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Ant mounds as a source of sediment in a tropical rainforest?

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HYDROLOGICAL PROCESSES

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Abstract

In Lutzito catchment on Barro Colorado Island, Panama, extraordinarily high suspended-sediment yields of $1-2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ were generated despite the dense forest cover coinciding with erosion-resistant soils. We hypothesized that ant mounding activity is an important zoogeomorphological mechanism in this area, providing relevant quantities of easily transportable material at the soil surface. To test this hypothesis, all ant mound material was collected collected for dry mass determination from thirty 4 m² plots installed in the study area every 1-3 days during the 39-day sampling period. Additionally, three ground-nesting ant species responsible for mounds in the study area, Ectatomma ruidum, Trachymyrmex cornetzi and Strumigenys marginiventris, were identified. On the basis of the total of 1.38 kg of material collected in the wet season of 2011, the estimate for the whole 8 months wet season amounts to 725 kg ha^{-1} . As this value is in the same order of magnitude as sediment output, it shows that ants may act as important ecosystem engineers and contribute to sediment production here by providing large quantities of fine-grained, readily erodible material at the soil surface for subsequent transport to the streambed. Copyright © 2014 John Wiley & Sons, Ltd.

Key Words ant mounds; soil erosion; sediment output; zoogeomorphology

Introduction

Although soil disturbance by animals has long been recognized as an important element in soil formation (Darwin, 1881), its role in landscape denudation was only acknowledged much later (e.g. Butler, 1995). But ever since, evidence for geomorphologic work accomplished by animals has been accumulating: For example, Black and Montgomery (1991) and Yoo et al. (2005) identified pocket gophers as the driving force of sediment transport in Marin County, California. This is supported by Phillips (2009), who showed that the seemingly minute expenditure of 0.1% of net primary production of plants is geomorphically significant and far exceeds the energy input to denudation from the conversion of potential to kinetic energy. Moreover, burrowing or scraping by larger animals has been shown to cause substantial soil movement and affect erosion across a variety of ecosystems (e.g. Richards et al., 2011; Eldridge et al., 2012). Most recently, the growing interest in this emerging field was reflected by the 42nd Annual Binghampton Geomorphology Symposium on Zoogeomorphology and Ecosystem Engineering, which featured a session on 'sediment movement and erosion from a variety of sources' (Butler and Sawyer, 2012).

The influence of fossorial animals other than mammals, such as ants, on erosion and sediment transport has received less attention. A few studies have explicitly investigated this question and identified ants as an important factor for soil erosion processes and sediment dynamics in agricultural areas (Cerdà and Jurgensen, 2008; Cerdà *et al.*, 2009; Cerdà and Jurgensen, 2011) and forest fire affected areas (Dragovich and Morris, 2002; Cerdà and Doerr, 2010). However, similar investigations in undisturbed tropical rainforests are lacking.

Recent research in tropical forests discounted the general assumption that forest cover is an effective erosion control: Zimmermann *et al.* (2012) demonstrated that suspended-sediment export of the intensively studied



Lutzito catchment on Barro Colorado Island (BCI), Panama, amounts to $1-2 \text{ Mg ha}^{-1} \text{ year}^{-1}$, ranging at the high end of reported sediment yields from forests worldwide. They argued that frequent overland flow acts as an important driver of erosion processes and that undisturbed forest ecosystems are especially susceptible to erosion if three conditions apply: active near-surface flowpaths, little ground vegetation and the absence of extensive root mats. However, given the low detachability of the soils as inferred from aggregate stability (unpublished data), these three conditions merely guarantee an effective transport of available material, but they do not necessarily reveal the source of sediment. Thus, the apparent low detachability does not accord well with the high sediment output. It is mainly through mechanisms providing loose, easily transportable soil material at the soil surface that the transport system can be effective (Dragovich and Morris, 2002). Adding to this, our personal observations of numerous ant mounds throughout Lutzito catchment and elsewhere on BCI support the reported high densities of some ground-nesting ant species in the area (Levings and Franks, 1982). To reconcile the latter observation with the former incongruity, we wished to test the hypothesis that ants overcome the putative low detachability of the soils. Hence, our objectives were to quantify the amount of material excavated by ants in the study area and to compare this amount with previous estimates of sediment export (Zimmermann et al., 2012).

Material and Methods

Study site description

The study site, the 3.3-ha Lutzito catchment (LC), is located on Barro Colorado Island, in Gatún Lake, Panama, which was formed because of the flooding of the Panama Canal in 1914 [Figure 1(a)–(b)]. The island was declared a reserve in 1923 and has been administered by the Smithsonian Tropical Research Institute since 1946. Its undisturbed vegetation is classified as tropical semi-deciduous forest (Foster and Brokaw, 1982).

