Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation.

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Abstract

Anthropogenic habitat change is a major driver of species extinctions and altered species communities worldwide. These changes are particularly rapid in the tropics, where logging of rainforests and conversion to agricultural habitats is widespread. Because species have varying effects on their abiotic environment, we expect shifts in species composition to drive changes in ecosystem processes. One important ecosystem process is animal-driven bioturbation: the turnover of soil material by soil-dwelling organisms. We developed a protocol for measuring aboveground bioturbation, and assessed how bioturbation rates and standing amounts of aboveground bioturbated soil change as primary tropical rainforests are logged and converted to oil palm plantation. By identifying the animals that created soil structures, we assigned bioturbation activity to different soil-dwelling groups. Across all habitats, most standing bioturbated soil was generated by termites (97.0%), while short-term, small-scale bioturbation was mainly generated by earthworms (87.3%). The species diversity of social insects (ants and termites) involved in bioturbation was higher in primary forest than in either logged forest or oil palm plantation. However, neither standing bioturbated soil, nor short-term bioturbation rate differed among habitats. Unexpectedly, in primary forest, high levels of bioturbation were associated with low bioturbator diversity. This was because two termite species, where present, conducted nearly all bioturbation. There was no relationship between levels of bioturbation and diversity in the other habitats. Our results emphasize the importance, across all habitats, of termites for generating standing aboveground soil structures, and earthworms for short-term soil turnover. In oil palm plantation, bioturbation relies on a smaller number of species, raising concerns about future environmental change and consequent species loss.

Key words: Bioturbation; Ecosystem function; Habitat change; Logging; Oil palm; Termites.

1. Introduction

Habitat change and habitat loss are the most important threats to biodiversity, ecosystem stability and nature conservation worldwide (McGarigal et al., 2005; Meffe and Carrol, 1997; Sala et al., 2000). The conversion of natural habitats, mainly to agricultural landscapes, leads to species loss and altered species composition due to modified abiotic conditions (Mack et al., 2000). The response of organisms and associated ecosystem functioning to disturbance are of particular importance in the tropics, which are experiencing rapid anthropogenic habitat change. Tropical forests are global biodiversity hotspots, yet are threatened by logging and conversion to agriculture (Basiron, 2007; Sodhi et al., 2004). In South East Asia, primary forests often undergo multiple rounds of logging before conversion to oil palm plantation (Woodcock et al., 2011). However, even severely logged forests still support numerous species (Fitzherbert et al., 2008) and some forest functions such as soil erosion protection can be restored within just five to ten years if the forest is left to regenerate naturally (Bruijnzeel, 2004; Douglas, 1999). In contrast, oil palm plantation supports a very low diversity of taxa compared to natural forests. According to a review 25 of 27 studies concerning various animal taxa demonstrated a reduction of species richness in oil palm compared to other habitats (Turner et al., 2011). Taken together, logging of rainforest and consequent conversion to oil palm plantation cause various changes, many of which are predicted to influence the community of organisms and hence to affect ecosystem functions.

Soil modification and development is a key ecosystem process driven by animals and plants that is likely to be affected by habitat change in the tropics. Although soil organisms represent a small fraction of the total soil mass, they are a vital functional component of the ecosystem: they affect water quality, water supply, erosion, and are important for climate regulation, pollutant attenuation and degradation, and pest and disease control (Barrios, 2007; Brussaard, 1998; Decaëns et al., 2006). From a soil processes perspective, soil organisms are responsible for decomposition of litter, soil organic matter dynamics at different spatial and temporal scales, and maintenance of soil structure and aeration (Frouz, 2018). They also store nutrients in their living tissues and faeces and thus reduce nutrient leaching (Cunha et al., 2016; Doran and Safley, 1997). All these activities performed by soil organisms affect overall soil health and as a result plant growth, and thus they are crucial in both natural habitats and agroecosystems (Brussaard et al., 2007; Kohl et al., 2014; Usman et al., 2016).

One of the main ways in which living things modify soil is through bioturbation; the reworking and mixing of soil by organisms (Kristensen et al., 2012). This process is sometimes called ‘mounding’ when only production of aboveground soil structures is taken in account (Wilkinson et al., 2009). Bioturbation relates not only to physical movement of soil by organisms, but also to transport of soil particles to soil layers with different oxygen and water levels. This movement significantly affects the redistribution of soil organic matter and the creation of biopores, and it hence enhances microbial activity and consequent organic matter decomposition and nutrient release due to increased water infiltration and soil aeration (Lobry De Bruyn, 1997; Meysman et al., 2006; Wilkinson et al., 2009; Yair, 1995). As a result of this importance, the presence of bioturbating organisms correlates with production, health and fertility of soils (Wilkinson et al., 2009).

Despite the importance of terrestrial bioturbation, methods for measuring this process are not yet well developed. Usually a single organism is studied in detail and extrapolations of its bioturbation are then made (Meysman et al., 2006). The most common way to estimate bioturbation involves direct measurements or collections of the soil structures on the soil surface, e.g. termite mounds, earthworm casts or ant nests (Wilkinson et al., 2009). It is important to note that the soil deposited on the surface does not necessarily reflect total animal-driven bioturbation. A significant share of soil mixing occurs underground, performed mostly by endogeic species of ants, termites, earthworms and other animals (e.g. Minter et al., 2012; Whalen et al., 2004). Methods to estimate the underground volume that is excavated by ants or termites comprise pouring dental plaster or molten aluminum into underground nests to obtain a solid casting of the hollow spaces (e.g. Mikheyev and Tschinkel, 2004) or direct observation of the movement of soil material in artificial arenas during excavation of underground spaces (Halfen and Hasiotis, 2010; Minter et al., 2012). However, these methods are often used only to describe nest architecture and do not account for backfilled or collapsed spaces, which often occur in ant nests (Halfen and Hasiotis, 2010). All of these approaches usually result good estimations of bioturbation activity of a single species or faunal group at one location or under laboratory conditions. However, measurements of bioturbation at the level of entire communities with comparisons between habitats are rare. Additionally, to our knowledge, there is no information about how overall bioturbation in any habitat is partitioned between different faunal groups for the tropics.

The most important groups of bioturbating invertebrates worldwide are ants, earthworms and termites (Paton et al., 1995). There is also a range of other invertebrates and burrowing vertebrates that affect soils. The importance of these groups varies with the climatic conditions. For example, ants and termites tend to dominate in drier environments, where they replace earthworms, which are the main bioturbating group in moister environments (Jones et al., 1994; Wilkinson et al., 2009). Understanding which organisms are responsible for bioturbation is important because soil organisms differ in the ways they manipulate the soil during the bioturbation process (Meysman et al., 2006). For example, ants or rodents mainly translocate mineral soil within the soil profile, while earthworms and termites not only translocate the soil, but also ingest various soil materials, so their faeces are moistened and enriched by a diverse spectrum of microorganisms (Brauman, 2000; Lavelle et al., 2004). Conversely, the casts of earthworms are often compacted and bacterial cells can be coated by clay materials that stabilizes the cast and lowers microbial activity in the long term (Guéi and Tondoh, 2012; Hopkins et al., 1998). Through these mechanisms, variation in bioturbator community composition gives rise to variation in the functional importance of resulting soil structures, with consequences for soil processes such as soil organic matter dynamics, especially in habitats being affected by anthropogenic change (Frouz, 2018; Lobry de Bruyn and Conacher, 1994).

Because of their ecological importance, impacts of anthropogenic habitat change on bioturbating organisms is of great concern. The abundance and species richness of bioturbating soil macrofauna in ecosystems is usually reduced with habitat degradation, and species composition is altered. Lower diversity in human-disturbed habitats has been reported for soil and leaf litter ants (e.g. Hernández-

Flores et al., 2016; Solar et al., 2016), termites (e.g. Dambros et al., 2013; Dosso et al., 2013), cicadas (e.g. Chiavacci et al., 2014; Karban, 2014) and earthworms (e.g. Guéi and Tondoh, 2012; Dey and Chaudhuri, 2014). For example, species richness of ants, termites and earthworms was lower in pasture or sugarcane plantation than in natural vegetation in Brazil (Franco et al., 2016). The same animal groups had lower abundance, biomass and diversity in logged lowland tropical forest, compared to primary forest in Malaysian Borneo (Ewers et al., 2015). This reduction in species richness compared to natural ecosystems is often attributed to lower habitat complexity with lack of niches and altered microclimatic conditions (Ewers et al., 2015; Foster et al., 2011). However, anthropogenic disturbance can also lead to higher abundances of certain taxa. For example, cicadas can increase in abundance in logged forest gaps (Karban, 2014) and along forest edges (Chiavacci et al., 2014), where there are more young saplings, which are vital for cicada nymph development. There can also be increases in the dominance of particular groups. For example, disturbed and converted habitats can be invaded and dominated by a single species of earthworm that contributes greatly to bioturbation (González et al., 2006). All of these compositional changes driven by human-induced habitat degradation result in changes in assemblages of bioturbating organisms. Animals that perform soil mixing differ in their efficiency, and hence disturbance is predicted to influence bioturbation rates via turnover of species.

Despite the plausibility of anthropogenic impacts on bioturbation, even comparisons of different faunal groups in terms of their contribution to bioturbation in a single habitat are rare, albeit called for by soil ecologists (Wilkinson et al., 2009). Similarly, studies of bioturbator groups or area-based bioturbation rates across contrasting habitats are uncommon. One study in Sweden found that earthworms performed the vast majority of bioturbation in most habitats (>98%), with the exception of abandoned fields (12% ant-mediated bioturbation) and spruce forest (93% ant bioturbation) (Persson et al., 2007). In tropical regions, to the best of our knowledge only one study has assessed impacts of logging on bioturbation. This focused solely on dung beetles and their small-scale effects in an area surrounding experimentally placed dung (França et al., 2017), finding that even low intensities of logging led to reduced bioturbation by this group. However, no work has attempted to quantify the activity of entire bioturbating animal communities on the soil surface.

In this study we develop and apply a novel method to quantify the aboveground soil structures created by animal-driven bioturbation. We investigate how bioturbation rates and standing amounts of bioturbated soil are affected by logging and conversion to oil palm of primary lowland dipterocarp rain forest in Sabah, Malaysia. By identifying the groups and species that generate bioturbated aboveground soil, we were able to measure for the first time the individual contributions of different ecological groups to the bioturbation process in the tropics. Specifically, we test the following hypotheses:

1. Bioturbation rate will decrease and there will be less standing bioturbated soil in more disturbed habitats.

2. Bioturbator diversity will decrease in more disturbed habitats.

3. Bioturbation rates and amounts of standing bioturbated soil will be higher in plots with greater bioturbator diversity.

2. Materials and methods

2.1. *Study sites*

The study sites were part of the Stability of Altered Forest Ecosystems (SAFE) project in Sabah, Malaysian Borneo (Ewers et al., 2011). Six sampling points were surveyed in each of the three habitats (N=18 plots in total): 1. Primary lowland rainforest at Maliau Basin Conservation Area (MBCA, SAFE Project site 'OG2'). This forest has never been logged and is part of a large continuous forest block: the 58,840 hectares of MBCA forest is surrounded by one million hectares of logged forest. 2. Continuous selectively logged forest in the SAFE Project experimental area, with two plots at each of the three SAFE Project sites: ‘LFE’ (Logged Forest Edge) and sites ‘B’ and ‘F’. All three sites have been at least twice logged (Struebig et al., 2013). Note that all sites were sampled before any SAFE project-related experimental fragmentation. 3. Oil palm plantations, with two plots at each of the SAFE Project sites ‘OP1’, ‘OP2’ and ‘OP3’. OP1 and OP2 were planted in 2006, and OP3 in 2000. These are managed by the company Benta Wawasan Sdn Bhd (see Ewers et al., 2011) and the SAFE Project (see www.safeproject.net for details). For sample site coordinates see Supplementary material 1. Data were collected from 22nd June to 18th August 2015 and from 9th July to 17th August 2016. This was during a two-year long El Niño event, although no fires occurred in the study area.

2.2. Sample collection and measurements

2.2.1. Assessing aboveground bioturbation

We defined and measured bioturbation activity as the amount of soil material moved to the soil surface by the activity of various animals. We carried out three kinds of surveys in order to: 1. Assess the distribution of larger aboveground bioturbated structures across larger spatial scales (‘standing bioturbated soil’); 2. Assess turnover of smaller aboveground structures at a smaller spatial scale (‘bioturbation rate’); 3. Measure growth and turnover of aboveground termite mounds (‘termite mound dynamics’). For further details of the measurements, see Supplementary material 2.

2.2.2. Assessing standing bioturbated soil

For large-scale surveys, at each of the six sampling points in each habitat a 25 m x 25 m (625 m^2) plot was searched thoroughly for any aboveground biogenic soil structure that could be seen without moving leaf litter, not including scrapes (resulting from shallow excavations such as digging) or plant-generated mounds and hollows, such as that caused by tree uprooting. Structures that were smaller than 6 cm in height were omitted from the standing bioturbation measurements. This excluded mainly epigeic and small anecic earthworms, some ant mounds and other small burrowers. We were able to distinguish five categories of larger structure: Cicada turret - a hollow cylinder of clay material, which was sometimes capped (Fig. 1b); Earthworm cast – a pile of soil extruded as a long cylinder (Fig. 1f); Ant mound - a pile of soil particles at a nest entrance (Fig. 1e); 'Burrow' – a heap (with no typical shape) of excavated soil usually around a tunnel/nest entrance, perhaps caused by large insects such as beetles, solitary wasps, small mammals or lizards.

These structures were collected in their entirety from the level of the soil surface upwards, identified, dried in an oven at 80°C for two days and weighed.

