Plant roots fuel tropical soil animal communities

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Abstract

Belowground life is traditionally considered to rely on leaf litter as the main basal resource, whereas the importance of roots remains little understood, especially in the tropics. Here, we analysed the response of 30 soil animal groups to root trenching and litter removal in rainforest and plantations in Sumatra and found that roots are similarly important to soil fauna as litter. Trenching effects were stronger in soil than in litter with animal abundance being overall decreased by 42% in rainforest and by 30% in plantations. Litter removal little affected animals in soil, but decreased the total abundance by 60% both in rainforest and rubber plantations but not in oil palm plantations. Litter and root effects were explained either by the body size or vertical distribution of specific animal groups. Our findings highlight the importance of root-derived resources for soil animals and quantify principle carbon pathways in tropical soil food webs.

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Abstract

Belowground life is traditionally considered to rely on leaf litter as the main basal resource, whereas the importance of roots remains little understood, especially in the tropics. Here, we analysed the response of 30 soil animal groups to root trenching and litter removal in rainforest and plantations in Sumatra and found that roots are similarly important to soil fauna as litter. Trenching effects were stronger in soil than in litter with animal abundance being overall decreased by 42% in rainforest and by 30% in plantations. Litter removal little affected animals in soil, but decreased the total abundance by 60% both in rainforest and rubber plantations but not in oil palm plantations. Litter and root effects were explained either by the body size or vertical distribution of specific animal groups. Our findings highlight the importance of root-derived resources for soil animals and quantify principle carbon pathways in tropical soil food webs.

Keywords: roots; litter; land use; soil fauna; deforestation; soil food web; carbon cycle; energy channel; basal resources; trenching

INTRODUCTION

The belowground system harbours a large portion of terrestrial biodiversity and delivers vital ecosystem services (Bardgett & van der Putten 2014; Guerra *et al.* 2021). In terrestrial ecosystems, 80%–90% of the carbon fixed by plants enters the belowground system via litter and roots, thereby fuelling the belowground food web (Bardgett & Wardle 2010; Gessner *et al.* 2010; Schmitz & Leroux 2020). Litter of aboveground plant compartments, in particular leaves, is assumed to form the major source of organic matter and thereby of crucial importance for energy flow in soil (Attiwill & Adams 1993; Kögel-Knabner 2002). Litter-derived carbon enters the belowground food web through saprotrophic fungi and bacteria or via direct consumption by litter-feeding soil fauna (Scheu & Setälä 2002). The alternative pathway, receiving increased attention recently, comprises photosynthates entering the belowground system via root-derived resources such as root exudates (Jones *et al.* 2009). These resources are taken up mainly by microorganisms including mycorrhizal fungi and may account for up to 54% of soil respiration in boreal forests (Högberg *et al.* 2001). Root-derived carbon has been shown to fuel belowground food webs across trophic levels and to represent another major source of organic matter in soil (Högberg *et al.*2001; Pollierer *et al.* 2007; Bradford 2016). However, the importance of the alternative root carbon pathway for soil animal communities has only been investigated in temperate and boreal ecosystems, whereas its role in tropical ecosystems with fundamentally different rhizosphere associations and processes is unknown (Averill*et al.* 2014).

Soil fauna comprise a huge diversity of forms and functions that supports element cycles in soil by controlling microbial communities and soil physicochemical properties (Bardgett & van der Putten 2014; Briones 2014; Potapov *et al.* 2022). The relative importance of litter and root resources vary across different soil animal taxa. For example, in temperate forests the importance of root resources for arthropods, earthworms and fungivorous nematodes may exceed that of litter resources (Pollierer *et al.* 2007, 2012; Gilbert *et al.* 2014; Kudrin *et al.* 2021), whereas in subtropical plantations litter resources have been found to be more important than root resources for earthworms (Chen *et al.* 2020). Also, in temperate forests oppiid mites, onychiurid springtails, proturans, and centipedes have been found to heavily rely on root-derived resources (Remén *et al.* 2008; Endlweber *et al.* 2009; Goncharov*et al.* 2016; Potapov *et al.* 2016b; Bluhm *et al.*2019b). However, the relative importance of these two pathways in fuelling soil food webs and its variation among forest types and biomes remain unclear. For uncovering general patterns, studies across a wide range of animal taxa and including functional traits of different soil fauna groups are needed. For instance, animals of large body size and high trophic position tend to feed on more diverse resources and integrate different energy channels in soil food webs (Wolkovich 2016). Thus, large-sized and predatory animal taxa may be less affected by deprivation of one specific resource pathway. Indeed, it has been shown that microarthropods are more sensitive to root trenching than macroarthropods in temperate forests (Bluhm *et al.* 2021). Differences in the vertical distribution of soil fauna may be another factor determining the use of litter vs. root resources (Li *et al.* 2022; Potapov 2022). In fact, root-derived resources have been found to be more important for soil- than for litter-dwelling springtails in coniferous forests (Potapov *et al.* 2016a), however, this pattern may not uniformly apply (Fujii *et al.* 2016; Li *et al.* 2020). Overall, studies from temperate ecosystems suggest that including functional traits of soil fauna may allow uncovering their link to litter and root resources. Testing these trait-based predictions in a distinct context, such as the tropics, can provide robust evidence for their generality.

