

Aboveground soil supports high levels of biological activity in oil palm plantations

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Oil palm plantations are expanding rapidly throughout Southeast Asia due to increasing global food demand, thereby putting greater pressure on local ecosystems. These plantations usually replace rainforests, resulting in major losses of soil structure and fertility, and belowground biodiversity. However, despite causing soil degradation, oil palms may provide a novel microhabitat for soil biota in suspended soil that accumulates in the axils of cut palm fronds attached to the trunks of these trees. We examined soil communities belowground and in frond axils in a 16-year-old oil palm plantation in Sumatra, Indonesia. Community metabolism of small arthropods, nematodes, and testate amoebae (protists) per gram of soil was much higher in axils (suspended soil) than in belowground soil, and accounted for approximately 28% of total soil fauna metabolism at the plantation scale (considering the top 5 cm of soil). Preserving these aboveground microhabitats of suspended soil as hotspots of biological activity during plantation management may therefore partly offset the detrimental impacts of oil palm plantations on soil-borne processes and biodiversity.

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Increasing global demand for food and other resources has driven large-scale deforestation in many tropical regions. In Southeast Asia, the main crop that is replacing natural forests is oil palm (Vijay *et al.* 2016). Oil palm expansion has been especially rapid over recent decades, with oil palm-dominated landscapes forming across Indonesia and Malaysia (Figure 1a; Corley and Tinker 2016). Such landscapes generally have 25-year commercial lifecycles, with replanting events usually involving the clearcutting of all previous palms (Figure 1b; Corley and Tinker 2016). Minimal labor requirements and high yields result in the profitability of oil palm plantations, but the expansion of these plantations poses a threat to many ecosystem functions (Clough *et al.* 2016). In comparison to rainforests, oil palm plantations have reduced soil fertility, water quality, gas efflux regulation, and genetic and medicinal resources (Dislich *et al.* 2017), as well as biodiversity (Fitzherbert *et al.* 2008; Clough *et al.* 2016).

Soil biota are responsible for a variety of ecosystem functions, including litter decomposition, nutrient mineralization, soil structure formation, and plant growth (Bardgett and van der Putten 2014). Different size classes of soil animals, such as micro-, meso-, and macrofauna, affect microbially driven processes via direct trophic interactions or modification of ecosystem structure. Energy fluxes in soil food webs and diversity of soil animals decline following conversion of rainforests to oil palm plantations (Barnes *et al.* 2014; Potapov *et al.* 2019), with negative impacts on the performance of ecosystem functions,

such as decomposition and top-down control (Barnes *et al.* 2014; Krashevska *et al.* 2018; Potapov *et al.* 2019). These impacts have led to calls for management strategies that reduce the negative effects of oil palm plantations on soil biodiversity and related ecosystem functions (Ashton-Butt *et al.* 2018). However, knowledge of soil biota and their contributions to ecosystem functions in oil palm plantations is poor.

In tropical forests, dead leaves and other detritus frequently accumulate on tree trunks and branches aboveground, forming “suspended soils” that usually support ferns and other epiphytic plants, and that serve as habitat for numerous arthropod species (Paoletti *et al.* 1991; Ellwood and Foster 2004). Animals that are common in soils, such as springtails and mites, can attain high abundances in suspended soils, though community composition typically differs from that belowground (Beaulieu *et al.* 2010; Rodgers and Kitching 2011). In oil palm plantations, suspended soils accumulate in the axils (angles between fronds and the stem) of cut fronds along oil palm trunks (Figure 1, c and d) and are inhabited by various insect groups, including soil-dwelling animals, thereby contributing to biodiversity and other aspects of ecosystem functioning (Ganser *et al.* 2017). To our knowledge, the degree to which animals in oil palm frond axils contribute to overall soil animal abundance in oil palm plantations has not been previously assessed.

