effect of termites is positive, i.e. they provide valuable ecosystem services to humans (Jouquet et al., 2011; Kaiser et al., 2017). Many such conclusions have been reached in savannah ecosystems, where termites construct productivity hotspots through concentration of nutrients and moisture in and around their nests and other physical structures (e.g. Lobry de Bruyn and Conacher, 1990). Similarly, the positive effect the termite created soil macropores can have on soil erosion control in such environments has been mentioned repeatedly. In contrast, our results demonstrate that in undulating landscapes macro-invertebrate activity may have a negative effect on landscape scale soil fertility. P is of particular interest here, as it is often found to be the limiting nutrient in tropical ecosystems (Reich and Oleksyn, 2004). We hypothesise that the 45–60% reduction in stocks due to the termite mediated export of the fine-earth fraction from the *catena*, we found here, results in an ecologically substantial reduction in plant available P at the landscape level in sloping environments, as these catenas are widely described across the tropics (Ahn, 1970). This hypothesis should be tested in other such environments with considerable bioturbation, and should be accounted for in future evaluations of the ecological implications of termite activity. The increasing density of termite mounds and decreasing soil depth with increasing elevation observed along a catena in Brazil (Sarcinelli et al., 2009) and at an inselberg in Ghana where we conducted a study previously (Kristensen et al., 2015) suggests that this process is widespread across tropical catenas. Moreover, bioturbation should be considered across taxa, as also vertebrate and floral bioturbation can result in similar downslope movement of soil material (Heimsath et al., 2002; Stockmann et al., 2013).

5. Conclusion

We assessed the combined effect of termite bioturbation and downslope water erosion on soil nutrient stocks along a catena in a moist semi-deciduous tropical forest in Ghana. The results suggested that this process reduced the nutrient stocks by up to 60% at the upper slope due to relative accumulation of chemically inert gravel, while the effect was negligible further downslope. This is most likely because water erosion transported the majority of the fine-grained material directly to the stream at the base of the catena during the major rainy season, as the surface erosion peak coincided with flooding of the catena base. Thus, the landscape scale net effect on soil nutrient stocks of this termite mediated downslope transport of fine-earth material (< 2 mm) was negative and should be considered in future ecosystem services evaluations.

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References

Adu, S.V., 1992. Soils of the Kumasi Region, Ashanti Region, Ghana. Ghana Ministry of Food and Agriculture Scientific Services Division. Soil and Land-use Survey Branch. Memoir 8, Kumasi.

Ahn, P.M., 1970. West African Soils. Oxford University Press, London.

Alexander, L.T., Cady, J.G., Whittig, L.D., Dever, R.F., 1956. Mineralogy and chemical changes in the hardening of laterite. In: Transactions of 6th International Congress of Soil Science, Paris. V, pp. 67–73.

Awadzi, T.W., Cobblar, M.A., Breuning-Madsen, H., 2004. The role of termites in soil formation in the tropical semi-deciduous forest zone, Ghana. Dan. J. Geogr. 104 (2), 27–34.

Breuning-Madsen, H., Awadzi, T.W., Mount, H.R., 2004. Classification of soils modified by termite activity in tropical moist semi-deciduous forests of West Africa. Soil Surv. Horizon 45, 111–120.

Breuning-Madsen, H., Awadzi, T.W., Koch, C.B., Borggaard, O.K., 2007. Characteristics and genesis of pisolitic soil layers in a tropical moist semi-deciduous forest of Ghana. Geoderma 141 (1–2), 130–138.

Breuning-Madsen, H., Kristensen, J.A., Awadzi, T.W., Murray, A.S., 2017. Early cultivation and bioturbation cause high long-term soil erosion rates in tropical forests: OSL based evidence from Ghana. Catena 151, 130–136.

Chapman, H.D., 1965. Cation exchange capacity. In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiologial Properties. ASA, Madison, pp. 891–901.

Christensen, E., Awadzi, T.W., 2000. Water balance in a moist semi-deciduous forest of Ghana. West Afr. J. Appl. Ecol. 1, 11–22.

Day, P.R., 1965. Particle fractionation and particle-size analysis. In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (Eds.), Methods of Soil Analysis. Agronomy 9. American Society of Agronomy, Madison, Wisconsin, pp. 545–567.

Dijkerman, J.C., Miedema, R., 1988. An Ustult-Aquult-Tropept catena in Sierra Leone, West Africa, I. Characteristics, genesis and classification. Geoderma 42, 1–27.

Elberling, B., Breuning-Madsen, H., Knicker, H., 2013. Carbon sequestration in iron-nodules in moist semideciduous tropical forest soil. Geoderma 200–201, 202–207.

ELTRA, 1995. CS500 Simultaneous Carbon/Sulfur Determinator. ELTRA GmbH, Neuss.

FAO, 1990. Guidelines for Soil Description, 3rd edition. Food and Agriculture Organization of United Nations, Rome.

Fritsch, E., Montes-Lauar, C.R., Boulet, R., Melfi, A.J., Balan, E., Magat, P., 2002. Lateritic and redoximorphic features in a faulted landscape near Manaus, Brazil. Eur. J. Soil Sci. 53, 203–217.