The tropics account for over half of the global annual production, and tropical rainforests play an important role as carbon sink in the global carbon cycle (Baccini *et al.* 2017; Mitchard 2018). Agricultural expansion is among the main threats to tropical ecosystems (Laurance*et al.* 2014; Hoang & Kanemoto 2021) that greatly reduces carbon storage, changes carbon cycling and redistribute the energy flow in soil food webs (Guillaume *et al.* 2018; Potapov *et al.* 2019a; Veldkamp *et al.*2020). However, changes in the importance of root-derived resources for soil animal communities with the conversion of rainforest into agricultural land-use systems remain unknown. Root supply varies among cropping systems (Scheunemann *et al.* 2015; Li *et al.* 2020) and tree species (Zieger *et al.* 2017). Strong shifts in plant communities, changes in soil microbial biomass and community composition, and depletion of litter resources associated with changes in tropical land use (Krashevska *et al.* 2015; Rembold *et al.* 2017) suggest that the availability of resources for soil animal communities is also changing. This is supported by recent studies indicating that the basis of soil animal food webs shifts towards the living plant energy channel in plantations (Susanti *et al.* 2019; Krause *et al.* 2021; Zhou *et al.* 2022), but the role of roots in this context remains unclear.

Here, we investigate the effects of deprivation of resource input via living roots or aboveground plant litter on soil fauna communities using a full-factorial root-trenching and litter-removal experiment in rainforest and plantations of rubber and oil palm in Sumatra, Indonesia. We assessed the response of 30 high-rank animal groups in litter and soil to evaluate the importance of living roots as an alternative major carbon source to aboveground litter for soil animal communities in tropical ecosystems.

Specifically we tested the following hypotheses:

1. Roots and aboveground litter are of similar importance for soil animal food webs in rainforest, whereas in plantations root resources are more important than litter due to depletion of litter resources in comparison to rainforest.
2. Root-trenching effects on soil animal communities are stronger in soil than in the litter layer.
3. Root trenching and litter removal restructures soil food webs through trait-specific effects, depending

on animal body sizes, vertical distributions, and trophic niches.

MATERIALS AND METHODS

Sampling sites and experimental set-up

The study was conducted in the framework of the collaborative research project CRC990/EFForTS investigating ecological and socio-economic changes associated with the transformation of lowland forest into agricultural systems (Drescher *et al.* 2016). The present study took place in Jambi province, Sumatra, Indonesia, which is a global hotspot of biodiversity, where over last 25–35 years rainforests have been largely replaced by intensively managed plantations, mostly oil palm and rubber, which lead to ecosystem degradation and biodiversity decline (Margono *et al.* 2012; Clough *et al.* 2016).

The experiment was established in three land-use types, rainforest, rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) plantations in October 2016, and was replicated four times in each land-use type, resulting in a total of 12 independent sites spread across an area of ca. 35 km diameter with adjacent sites being spaced by 0.5–5 km. Four experimental treatments (plots) were established at each experimental site: control, root trenching, litter removal, and both root trenching and litter removal (Fig. 1); each experimental plot measured 75 x 75 cm. Root trenching was performed by digging a trench around the treatment area and establishing a 0.6 mm think plastic screen to a depth of 60–70 cm around the plot. All weeds were removed regularly (every two weeks) from the trenched plots throughout the experiment. Litter removal was performed by removing the litter layer and installing a roof (metal mesh of 5 mm and plastic mesh of 2 mm; Fig 1) above the experimental plots to avoid fresh litter to enter the plots. In the litter removal plots the litter was replaced by plastic bamboo leaves to fully cover the soil surface and minimize confounding effects due to erosion and soil drying, and to focus on effects of litter as food resource. Experimental plots were checked every two weeks and litter occasionally fallen into the plots from the side was removed.

Sampling, extraction and classification of soil fauna

Soil fauna was sampled after one year in September–October 2017. In each plot one 16 x 16 cm sample was taken with a spade and divided into three layers: (1) litter (plastic leaves were not sampled), (2) 0–5 and (3) 5–10 cm of soil, resulting in total of 112 samples. The samples were transported to the laboratory and animals were extracted under a temperature gradient between 45degC above and 15degCbelow the substrate (Kempson *et al.* 1963) until the substrate was completely dry (6–8 days). Animals were collected in a glycerol: water (1 : 1) solution and subsequently stored in 80% ethanol. Animals were classified into 30 high-rank taxonomic groups (Oribatida, Collembola, Protura, Mesostigmata, Pauropoda, Hymenoptera, Hemiptera, Diptera, Thysanoptera, Prostigmata, Psocoptera, Auchenorrhyncha, Symphyla, Pseudoscorpiones, Lepidoptera, Diplopoda, Campodeidae, Isopoda, Formicidae, Opiliones, Schizomida, Araneae, Japygidae, Heteroptera, Coleoptera – predators, Coleoptera – Staphylinidae, Coleoptera – herbivores, Isoptera, Orthoptera, Dermaptera, Chilopoda, Blattodea, Lumbricina), roughly representing trophic/functional groups (Potapov *et al.* 2022).

Statistical analysis

All analyses were done in R 4.0.3 (R Core Team 2020). To assess the effects of litter removal and root trenching on total abundance and on each animal group, we fitted linear mixed-effects models (LMMs) using log-transformed abundance values or generalized linear mixed-effects models with Poisson distribution (GLMMs) and then applied contrasts between resource exclusion (either no litter or no root) and resource inclusion (either litter or root) to estimate effect sizes. We focussed on the effects of the litter removal and root trenching instead of the full-factorial design as explorative models did not show significant interactions between the two treatments. The litter removal effect represents the difference between 'control' + 'trenching' versus 'litter removal' + 'litter removal and root trenching'. The root trenching effect represents the difference between 'control' + 'litter removal' versus 'trenching' + 'litter removal and root trenching'. We checked model assumptions of the most parsimonious models by fitting model residuals versus the results of fitted models, and simplified models based on the Akaike information criterion (AIC).