We collected protists (testate amoebae) and micro-, meso-, and macrofauna (Figure 2) from the suspended soils in frond axils and in belowground microhabitats typical of oil palm plantations – such as under frond piles (pruned senesced fronds, which are linearly stacked after every second row of palms), in the inter-rows (the spaces between oil palms that permit the passage of plantation workers and that receive only moderate herbicide application), and inside the palm fertilization circle (the area around the base of an oil palm trunk, with a radius of 1–2 m, that receives intensive

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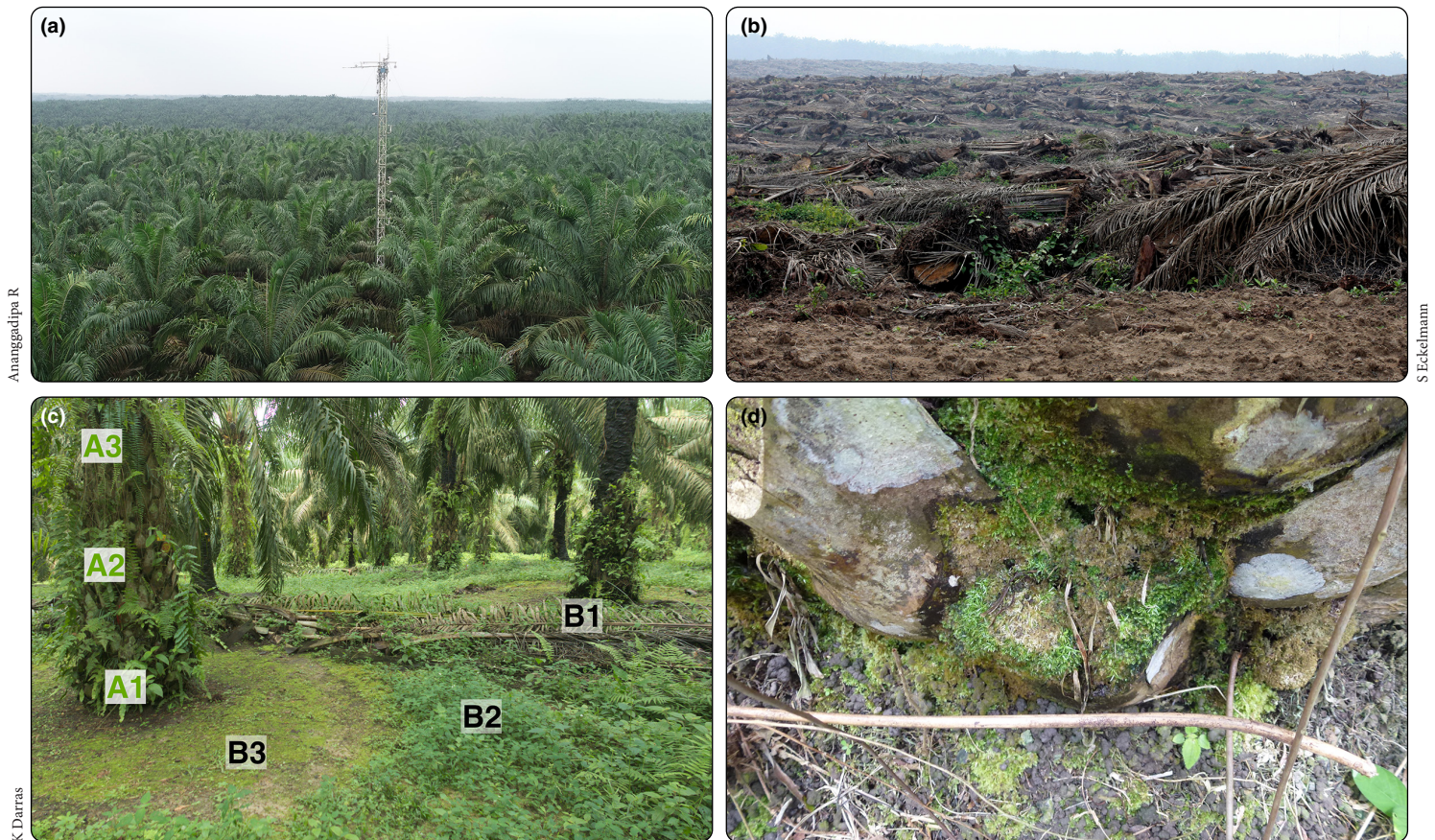