Termite mounds - All intact, standing termite mounds, fragments of mounds and dead (fallen) mounds were counted in each plot. Aboveground mounds built by the three species of termite present in the plots were identified based on mound morphology and species identification from voucher samples. *Dicuspiditermes nemorosus* (Haviland, 1898) made dark-coloured mounds with multiple turrets emerging from an aboveground basal plate (Fig. 1a) while *Dicuspiditermes minutus* (Akhtar and Riaz, 1992) made single standing turret-shaped mounds (Fig. 1c). *Macrotermes gilvus* (Hagen, 1858), made large, dense, mounds with clay that was generally yellow (Fig. 1d). However, species boundaries between *Dicuspiditermes* termites were not clear in all cases, and so for mound growth and turnover analyses the two species in the genus were pooled as *Dicuspiditermes* spp.

The mound height from the soil surface and the most representative diameter were measured for each mound structure. Where the base of the mound was elliptical rather than circular, the mean of two perpendicular measurements of diameter was used. In cases of multiple turrets within one mound, separate measurements were made for each turret and the values were summed. The mound volume was then calculated by approximating the mound shape to a cylinder, using a standard formula for cylinder volume $V = \pi r^2 h$ for *D. nemorosus* and *D. minutus*, while a standard formula for cone volume $V = \pi r^2 h/3$ was used for *M. gilvus* nests. This value was converted to soil mass using soil samples of a known volume of mound material from each species, which were dried in an oven for two days at 80°C before weighing.

2.2.3. Assessing bioturbation rate

To assess bioturbation performed by smaller organisms at smaller scales, which was not recorded during large-scale surveys (those that fell below the threshold of 6 cm in height), we established two 1 m^2 plots per sampling point (N=12 per habitat). This assessment was performed in the same time as standing bioturbation was measured, and in the same area. First, we cleared all litter and soil structures caused by bioturbation from the plot. This was necessary because distinguishing bioturbated soil from other soil within the leaf litter layer was not possible. After five days we collected all the soil structures that had appeared on the soil surface. The five day period was established on basis of the prior measurement trials. This period was long enough for new structures to emerge, but also not excessively long for the effect of repeated rain to break and wash away the bioturbated soil structures. Rain is the main limiting factor in this kind of measurement, as it restricts the maximal time between the setup and re-visit of the plot. The collected structures were dried in an oven at 80°C for two days and weighed.

2.2.4. Assessing termite mound dynamics

In addition to small-scale bioturbation rate, it is important to consider turnover of larger aboveground structures. This was not feasible at the scale of whole plots and for all types of bioturbated structures. However, we observed that the majority of such translocated soil originated in termite mounds of the three mound-building species present in the plots, presumably accumulated over longer timescales. Hence we measured the growth and turnover of termite mounds of *M. gilvus* and *Dicuspiditermes* spp. in primary forest, logged forest and oil palm plantation. We marked and measured all the standing soil termite mounds in the 25 m by 25 m plots in which large-scale standing bioturbated soil was surveyed (N=18, see above). We selected five of the *M. gilvus* and *Dicuspiditermes* spp. mounds in each habitat in which the species were present, and applied thin plastic sticks with a measuring scale, vertically in the body of the mound. Termites did not preferentially cover the measuring sticks with mound material. After one year, we re-surveyed all the plots and recorded the number and size of dead or newly-emerged mounds. Dead mounds were considered those that had fallen to the ground and newly-emerged ones those that were not present in the initial survey. For mound growth, the one-year increase of soil covering the measuring sticks was recorded (for further details of the measurements see the Supplementary material 2).

2.2.5 Limitations

Using these methods, we obtained a "snapshot" of aboveground bioturbation. We did not aim to evaluate the bioturbation activity of any particular animal in detail (apart from for termite mound dynamics). This method also necessarily underestimates total bioturbation values in the following ways:

1. The method measures only aboveground soil and it is known that underground soil mixing can account for a significant, but mostly unknown share of the overall bioturbation (Hasiotis and Halfen, 2010; Minter et al., 2012).
2. The method omits very small bioturbation conducted by certain meso- and micro-fauna, such as small earthworms and Enchytraeidae, dipterian larvae, nematodes etc.
3. In order to obtain a complete picture of aboveground bioturbation in certain habitat, multiple measurements during the year, both of standing structures and of mixing rate would have to be taken to record the creation and decay of more temporal structures (such as cicada turrets and earthworm casts).

Nevertheless, we believe that our combined method for measuring aboveground bioturbation is of utility when the habitats are compared within the same region and over the same period.

2.3. Data analysis

The effects of habitat on standing bioturbated soil and bioturbation rate were tested using generalized linear models (GLM, family=Gaussian; link=log, log link used to account for non-normal distribution of errors). Chi-square tests of deviance were used to compare and simplify models. The contribution of various animal groups to the total bioturbation in different habitats was tested using ANOVAs (since data were normally distributed) with Tukey HSD post-hoc comparisons, where applicable. In order to assess the diversity of the animals contributing to soil bioturbation, a bioturbator diversity index was calculated based on Simpson's diversity index, D (Simpson, 1949). The sum of squared proportional contribution of individual bioturbator species to the total bioturbation within the plot was subtracted from 1, so $D=1-\sum (n/N)^2$, where n denotes bioturbation performed by one type of bioturbator and N is the sum of measured bioturbation of all bioturbators within individual plot. This denotes the probability that two randomly chosen small particles of bioturbated soil were brought to the surface by different animal groups/species. The index was calculated for each plot, for both standing bioturbated soil and bioturbation rate measurements. Note that this index is based on relative amounts of soil uplifted, and not on numbers of individuals of different species. Differences between habitats in this index were tested using ANOVAs with Tukey HSD post-hoc comparisons, where applicable. The difference in growth rates of surviving *Dicuspiditermes* spp. nests in primary forest and logged forest (the two habitats in which they were present) was tested by standard unpaired t-test. The same test was used to compare the amount of soil brought up by new *Dicuspiditermes* spp. nests in primary forest and logged forest. The total amount of soil brought up by *Dicuspiditermes* spp. mounds was calculated as the mean number of live nests multiplied by their mean growth, and the mean amount of soil found in new *Dicuspiditermes* spp. mounds was added to this value. To test whether habitats with more diverse bioturbating soil fauna had higher levels of bioturbation we used generalized linear models (GLM, family=Gaussian; link=log) predicting mean standing bioturbated soil as a function of bioturbator diversity index. Statistical analyses were performed using R Statistical Software (version 3.6.0).

3. Results

3.1. Standing bioturbated soil and bioturbation rate across different land uses

The mean mass of standing bioturbated soil at large scales (25 m x 25 m plots) was highly variable. Although mean values were lowest in primary forest (828 kg ha^{-1} ± 689; all numbers are presented as means with standard deviation), intermediate in logged forest (1900 kg ha^{-1} ± 2260) and highest in oil palm plantation (2140 kg ha^{-1} ± 3019, Fig. 2a), there was no significant difference between habitats in standing mass of bioturbated soil (GLM, χ^2_{15}=5848485, p=0.551); note that χ^2 values are large as they are calculated using deviance, which is on the scale of kg ha^{-1}). The mean small-scale bioturbation rate was also highly variable, being highest in primary forest (3952 kg ha^{-1} $year^{-1}$± 2665), intermediate in logged forest (2338 kg ha^{-1} $year^{-1}$± 2760), and lowest in oil palm (1643 kg ha^{-1} $year^{-1}$± 1902, Fig. 1b). However, there was no significant difference in small-scale bioturbation rates between the habitats (GLM, χ^2_{15}=16842008 p=0.318).

3.2. Contribution of different faunal groups to standing bioturbated soil and bioturbation rate across different land uses

The standing bioturbated soil across all habitats (Fig. 3a) was overwhelmingly generated by termites, comprising 97.0 % of total bioturbation, with no significant difference in this total amount between habitats (ANOVA between habitats: $F_{2, 15}$=0.10, p=0.904). A single termite species *Macrotermes gilvus* brought up on average 99.8 % of all standing bioturbated soil in oil palm, 67.7 % in logged forest and 1.1 % in primary forest. Cicadas were responsible for 1.4% of the standing bioturbated soil across all habitats, also with no significant difference between primary and logged forest ($F_{1, 10}$=0.627, p=0.447), while other unidentified bioturbators were responsible for 0.7 % of bioturbation across all habitats, with higher bioturbation in primary forest than in both logged forest and oil palm (ANOVA: $F_{2, 15}$=20.21, p<0.001, Tukey HSD: primary-logged p=0.012, primary-oil palm p<0.001). Earthworms (0.7 %, with no difference between primary and logged, $F_{1, 10}$=0.807, p=0.390) and ants (0.2 %, with no difference between habitats, $F_{2, 15}$=0.62, p=0.549) also made minor contributions to standing bioturbated soil. Note that there was no standing bioturbated soil >6 cm generated by either earthworms or cicadas in oil palm.

The majority of contributions to small-scale bioturbation rate across all habitats (Fig. 3b) was from earthworms (87.3 %), followed by ants (10.4 %) and other unidentified animals (2.2 %). Bioturbation rate across habitats did not differ significantly for ants between primary forest and oil palm (ANOVA, $F_{1, 9}$=0.179, p=0.682) but it approached significance for earthworms (ANOVA, $F_{2, 15}$=3.219, p=0.069).

There was no significant difference in bioturbator diversity for standing bioturbated soil between habitats (note the outlier in oil palm; Fig. 3c, ANOVA, $F_{2, 15}$=2.0, p=0.169), or for bioturbation rate between primary forest and oil palm (Fig. 3d, ANOVA, $F_{2, 15}$=1.54, p=0.245; note that logged forest was not tested as all values were zero).

3.3. Social insect bioturbator diversity across different land uses

When considering social insects that generated standing bioturbated soil (ants and termites) and which we were able to identify to species level (Fig. 4c), there was a significant difference in social insect bioturbator diversity index between habitats (Fig. 4a, ANOVA, $F_{2, 15}$=17.43, p<0.001) with primary forest having higher values than logged forest and oil palm plantation (Tukey HSD, p<0.001 and p<0.001 respectively). For small-scale bioturbation rate, bioturbation was carried out solely by ants in primary forest and oil palm (Fig. 4b), and there was no social insect contribution in logged forest (see also above section). Although two species of ants performed bioturbation in oil palm (Fig. 4d), they never occurred in the same plot. Hence all values of the diversity index were zero in both disturbed habitats, making statistical comparisons with the primary forest impossible.

3.4. The relationship between diversity index of bioturbators and aboveground bioturbation

The bioturbator biodiversity index for broader taxonomical categories was significantly and negatively correlated with standing bioturbated soil in primary forest (GLM, t_4=-5.505, p=0.005) but not in logged forest (GLM, t_4=-0.889, p=0.424) or in oil palm (GLM, t_4=1.128, p=0.322; Fig. 5). There was no significant correlation between bioturbation rate and diversity of small-scale bioturbators across habitats (GLM, t_4=0.135, p=0.899) for primary forest and (GLM, t_1=-5.402, p=0.117) for oil palm. There was no possible correlation for logged forest due to a lack of valid data points (see above), because only earthworms contributed to bioturbation rate.

3.5. Termite mound dynamics (the growth, turnover and densities of termite mounds)

Mounds of the termite *Dicuspiditermes* spp. grew by an average of 10.4 cm per mound per year, which accounted for 74.7 grams of dry soil per mound per year (N=5 measured in each habitat) across forested habitats. There was no significant difference in growth rate of individual *Dicuspiditermes* mounds between primary forest and logged forest (Fig. 6a, t_8=-0.586, p=0.574). We did not record any growth of the mounds of *M. gilvus* in one year across all habitats. The mean mass of soil brought up by new *Dicuspiditermes* spp. mounds was 2.6 kg ha^{-1} year^{-1} in primary forest, 1.5 kg ha^{-1} year^{-1} in logged forest and 0.0 kg ha^{-1} year^{-1} in oil palm, although with no significant difference between primary forest and logged forest (Fig. 6b, t_{10}=-0.509, p=0.615). There was an average of 109.3 living *Dicuspiditermes* spp. mounds per hectare in primary forest (min. 0, max. 265), 69.3 mounds per hectare in logged forest (min. 0, max. 160) and no mounds in oil palm plantation (Fig. 6c). After one year, we recorded a reduction in density of living mounds (Fig. 6d) in primary forest by 26.8 % (32.0 mounds built, 61.3 died per hectare) and in logged forest by 57.7 % (5.3 mounds built, 45.3 died, per hectare). Regarding *Macrotermes gilvus*, there were 2.7 living mounds per hectare in primary forest, 13.3 mounds per hectare in logged forest and 16.0 mounds per hectare in oil palm, with no recorded appearance, growth or death of mounds. Taking together growth of existing mounds and appearance of new mounds, the total amount of soil brought up by living termite mounds, which was entirely due to *Dicuspiditermes* spp., was 42.7 kg ha^{-1}

year^{-1} in primary forest, 28.6 kg ha^{-1} year^{-1} in logged forest and 0.0 kg ha^{-1} year^{-1} in oil palm (the latter due to lack of any live growing nests).

4. Discussion

Our study represents the first assessment and quantification of the contributions of invertebrates to aboveground bioturbation in tropical forest ecosystems. Furthermore, we were able to compare their contributions across a gradient of anthropogenic habitat modification. Despite high variability in bioturbation values within and across habitats and hence lack of significant differences in bioturbation measures among the primary forests, logged forests and oil palm, we show the importance of changes in bioturbator community composition. Termites were the major generators of standing bioturbated soil across all habitats. However, mound growth was very slow, and hence turnover was dominated by non-termite groups carrying out soil uplift over small spatial and temporal scales.