Funch, R.R., 2015. Termite mounds as dominant land forms in semiarid northeastern Brazil. J. Arid Environ. 122, 27–29.

Grossman, R.B., Reinsch, T.G., 2002. Bulk Density and Linear Extensibility. In: Dane, J.H., Topp, G.C. (Eds.), Methods of Soil Analysis: Physical Methods, Part 4. Soil Science Society of America, Madison, pp. 201–228.

Heimsath, A.M., Chappell, J., Spooner, N.A., Questiaux, D.G., 2002. Creeping soil. Geology 30 (2), 111–114.

IUSS Working Group WRB, 2006. World reference base for soil resources. In: World Soil Resources Reports No. 103. FAO, Rome.

Jouquet, P. et al., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. 47: 215–222.

Jouquet, Pascal, Bottinelli, Nicolas, Shanbhag, Rashmi R., Bourguignon, Thomas, Traoré, Saran, Abbasi, Shahid Abbas, 2016. Termites: the neglected soil engineers of tropical soils. Soil Sci. 181, 157–165.

Jouquet, P., Caner, L., Bottinellia, N., Chaudhary, E., Cheik, S., Riotte, J., 2017. Where do South-Indian termite mound soils come from? Appl. Soil Ecol. 117–118, 190–195.

Kaiser, D., Lepage, M., Konaté, S., Linsenmair, K.E., 2017. Ecosystem services of termites (Blattoidea: Termitoidae) in the traditional soil restoration and cropping system Zaï in northern Burkina Faso (West Africa). Agric. Ecosyst. Environ. 236, 198–211.

Kristensen, J.A., Thomsen, K.J., Murray, A.S., Buylaert, J.-P., Jain, M., Breuning-Madsen, H., 2015. Quantification of termite bioturbation in a savannah ecosystem: application of OSL dating. Quat. Geochronol. 30, 334–341.

Lawson, G.W., Armstrong-Mensah, K.O., Hall, J.B., 1970. A catena in the tropical moist semi-deciduous forest near Kade, Ghana. J. Ecol. 58, 371–398.

Lobry de Bruyn, L.A., Conacher, A.J., 1990. The role of termites and ants in soil modification: a review. Aust. J. Soil Res. 28, 55–93.

Mujinya, B.B., Adam, M., Mees, F., Bogaert, J., Vranken, I., Erens, H., Baert, G., Ngongo, M., Van Ranst, E., 2014. Spatial patterns and morphology of termite (Macrotermes falciger) mounds in the Upper Katanga, D.R. Congo. Catena 114, 97–106.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.

Nahon, D.B., 1986. Evolution of iron crusts in tropical landscapes. In: Colman, S.M., Dethier, D.P. (Eds.), Rates of Chemical Weathering of Rocks and Minerals. Academic Press, Orlando.

Nye, P.H., 1954. Some soil-forming processes in the humid tropics. A field study of a catena in the West African forest. J. Soil Sci. 5, 7–21.

Nye, P.H., 1955. Some soil-forming processes in the humid tropics. The action of the soil fauna. J. Soil Sci. 6, 73–83.

Obi, J.C., Ogunkunle, A.O., 2009. Influence of termite infestation on the spatial variability of soil properties in the Guinea savanna region of Nigeria. Geoderma 148, 357–363.

Owusu-Bennoah, E., Awadzi, T.W., Boateng, E., Krogh, L., Breuning-Madsen, H., Borggaard, O.K., 2000. Soil properties of a toposequence in the moist semi-deciduous forest zone, Ghana. West Afr. J. Appl. Ecol. 1, 1–10.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proc. Natl. Acad. Sci. 101 (30), 11001–11006.

Sarcinelli, T.S., Schaefer, C.E.G.R., Lynch, L.S., Arato, H.D., Viana, J.H.M., Filho, M.R.A., Gonçalves, T.T., 2009. Chemical, physical and micromorphological properties of termite mounds and adjacent soils along a toposequence in Zona da Mata, Minas Gerais State, Brazil. Catena 76, 107–113.

Sarcinelli, T.S., Schaefer, C.E.G.R., Filho, E.I.F., Mafia, R.G., Neri, A.V., 2013. Soil modification by termites in a sandy-soil vegetation in the Brazilian Atlantic rain forest. J. Trop. Ecol. 29, 439–448.

Stockmann, U., Minasny, B., Pietsch, T.J., McBratney, A.B., 2013. Quantifying processes of pedogenesis using optically stimulated luminescence. Eur. J. Soil Sci. 64 (1), 145–160.

Thomas, M.F., 1994. Geomorphology in the Tropics. A Study of Weathering and Denudation in Low Latitudes. John Wiley and Sons, Chichester.

Thomas, G.W., 1996. Soil pH and soil acidity. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. Soil Science Society of America and American Society of Agronomy, Madison, pp. 475–490.

Wilkinson, M.T., Richards, P.J., Humphreys, G.S., 2009. Breaking ground: pedological, geological, and ecological implications of soil bioturbation. Earth Sci. Rev. 97 (1–4), 257–272.

Wills, J.B., 1962. Agriculture and Land Use in Ghana. Ghana Ministry of Food and Agriculture. Oxford University Press, London.