Figure 1. (a) Aerial view of a mature oil palm plantation in Sumatra, Indonesia, that contains an EFForTS meteorological tower. (b) Transformed landscape during a large-scale oil palm replanting event. (c) Depiction of the microhabitats included in our analysis – A1 to A3: frond axils on the palm trunk; B1: soil and litter beneath piles of cut palm fronds; B2: soil between palms in the inter-row; and B3: soil within the palm fertilization circle. (d) Suspended soil with moss in a cut palm frond axil.

herbicide application and fertilization) (Figure 1c and WebPanel 1) – in a palm plantation in Sumatra, Indonesia. Individual animals and protists were measured in order to calculate biomass and community metabolism of different size classes, which served as proxies for their impacts on ecosystem processes. We hypothesized that the abundance and activity of fauna per unit of soil mass are higher in suspended soils than in topsoil, and that suspended soil biota therefore make considerable contributions to total soil biological activity at the plantation scale.

Methods

Our study was conducted within the framework of the integrated research project CRC990/EFForTS (www.uni-goettingen.de/en/310995.html), which focuses on the ecological and socioeconomic changes associated with the transformation of lowland rainforests into agricultural systems. Samples were collected on 17 Oct 2016, at a 16-year-old smallholder oil palm plantation (site HO4; 01°47'12.7" S, 103°16'14.0" E; Drescher *et al.* 2016) in Jambi Province, Sumatra, Indonesia. Aboveground soil (A) for use in fauna extraction was collected by hand from frond axils on palm trunks; for each

sample, suspended soil was collected from three axils at a certain height (see below) and pooled. Fauna in belowground soil (B) were analyzed by collecting 16-cm × 16-cm soil samples with a spade to a depth of 5 cm, including litter on the soil surface (if present). Six microhabitats were identified, consisting of A1: suspended soil in frond axils at the bottom axil row of the palm trunk; A2: suspended soil in frond axils at a height of 90 cm; A3: suspended soil in frond axils at a height of 180 cm; B1: soil and litter beneath piles of cut palm fronds; B2: soil between palms in inter-rows; and B3: soil within the palm fertilization circle around the trunk (Figure 1c; see WebPanel 1 for more detailed descriptions). Six randomly selected oil palms and adjacent belowground microhabitats (as replicates) within a 50-m × 50-m area were sampled, resulting in 36 soil samples. Soil samples were also collected from each microhabitat for extraction of nematodes and protists (testate amoebae), as well as measurement of several environmental factors, including basal respiration, microbial biomass, pH, and total carbon (C) and nitrogen (N) concentrations (WebPanel 1).

Different size classes of soil fauna were extracted separately, using standard heat and water extraction methods (WebPanel 1). All extracted fauna were sorted, counted, and