Total annual rainfall averages $2649 \pm 487 \text{ mm}$ [mean ± 1 standard deviation (SD), data from 1929 to 2011; data courtesy of the Environmental Sciences Program, Smithsonian Tropical Research Institute, Republic of Panama] and occurs mostly in the distinct wet season, lasting from May to mid-December. In 2011, when this study was conducted, total annual rainfall amounted to 3299 mm. The high rainfall amounts and intensities coupled with low soil saturated hydraulic conductivities at shallow depths result in frequent and widespread saturation overland flow (Godsey *et al.*, 2004; Zimmermann *et al.*, 2012; Zimmermann *et al.*, 2013).

Soils in LC were identified as Eutric Cambisols (FAO, 1998) and reach depths between 0.3 and 1 m (Baillie *et al.*, 2007). Topsoil aggregate stability is 0.97 ± 0.025 (mean ± 1 SD, unpublished data).

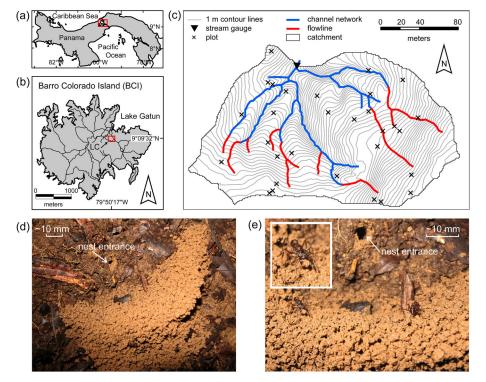


Figure 1. Location of the research area (a) in Panama and (b) on Barro Colorado Island. (c) Plot locations and catchment boundaries of Lutzito catchment (LC). Flow lines (red lines) mark areas where overland flow drains into the stream channel system (blue lines). (d) View of an *Ectatomma ruidum* nest entrance with the associated characteristic mound. (e) *E. ruidum* specimen adding grains of soil to the mound



Levings and Franks (1982), Levings (1983), Kaspari (1996), Kaspari and Weiser (2000) and Hahn and Wheeler (2002) studied litter ant assemblages in detail in the study area but did not distinguish between groundnesting or litter-nesting, twig-dwelling and even arboreal ants, all of which may forage in the leaf litter. Thus, information on species composition and abundances of the ground-nesting ant community, which is potentially relevant to sediment dynamics, is very limited. In this study, collected ant specimens from 18 different colonies were identified as *Ectatomma ruidum* (eight collections) [Figure 1(e)], *Trachymyrmex cornetzi* (nine collections) and Strumigenys marginiventris (one collection). However, there may be many more species potentially relevant for sediment dynamics in the study area. Nevertheless, no leaf-cutting ant colonies (Atta colombica), producing much larger mounds and thus greater amounts of potential sediment, were found in the study area.

Experimental design and collection of mound material Thirty plots of 1×4 m size were randomly chosen and marked in the study area [Figure 1(c)]. The rectangular shape of the plots allowed collection of mound material without disturbing the soil surface. Initially, the plots were carefully cleared of all leaf litter to ensure easy detectability of all present mounds, which was repeated twice a week during the course of sampling from 6 October until 13 November.

The ant mounds concerned in this study consist of loose, fine-grained soil material deposited by ants on the surface around or near the nest entrances in the process of nest building. They are mostly small and are classified as 'type 1' mounds (Paton *et al.*, 1995), as they do not form an integral part of the nest [Figure 1(d)–(e)]. In contrast to larger 'type 2' mounds, which are built to persist at the soil surface for many years, type 1 mounds are described as more easily erodible (Paton *et al.*, 1995).

The positions of all mounds found within the plots were marked, and all present mound material was collected at intervals of 1–3 days. Only mounds that could be assigned to ants unambiguously (because ants were adding material at the time of collection or the mound had the same distinct shape and features as other mounds that had been observed as accumulated by ants before) were considered in the analysis.

After removal of organic material such as roots, insects and leaves that formed part of the mound, the mound material was dried at 105 °C until consecutive weighing differed by less than 0.001 g.

Results and Discussion

Within the 39-day monitoring period, mounds were collected on 22 days, adding up to a total of 274 mounds

and 1384 g of mound material. Mound diameters at the time of collection averaged 4.92 cm and ranged from 0.5 to 17 cm.

Of all collected mounds, 15.4% were partly eroded at the time of collection. This highlights that all mentioned values of material provided by ants include excavation by ants as well as erosion and thus potentially represent an underestimate, as it was impossible to effectively shield the mounds from erosive forces. Further, the number of mounds that were eroded entirely before they could be collected is uncertain.