4.1. Termites as a dominant generators of standing bioturbated soil

Most of the standing bioturbated soil was produced by the mound-building activity of termites, with a single termite species, *Macrotermes gilvus*, dominating in the disturbed habitats. The second most important bioturbator in primary forest and logged forest was the soil-feeding termites *Dicuspiditermes* spp., which build phallic-shaped mounds from organic matter-rich soil. This finding supports a long-standing claim, that termite mounds trap significant amounts of soil (e.g. Dangerfield, 1998; Tilahun et al., 2012), although such measurements necessarily neglect the bioturbation taking place in underground mound spaces for these species and also all bioturbation performed by strictly hypogeic termites. Additionally, the aboveground mounds of *M. gilvus* are made of sand/silt and clay soil and have a thick outer wall. Hence they had proportionally higher bulk density (1.66 g cm^3) than the lighter mound material of *Dicuspiditermes* spp. (0.53 g cm^3), with more hollow spaces represented by chambers and tunnels. *Dicuspiditermes* spp. were absent or rare in oil palm plantation (with only one dead nest found), probably due to high temperature, low humidity and patchy food resources.

4.2. Earthworms as a dominant driver of bioturbation rate

Our results highlight the importance of termites for standing bioturbated soil in this system, and that the density of mound material (not only the volume of the mound) should be taken in account during such comparisons. The bioturbation rate (on a small scale) however, was mainly driven by earthworms (Oligochaeta), contributing 63-99 % of the total bioturbation across all habitats through production of small soil casts (details of other bioturbator groups are given in Supplementary material 3). Note however, that this does not reflect the bioturbation of the whole earthworm community, but probably only the activity of anecic (mainly vertically moving) earthworms (Lamandé et al., 2003; Whalen et al., 2004). Earthworms generated the greatest proportion of small-scale bioturbation in all three habitats, and were the only small-scale bioturbator in logged forest. This shows the importance of earthworms for maintaining small-scale bioturbation rate over short time periods when other organisms are absent. This is especially important because of the ecosystem services earthworms are known to provide: facilitation of water and gas transport, incorporation of litter into the soil, and breaking down soil organic matter, with impacts on vegetation dynamics and diversity (Jouquet et al., 2006).

4.3. Variability in standing bioturbated soil across habitats

The lack of difference between habitats in standing bioturbated soil probably relates to increases in the creation of aboveground soil structures by termites, which balances the decreases in the activity of other bioturbator groups. An additional factor is the high variability in these measures among plots, reflecting spatial patchiness. Indeed, the standing bioturbated soil was mainly generated by termites in all three habitats, although *M. gilvus* was not a dominant species in primary forest, in contrast to logged forest and oil palm plantation (Fig. 4a; Supplementary material 4). However, the two *Dicuspiditermes* termite species, combined with a diverse range of other bioturbating animals, generated similar levels of standing bioturbated soil in primary forest compared to logged forest and oil palm plantation. Compared to primary forest, the amount of soil brought up by *M. gilvus* was higher in logged forest and highest in oil palm plantation, where it accounted for the majority of total standing bioturbated soil (see above). In oil palm, *M. gilvus* was able to compensate for the amount of standing bioturbated soil in logged and primary forest attributable to other bioturbators. It seems that *M. gilvus* replaces other termites in more degraded habitats and becomes the main species producing long-lived above ground soil structures. The dominance of *M. gilvus* in disturbed habitats is explicable in terms of it being a fungus-growing and wood/litter-feeding species and hence, in contrast to most rainforest termite species, it can tolerate the high temperatures and low air humidity typical of disturbed areas (Bandeira et al., 2003; Eggleton and Tayasu, 2001; Hassall et al., 2006; Jones et al., 2003; Luke et al., 2014). A similar increase in the relative importance of *M. gilvus* in oil palm plantation as compared with primary and logged forest has been observed in terms of litter decomposition (Foster et al., 2011).

4.4. Termite mound dynamics

In primary and logged forest greater numbers of mounds died than were created during the year, which might be due to the hot, dry El Niño conditions. However, this effect was more extreme in logged forest. There were almost six times fewer new *Dicuspiditermes* spp. mounds in logged forest than in primary forest, but only 1.4 times fewer newly dead mounds. Taken together, there were 1.6 times more living mounds in primary forest, with fewer mounds dying and more mounds created, compared with logged forest (Fig. 6c). This might be due to disturbance from past logging activities, which could physically damage mounds. The mounds in logged forests could also suffer from a higher frequency of treefalls (we observed this on at least two plots), from soil compaction caused by logging vehicles (Edwards et al., 2014), and possibly by more extreme impacts of the two-year El Niño event (NOAA, 2019) in more degraded forest. The higher number of newly-created mounds in primary forest could result from the higher overall mound densities in this habitat and hence greater production of alates. We did not record any growth or turnover of *M. gilvus* mounds in any habitat. Furthermore, our measurement did not record any termite sheeting in this species (temporary protective soil layers build over food items and passageways) which is known to contribute greatly to overall termite bioturbation (Kooyman and Onck, 1987; Lee and Wood, 1971). This means that either mound growth is very slow for *M. gilvus*, or that termites favour more humid conditions for mound and sheetings building than those experienced during El Niño (Woon et al., 2019). However, when compared to *Dicuspiditermes* spp., there were disproportionally fewer *M. gilvus* mounds in all the habitats, and mound dynamics are expected to be slower. Additionally, *M. gilvus* mounds decompose slowly (Coventry et al., 1988), as the mound material is very dense. Hence, we would expect that the less dense *Dicuspiditermes* spp. mounds should decompose faster than those of *M. gilvus*, especially in humid conditions (supported by personal observation of Jiri Tuma).

4.5. Bioturbation rate and its relation to mass of standing bioturbated soil

The mean values of small-scale bioturbation rate were double or even triple those of large-scale standing bioturbated soil, when extrapolating to annual values in forested habitats, but not in oil palm (Supplementary material 5). This emphasizes the potential importance of bioturbators at small temporal and spatial scales. However, these values were extrapolated from a five-day observation period, and so we would advise caution in interpreting these results. We would recommend future work be conducted with repeated measurements of these bioturbation rates throughout the year (details of the methods and discussion on limitations are available in the Supplementary material 3). Despite this limitation, our measurements of growth of termite mounds indicates such a low rate of bioturbation generated by this group (42.7 kg ha^{-1} year^{-1}in primary forest and 28.6 kg ha^{-1} year^{-1} in logged forest), that the annual termite bioturbation figure is still an order of magnitude less than even the five-day small-scale short term bioturbation rate (not multiplied up to annual time scale). Previous work has emphasized the importance of termites as apparent bioturbators in tropical ecosystems (Holt and Lepage, 2000; Seymour et al., 2014). However, our work shows that small-scale bioturbators such as worms and ants, previously thought to be important mainly in temperate and drier sub-tropical systems (Persson et al., 2007), can contribute greatly to tropical bioturbation, with probably more rapid breakdown of bioturbated structures and hence possible incorporation back into the soil profile (which is one reason why this has been poorly documented). However, more measurements are needed during wetter periods, since growth of termite mounds might increase after rains, because termites are generally more active in humid conditions (Dibog et al., 1998). This is important, because the balance between species that slowly produce longer-lived mounds (termites) and those that rapidly produce smaller short-lived structures (worms and ants) is affected by habitat change (Fig 4a, this paper; Luke et al., 2014).

4.6. The relationship between diversity of bioturbators and its relation to bioturbation

Bioturbation is mediated by a more diverse community in less disturbed habitats, with a greater number of groups/species contributing similar amounts. Unexpectedly, in primary forest plots with higher bioturbator diversity, standing bioturbated soil was lower (Fig. 5). This is caused by termites bringing up, proportionally, the majority of soil in primary forest (note that the diversity index was calculated using proportions of soil brought up, rather than direct measures of abundances). Therefore, when there were fewer termite mounds in the area, the remaining bioturbators did not compensate for the bioturbation done by termites, despite the bioturbator diversity index being higher (because termites did not dominate). However, our method did not distinguish between different kinds of bioturbation qualitatively and the question remains whether the overall bioturbation caused by higher variety of bioturbators is more beneficial for the soil environment and nutrient cycling. There could also be some degree of competition for soil as a living space, or even in terms of soil nutrients, which would also explain our results, with termites outcompeting other bioturbating species.

4.7. Redundancy of bioturbators across habitats

It appears that the dominant bioturbator *M. gilvus* is able to maintain soil mounds in logged forest and to a greater extent in oil palm plantations. However, it remains unclear whether this species can balance the contribution of other bioturbators in the system in terms of nutrient redistribution and maintenance of soil quality. Because *M. gilvus* mounds are very dense clay structures, they are very long-lived, and their importance in terms of nutrient dynamics might not be as great as their imposing appearance suggests. The dominance of this species also means that aboveground bioturbation in oil palm plantations depends almost entirely on one species, which could make this converted habitat potentially vulnerable to species extinctions (Mack et al., 2000) and to loss of the ecosystem services provided by *M. gilvus*. However, such resilient bioturbating termite species may be vital for the initial recovery of disturbed habitats, for example by providing better soil hydrological functions (i.e. water infiltration), or decomposing dead plant matter (Dawes, 2010; Foster et al., 2011). In contrast, small-scale bioturbators like ants and earthworms still performed relatively well in plantations, highlighting their significance for contributing to total bioturbation in disturbed habitats. Logged forest represented an intermediate habitat. Some primary forest groups could still survive, for example efficient bioturbators such as soil-feeding termites, earthworms and cicadas, but there was also a higher density of *M. gilvus* mounds, keeping the standing bioturbated soil levels high. Hence, bioturbator redundancy remained high when the primary forest was logged, but not when the forest was converted to oil palm plantation.

5. Conclusion

Our work indicates that aboveground bioturbation in the tropics may be dominated by an important group of “hidden bioturbators”, whose small structures are rapidly broken down after construction, and hence whose importance has previously been underestimated. Although amounts standing of bioturbated soil and bioturbation rate did not differ between habitats, in oil palm plantation, the standing bioturbated soil was created almost exclusively by one species of termite – *Macrotermes gilvus*. Primary and logged forest, on the other hand, maintained a high diversity of bioturbators. This reliance on a single bioturbator species in oil palm plantation over larger scales is of concern because it leaves this important ecosystem process vulnerable to future extinction events.

Figures:

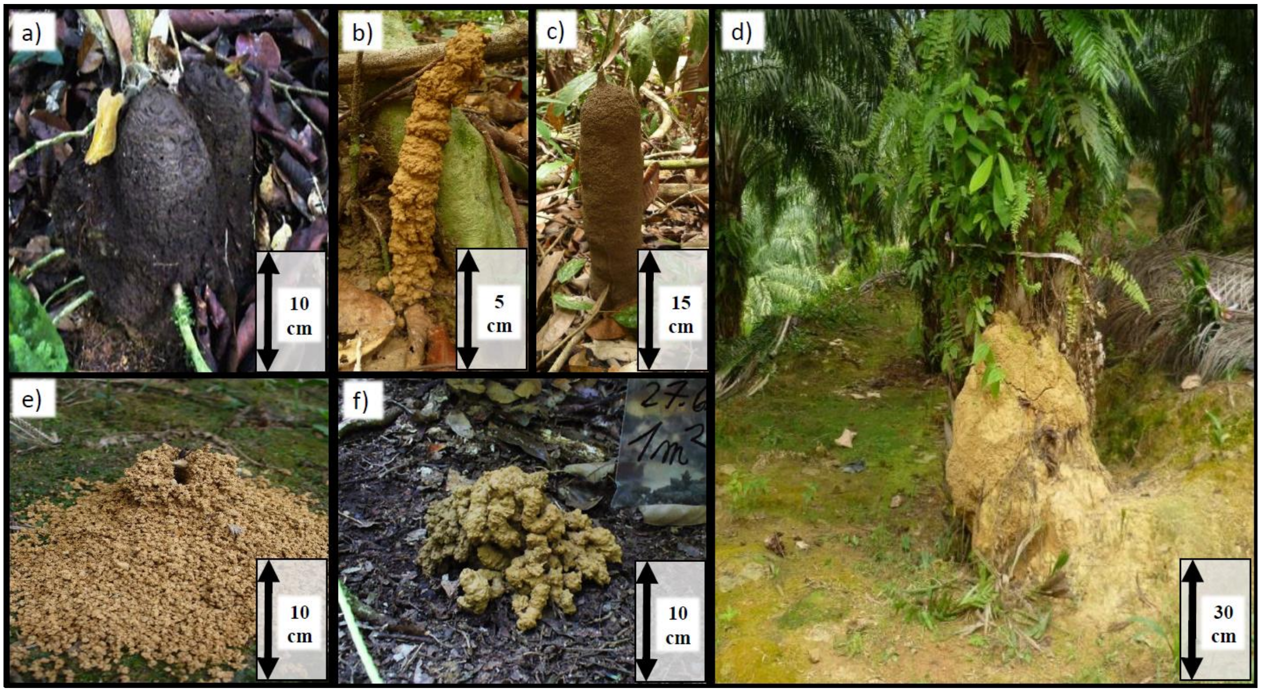

Fig. 1. Epigeous soil structures measured during surveys of standing bioturbated soil: (a) *Dicuspiditermes nemorosus* mound (note the two turrets emerging from the basal plate); (b) cicada turret; (c) *Dicuspiditermes minutus* mound; (d) *Macrotermes gilvus* mound at the base of an oil palm tree; (e) ant mound (*Odontoponera transversa*), at entrance to nest; (f) large earthworm cast. Scales vary between panels, and are indicated in the lower right corner of each panel.