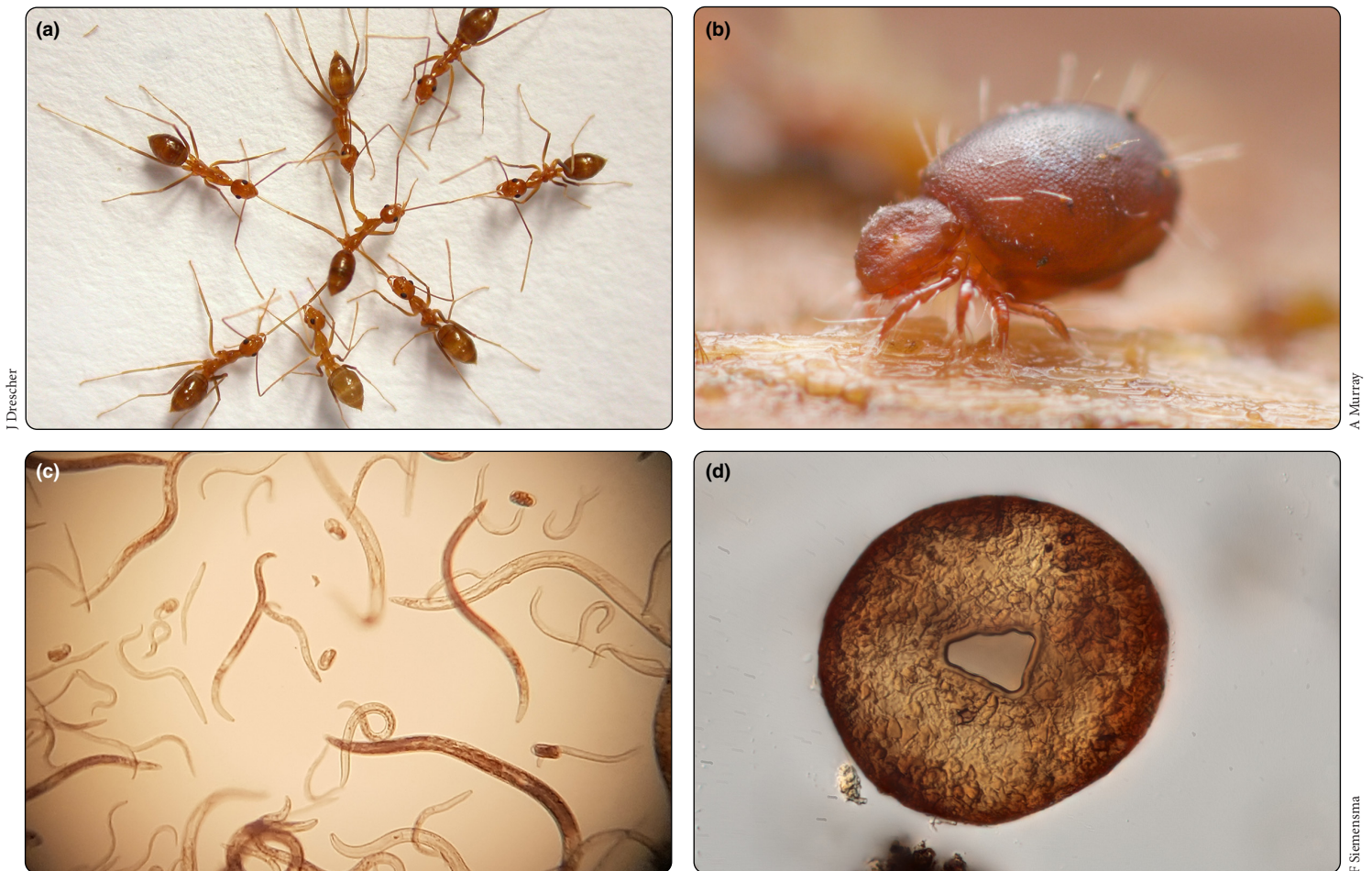


Figure 2. Abundant groups of fauna in suspended soils of palm frond axils include (a) ants (macrofauna), (b) soil mites (mesofauna), (c) nematodes (microfauna), and (d) testate amoebae (protists).

measured individually for body length and width under a microscope. From the size measurements, individual living body masses and individual metabolic rates were calculated to estimate the biological activity of these fauna, based on a set of group-specific allometric regressions (WebPanel 1; WebFigure 1). Fauna metabolism and basal respiration were corrected for temperature using the Arrhenius equation (air temperature of 24.6°C for aboveground and 26.2°C for belowground microhabitats). To calculate community metabolism (alternatively, “biological activity”), we summed the metabolic rates (expressed in joules per hour) of all individuals in a sample.

