SOIL ORGANISMS **93** (2) · August 2021 pp. 83–95

Impact of rainforest conversion into monoculture plantation systems on pseudoscorpion density, diversity and trophic niches

Dana Fabienne Liebke[1]*, Danilo Harms[2], Rahayu Widyastuti[3], Stefan Scheu[1,4] and Anton M. Potapov[1,5]

[1] J. F. Blumenbach Institute of Zoology and Anthropology, Animal Ecology, University of Goettingen, Untere Karspühle 2, 37073 Göttingen, Germany

[2] Zoological Museum Hamburg, Leibnitz Institute for the Analysis of Biodiversity Change (LIB), Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

[3] Department of Soil Sciences and Land Resources, Institut Pertanian Bogor-IPB, Damarga Campus, Bogor, 16680, Indonesia

[4] Centre of Biodiversity and Sustainable Land Use, Büsgenweg 1, 37077 Göttingen, Germany

[5] A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071 Moscow, Russia

* Corresponing author, Email: d.liebke@stud.uni-goettingen.de

Received 18 December 2020 | Accepted 11 May 2021
Published online at www.soil-organisms.de 1 August 2021 | Printed version 15 August 2021
DOI 10.25674/so93iss2id147

Abstract

Indonesia's biodiversity is at risk due to large forest areas being transformed into rubber and oil palm monoculture plantations. The effects of this land-use change on local fauna have been studied in a variety of organisms, including invertebrates from leaf litter and soil habitats. Litter and soil organisms are important drivers of essential ecosystem functions, such as nutrient cycling and carbon sequestration, which are impacted heavily by monoculture plantations. Pseudoscorpions (Arachnida: Pseudoscorpiones) are predatory arthropods in such litter and soil habitats and are an ubiquitous, although typically not very abundant, component of the soil animal food web. Since virtually nothing is known on their functional role diversity in tropical soil food webs, this study aims at contributing filling this gap of knowledge. We studied the impact of the conversion of rainforest into rubber and oil palm plantations on the density and diversity of pseudoscorpions in two landscapes of Jambi province, Sumatra, Indonesia, and applied stable isotope analysis to investigate changes in their trophic niches. Among 266 sorted individuals, only one described species was recorded, while the others were sorted to a total of nine morphospecies. Pseudoscorpions in the study region predominantly colonized mineral soil rather than the litter layer. As expected, the density declined from rainforest to rubber (-83%) and oil palm (-87%), and the number of species declined from rainforest to rubber (-37%) but in particular to oil palm (-47%). The density in riparian areas was five times lower than in non-riparian sites, however, species richness was almost the same. Further, the community composition of pseudoscorpions differed between land-use systems and landscapes; no species was present across all land-use systems, and the majority of species was only present in one land-use system indicating high habitat dependence. Stable isotope analysis suggested that the pseudoscorpion community shifted from species associated with the detritus-based energy channel in rainforest to species associated with the plant-based energy channel in monoculture plantations, indicating shifts in the use of basal resources by the soil community cascading up into predators. Overall, the results indicate that tropical pseudoscorpion communities comprise high-level predators that prefere to inhabit soil rather than litter and respond sensitively to land-use change. Due to this sensitivity, pseudoscorpion abundance may serve as bioindicator for ecosystem changes in the tropics. To mitigate negative effects of changes in land use in tropical ecosystems on cryptic and unexplored soil biodiversity, reduced herbicide use resulting in increased understory vegetation and mulching practices might be adopted.

Keywords Stable isotopes | soil | predation | Indonesia | land-use change | rubber | oil palm

ISSN 1864-6417 (print) · **ISSN** 2509-9523 (online)

1. Introduction

Tropical forests are increasingly being transformed to cash-crop monocultures such as rubber and oil palm, causing widespread habitat and biodiversity loss in tropical ecosystems (Drescher et al. 2016). Today, the biodiversity hotspot Indonesia (Sodhi et al. 2004) is the number one producer of palm oil in the world and only second to Thailand in rubber production (FAO 2020). Between 1990 and 2013 the Indonesian rainforest land cover decreased by 70 % and land used for rubber and oil palm cultivation increased by 23 %. The associated increase in the profits of farmers came at the costs of local biodiversity and key ecosystem functions (Grass et al. 2020). Negative impacts on biodiversity have been documented for a wide variety of organisms, including those belowground (Drescher et al. 2016, Clough et al. 2016, Klarner et al. 2017, Krashevska et al. 2018, Nazarreta et al. 2020, Potapov et al. 2020).