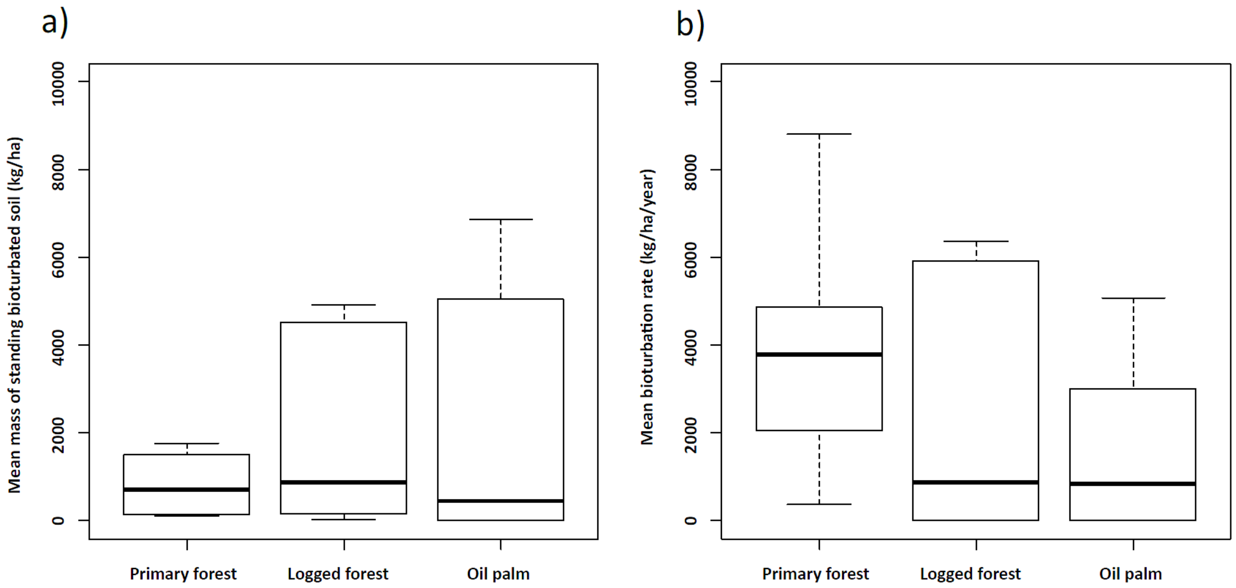

Fig. 2. (a) Mass of standing bioturbated soil in across different land uses measured at large scale (25 m x 25 m). (b) Bioturbation rate at small scale (2 m x 2 m plots measured over five days). Medians are denoted by bold horizontal lines, the interquartile range box represents the middle 50% of the data, and the whiskers represent full data ranges.

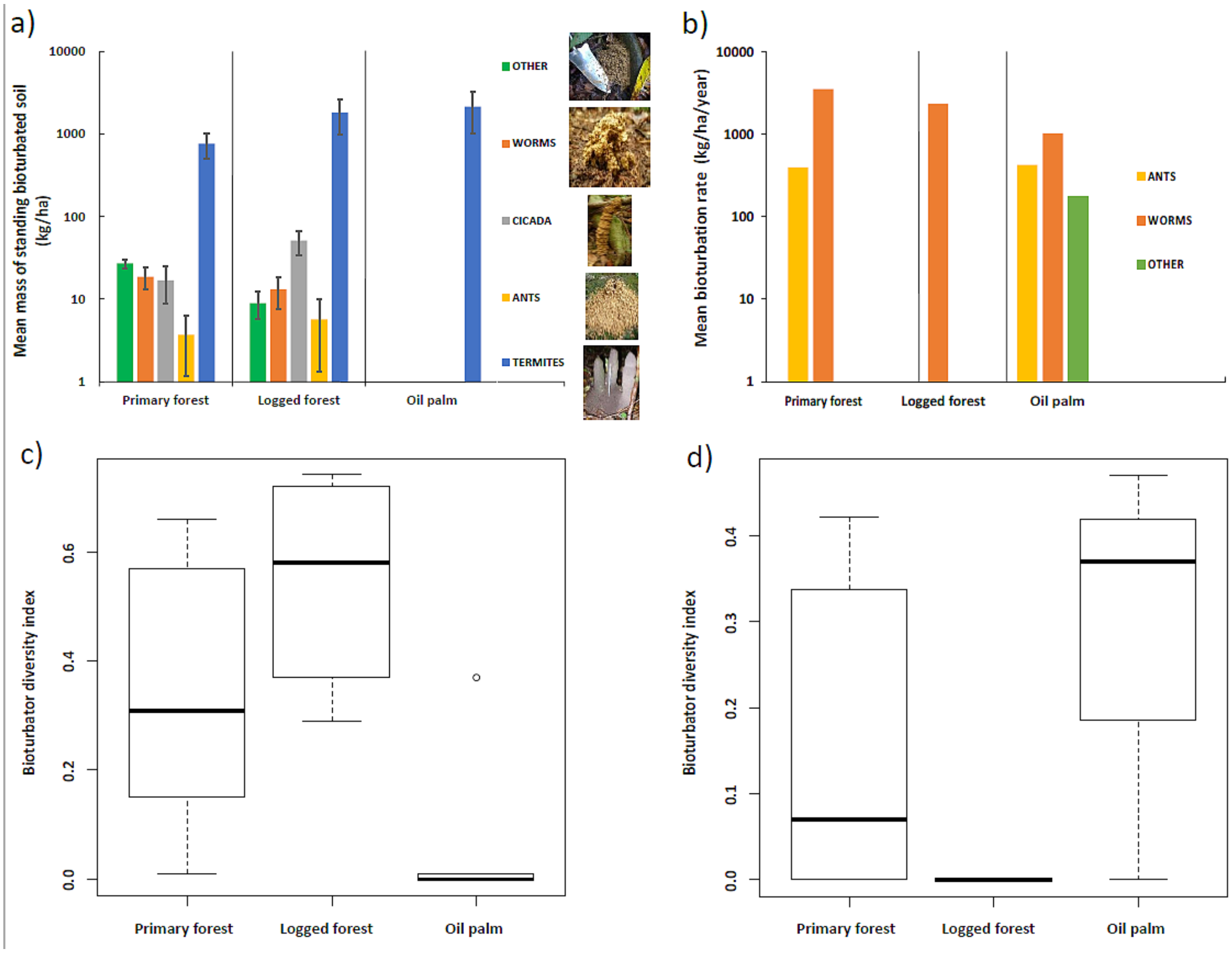

Fig. 3. The relative contribution of bioturbator groups to standing bioturbated soil and bioturbation rate across different land uses. (a) Large-scale standing bioturbated soil (note that the minimal values for ‘ants’ and ‘other’ groups are not visible in this graph for oil palm). (b) Small-scale bioturbation rate of different animal groups. Note the logarithmic y-axes in graphs (a) and (b) The error bars represent the standard error of mean. In graph (b) the SEM were removed for better data visualisation and are available in Supplementary material 6. (c) The bioturbator diversity index for standing bioturbated soil. (d) The bioturbator diversity index for small-scale bioturbation rate. In both c) and d) broadly defined taxonomic groups were used for the index calculation (see methods for details). In boxplots the median is denoted by a bold horizontal line, the interquartile range box represents the middle 50% of the data and the whiskers represent the full data range excluding outliers. Outliers are represented by open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles.

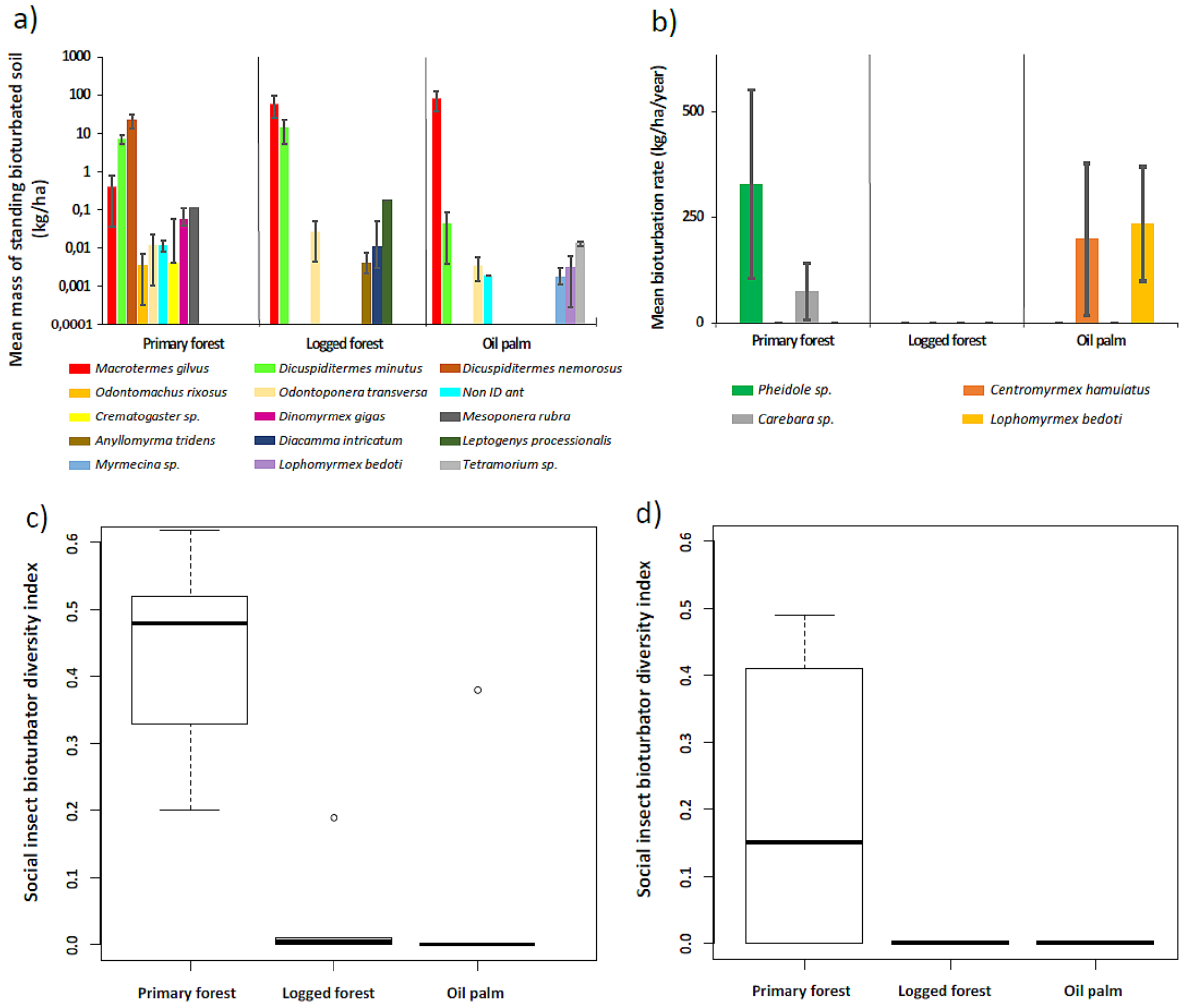

Fig. 4. Bioturbator diversity index and mass of standing bioturbated soil and bioturbation rates of social insects across different land uses. (a) Visualization of all social insect species generating standing bioturbated soil. All the SEM values are available in Supplementary material 6. Note the logarithmic y-axis. (b) Visualization of social insect small-scale bioturbation rate (note that no termite bioturbation was found in any habitat and no ant bioturbation was found in logged forest). The error bars represent the standard errors of means. (c) The bioturbator diversity index for social insects (ants and termites) identified to species level for standing bioturbated soil. (d) The bioturbator diversity index for social insects (ants and termites) for bioturbation rate. In boxplots the median is denoted by a bold horizontal line, the interquartile range box represents the middle 50% of the data and the whiskers represent the full data range excluding outliers. Outliers are represented by open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles.

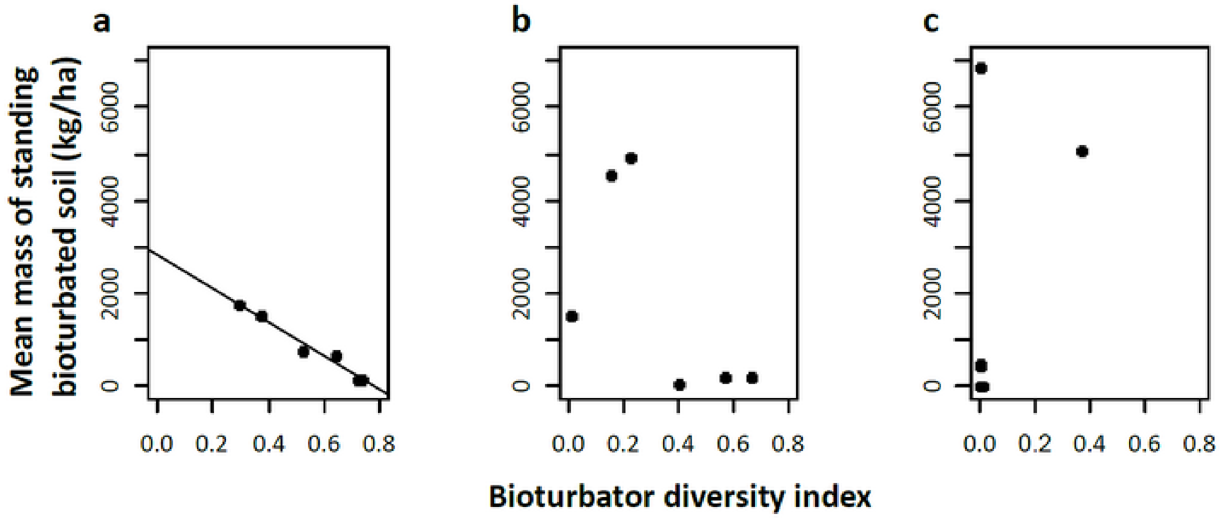

Fig. 5. The mass of standing bioturbated soil in relation to bioturbator diversity index in (a) primary forest, (b) logged forest and (c) oil palm plantation. Points represent individual plots (N=6 per habitats) at which standing mass of bioturbated soil and diversity of bioturbating animals were measured. The fitted line denotes a significant relationship.