Sample calculations of density, biomass, and community metabolism were converted to their respective levels per gram (g) of dry soil using data on sample weights; community metabolism was also recalculated per g of organic C, using the C content in each sample (WebPanel 1; WebTable 1). To estimate the total contribution of aboveground soil microhabitats to total biological activity of fauna at the plantation scale, parameters were recalculated on a per-hectare (ha) basis. According to our estimates, the dry mass of suspended soil per unit area was around 0.8% of that in the top 5 cm of belowground soil. Palm frond piles and palm circles occupied about 15% and 7% of the

ground surface, respectively. Estimated parameters for each microhabitat were scaled according to the contribution of the microhabitat to total dry mass of soil per ha (WebPanel 2).

Calculations and statistical analyses were performed in R (v3.4.0) with RStudio (v1.0.143). The effects of the studied fauna group, habitat above- or belowground, microhabitats within the habitats, and pairwise interactions between them (fixed factors) on community metabolism and basal respiration were analyzed using linear mixed-effects models, with oil palm replicate (six replicates in total) set as the random effect, using the R package *lme4*. Response variables were log-transformed prior to analysis, which greatly improved descriptions of the data by the model. We used Type III analysis of variance (ANOVA) (WebTable 2) and Tukey’s honest significant difference (HSD) post-hoc pairwise comparisons to estimate the significance of the effects in the model for each of the variables using the R package *agricolae*.

Results

In total, 9205 macrofauna (earthworms and large arthropods – mainly ants, fly larvae, millipedes, booklice, symphylans),

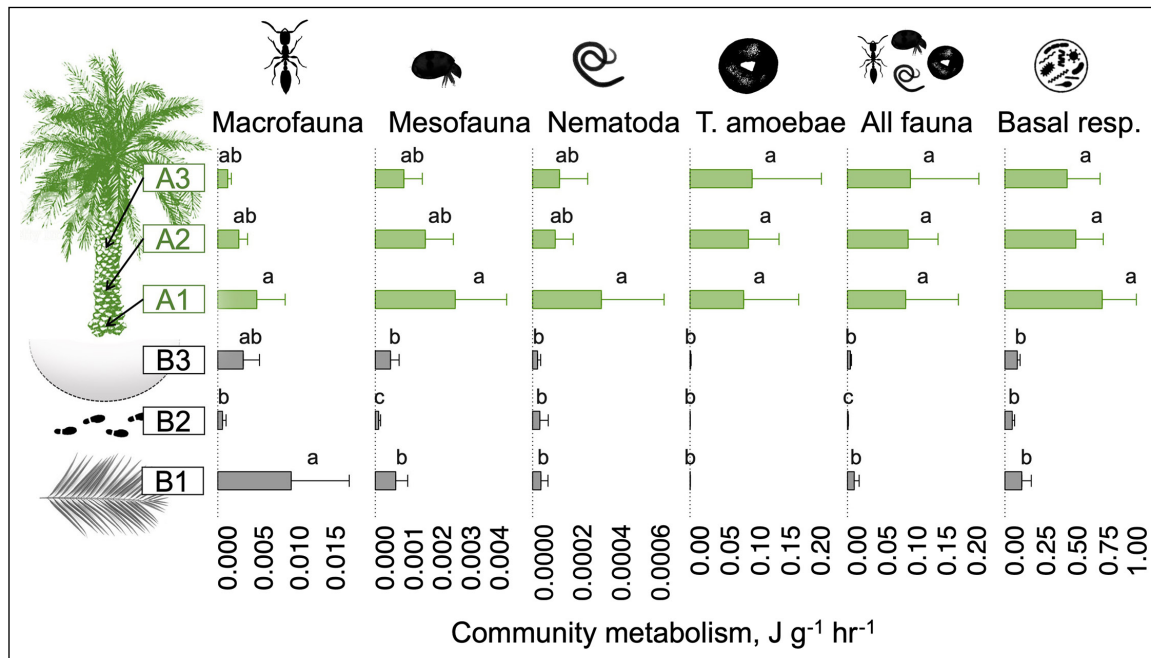


Figure 3. Community metabolism of different groups of soil fauna, including protists (testate amoebae), and basal respiration in microhabitats of the studied oil palm plantation. Data are given in joules per g of soil (dry weight) per hour. Means and standard deviations ($n = 6$); bars sharing the same letter were not significantly different (Tukey's HSD test, $P < 0.05$). Microhabitats: A1 to A3: soil in frond axils at the bottom, 90 cm, and 180 cm height of palm trunks; B1: soil and litter beneath piles of cut palm fronds; B2: soil between the palms in the inter-row; and B3: soil within the palm fertilization circle.