In Sumatra, one of the hotspots of rainforest transformation (Margono et al. 2012), rubber and oil palm monocultures dominate among plantations and are accompanied by complex alterations of root functional traits, diminished nutrient concentrations (Sahner et al. 2015), and changes in soil microbial communities amongst others (Krashevska et al. 2018). In comparison to rainforest, about 90 % of the energy in soil food webs is channeled from basal resources to large decomposers and total soil animal density is decreased by about 60 %, with predator populations suffering the most (Potapov et al. 2019b). Since soil animals are involved in processes, such as ecosystem engineering, nutrient cycling, litter decomposition and carbon sequestration, losses of animal diversity in soil may strongly impact ecosystem functioning (Briones 2018). While conversion of rainforest into plantation systems detrimentally affects diversity and density of macro-predators (Klarner et al. 2017, Potapov et al. 2020) and is associated with shifts in micro-decomposer communities (Krashevska et al. 2018), the effects on meso-predator communities are poorly studied. Since predators of all body size contribute to the channeling of energy through food webs (Brose & Scheu 2014, Potapov et al. 2019b), studying their role is important to comprehensively understand the functioning of soil communities in both rainforest and transformed ecosystems.

Soil meso-predators commonly feed on more than one trophic level and take part in intraguild predation and cannibalism (Scheu 2002, Digel et al. 2014), thereby supporting system stability (Rooney et al. 2006). In Jambi province, Sumatra, Indonesia, pseudoscorpions (Arachnida: Pseudoscorpiones) are the second most abundant meso-predator group in soil following predatory mites (Mesostigmata) (Potapov et al. 2019b). Pseudoscorpions are small arachnids (2–8 mm) (Fig. 1) that occur in almost every terrestrial ecosystem (Harvey 1988) and feed on other small arthropods, such as springtails, mites and small beetles, but also larger prey, such as other non-mite arachnids, woodlice, centipedes and ants (Weygoldt 1969, Harvey 1988). Food web studies have shown that soil inhabiting pseudoscorpions in temperate forests often feed on secondary decomposers, such as springtails and oribatid mites, and probably also engage in intraguild predation and cannibalism (Pollierer et al. 2009, Oelbermann & Scheu 2010). Some soil inhabiting pseudoscorpions from seasonally flooded regions of the Amazonian rainforest have been observed to migrate to tree trunks and even the canopy of trees 5–6 weeks before the area was flooded, where they stay with an abundance of prey species, until they migrate downwards back into the soil at the beginning of the emersion phase (Adis 1981; Battirola et al. 2017). This shows the sensitivity of pseudoscorpions to soil moisture and its relevance to the occurrence of certain species. Pseudoscorpions are

Figure 1. Four species of pseudoscorpions found at the study sites. From left to right: Atemnidae sp.1, *Lagynochthonius* sp.1, Atemnidae sp.2, *Hya minuta*.

also sensitive to anthropogenic changes in litter layer thickness and total plant cover in forests, and therefore have been proposed to be useful bioindicators (Yamamoto et al. 2001; Lencinas et al. 2015). However, very little is known about the functional importance and the ecology of most pseudoscorpion species, their place in soil food webs, and their response to land-use changes, especially in the tropics (Dennis et al. 2001).

Soil food webs are difficult to investigate due to their complex, multi-trophic interactions and the obstructing nature of soil (Brose & Scheu 2014). Thus, molecular tools, such as the analysis of natural variations in the stable isotope ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$, now are commonly used to understand the trophic structure and basal resources of soil food webs, respectively (Maraun et al. 2011, Huang et al. 2012, Klarner et al. 2017, Potapov et al. 2019a). Analyzing the ^{15}N concentration in animal tissue allows the assignment of species to trophic levels, since animals are enriched by 3–4‰ in ^{15}N relative to their diet (Post 2002, Haubert et al. 2006). By contrast, ^{13}C concentrations can be utilized to link species to either plant or detrital energy channels, since changes in ^{13}C concentrations in trophic interactions typically are small, but primary decomposers in soil food webs are considerably enriched in ^{13}C compared to living plants (Potapov et al. 2019a).