Firstly, we estimated the effect sizes of litter removal and root trenching on the total abundance and richness in different layers using separate models as litter was absent in the litter removal treatment. The GLMMs (with Poisson distribution) included litter (removal/no removal), root (trenching/no trenching), land-use type (rainforest, rubber and oil palm plantations) and layer (litter layer, 0-5 and 5-10 cm soil depth for the root trenching model, and 0-5 and 5-10 cm soil depth for the litter removal model) as fixed effects, with treatment nested within plot as random effect to account for interdependence of layers from the same soil core and treatments from the same plot. In addition, we estimated the effect sizes of litter removal and root trenching on the total abundance and richness (pooled across layers). The GLMMs included treatment and land-use type as fixed effects, with plot as random factor to account for interdependence of treatments from the same plot.

Next, we estimated the effect size of litter removal and root trenching on the abundance of each taxonomic group (lumped data across layers) by LMMs. The model included litter (removal/no removal), root (trenching/no trenching), land-use type, taxonomic group as fixed effects, and plot as random effect. In this model we excluded groups which occurred less than 5 times among all 120 samples, namely Auchenorrhyncha, Lepidoptera and Dermaptera. Besides, data that were 0 in the control and the treatment were excluded from the model since effect size for double zero data cannot be reliably estimated.

To relate effects of the litter/root exclusion to traits of soil animal groups, we used the effect sizes of litter removal and root trenching for each taxonomic group from the above described models. We used the following traits/characteristics assigned at animal group level: average body mass, abundance in the control treatment, vertical distribution in the control treatment, and trophic niche as indicated by stable isotope values ($\delta^{13}C$ and $\delta^{15}N$). The vertical distribution was represented by scaled values between 0 (the group only in litter) and 1 (the group only at 5-10 cm depth), accounting for the abundance in each layer. For the average body mass of taxonomic groups and trophic niche ($\delta^{13}C$ and $\delta^{15}N$ values), we used our previous data from the same study sites (Potapov*et al.* 2019c; Zhou *et al.* 2022). Stable isotope values of animals were calibrated to the respective values of litter in the respective plot. $\delta^{15}N$ values reflect the trophic position (Post 2002; Potapov *et al.* 2019b) and $\delta^{13}C$ values indicated the use of different basal carbon resources, e.g. fresh and old organic matter (Pollierer *et al.* 2009; Potapov *et al.* 2019b).

Principal component analysis (PCA) and PERMANOVA were used to analyse the influence of land use and treatments on soil animal community composition (pooled data across layers). We used Hellinger and Bray–Curtis distance transformation prior to PCA and PERMANOVA, respectively, to test the effects of land use and treatment on animal community composition.

Vegan package was used for PCA and PERMANOVA analysis (Oksanen*et al.* 2020); *nlme* and *lme4* package were used to fit LMMs and GLMMs, respectively (Bates *et al.* 2015; Pinheiro*et al.* 2022), and *emmeans* package was used to conduct planned contrasts (Lenth 2021). All mixed models were visually checked to meet the assumption of residual homogeneity of variance. Results were visualized using the *ggplot2* package (Wickham 2016).

RESULTS

1. Effects of litter removal and root trenching on faunal abundance and richness

Root trenching reduced the total abundance of soil fauna by 42.6 ± 12.7%, 28.5 ± 15.7% and 29.9 ± 15.6% (estimated means ± standard errors) in rainforest, rubber and oil palm plantations, respectively (Fig. 2; Table S1). Litter removal reduced the total abundance of soil fauna in rainforest and rubber plantations by 63.6 ± 8.7% and 60.0± 9.3%, respectively, but the effect was not significant in oil palm plantations. Generally, effects of root trenching on soil fauna abundance were stronger in soil than in litter. Soil fauna abundance was reduced by 64.2 ± 8.8% and 50.4 ± 12.5% in 0–5 and 5–10 cm soil depth in rainforest, and by 36.0 ± 15.3% and 36.1 ± 15.5% in 0–5 cm depth in rubber and oil palm plantations, respectively, while the abundance in the litter layer did not change significantly. Litter removal generally did not change soil fauna abundance in soil. Total richness of soil fauna (30 taxonomic groups) declined in rainforest by both root trenching (23.1 ± 10.9%) and litter removal (27.6 ± 10.2%). In rubber plantations root trenching reduced the richness of soil fauna by 43.1 ± 14.9% in the litter layer, whereas in oil palm plantations it was reduced by 33.7 ± 12.6% in the 0–5 cm soil. Litter removal did not change the richness of soil fauna in soil across land-use types.