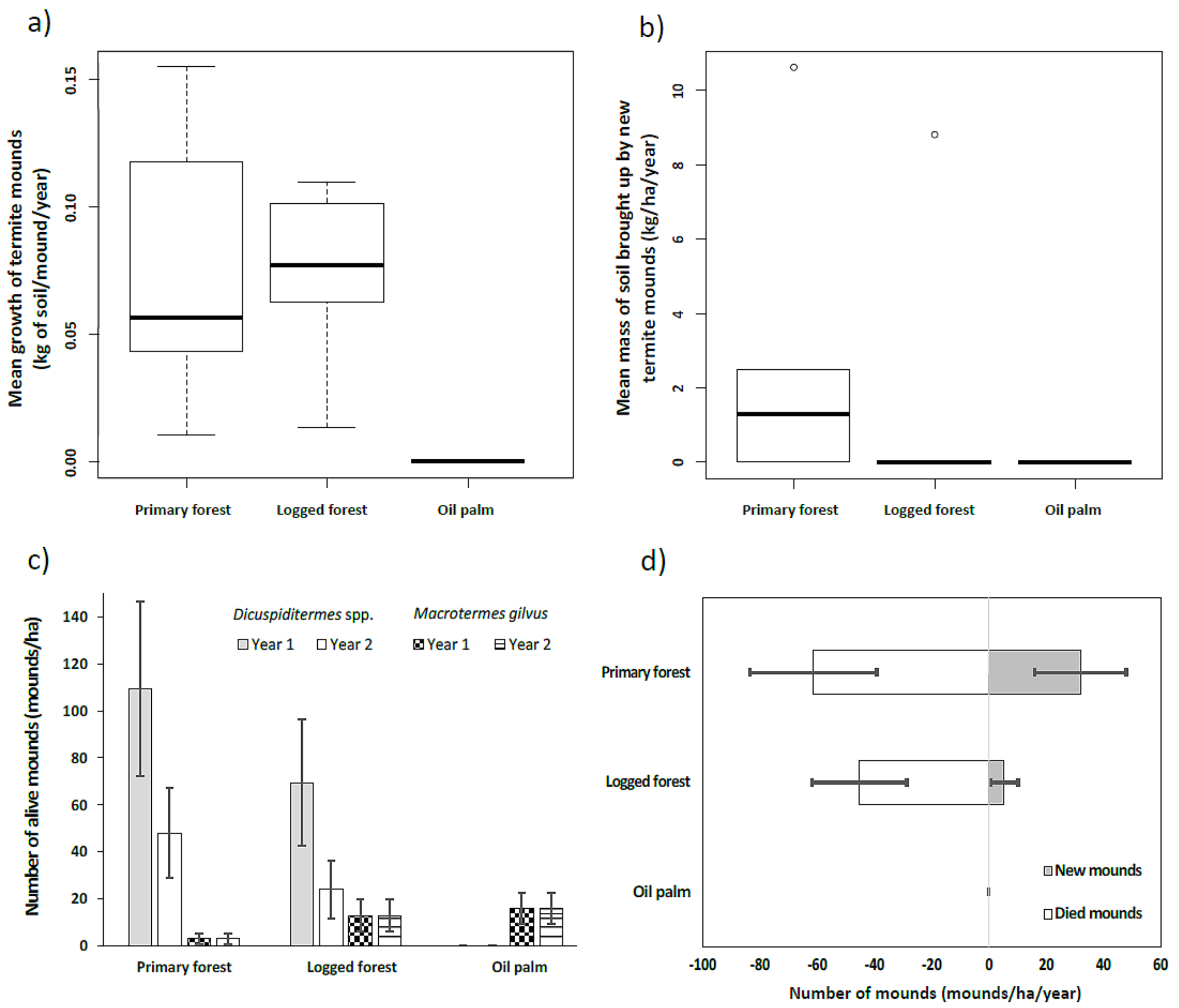

Fig. 6. Termite mound dynamics. Note that no growth or turnover of *M. gilvus* mounds was recorded during the one-year study period hence all such data presented here relate only to *Dicuspiditermes* spp. mounds. (a) The growth of *Dicuspiditermes* spp. termite mounds across different land uses measured over a one-year period. (b) The mass of soil brought up to the surface by newly emerged *Dicuspiditermes* spp. mounds. In boxplots the median is denoted by a bold horizontal line, the interquartile range box represents the middle 50% of the data and the whiskers represent the full data range excluding outliers. Outliers are represented by open points, and are defined as values being more extreme than 1.5 times the interquartile range from the upper or lower quartiles. Note that the absence of the upper whisker for primary forest is because the 75th percentile is the same value as the maximum value in the data, once the upper outlier is excluded. (c) Termite mound densities and relative changes over a one year period measured on 25 m x 25 m plots. (d) Number of recently dead and newly created *Dicuspiditermes* spp. mounds on 25 m x 25 m plots after one year.

Data Availability

Full datasets for all analyses in this paper are available at https://doi.org/10.5281/zenodo.3344504.

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References

Akhtar, M.S., Riaz, S., 1992. A new termite from Malaysia. Pak. J. Zool. 24, 35–37.

Bandeira, A.G., Vasconcellos, A., Silva, Moabe, P., Constantino, R., 2003. Effects of habitat disturbance on the termite fauna in a highland humid forest in the caatinga domain, Brazil. Sociobiology 42, 1–11.

Barrios, E., 2007. Soil biota, ecosystem services and land productivity. Ecol. Econ. 64, 269–285. https://doi.org/10.1016/j.ecolecon.2007.03.004

Basiron, Y., 2007. Palm oil production through sustainable plantations. Eur. J. Lipid Sci. Technol. 109, 289–295. https://doi.org/10.1002/ejlt.200600223

Brauman, A., 2000. Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: A review. Eur. J. Soil Biol. 36, 117–125. https://doi.org/10.1016/S1164-5563(00)01058-X

Bruijnzeel, L.A., 2004. Hydrological functions of tropical forests: Not seeing the soil for the trees? Agric. Ecosyst. Environ. 104, 185–228. https://doi.org/10.1016/j.agee.2004.01.015

Brussaard, L., 1998. Soil fauna, guilds, functional groups and ecosystem processes. Appl. Soil Ecol. 9, 123–135. https://doi.org/10.1016/S0929-1393(98)00066-3

Brussaard, L., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233–244. https://doi.org/10.1016/j.agee.2006.12.013

Chiavacci, S.J., Bednarz, J.C., McKay, T., 2014. The emergence densities of annual cicadas (Hemiptera: Cicadidae) increase with sapling density and are greater near edges in a bottomland hardwood forest. Environ. Entomol. 43, 859–867. https://doi.org/10.1603/EN13338

Coventry, R., Holt, J., Sinclair, D., 1988. Nutrient cycling by mound-building termites in low-fertility soils of semi-arid tropical Australia. Aust. J. Soil Res. 26, 375–390.

Cunha, L., Brown, G.G., Stanton, D.W.G., Da Silva, E., Hansel, F.A., Jorge, G., McKey, D., Vidal-Torrado, P., Macedo, R.S., Velasquez, E., James, S.W., Lavelle, P., Kille, P., 2016. Soil animals and pedogenesis: The role of earthworms in anthropogenic soils. Soil Sci. 181, 110–125. https://doi.org/10.1097/SS.0000000000000144

Dambros, C. de S., da Silva, V.N.V., Azevedo, R., de Morais, J.W., 2013. Road-associated edge effects in Amazonia change termite community composition by modifying environmental conditions. J. Nat. Conserv. 21, 279–285. https://doi.org/10.1016/j.jnc.2013.02.003

Dangerfield, J.M., McCarthy, T.S., Ellery, W.N., 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. J. Trop. Ecol. 14, 507–520. https://doi.org/10.1017/S0266467498000364

Dawes, T.Z., 2010. Impacts of habitat disturbance on termites and soil water storage in a tropical Australian savanna. Pedobiologia. 53, 241–246. https://doi.org/10.1016/j.pedobi.2009.11.003

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J., Lavelle, P., 2006. The values of soil animals for conservation biology. Eur. J. Soil Biol. 42, S23–S38. https://doi.org/10.1016/j.ejsobi.2006.07.001

Dey, A., Chaudhuri, P.S., 2014. Earthworm community structure of pineapple (*Ananas comosus*) plantations under monoculture and mixed culture in West Tripura, India. Trop. Ecol. 55, 1–17.

Dibog, L., Eggleton, P., Forzi, F., 1998. Seasonality of soil termites in a humid tropical forest, Mbalmayo, southern Cameroon. J. Trop. Ecol. 14, 841–850. https://doi.org/10.1017/S0266467498000601

Doran, J.W., Safley, M., 1997. Defining and assessing soil health and sustainable productivity, in: Pankhurst, C., Doube, B.M., Gupta, V.V.S.R. (Eds.), Defining and Assessing Soil Health and Sustainable Productivity. Cabi Publishing, Oxon, UK, p. 1275.

Dosso, K., Deligne, J., Yéo, K., Konaté, S., Linsenmair, K.E., 2013. Changes in the termite assemblage across a sequence of land-use systems in the rural area around Lamto Reserve in central Côte d'Ivoire. J. Insect Conserv. 17, 1047–1057. https://doi.org/10.1007/s10841-013-9588-2

Douglas, I., 1999. Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 354, 1725–1738. https://doi.org/10.1098/rstb.1999.0516

Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., Laurance, W.F., 2014. Maintaining ecosystem function and services in logged tropical forests. Trends Ecol. Evol. 29, 511–520. https://doi.org/10.1016/j.tree.2014.07.003

Eggleton, P., Tayasu, I., 2001. Feeding groups, lifetypes and the global ecology of termites. Ecol. Res. 16, 941–960. https://doi.org/10.1046/j.1440-1703.2001.00444.x

Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P., Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathevi, R., Kitching, R.L., Khoo, M.S., Luke, S.H., March, J.J., Nilus, R., Pfeifer, M., Rao, S. V., Sharp, A.C., Snaddon, J.L., Stork, N.E., Struebig, M.J., Wearn, O.R., Yusah, K.M., Turner, E.C., 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nat. Commun. 6, 1–7. https://doi.org/10.1038/ncomms7836

Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., Turner, E.C., 2011. A large-scale forest fragmentation experiment: The stability of altered forest ecosystems project. Philos. Trans. R. Soc. B Biol. Sci. 366, 3292–3302. https://doi.org/10.1098/rstb.2011.0049

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545. https://doi.org/10.1016/j.tree.2008.06.012

Foster, W. a., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Ellwood, M.D.F., Broad, G.R., Chung, a. Y.C., Eggleton, P., Khen, C. V., Yusah, K.M., 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. Philos. Trans. R. Soc. B Biol. Sci. 366, 3277–3291. https://doi.org/10.1098/rstb.2011.0041

França, F.M., Frazão, F.S., Korasaki, V., Louzada, J., Barlow, J., 2017. Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. Biol. Conserv. 216, 115–122. https://doi.org/10.1016/j.biocon.2017.10.014

Franco, A.L.C., Bartz, M.L.C., Cherubin, M.R., Baretta, D., Cerri, C.E.P., Feigl, B.J., Wall, D.H., Davies, C.A., Cerri, C.C., 2016. Loss of soil (macro)fauna due to the expansion of Brazilian sugarcane acreage. Sci. Total Environ. 563–564, 160–168. https://doi.org/10.1016/j.scitotenv.2016.04.116

Frouz, J., 2018. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma 332, 161–172. https://doi.org/10.1016/j.geoderma.2017.08.039

González, G., Huang, C.Y., Zou, X., Rodríguez, C., 2006. Earthworm invasions in the tropics. Biol. Invasions 8, 1247. https://doi.org/https://doi.org/10.1007/s10530-006-9023-7

Guéi, A.M., Tondoh, J.E., 2012. Ecological preferences of earthworms for land-use types in semi-deciduous forest areas, Ivory Coast. Ecol. Indic. 18, 644–651. https://doi.org/10.1016/j.ecolind.2012.01.018

Hagen, H.A., 1858. Special monograph on termites. Linnea Entomol. 12, 4–342.

Halfen, A.F., Hasiotis, S.T., 2010. Downward Thinking: Rethinking the “Up” in Soil Bioturbation, in: 19th World Congress of Soil Science, Soil Solutions for a Changing World. pp. 21–24. https://doi.org/10.1039/c3lc00031a

Hasiotis, S.T., Halfen, A.F., 2010. The Story of O: The dominance of organisms as a soil-forming factor From an integrated geologic perspective and modern field and experimental studies, in: World Congress of Soil Science. Brisbane/Australia, pp. 100–103.

Hassall, M., Jones, D.T., Taiti, S., Latipi, Z., Sutton, S.L., Mohammed, M., 2006. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. Eur. J. Soil Biol. 42, 197–207. https://doi.org/10.1016/j.ejsobi.2006.07.002

Haviland, G.D., 1898. Observations on termites; with descriptions of new species. J. Linn. Soc. London, Zool. 26, 358–442. https://doi.org/10.1111/j.1096-3642.1898.tb00405.x

Hernández-Flores, J., Osorio-Beristain, M., Martínez-Garza, C., 2016. Ant foraging as an indicator of tropical dry forest restoration. Environ. Entomol. 45, 991–994. https://doi.org/10.1093/ee/nvw054

Holt, J.A., Lepage, M., 2000. Termites and soil properties, in: Termites: Evolution, Sociality, Symbioses, Ecology. Springer Netherlands, Dordrecht, pp. 389–407. https://doi.org/10.1007/978-94-017-3223-9_18

Hopkins, D.W., Chudek, J.A., Bignell, D.E., Frouz, J., Webster, E.A., Lawson, T., 1998. Application of 13C NMR to investigate the transformations and biodegradation of organic materials by wood- and soil-feeding termites, and a coprophagous litter-dwelling dipteran larva. Biodegradation 9, 423–431. https://doi.org/10.1023/A:1008313309557

Jones, D.T., Susilo, F.X., Bignell, D.E., Hardiwinoto, S., Gillison, A.N., Eggleton, P., 2003. Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. J. Appl. Ecol. 40, 380–391. https://doi.org/10.1046/j.1365-2664.2003.00794.x

Jones, G.C., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. OIKOS 69, 373–386.