40,229 mesofauna (small arthropods – mainly springtails and mites), 2895 nematodes (ie microfauna), and 4467 living testate amoebae (ie protists) were collected across the six microhabitats.

Soil parameters differed distinctly between aboveground and belowground microhabitats. Aboveground soil was more acidic ($\text{pH} = 3.7$) than belowground soil ($\text{pH} = 6.0$) and had several times higher total C, microbial C, and total N levels (WebTable 1). All size groups of fauna, with the exception of macrofauna, had much higher densities, biomasses, and community metabolism per g of dry soil in the aboveground than the belowground soils. This effect was most prominent in testate amoebae, where density, biomass, and community metabolism per g of soil aboveground were 60–250 times that belowground. For mesofauna and nematodes, the same parameters in aboveground soil were 3–9 times that in belowground soil. In contrast, macrofauna were five times as dense but had one-eighth of the biomass and slightly lower community metabolism per g of soil in above- than belowground soils (Figure 3; WebTable 1), and their community metabolism per g of organic C in aboveground soil was approximately one-tenth of that in belowground soil. Community metabolism per g of organic C of mesofauna and nematodes was slightly lower in above- than belowground soils, whereas for testate amoebae it was 20 times as high. The community metabolism per g of organic C for all faunal groups combined was ~65% higher in above- than belowground soils (WebTable 1).

Aboveground, activity for nematodes, macrofauna, and mesofauna was highest at the bottom of palm trunks. Belowground, faunal activity was concentrated beneath the stacks of palm fronds, although this effect was strong only for macrofauna (Figure 3; WebTables 3–6). Soil faunal activity was generally lowest in inter-rows. Total community metabolism of fauna per g of soil aboveground was, on average, 17 times that belowground, and basal respiration aboveground was six times that belowground (WebTable 1).

Extrapolating the data per ha of the oil palm plantation, the contribution of aboveground soil biological activity to total soil biological activity above- and belowground (litter and top 5 cm of soil) was estimated to be $1.7 \pm 0.9\%$ (mean \pm SD, palms were treated as replicates) for macrofauna, $7.9 \pm 3.8\%$ for mesofauna, $6.9 \pm 5.6\%$ for microfauna (ie nematodes), and $64.4 \pm 20.5\%$ for protists (ie testate amoebae). Total activity aboveground and total basal respiration aboveground accounted for $27.7 \pm 15.5\%$ and $8.3 \pm 3.2\%$, respectively, of the total (aboveground + belowground) activity and respiration per ha of the oil palm plantation.

Discussion

We have demonstrated that biological activity of soil fauna and microorganisms per unit mass was much higher in suspended soils than in the topsoil between oil palms in an oil palm plantation. Aboveground activity was more or less evenly distributed along the trunks of the palms, albeit slightly higher

toward the bottom of the trunk for metazoan groups (macrofauna, mesofauna, nematodes). Belowground activity was concentrated under cut palm fronds due to the high abundance of large invertebrates (macrofauna), but abundances of other animal groups were only slightly higher in this microhabitat. Our estimates suggest that aboveground activity of soil fauna (including protists) contributes greatly to total soil biological activity in mature oil palm plantations.