2. Soil animal community structure

Soil animal community composition varied significantly among the three land-use types (PERMANOVA; F = 5.54, $p < 0.001$) as well as experimental treatments (PERMANOVA; F = 3.50, $p < 0.001$), with the difference among treatments being most pronounced in rainforest and least in rubber plantations (PERMANOVA; Land use × Treatment interaction, F = 2.74, $p < 0.001$; Fig. 3). The effects of root trenching on soil animal abundances were generally independent of litter removal (Table 1). The root-trenching effects on the abundance of each group were universal across different land-use types (Table 1), but the average effects across soil animal groups were stronger in rainforest (-29.6 ± 9.8%) than in rubber (-17.4 ± 8.1%) and oil palm plantations (-18.4 ± 8.9%) (Fig. 4a). Litter-removal effects on the abundance of each group varied across land-use types (Table 1). In contrast to effects of root trenching, the average effects of litter removal across groups were negative in rainforest and rubber plantations (-25.0 ± 11.5% and -27 ± 6.5%, respectively), but positive in oil palm plantation (57 ± 38.4%) (Fig. 4b).

The response of animal groups to root trenching and litter removal varied with land-use type (significant three-factor interaction for both; Table 1). Root trenching significantly decreased the abundance of Protura, Mesostigmata, Prostigmata, Symphyla, Schizomida and Japygidae in rainforest, that of Prostigmata, Psocoptera, Formicidae and Araneae in rubber, and that of Protura, Pauropoda, Hemiptera and Formicidae in oil palm plantations (Fig. 4c, Table S2). Litter removal significantly decreased the abundance of nine animal groups in rainforest including Oribatida, Mesostigmata, Diptera, Thysanoptera, Psocoptera, Pseudoscorpiones, Diplopoda, Campodeidae and herbivorous Coleoptera, and decreased six groups in rubber including Oribatida, Collembola, Mesostigmata, Thysanoptera, Psocoptera and Formicidae. Conversely, litter removal increased the abundance of Prostigmata in oil palm plantations, but it decreased the abundance of Hemiptera (Fig. 4c, Table S3).

3. Linking effects of litter removal and root trenching to animal traits

In root trenching treatments the decline in animal density (measured as effect size) was more pronounced in small- than large-sized taxa; although this was also the case in litter removal treatments in rainforest and rubber, overall this was not significant (Fig 5a, b; Table S4). Accordingly, abundant taxonomic groups (usually represented by groups with smaller body size) declined more with both litter removal and root trenching than rare ones (Fig 5c, d; Table S4). Litter-removal effects were much stronger in taxa inhabiting predominantly the litter layer, whereas root-trenching effects were not related to the vertical distributions of animal taxa (Fig 5e, f; Table S4). Both litter and root effects were not universally related to the trophic position (Δ^{15}N values) or use of basal resources (Δ^{13}C values) of animal taxa; however, in litter removal treatments the response was more pronounced in animal taxa with low Δ^{15}N values but only in rainforest and rubber, and in trend this also applied to animals with low Δ^{13}C values but only in rainforest and oil palm (Fig. 5g-j; Table S4).

DISCUSSION

We analysed the effects of litter removal and root trenching on soil animals in rainforest and plantations, for the first time testing the importance of living root carbon supply for tropical soil fauna communities. We found that root-trenching effects are of similar magnitude and more uniform across land-use types than litter-removal effects. Root-trenching effects were more pronounced in soil than in the litter layer, while litter removal little affected animal abundance in soil. Litter removal decreased animal abundance in rainforest and rubber plantations but not in oil palm plantations. Root and litter exclusion shaped soil food webs through different mechanisms. Root trenching affected stronger small-sized and abundant animal groups, with the effect being independent of the initial vertical distribution. By contrast, litter removal affected more abundant groups that inhabited litter in control plots.

1. Litter and root resources across land-use types and soil layers

Compared to litter removal, root-trenching effects on soil animals were more universal across land-use types and in oil palm plantations they even exceeded effects of litter removal. This suggests that living roots are of similar importance than leaf litter in fuelling soil animal food webs in tropical ecosystems, and are even more important than litter in oil palm plantations, which supports our first hypothesis. Root-derived carbon predominantly comprises easily available carbon compounds entering the belowground food web via mycorrhizae and root exudates, which are rapidly consumed by microorganisms and thereby propagated to higher trophic levels in the rhizosphere (Bradford 2016; Zieger *et al.* 2017). By contrast, leaf litter comprises a variety of complex compounds including lignin and waxes but also secondary compounds deterring incorporation of its compounds into animal consumers (Vitousek 1984; Pollierer *et al.* 2007), and this may in particular apply to leaf litter material in the tropics (Hättenschwiler & Jørgensen 2010; Butenschoen *et al.* 2014; Marian *et al.* 2018). Litter-removal effects on soil animals varied with land use, changes of both total abundance and mean effect size across animal groups indicated that litter resources were more important in rainforest and rubber plantations but less in oil palm plantations with poorly developed litter layer. In rubber plantations the trees were tapped for collecting latex, which likely reduces the input of assimilates to roots, and therefore soil organisms may rely more on litter resources than in rainforest, although the litter layer in rubber plantations also is reduced compared to rainforest. However, as opposed to rainforest and rubber plantations, the mean effect of litter removal across groups in oil palm plantations was positive (increase in effect sizes by 57%) and the total abundance was not significantly affected. Litter not only serves as food resource for detritivore soil animals, but also comprises the habitat of litter living species (Sayer *et al.* 2006; Fujii*et al.* 2020). To consider the role of litter as habitat we not just removed the litter layer but replaced it by plastic leaves. Covering the nearly bare soil in oil palm plantations by these leaves may have reduced desiccation and thereby beneficially affected soil animals. The results suggest that in oil palm plantations litter-derived food resources are of minor importance and that the physical absence of the litter layer expose soil animals to detrimental environmental conditions. This points to the great restoration potential of e.g. mulching for soil animal communities in oil palm plantations which will improve the buffering ability, habitat structure, and provide food resources for soil fauna (Tao *et al.* 2018; Potapov *et al.*2020).