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. Appl. Soil Ecol. 32, 153–164. https://doi.org/10.1016/j.apsoil.2005.07.004

Karban, R., 2014. Transient habitats limit development time for periodical cicadas. Ecology 95, 3–8. https://doi.org/10.1890/13-1518.1

Kohl, L., Oehl, F., van der Heijden, M.G.A., 2014. Agricultural practices indirectly influence plant productivity and ecosystem services through effects on soil biota. Ecol. Appl. 24, 1842–1853. https://doi.org/10.1890/13-1821.1

Kooyman, C., Onck, R.F.M., 1987. The interactions between termite activity, agricultural practices and soil characteristics in Kisii District, Kenya. Agricultural University Wageningen Papers, Wageningen.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G.T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302. https://doi.org/10.3354/meps09506

Lamandé, M., Hallaire, V., Curmi, P., Pérès, G., Cluzeau, D., 2003. Changes of pore morphology, infiltration and earthworm community in a loamy soil under different agricultural managements. Catena 54, 637–649. https://doi.org/10.1016/S0341-8162(03)00114-0

Lavelle, P., Charpentier, F., Villenave, C., Rossi, J.-P., Derouard, L., Pashanasi, B., André, J., Ponge, J.-F., Bernier, N., 2004. Effects of earthworms on soil organic matter and nutrient dynamics at a landscape scale over decades. Earthworm Ecol. 2, 145–160.

Lee, K.E., Wood, T.G., 1971. Termites and soils. Academic press, London. https://doi.org/10.1017/S0014479700005354

Lobry De Bruyn, L.A., 1997. The status of soil macrofauna as indicators of soil health to monitor the sustainability of Australian agricultural soils. Ecol. Econ. 23, 167–178. https://doi.org/10.1016/S0921-8009(97)00052-9

Lobry de Bruyn, L.A., Conacher, A.J., 1994. The bioturbation activity of ants in agricultural and naturally vegetated habitats in semi-arid environments. Aust. J. Soil Res. 32, 555–570.

Luke, S.H., Fayle, T.M., Eggleton, P., Turner, E.C., Davies, R.G., 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodivers. Conserv. 23, 2817–2832. https://doi.org/10.1007/s10531-014-0750-2

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: casuses, epidemiology, global consequences and control. Ecol. Appl. 10, 689–710. https://doi.org/10.1890/0012-9623(2005)86[249b:IIE]2.0.CO;2

McGarigal, K., Cushman, S., Regan, C., 2005. Quantifying terrestrial habitat loss and fragmentation: A protocol. Amherst, MA Univ. Massachusetts, Dep. Nat. Resour. Conserv.

Meffe, G.K., Carrol, C.R., 1997. Principles of conservation biology, 2nd ed. MA: Sinauer Associates., Sunderland, Massachusetts.

Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol. 21, 688–695. https://doi.org/10.1016/j.tree.2006.08.002

Mikheyev, A.S., Tschinkel, W.R., 2004. Nest architecture of the ant *Formica pallidefulva*: Structure, costs and rules of excavation. Insectes Soc. 51, 30–36. https://doi.org/10.1007/s00040-003-0703-3

Minter, N.J., Franks, N.R., Robson Brown, K.A., 2012. Morphogenesis of an extended phenotype: Four-dimensional ant nest architecture. J. R. Soc. Interface 9, 586–595. https://doi.org/10.1098/rsif.2011.0377

NOAA, 2019. http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_advisory/

Paton, T.R., Humphreys, G.S., Mitchell, P.B., 1995. Soils: a new global view. Yale University Press, New Haven.

Persson, T., Lenoir, L., Taylor, A., 2007. Bioturbation in different ecosystems at Forsmark and Oskarshamn. Stockholm.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H. a, Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Seymour, C.L., Milewski, A. V, Mills, A.J., Joseph, G.S., Cumming, G.S., Cumming, D.H.M., Mahlangu, Z., 2014. Do the large termite mounds of Macrotermes concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? Soil Biol. Biochem. 68, 95–105. https://doi.org/10.1016/j.soilbio.2013.09.022

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. https://doi.org/10.1038/163688a0

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L., 2004. Southeast Asian biodiversity: An impending disaster. Trends Ecol. Evol. 19, 654–660. https://doi.org/10.1016/j.tree.2004.09.006

Solar, R.R. de C., Barlow, J., Andersen, A.N., Schoereder, J.H., Berenguer, E., Ferreira, J.N., Gardner, T.A., 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biol. Conserv. 197, 98–107. https://doi.org/10.1016/j.biocon.2016.03.005

Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., Bell, D., 2013. Quantifying the biodiversity value of repeatedly logged rainforests. Gradient and comparative approaches from Borneo. Adv. Ecol. Res. 48, 183–224. https://doi.org/10.1016/B978-0-12-417199-2.00003-3

Tilahun, A., Kebede, F., Yamoah, C., Erens, H., Mujinya, B.B., Verdoodt, A., Van Ranst, E., 2012. Quantifying the masses of *Macrotermes subhyalinus* mounds and evaluating their use as a soil amendment. Agric. Ecosyst. Environ. 157, 54–59. https://doi.org/10.1016/j.agee.2011.11.013

Turner, E.C., Snaddon, J.L., Ewers, R.M., Fayle, T.M., Foster, W. a, 2011. The impact of oil palm expansion on environmental change: putting conservation research in context. Environ. Impact Biofuels 19–40. https://doi.org/10.5772/960

Usman, S., Muhammad, Y., Chiroman, A., 2016. Roles of soil biota and biodiversity in soil environment – A concise communication. Eurasian J. Soil Sci. 5, 255. https://doi.org/10.18393/ejss.2016.4.255-265

Whalen, J.K., Sampedro, L., Waheed, T., 2004. Quantifying surface and subsurface cast production by earthworms under controlled laboratory conditions. Biol. Fertil. Soils 39, 287–291. https://doi.org/10.1007/s00374-003-0715-1

Wilkinson, M.T., Richards, P.J., Humphreys, G.S., 2009. Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. Earth-Science Rev. 97, 257–272. https://doi.org/10.1016/j.earscirev.2009.09.005

Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C. V., Bottrell, S.H., Hamer, K.C., 2011. The conservation value of South East Asia’s highly degraded forests: evidence from leaf-litter ants. Philos. Trans. R. Soc. B Biol. Sci. 366, 3256–3264. https://doi.org/10.1098/rstb.2011.0031

Woon, J.S., Boyle, M.J.W., Ewers, R.M., Chung, A., Eggleton, P., 2019. Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. Insectes Soc. 66, 57–64. https://doi.org/10.1007/s00040-018-0664-1

Yair, A., 1995. Short and long term effects of bioturbation on soil erosion, water resources and soil development in an arid environment. Geomorphology 13, 87–99. https://doi.org/10.1016/0169-555X(95)00025-Z

Supplements

Supplement 1

SAFE project sites at which the bioturbation survey plots were located, and their GPS coordinates.

Sampled sites	GPS coordinates	Mean altitude (m a.s.l.)
OG2	4.747133 - 116.972182	279
B	4.729231 - 117.616939	428
F	4.699606 - 117.546201	445
LFE	4.740113 - 117.589789	494
OP1	4.656591 - 117.453272	405
OP2	4.647143 - 117.441597	471

OP3	4.640273 - 117.453208	306

Supplement 2

Field bioturbation assessment protocol

This guide aims to provide a straightforward method for estimation of terrestrial bioturbation activity performed by various soil organisms from appearance of soil above ground level. It can be used to compare the relative importance of various macro- and megafauna performing bioturbation, and to compare bioturbation values between habitats or biomes. The protocol described here is implemented in Tuma et al. (In preparation).

Methods:

1. Plot establishment

Individual sampling plots were of dimensions 25 m x 25 m. Preliminary observations indicated that this size is small enough for effectively surveying all activity within each plot, but sufficiently large for recording the potentially clumped distribution of particular structures created by bioturbation (e.g. cicada turrets). The number of replicates of these plots will depend on the particular research question, the expected magnitude of effect sizes, and the expected within habitat heterogeneity. The replicates should be randomly distributed within the sampled habitat, unless the aim is to sample a specific place in the area of interest. Before starting the survey, the plot should be marked using tape or string on its edges and corners. Two different kinds of surveys are then carried out within each plot. One for measuring larger structures over the entire 25 m x 25 m plot (3. Standing bioturbated soil), and a second for measuring creation of smaller structures in a 1 m by 1 m sub-plot (4. Bioturbation rate).

2. Types of soil structures

In advance of the whole procedure, it is recommended to make several trial surveys. During these, one can learn to recognise the structures present in the habitat. The soil casts can be dissected to see the internal organisation and in some cases to find and sample the animal creating it, in order to become familiar with types of structures. In most cases the bioturbator can then be placed in a broad taxonomic/functional category solely from the appearance of the cast. The variability between and within groups of bioturbators from our field sites in Sabah (Malaysia) is depicted in Figures 1 - 4.

For example, earthworms typically produce shaped casts, compressed, smooth soil structures, roughly mirroring the shape and the size of the earthworm itself. The casts of large tropical earthworms could be mistaken for cicada emergence turrets. However, cicada turrets have a large cavity in the middle of the cast. Ant mounds are, in contrast, formed by loose grains formed in variously shaped heaps and mounds. For ants it is also possible to use a bait dropped near the mound structure (e.g. crushed biscuit) and observe whether the resulting foraging trail leads to the mound. A voucher sample of the ant species can then be obtained. These examples demonstrate the importance of observing the structures, learning their most common shapes, and trialling the procedure beforehand.

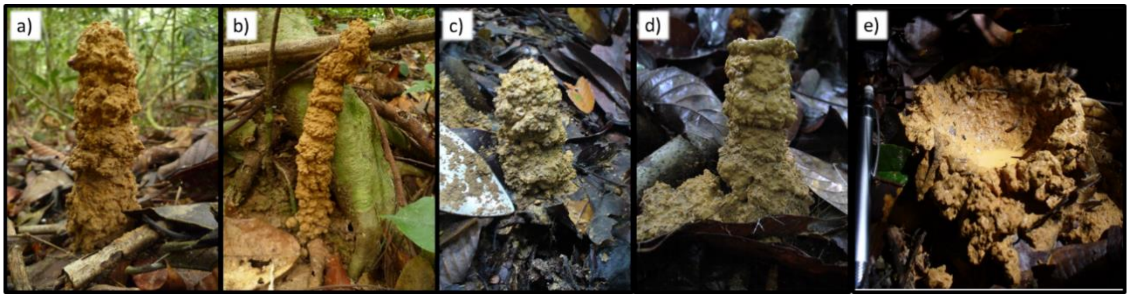


Figure 1. Diversity of cicada turrets around emergence holes. a) – c): different sizes and shapes of capped turrets, d) fresh, uncapped turret, e) a turret damaged by rain, but still recognizable.

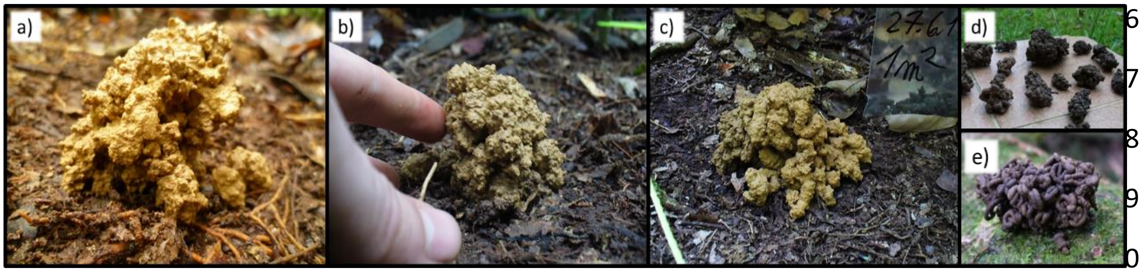


Figure 2. Diversity of earthworm casts. a)-c) different shapes of yellow, clay-rich casts, extruded by large earthworms. d) large, red/brown casts, created by large earthworms ingesting clay which is rich in iron. e) smaller, dark-brown/black casts produced by small earthworms living in upper soil layers rich in organic matter.