In tropical ecosystems, suspended soils associated with ferns and other epiphytes are populated by a large number of invertebrates (Ellwood and Foster 2004). In rainforests, for instance, the abundance of meso- and macroinvertebrates (per unit mass) in suspended soils is approximately ten times that in belowground soils (Paoletti *et al.* 1991). When recalculated per unit of area, arthropods are as abundant in ferns as in litter in both rainforest and oil palm plantations (Turner and Foster 2009). Notably, we found that testate amoebae density may be two orders of magnitude higher in above- than in belowground soils, and therefore predominate in terms of aboveground soil fauna biomass and metabolic activity. Only a few (less than 5% of counted specimens) testate amoebae cysts were observed during sample inspection, suggesting that most testate amoebae were active, and therefore our community metabolism estimate is likely to be realistic. These protists are common in soils around the globe and play important roles in nutrient cycling – especially of silicon – because they feed on other eukaryotes and microorganisms (Geisen *et al.* 2018).

Suspended soils provide numerous ecosystem services. First, they provide unique habitats that support high biodiversity; many species of insects and mites colonize suspended soils and, for at least parts of their life cycles, are often restricted to this habitat (Beaulieu *et al.* 2010; Rodgers and Kitching 2011). Second, ferns that are associated with suspended soils in tropical rainforests support large invertebrate biomasses, including several specialized species (Ellwood and Foster 2004); moreover, although epiphyte diversity is lower in oil palm plantations than in rainforests, epiphytes are more abundant in oil palm plantations (Turner and Foster 2009; Böhnert *et al.* 2016), suggesting that suspended soils contribute greatly to invertebrate density and diversity at the plantation and landscape scales. For example, ferns in oil palm plantations support a remarkable diversity of ant species (Fayle *et al.* 2010). Because community metabolism usually scales positively with biodiversity (Barnes *et al.* 2014), the high soil fauna activity that we observed in suspended soils is an indication that these habitats likely harbor species-rich communities and therefore contribute to biodiversity in plantation systems. Biodiversity-related ecosystem services in oil palm plantations, such as decomposition, pollination, and pest control, are associated with a variety of invertebrates living on palm trunks (Ganser *et al.* 2017).

The high biological activity we observed in suspended soils suggests that this microhabitat plays a key role in nutrient cycling in oil palm plantations. In rainforests, suspended soils

and associated vegetation have been shown to contribute substantially to nutrient pools and nutrient cycling (Nadkarni *et al.* 2004). Furthermore, as demonstrated in a recent study, nitrous oxide (N₂O) and methane (CH₄) emissions per unit mass of suspended soil in oil palm plantations is high, constituting about 1% of the total emissions of a middle-aged plantation, but potentially having larger impacts at the landscape scale (Allen *et al.* 2018). In our study, we found that the contribution of fauna in suspended soils to C mineralization at the plantation scale is considerably greater than 1%, and may comprise about 28% of the total contribution of all soil fauna. This discrepancy may be due to the fact that the majority of belowground animal biomass is concentrated in the upper 5 cm of soil, whereas microorganisms are abundant throughout the soil profile and thus are found predominately belowground.

Aboveground soil in oil palm plantations is not isolated; rather, it is linked to other ecosystem compartments, contributing to soil-related ecosystem functions beyond the microhabitat itself. The suspended soil samples that we analyzed were colonized by many fly larvae, and 33% of the beetles in this habitat were also in larval stages, suggesting that frond axils form an important microhabitat for winged insects to complete their life cycles. These insects likely contribute to ecosystem services such as pollination and pest control at the plantation scale. In addition, non-winged mobile predators, such as spiders, may use frond axils as refuges or for hunting. Even small invertebrates, such as mites and springtails, migrate between below- and aboveground soils (Beaulieu *et al.* 2010), but vertical migration is particularly pronounced in ants and termites, which forage over large spatial scales and thereby contribute to energy and nutrient exchange between ecosystem compartments. Moreover, nutrient and energy exports in the form of invertebrate excrement, exuvia (molted exoskeletons), or carrion from aboveground soils and the canopy to the ground may provide supplementary resources for belowground soil communities, as has been reported for temperate ecosystems (Rozanova *et al.* 2019). In tropical ecosystems, such exports are likely to be more pronounced due to the much richer canopy fauna. Finally, suspended soils may also contribute to the preservation of plant seeds and microbial diversity, though these potential functions require further study.