On the basis of the 120 m^2 of sampled area, the estimated yield for the whole 3.3-ha catchment area amounts to 380.6 kg within the 39-day monitoring period and to 725 kg ha^{-1} extrapolated to the whole 8-month wet season (from May to December). However, material deposition showed a declining trend from the beginning to the end of collections, and a disturbance of the present colonies due to leaf litter removal or the collection of mounds cannot be ruled out. We therefore calculated two estimates for the whole wet season, assuming the first and last 10 days of collections to be representative, respectively. Despite the considerable difference between the resulting estimates of 1049 kg ha^{-1} for the first and 402 kg ha^{-1} for the last 10 days of collections, respectively, all values are in the same order of magnitude. Also, these values are likely to be underestimates as they do not include material that may be brought to the surface by ants during the dry season, as dry season data of mound production are lacking. Thus, we have no means of estimating how production changes in the dry season and whether material deposited then is relevant for sediment dynamics.

Comparing these estimates to the sediment output for Lutzito catchment $(1-2 \text{ Mg ha}^{-1} \text{ year}^{-1}; \text{ Zimmermann}$ et al., 2012), even the lowest estimate of $402 \text{ kg} \text{ ha}^{-1}$ would indicate a substantial potential contribution of ant mounding activity to sediment output. Further, the small sizes of the grains deposited at the surface by ants in loosely structured mounds point at an easy transportability of single grains. This is emphasized by the observation that many mounds were partly eroded at the time of collection after rainfall events and that no mounds could be found after heavy rainstorms on two occasions in this study. Our results are in line with the findings of several previous studies in arid and temperate regions, which associated the presence of ant mounds with elevated sediment transport (Table I). Yet, comparability amongst studies is limited, and at least two studies either considered the influence of ants on erosion to be negligible (Aalders et al., 1989) or detected an even lower sediment yield in areas prone to ant activity, which was explained by an increased infiltrability and hence lower surface run-off compared with ant-free control areas (Cerdà and Jurgensen, 2008). In areas prone



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Reference	Study area	Target variable	Sediment yield [units]
Aalders et al., 1989	Cultivated area, France	Mound degradation	$1.3 [\text{kg ha}^{-1} \text{year}^{-1}]$
Cerdà and Jurgensen, 2008	Orange orchard, Spain	Run-off sediment concentration	50 (ants), 160 (no ants) $[kg ha^{-1} year^{-1}]$
Cerdà et al., 2009	Orange orchard, Spain	Run-off sediment concentration	42 (ants), 12 (no ants) $[kg ha^{-1}]$
Cerdà and Doerr, 2010	Fire affected shrub area, Spain	Run-off sediment concentration	Summer: 96 (ants), 30 (no ants) Winter: 817 (ants), 933 (no ants) $[kg ha^{-1}]$
Cerdà and Jurgensen, 2011	Orange orchard, Spain	Run-off sediment concentration	590 (ants), 360 (no ants) [kg ha ⁻¹ year ⁻¹]
Dragovich and Morris, 2002 ^a	Fire affected forest, Australia	Sediment transfer	0.47 (many ants), 0.035 (few ants) $[kg m^{-1}]$

Table I. The influence of ants on sediment yields

^a According to Dragovich and Morris (2002), ant mounds contributed >90% to the total weight of transferred sediment; the remaining sediment was ascribed to scratching by bandicoots.

to frequent overland flow, as at our study site (Zimmermann *et al.*, 2012; Zimmermann *et al.*, 2014), a high erodibility of the mounds would suggest that a large portion of the material made available by ground-nesting ants may be transported and hence contribute to the reported sediment yields. However, future research is needed to quantify the portion of material that is transported to the streambed as well as the associated travel time and to explore possible variations in mound production with topography or soil moisture.

Our results suggest that ant mounding activity could be an important zoogeomorphological mechanism, providing loose, easily transportable soil material at the soil surface and feeding the effective transport system, as material displacement by ants is in the same order of magnitude as suspended-sediment yields in the study area. Biotic influences can thus explain the origin of the unexpected sediment yields, especially as there may be many more relevant biotic processes than just ant mounding activity, such as burrowing or scraping by larger animals, which have been shown to cause substantial soil movement and affect erosion in other ecosystems (e.g. Black and Montgomery, 1991; Richards *et al.*, 2011; Eldridge *et al.*, 2012).

Conclusions

Our results show that the quantity of material deposited at the soil surface by ants is in the same order of magnitude as the sediment output in the study area. Furthermore, the mound erodibility can be assumed to be high because about 1/6 of all mounds were partly eroded at the time of collection and no mounds were found after heavy rainstorms. This is also supported by other studies investigating the erodibility of similar mounds. In addition, frequent and widespread overland flow serves as an effective transport system that links mound production and sediment export. We conclude that ant mounding activity plays a crucial role in the sediment dynamics in the study area. It remains to be seen, however, which portion of the mound material actually arrives at the streambed and how long it takes to do so.

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