Root-trenching effects were stronger in soil than in the litter layer, which supports our second hypothesis. Soil biota are known to essentially rely on root-derived resources and this applies to both soil microorganisms as well as soil animals (Pollierer *et al.* 2007; Bluhm *et al.* 2019a, 2021). Trenching cuts off the input of 'green energy' into the soil from above the ground thereby eliminating mycorrhizal fungi but also reducing saprotrophic rhizosphere microorganisms (Díaz-Pinés *et al.* 2010; Bluhm *et al.*2019a). However, it also leaves the cut roots inside of the trenched plots, which may increase the supply of resources to the decomposer system. Nevertheless, soil animal abundance was strongly reduced by root trenching reflecting the overwhelming importance of resources derived from living roots. Meanwhile, trenching little affected animals in the litter layer although decomposers in litter layer may also benefit from root-derived resources transferred via fungal hyphae from the soil into the litter (Frey *et al.* 2003; Wallander *et al.* 2006). Litter removal little affected animal abundance in soil suggesting that similar to root resources in litter, litter resources are of very limited importance for the nutrition of soil living animal taxa. Overall, this suggests that both root-derived and litter resources are consumed mainly in close vicinity where they are located with very limited translocation to other layers. This points on potential spatial compartmentalisation of soil animal food webs, i.e. litter and soil animal communities are partly independent and fuelled by food resources channelled to the belowground system via different pathways.

2. Trait-specific responses of soil animals

Partially confirming our third hypothesis, the exclusion of basal resources restructured the belowground food web in respect to body size, vertical distribution and abundance as well as trophic niches of taxonomic groups. Deprivation of root-derived resources detrimentally affected in particular small-sized groups. Resources from living roots, particularly labile compounds such as root exudates, are readily used by rhizosphere microorganisms and thereby transferred to higher trophic levels such as mesofauna depending heavily on microorganisms as food (Albers *et al.* 2006; Sokol *et al.* 2019; Li *et al.*2021). In fact, the root-derived energy channel is viewed as fast energy channel in the belowground system (Pollierer *et al.* 2012; de Vries & Caruso 2016). Small-sized soil animals typically are characterized by faster energy turnover than large-sized species (Brown*et al.* 2004; Potapov *et al.* 2021b) underlining that in soil the fast energy channel based on root-derived resources is particularly important for small-sized animals. Further, the porous structure of soil may restrict the access of root-derived resources by large-sized animals (Erktan *et al.* 2020), and large-sized animals are likely to more intensively integrate different energy channels by foraging at larger spatial scales (Wolkovich 2016) allowing them to more flexibly respond to the exclusion of root resources. The effect of root-trenching was more pronounced in abundant animal groups as abundance typically scales negatively with body size (Brown *et al.* 2004; White *et al.* 2007).

Exclusion of litter little affected animal groups inhabiting the mineral soil, whereas the effects of root trenching were independent of the vertical distribution of soil animal groups. Stable isotope labelling studies reported that root-derived resources also propagate into animal species typically inhabiting the litter layer (Pollierer *et al.* 2007), suggesting that soil animals benefit from root-derived resources independent of their vertical habitat preferences. Notably, as discussed above, root trenching in particular reduced total abundance in soil and not in the litter layer, which means the faunal decline in soil layer were not because the groups with deeper vertical distribution were affected more by trenching, but because the animals initially inhabiting soil layers migrated up to the litter layer after trenching lowered the food-resources availability in the soil.

Root-trenching effects were independent of the trophic niche of soil animals as indicated by $\Delta^{15}N$ and $\Delta^{13}C$ values suggesting that root-derived resources are of similar importance for taxa across food chains (Glavatska *et al.* 2017; Zieger *et al.* 2017). The litter-removal effects, however, were less pronounced in low trophic level taxa in rainforest and oil palm plantations, and also in taxa using 'older' microbially processed carbon in rainforest and rubber plantations. This suggests that predators are in general less affected by deprivation of litter resources than primary decomposers, at least in certain ecosystem types. However, our stable isotope analysis represented only two dimensions of the trophic niche of species (Potapov *et al.* 2021a) and studies on other trophic niche-related dimensions, e.g. animal stoichiometry, need to be included in future.

CONCLUSIONS

For the first time we evaluated the importance of litter and root-derived resources for the soil animal food web in tropical ecosystems including rainforest and plantations. The response of a wide range of soil animal taxa indicates that both litter and root-derived resources shape belowground food webs in tropical ecosystems. Our results document the importance of living root supply as an alternative to leaf litter resource pathway in soil animal food webs of tropical ecosystems, which is even more important than litter-based resources in oil palm plantations. Beneficial effects of the addition of artificial leaves in oil palm plantations point to the potential of improving habitat structure, e.g. via mulching, to promote soil food webs and the services they provide. Root-derived resources altered the body size structure of soil animal communities by favouring in particular small and abundant taxa, reflecting that living roots essentially structure soil food webs and their functioning. Our study sheds light on the principle carbon pathways in tropical soil animal food webs and how they change with anthropogenic land use. This knowledge provides the basis for animal-cantered carbon modelling, ecosystem-friendly agricultural management, and conservation of soil animal biodiversity in the tropics.