The results of our analysis demonstrate that suspended soils form a rich and biologically active microhabitat in oil palm plantations. Although we examined only a single plantation, the microhabitats we studied occur in virtually all oil palm plantations in the region (Corley and Tinker 2016), suggesting that our findings are likely relevant at both the regional and broader scales. However, additional research is needed to explore temporal and spatial variation in the contributions of suspended soils to ecosystem functioning of oil palm plantations (eg for plantations of various ages). Suspended soils cannot compensate for the biodiversity loss resulting from deforestation (Turner and Foster 2009; Clough *et al.* 2016), but preserving this habitat may help somewhat in mitigating the loss of biodiversity and fauna activity

in plantations. Suspended soil environments in oil palm plantations have received little attention to date, and are not usually managed during the plantation life cycle. Such plantations are often replanted after ~25 years, at which time palm trunks are cut, injected with fungi, or in some cases burned (Corley and Tinker 2016), resulting in the loss of associated microhabitats, including suspended soils. In response, zero-burning land clearance practices are now being promoted as viable alternatives (eg by the Roundtable on Sustainable Palm Oil; <https://rspo.org>). In many cases, oil palm trunks are cut with heavy machinery and used as mulch during replanting (Corley and Tinker 2016). Such practices may partly mitigate the negative impacts of land clearance by enabling the survival of some aboveground-living soil species, which can then recolonize the trunks of the newly planted oil palms. Regardless, such practices destroy the complex vegetation structure of these systems, including aboveground soil habitats, and initial oil palm replantings may result in a “second wave” of biodiversity loss (Ashton-Butt *et al.* 2019). To mitigate such negative effects and to maintain biodiversity in the suspended soils of plantations, we advise that palms of different ages be combined within plantations (eg by underplanting or preventing large areas from being cleared simultaneously; Corley and Tinker 2016). This would facilitate the colonization of newly planted palm trunks by winged and mobile soil fauna, while smaller fauna and microorganisms could disperse passively (Lehmitz *et al.* 2011). Considering the rapid expansion of oil palm plantations throughout Indonesia and other tropical regions (Vijay *et al.* 2016), replanting events will become more common in the future. A better understanding of the distribution and dynamics of soil biodiversity across microhabitats in oil palm plantations may help in developing more sustainable plantation management systems that preserve ecosystem functioning.

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Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2174/supinfo>



It's a trap!

Jack-in-the-pulpit (*Arisaema* spp) have flowers shaped like the flowers of carnivorous pitcher plants. Unlike pitcher plants, however, *Arisaema* species do not absorb nutrients from insects. Instead, the trapped insects (frequently fungus gnats; various genera within the family Mycetophilidae) become part of a unique pollination system. Victims are handled differently between *Arisaema* sexual morphs: the



male plants allow fungus gnats to escape unharmed, but the gnats die when they are trapped in female flowers. In Shizuoka, Japan, we observed corpses of fungus gnats trapped at the bottom of the spathe (the large bract that surrounds the inflorescence) of the female *Arisaema stenophyllum*.

In male plants, individual fungus gnats enter the upper part of the floral tube and then slide down the tube's inner wall, which is very slippery (preventing the gnats from climbing back out). The more the gnats struggle to escape, the greater the number of pollen grains attach to the gnats, which eventually find a small gap at the bottom of the spathe and leave. The escapees then enter a female spathe, where a more sinister fate awaits. Unlike male spathes, female spathes have no exit holes. The trapped insects continue to struggle inside the spathe searching an exit, but are trapped there until death. Thus, the fungus gnats are forced to pollinate female *Arisaema* flowers. The genus *Arisaema* represents the only known floral trap that permanently imprisons its victims. Harming the pollinator is considered an evolutionarily unstable strategy. We therefore seek answers to the following questions: what is the cost to the pollinators, and why does this unique pollination system not collapse?

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