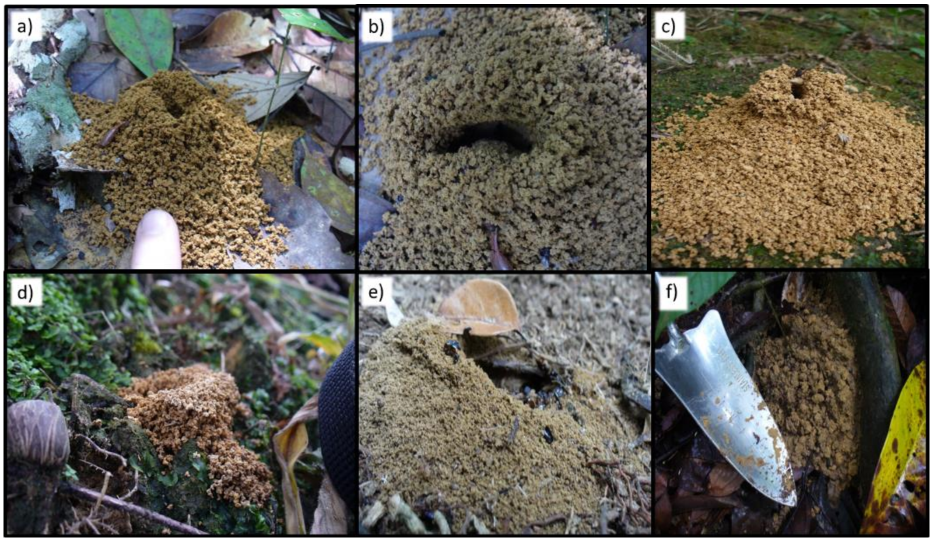


Figure 3. Diversity of ant nests. a) excavated soil around the nest entrance of *Diacamma intricatum*. b) typical U-shaped, slit-like entrance of a *Diacamma intricatum* nest. c) nest entrance of *Odontoponera transversa*. d) small heap of soil around another *Odontoponera transversa* nest. e) soil wall with food remnants around nest entrance of *Pheidole* sp. f) a structure superficially like an ant nest, but classed as 'burrow' created by unidentified digging.

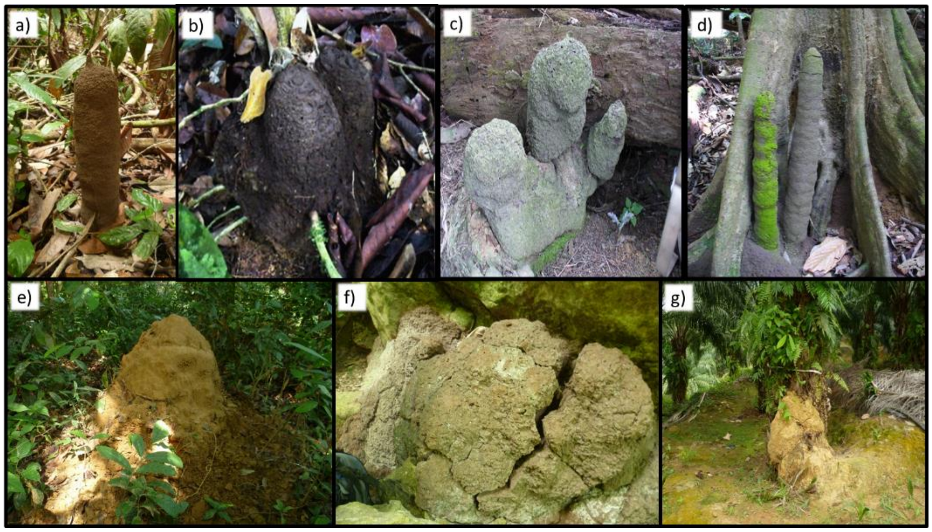


Figure 4. Diversity of termite mounds. a) *Dicuspiditermes minutus* typical mound. b) *D. nemorosus* typical mound. c) *Dicuspiditermes minutus* in oil palm plantation d) *Dicuspiditermes* sp. in logged forest (SAFE site 'LFE' plot). e) *Macrotermes gilvus* mound in primary forest. f*) M. gilvus* in logged forest – a mound made from soil rich in iron (SAFE site 'F'). g) *M. gilvus* mound in oil palm plantation attached to an oil palm tree.

3. Standing bioturbated soil (large-scale)

Searching for the soil structures created by bioturbation should be done in one or two-meter strips, depending on undergrowth density and terrain complexity, starting from a corner of the 25 m by 25 m plot. A good approach is to mark the strips that have already been surveyed by attaching tape to the vegetation, especially in dense vegetation.

It is unmanageable to collect all of the smaller soil structures on the soil surface as they are covered by litter, too small to spot, or difficult to distinguish from soil between dead leaves that were not necessarily generated by bioturbators. Therefore it is useful to set a minimum threshold for dimensions (mainly height) of the soil structures to be collected. In our study, we set the threshold to 6 cm. This excluded mainly epigeic and small anecic earthworms, some ant mounds and other small burrowers falling below this threshold. However, these were recorded in 1 m x 1 m plots (see section 4 below).

The soil structures should be collected in separate plastic bags, each type into an individual bag for each plot. It is recommended to use a small trowel for scooping the soil. The whole structure above the soil surface should be collected, including the soil stacked between living or dead leaves, and the soil that has been splashed or scattered around, but clearly originated in the focal soil structure. Usually, it is possible to distinguish this soil from the unchanged soil as the bioturbated soil is often of different colour and texture. The individual samples of collected soil should be oven dried at 80°C for 48 hours and weighed.

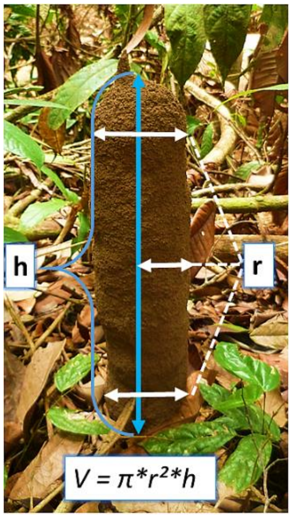


Figure 5. Measurement procedure on *Dicuspiditermes minutus* mound in order to calculate the total volume of aboveground soil trapped in the mound.

Figure 6. Reference soil core taken from *Dicuspiditermes minutus* mound to obtain specific volumetric weight for estimation of total mound weight.

Larger soil structures, represented mainly by termite mounds, cannot be collected easily. In such cases, the dimensions of the mound are measured and the weight calculated through a "specific volumetric weight" approximation. First, the dimensions of the mounds in the field are measured. This depends on the most usual shape of the mounds, as it needs to be decided what geometric object will be used to estimate weight of each mound. For the termite *Macrotermes gilvus*, we measured the height and the diameter of the mound and applied the formula for cone volume calculation: $V=\pi*r^2*h/3$ (A). Then the density of the mound material was measured by inserting a sampling tube with known dimensions into the mound body thus obtaining a known volume of the mound substrate (Fig. 6). We sampled three mounds for each termite species across all habitats and took an average value for volumetric weight. These voucher samples are then oven-dried at 80°C for 48 hours and weighed. We then calculated the volume of the tube for the specific volumetric weight sampling (B) and divided it by the weight of the dry soil in this tube from *M. gilvus* voucher mound (C). Then we calculated the estimated total weight (D) of the sampled mound as $D= A*C/B$ (g). In case of the termite *Dicuspiditermes* spp., the mound volume was measured in the same way, but using an equation for the volume of cylinder, instead of a cone (Fig. 5). Note that the method described in this section estimates total standing bioturbated soil over a large area, rather than measuring the rate of soil turnover.

4. Bioturbation rate (small scale)

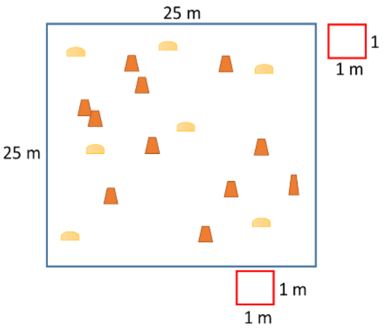


Figure 7. The layout of the bioturbation survey plots in the field. The blue square represents 25 x 25 m plot for surveying the standing bioturbated soil. The two red squares represents 1 x 1 m plots for survey of bioturbation rate done by smaller organisms.

The second type of measurement considers the bioturbation done by smaller animals, which are not included in the survey of the 25 x 25 m plot. This method also allows measurement of the rate of bioturbation (as distinct from the standing amount of bioturbated soil measured in the larger plots). For these smaller animals, the plot dimensions are 1 m x 1 m. Two 1 m^2 plots should be established at the edge of the 25 m x 25 m plot, but outside of it, in order to record small and large scale bioturbation in similar microhabitat conditions (Fig. 7). These two plots are placed avoiding any of the large structures that would have been surveyed in the 25 m x 25 m plot survey. Again, the perimeter should be marked using colourful string or tape. Before starting surveys, it is necessary to remove all leaf litter and dead plant material from the plot as well as all the soil structures formed by previous bioturbation (see Fig. 8). These are mostly small coprolites (typically of brown/black colour), smaller ant mounds (e.g. from *Pheidole* spp., *Carebara* spp., *Diacamma* spp.), small heaps of soil created by beetle larvae, solitary wasps and other animals. The aim of this clearing is to remove any soil structures that could later be misidentified as new bioturbation on this plot. In certain cases it is difficult to judge if a particular structure has been created by bioturbation, or sometimes it is be too demanding to remove it without severely destroying the plot. In such cases, these structures are marked with colourful toothpicks in order to avoid counting them later as newly emerged structures. This completes the first phase of the survey.

The second phase involves re-visiting the plot after five days. This is long enough for new structures to emerge, but also not excessively long for the effect of the rain to wash away the bioturbated material. Rain is the main limiting factor in this kind of measurement, as it restricts the maximal time between the setup and re-visit of the plot.

The survey phase is based on the same principle as for the larger plot described above. Although the searching has to be done at a smaller scale in order to record even minimal bioturbation. The structures were collected in separate bags and their animal-group identity recorded. The soil was then dried and weighed in the same way as for the large-scale method.

The bioturbation rate values obtained by the small-scale method represent temporal information about soil reworking. However, this is not true for the measurement of the large-scale bioturbation. We therefore propose that for future projects, the large and small-scale surveys are performed repeatedly through the year, or at least, the surveys repeated in the main seasonal periods, in order to record the changes in bioturbation in relation to the main environmental conditions (e.g. dry and wet season). The impact of environmental conditions on bioturbation could then be assessed, and total yearly bioturbation could be more accurately calculated.


Figure 8. Established 1 m^2 plot for small-scale bioturbation rate survey. Note that the plot is marked with bright coloured string and the litter and pre-existing bioturbated structures are removed.

Termite mound dynamics

5. Termite mound growth

To obtain information on relative growth of termite mounds we used plastic sticks with measuring scales, which were pushed horizontally and vertically in the body of the mound (Fig. 9: a). The sticks should be firm and pointed as the mound material can be very dense and difficult to penetrate. It is also easy to damage the mound, so inserting the sticks has to be done carefully. Opening the mound during this procedure can provoke the termites to cover not only the opening, but also the scale itself. The sticks should be long enough and extending above the mound surface to be still visible after one year of mound growth. The scales (cm) on the sticks should be carved/incised into the scale body as the field conditions can otherwise obscure scale marks. The position of the scales have to be recorded and photographed for future reference. A variety of mound sizes should be chosen for the mound growth measurement, as smaller or younger mounds can grow faster than older ones (Jiri Tuma, personal observation). After one year, the mounds with the measuring sticks should be checked and the level of mound material covering the scale

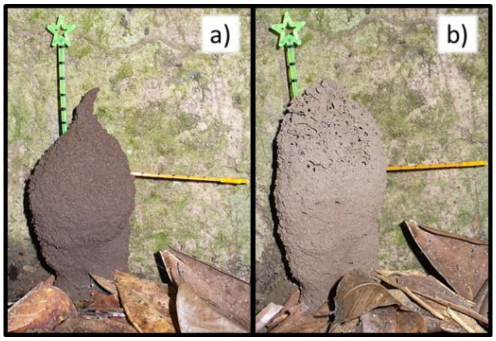


Figure 9. a) Sticks with measuring scales inserted in the body of a *Dicuspiditermes* spp. termite mound. b) The growth of the mound after one year – new soil mass covers the measuring scales. Note, that the vertical scale would not have been high enough in this case had the mound not died, as small mounds have the potential to completely overgrown the scale. Note broken appearance of the mound after one year, due to death of the colony.

should be recorded (Fig. 9: b). By this method, the initial size and the relative change of mound size can be determined, and hence the amount of up-lifted material incorporated into the mound structure can be calculated using cone/cylinder formula and specific volumetric weight of the mound material (calculation described in section 3. Standing bioturbated soil, see above).

6. Termite mound turnover

This assessment is based on section 3, in which all the standing termite mounds in the 25 m x 25 m plots were measured. To obtain the mound turnover in these plots, all the standing mounds should be marked with firm stick and a colourful flag with a mound specific number, or customized labelling. Additionally, the position of the individual live mounds in the plot should be recorded as well as the prominent features of the plot (logs, big trees etc.) for better navigation within the plot. After one year, the plot should be re-surveyed. The newly emerged mounds should be recorded and the state of the labelled mounds checked. If the mound fell to the ground, or is abandoned and in a bad state, the decomposition processes begins and it can be classified as dead in case of *Dicuspiditermes* spp. In case of large and stable mounds, as *Macrotermes gilvus*, the state of the mound should be inspected in detail. The mound has to be opened to confirm the presence of living individuals inside, or for the state of the symbiotic fungus. By this method, the number of surviving, newly-emerged and newly-dead mounds, in the plot over the course of one year can be obtained and thus the turnover rate of termite mounds can be calculated. Note that this method will not detect any mounds that have appeared and died within the course of one year.

5. Concluding remarks

By combining all these approaches, it is possible to obtain a representative picture of bioturbation in terrestrial habitats. It is also possible to calculate the comparative contribution of different macro and mega faunal groups to the overall bioturbation. However, a user of this guide should be aware of the limitations of this method and take them in account when interpreting the results. With the method we developed, we obtained a “snapshot” of aboveground bioturbation present. Principally, we did not aim to evaluate the bioturbation activity of any particular animal in detail apart from for termite mound dynamics. This method also necessarily underestimates total bioturbation values in following aspects:

1. The method measures only aboveground soil presence and it is known that underground soil mixing can reach significant, but mostly unknown share of the overall bioturbation (Hasiotis and Halfen, 2010; Minter et al., 2012).
2. It omits very small bioturbation done by certain meso- and micro-fauna, such as small earthworms and Enchytraeidae, dipterian larvae, nematodes etc.
3. In order to obtain a complete picture of bioturbation in certain habitat, multiple measurements during the year, both of standing and of mixing rate would have to be taken to record the creation and decay of more temporal structures (such as cicada turrets and earthworm casts). Nevertheless, we believe that our combined method for measuring terrestrial bioturbation can be of use when the habitats are compared within the same region and over the same time frame.