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Table 1. ANOVA table of F- and p-values of linear mixed-effects models on the effect of litter removal, root trenching, land use system (rainforest, rubber and oil palm plantations) and taxonomic groups (total n = 24) on abundance of groups, with plot as random factor; num DF, numerator degrees of freedom; den DF, denominator degrees of freedom.

	num DF	den DF	F-value	p-value
Root	1	556.34	50.62	< 0.001 ***
Litter	1	453.54	18.90	< 0.001 ***
Land Use (LU)	2	7.43	2.78	0.125
Group	23	561.00	92.98	< 0.001 ***
Root ? Litter	1	556.37	0.03	0.855
Root ? LU	2	556.36	2.47	0.086
Litter ? LU	2	464.59	12.75	< 0.001 ***
Root ? Group	23	556.93	1.51	0.060
Litter ? Group	23	557.62	2.95	< 0.001 ***
LU ? Group	46	560.44	4.37	< 0.001 ***
Root ? Litter ? LU	2	556.36	2.97	0.052
Root ? Litter ? Group	23	556.25	1.14	0.296
Root ? LU ? Group	46	556.85	1.69	0.004 **
Litter ? LU ? Group	46	557.42	1.42	0.040 *

Asterisks denote significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Figure 1. Experimental design. Control (C), litter removal (L), root trenching (R), and combined treatment (RL) were established at 12 sites, four of each rainforest, rubber and oil palm plantations in Jambi Province, Sumatra.

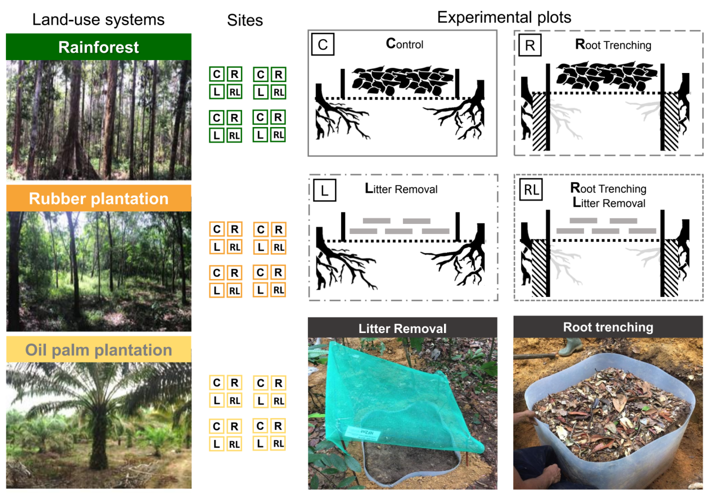
Figure 2. Effect sizes of litter removal and root trenching on abundance and richness of soil fauna in each layer and in total. Effect sizes are given as log-response ratios of litter or root exclusion compared to litter or root inclusion, respectively [ln (value in litter or root exclusion /values in litter or root inclusion)]. Asterisks

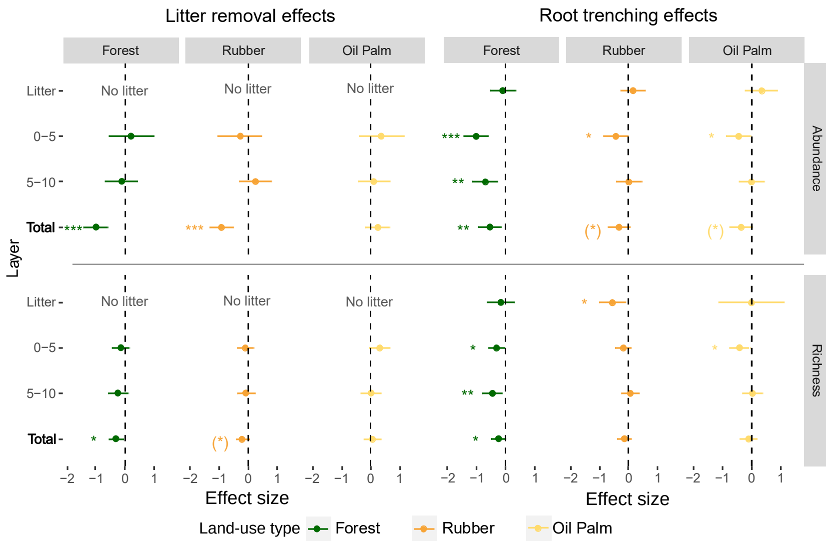
indicate significant effects, with (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$ and ***$p < 0.001$. Bars represent 95% confidence intervals (n = 8).

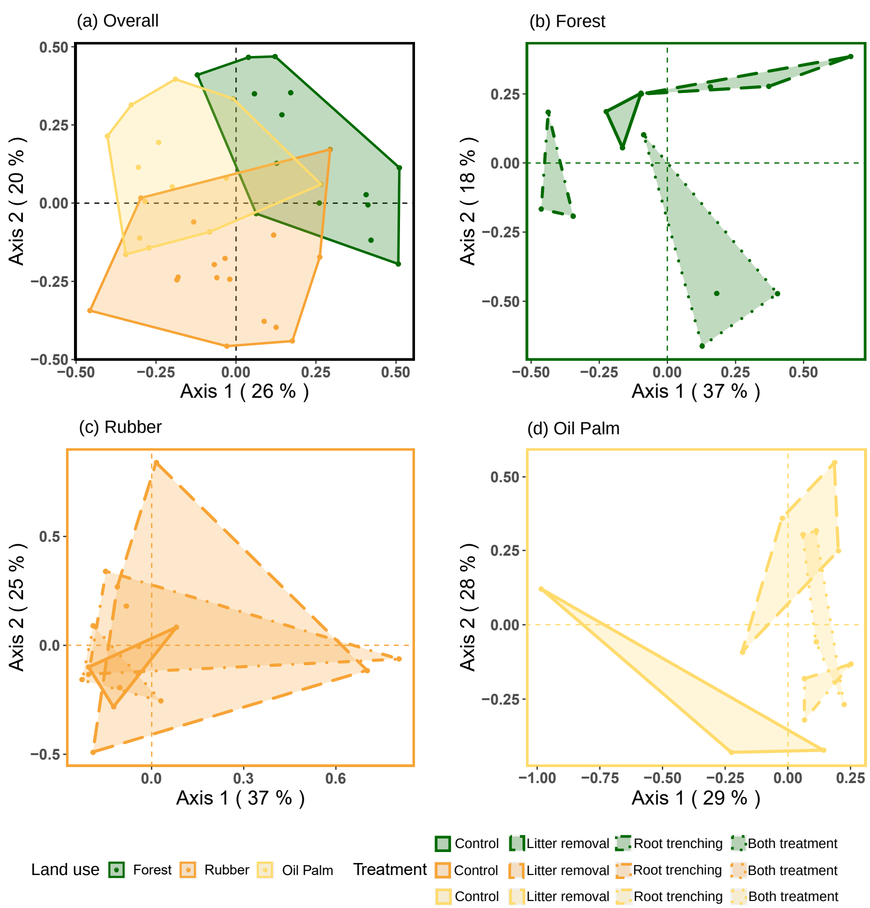
Figure 3. Principal component analysis of soil animal community composition varying with land-use types across experimental treatments (a), and among the different experimental treatments in rainforest (b), rubber (c) and oil palm plantations (d). Experimental treatments are coded by different line types: Control (solid line), litter removal (long dash), root trenching (dot dash) and litter removal + root trenching (dotted).

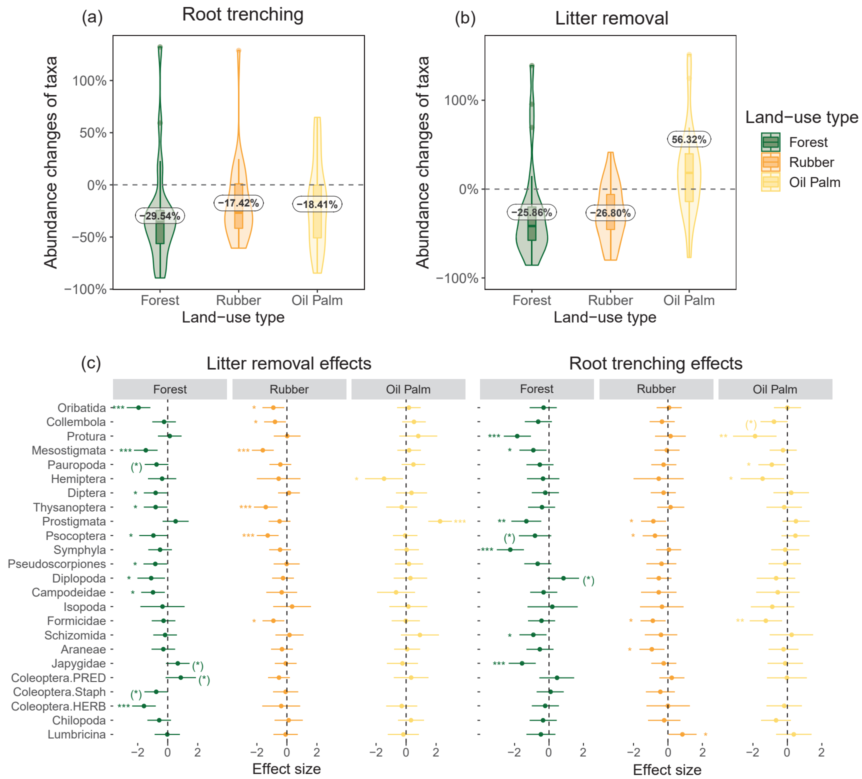
Figure 4. Effects of litter removal and root trenching on different taxonomic groups. Relative changes in abundance due to (a) root trenching and (b) litter removal, values represent mean effects across groups. (c) Effects of litter removal and root trenching on abundance of individual taxonomic groups. Effect sizes are given as log-response ratios of litter or root exclusion compared to litter or root inclusion [ln (value in litter or root exclusion /values in litter or root inclusion)]. Soil fauna abundance were summed across three depths (litter, 0–5 and 5–10 cm soil depth). Asterisks indicate significant effects, (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Bars represent 95% confidence intervals (n = 8). Taxonomic groups are ordered by increasing mean body mass.