A simplified outline of the procedure for bioturbation estimation:

1. Preliminary identification of structures done by bioturbation and their creators present in studied system.

2. Establishing the survey plot for large-scale standing bioturbated soil measurement.

3. Large-scale survey. Collection of bioturbated soil structures and separation of them according to the animal group.

4. Sampling of the larger (non-collectable) structures for ‘specific volumetric weight’ and measuring the dimensions of these structures.

5. Establishing the plots for small-scale bioturbation rate survey. Marking the plot, removing the litter layer and existing bioturbation structures, marking larger, bioturbation-like structures for future reference.

6. After a period of five days, surveying the plots for small-scale bioturbation activity, identification, collection and separation of the collected bioturbated structures into bioturbator groups.

References

Hasiotis, S.T., Halfen, A.F., 2010. The Story of O: The dominance of organisms as a soil-forming factor From an integrated geologic perspective and modern field and experimental studies, in: World Congress of Soil Science. Brisbane/Australia, pp. 100–103.

Minter, N.J., Franks, N.R., Robson Brown, K.A., 2012. Morphogenesis of an extended phenotype: Four-dimensional ant nest architecture. Journal of the Royal Society Interface 9, 586–595. doi:10.1098/rsif.2011.0377

Supplement 3

A more detailed explanation of the results relating to different soil fauna contributing to bioturbation in our system. Note that references to figures reference to the main manuscript.

Apart from termites, the other animal groups contributing to standing bioturbated soil were cicadas, earthworms, other unidentified bioturbators and ants. **Cicada** larvae build a soil turret from clay around the emergence holes in their last year of underground life (Béguin, 2017). They contributed to total bioturbation in our large scale assessment by between 0 – 2.7 %. The highest mean weight of soil represented by cicada turrets was found in logged forest, followed by primary forest and there was none found in oil palm plantation. This situation probably reflects the availability of food resources and environmental conditions cicadas require in the assessed habitats, as cicada larvae rely on young saplings and trees (Chiavacci et al., 2014). There are enough saplings and low vegetation available in forested habitats but not in the plantation. Additionally, sapling density can be connected with sun-affected spots along with continuous treefall gap dynamics (Arihafa and Mack, 2013). The logged forest has a more open canopy due to physical damage from the removal of large trees, skid trails and logging roads (Douglas, 1999). Cicadas prefer these areas, as there is significant re-growth triggered by better light conditions (Chiavacci et al., 2014). Finally, the absence of cicada turrets in intensively managed oil palm plantations could be caused by the absence of any tree saplings and other vegetation on which cicadas could feed.

Earthworms (Oligochaeta) are widespread bioturbators in humid habitats that produce casts. Their contribution to total bioturbation in our standing bioturbated soil assessment was: 0–2.26 %, but 63 –99 % at for small scales bioturbation rate. The mean weight of collected casts for standing bioturbated soil was highest in primary forest and comparable with logged forest values. There was no bioturbation caused by large earthworms in oil palm plantations measurable by our method. Note, that only the larger coprolites (> 6 cm in height) were collected during standing bioturbated soil assessment. Tropical earthworms in general depend on litter quality, organic matter content in the soil, humidity, and seasonality (Dey and Chaudhuri, 2014), but they also vary in species composition, depending on land use (Guéi and Tondoh, 2012). The lack of large earthworm activity in oil palm can be explained by the very poor litter layer, as this condition directly results in low input of organic matter into the soil and an absence of humid microclimate near the soil surface (Turner and Foster, 2009; Brühl and Eltz, 2010). However, we found a number of smaller earthworm casts in oil palm plantation the bioturbation rate assessment, so there must be another factor negatively affecting large earthworms in oil palm habitats.

Ants are known as major bioturbators in a number of habitats (Mandel and Sorenson, 1982; Carlson and Whiteford, 1991; Nkem et al., 2000; Persson et al., 2007; Evans et al., 2011). Nonetheless, their contribution to total bioturbation in our standing bioturbated soil assessment was the least: 0 - 0.5 % and 0 – 26.2 % for small scale bioturbation rate. We did not see any tall soil ant mounds with complex internal structure. Most of the soil excavated by ants and deposited on the soil surface appeared to be just 'soil dumps', rather than true functional structures that are created in some places e.g. in the temperate zone (*Formica, Lasius*). Only the slit-shaped and turret-like entrance of *Diacamma intricatum* and soil walls around nest entrances of *Carebara* sp. and *Pheidole* sp. seemed to serve as protection of the nest entrance hole. In the contrast to this, the soil scattered around *Odontoponera transversa* nest entrance in oil palm was loose and seemed to be only temporary, being easily washed away by rain. Hence, ants appear to be important bioturbators at small scales, with unexplored bioturbation potential as they often do not form permanent aboveground mounds.

There was a significant bioturbation caused by animals that we were not able to identify (**Other** category). Generally, the bioturbated soil was found in heaps, mounds or placed without order, but was evidently excavated. Based on our experience and on animals present in these habitats, we speculate that this bioturbation was generated by rodents, lizards (e.g. Agamidae), snakes, myriapods, solitary wasps, beetles and other digging insects, including their larval stages. The contribution to standing bioturbated soil of this group was 0 – 3.3 %, and 0 – 11% for small scale bioturbation rate. Bioturbators in this category performed well in forested habitats, but not in oil palm plantations. This could be attributed to lower overall animal diversity in oil palm (Fitzherbert et al., 2008; Turner et al., 2011) in the standing bioturbated soil assessment. This trend is supported also by our results concerning bioturbator diversity (Fig. 3). Hence, there is decreased probability that a given animal living in oil palm plantations would act as an efficient bioturbator. On the other hand, oil palm plantations are known for cases of hyper-abundances of particular species (Senior et al., 2013), so there is a theoretical potential that a hyper-abundant, or even invasive species would be an efficient bioturbator. This raises the question, if we could consider the termite *M. gilvus* termite as a disturbed habitat species but also an efficient bioturbator in oil palm plantations.

References

Arihafa, A., Mack, A.L., 2013. Treefall gap dynamics in a tropical rain forest in Papua New Guinea. Pacific

Science 67, 47–58. doi:10.2984/67.1.4

Béguin, C.F., 2017. An architect cicada in brazilian rainforest: Guyalna chlorogena (Walker). Neotropical Entomology 46, 159–168. doi:10.1007/s13744-016-0464-0

Brühl, C.A., Eltz, T., 2010. Fuelling the biodiversity crisis: Species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). Biodiversity and Conservation 19, 519–529. doi:10.1007/s10531-009-9596-4

Carlson, S.R., Whiteford, W.G., 1991. Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. American Midland Naturalis 126, 125–139. doi:doi:10.2307/2426157

Chiavacci, S.J., Bednarz, J.C., McKay, T., 2014. The emergence densities of annual cicadas (Hemiptera: Cicadidae) increase with sapling density and are greater near edges in a bottomland hardwood forest. Environmental Entomology 43, 859–867. doi:10.1603/EN13338

Dey, A., Chaudhuri, P.S., 2014. Earthworm community structure of pineapple (Ananas comosus) plantations under monoculture and mixed culture in West Tripura, India. Tropical Ecology 55, 1–17.

Douglas, I., 1999. Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 354, 1725–1738. doi:10.1098/rstb.1999.0516

Evans, T.A., Dawes, T.Z., Ward, P.R., Lo, N., 2011. Ants and termites increase crop yield in a dry climate. Nature Communications 2, 262. doi:10.1038/ncomms1257

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends in Ecology and Evolution. doi:10.1016/j.tree.2008.06.012

Guéi, A.M., Tondoh, J.E., 2012. Ecological preferences of earthworms for land-use types in semi-deciduous forest areas, Ivory Coast. Ecological Indicators 18, 644–651. doi:10.1016/j.ecolind.2012.01.018

Mandel, R.D., Sorenson, C.J., 1982. The role of the western harvester ant (Pogonomyrmex occidentalis) in soil formation. Soil Science Society of America Journal 46, 785. doi:10.2136/sssaj1982.03615995004600040024x

Nkem, J.N., Bruyn, L.A.L. De, Grant, C.D., Hulugalle, N.R., 2000. The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia 44, 609–621.

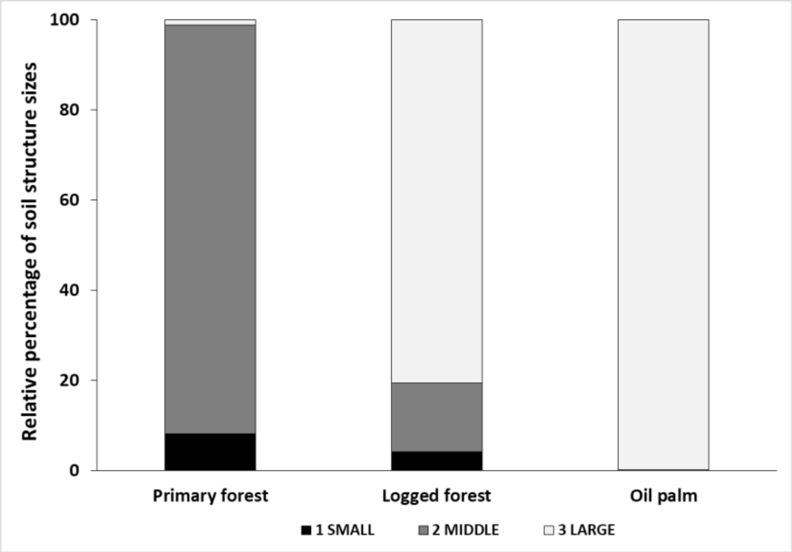
Persson, T., Lenoir, L., Taylor, A., 2007. Bioturbation in different ecosystems at Forsmark and Oskarshamn. Stockholm.

Senior, M.J.M., Hamer, K.C., Bottrell, S., Edwards, D.P., Fayle, T.M., Lucey, J.M., Mayhew, P.J., Newton, R., Peh, K.S.H., Sheldon, F.H., Stewart, C., Styring, A.R., Thom, M.D.F., Woodcock, P., Hill, J.K., 2013. Trait-dependent declines of species following conversion of rain forest to oil palm plantations. Biodiversity and Conservation 22, 253–268. doi:10.1007/s10531-012-0419-7

Turner, E.C., Foster, W. a., 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. Journal of Tropical Ecology 25, 23. doi:10.1017/S0266467408005658

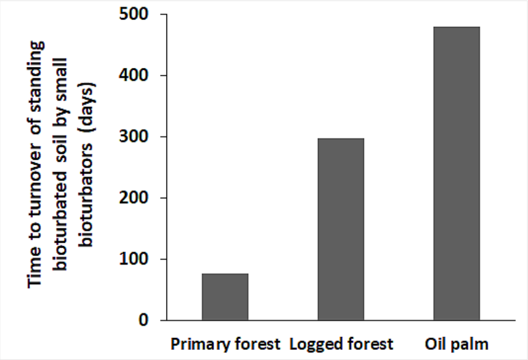
Turner, E.C., Snaddon, J.L., Ewers, R.M., Fayle, T.M., Foster, W. a, 2011. The impact of oil palm expansion on environmental change: putting ponservation research in context. Environmental Impact of Biofuels 19–40. doi:10.5772/960

Supplement 4



Proportional representation of structure sizes across different land uses measured on large scale (standing bioturbated soil). The categories were established as: SMALL – all soil bioturbated structures above six centimetres from soil surface belonging to ‘ANTS’, ‘CICADAS’, ‘WORMS’ and ‘OTHER’ category. MIDDLE – *Dicuspiditermes* spp. mounds and LARGE – *Macrotermes gilvus* mounds.

Supplement 5



The potential of small bioturbating organisms (bioturbation rate) for turnover of all aboveground soil structures created by large-scale bioturbators (standing bioturbated soil). The minimal time to the total turnover of standing bioturbated soil by small-scale bioturbators was calculated as the mean mass of standing bioturbated soil divided by one-day mean of bioturbative performance of small scale bioturbators (days). Because some plots had either zero standing soil or a rate of zero, we were only able to make these calculations for values summed across all plots in each habitat, and hence no statistical comparisons were possible.

Supplement 6

Standard error of mean values (SEM) of standing bioturbated soil generated by social insects, measured on large scale (Fig.4a).

Ant/termite species	Primary forest	Logged forest	Oil palm
Macrotermes gilvus	0.373	34.504	43.971
Dicuspiditermes minutus	1.874	8.787	0.040
Dicuspiditermes nemorosus	8.971	0.000	0.000
Odontomachus rixosus	0.003	0.000	0.000
Odontoponera transversa	0.011	0.023	0.002
Non ID ant	0.011	0.000	0.002
***Crematogaster* sp.**	0.004	0.000	0.000
Dinomyrmex gigas	0.052	0.000	0.000
Mesoponera rubra	0.104	0.000	0.000
Anillomyrma tridens	0.000	0.004	0.000
Diacamma intricatum	0.000	0.010	0.000
Leptogenys processionalis	0.000	0.164	0.000
***Myrmecina* sp.**	0.000	0.000	0.002
Lophomyrmex bedoti	0.000	0.000	0.003
***Tetramorium* sp.**	0.000	0.000	0.012

Standard error of mean values (SEM) of bioturbation rate measured at small scale (Fig.3b).

Category	Primary forest	Logged forest	Oil palm
ANTS	211.5	0.0	185.6
WORMS	1041.3	1125.8	624.3
OTHER	0.0	0.0	161.0