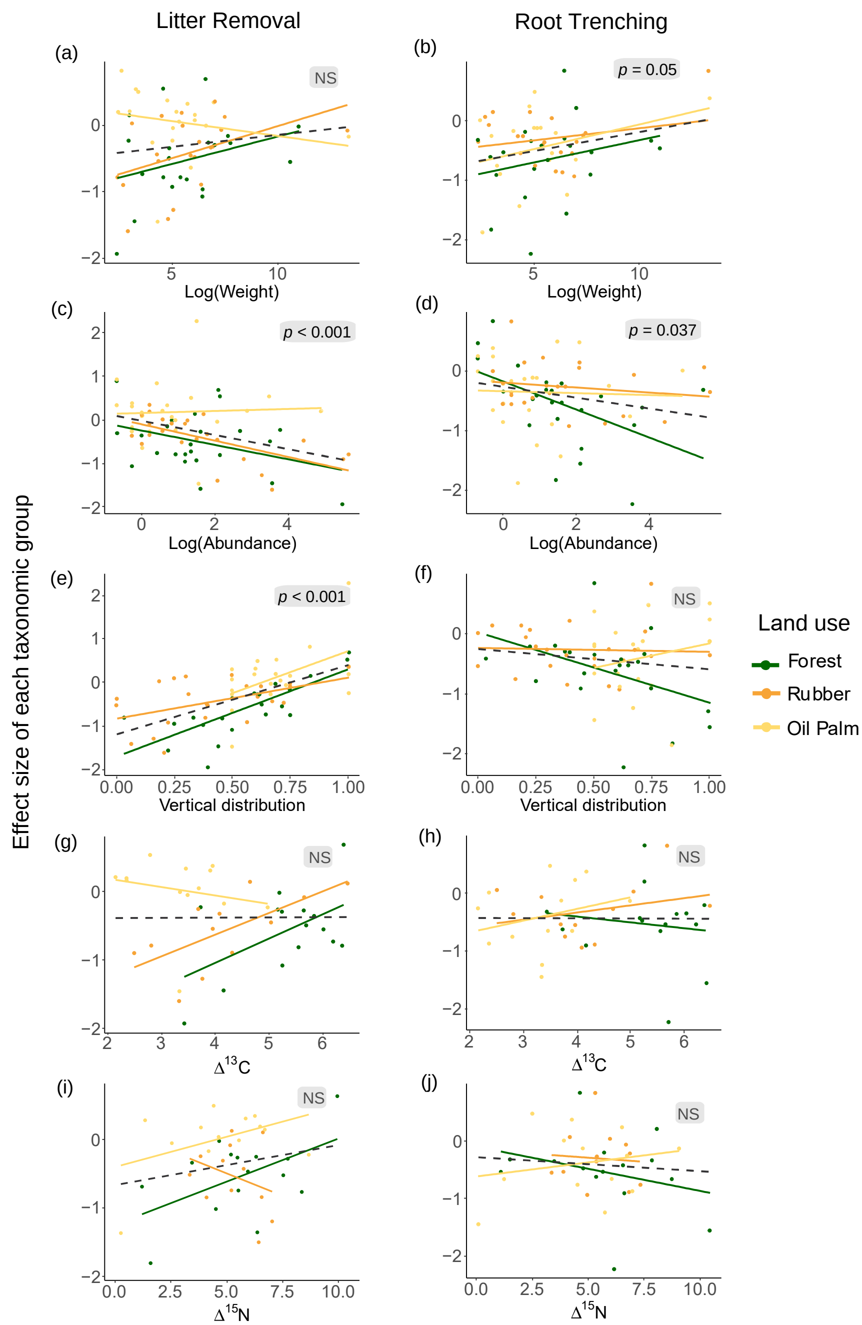
Figure 5 Relationship between the responses of animal groups to litter removal or root trenching and animal traits or community parameters: body mass (a, b), abundance (c, d), vertical distribution (e, f), Δ^{13}C (g, h) and Δ^{15}N (i, j). Black dashed lines denote overall model fits and coloured lines indicate different land-use types. The model outputs are reported in Table S4.




Litter removal effects
Root trenching effects
Forest
Rubber
Oil Palm
Abundance
Richness
Layer
Litter
0–5
5–10
Total
No litter
Effect size
Land-use type
Forest
Rubber
Oil Palm


(a) Overall
(b) Forest
(c) Rubber
(d) Oil Palm
Axis 1 (26 %)
Axis 2 (20 %)
Axis 1 (37 %)
Axis 2 (18 %)
Axis 1 (37 %)
Axis 2 (25 %)
Axis 1 (29 %)
Axis 2 (28 %)
Land use
Forest
Rubber
Oil Palm
Treatment
Control
Litter removal
Root trenching
Both treatment


(a)
Root trenching
Abundance changes of taxa
100%
50%
0%
−50%
−100%
−29.54%
−17.42%
−18.41%
Forest
Rubber
Oil Palm
Land−use type
(b)
Litter removal
Abundance changes of taxa
100%
0%
−100%
−25.86%
−26.80%
56.32%
Forest
Rubber
Oil Palm
Land−use type
Land−use type
Forest
Rubber
Oil Palm
(c)
Litter removal effects
Root trenching effects
Forest
Rubber
Oil Palm
Oribatida
Collembola
Protura
Mesostigmata
Pauropoda
Hemiptera
Diptera
Thysanoptera
Prostigmata
Psocoptera
Symphyla
Pseudoscorpiones
Diplopoda
Campodeidae
Isopoda
Formicidae
Schizomida
Araneae
Japygidae
Coleoptera.PRED
Coleoptera.Staph
Coleoptera.HERB
Chilopoda
Lumbricina
Effect size


Litter Removal
Root Trenching
(a) NS
(b) p = 0.05
Log(Weight)
(c) p < 0.001
(d) p = 0.037
Log(Abundance)
(e) p < 0.001
(f) NS
Vertical distribution
(g) NS
(h) NS
Δ13C
(i) NS
(j) NS
Δ15N
Effect size of each taxonomic group
Land use
Forest
Rubber
Oil Palm