Previous studies found that the community composition of soil predators is strongly affected by land-use change from rainforest to oil palm and rubber plantations (Klarner et al. 2017, Potapov et al. 2020). By using stable isotope analyses, it has been shown that land-use change also impacts trophic niches of soil predators such as centipedes (Klarner et al. 2017). The few resilient centipede species also colonizing monoculture plantations switch their basal resource from detritus-based carbon towards plant carbon in those systems, either by modifying prey choice or through changes in the resources their prey species are feeding on (Klarner et al. 2017). Oribatid mites also shift both their trophic niches and use of basal resources when rainforest is being transformed into agricultural land-use systems (Krause et al. 2019). Compared to rainforest, oil palm and rubber monoculture plantations are characterized by thin litter layers and a dense herb layer, which may explain shifts in the detrital community towards a plant-based diet. This was confirmed by fatty acid analysis, which showed that food webs in rainforest rely more on the bacterial energy channel, whereas those in plantation systems rely more heavily on the plant-based energy channel (Susanti et al. 2019). However, little is known on meso-predator communities and their prey in plantation systems. Only few food web studies have included pseudoscorpions as meso-predator group (Pollierer et al. 2007, 2009; Oelbermann & Scheu 2010), and changes in stable isotope ratios and trophic niches of pseudoscorpions when rainforests are being transformed into plantations remain unknown. Addressing this gap of knowledge, we studied population density, diversity and trophic niches of pseudoscorpions with the conversion of rainforest into plantation systems in Jambi province, Sumatra, Indonesia. We hypothesized that (1) the density and diversity of pseudoscorpions is lower in monoculture plantations than in rainforest and lower in riparian than in non-riparian areas, (2) only few rainforest species are present in monoculture plantations, and (3) trophic niches of the species present are shifted from detritivore prey in rainforest to more herbivore prey in plantation systems. The latter is associated with a narrower spectrum of trophic levels of pseudoscorpions in plantations. Further, we also tested if ^{15}N and ^{13}C concentrations correlate positively with body mass of pseudoscorpion species, thereby assessing body mass as potential predictor of their trophic niches.

2. Materials and methods

2.1 Study sites and sampling

The study formed part of the interdisciplinary project 'Ecological and socioeconomic functions of tropical lowland rainforest transformation systems, Sumatra, Indonesia' – EFForTS (for details see Drescher et al. 2016). The samples were taken from 50 m × 50 m 'core plots' established in each of three different land use systems (rainforest, rubber monoculture and oil palm monoculture) in two different landscapes (Bukit Duabelas and Harapan). In each of the landscapes four replicates of each land-use system were established. In addition to these well drained areas, we also sampled riparian areas in each land-use system of the Harapan landscape with four replicates to cover the heterogeneity of the region, resulting in a total of 36 plots. The riparian areas were flooded during the rainy season approximately from October until February. The rainforest systems were primary degraded rainforests, which had undergone selective logging and extraction of large trees some 30 years ago. The rubber plantations were between 7 and 16 and the oil palm plantations between 8 and 15 years old when the plots were set up in 2012. The loam acrisol soil in the Harapan landscape comprised of even fractions of sand, clay and silt, while the Bukit Duablelas landscape had a higher proportion of clay.

In each plot, samples were taken from each of three fixed, randomly assigned subplots each, resulting in a total of 108 samples. Soil cores of 16 cm × 16 cm were dug up to a depth of 5 cm with a spade in October-November

2016, and in the laboratory litter and soil samples were extracted separately using heat (Kempson et al. 1963), collected in 50:50 glycerol-water mixture and then stored in 80 % ethanol. Adult pseudoscorpions were identified to morphospecies level using Beier (1932), Harvey (1988), Harvey & Volschenk (2007), Cullen & Harvey (2008) and Harvey (2011). Body size of each individual was measured using a stereomicroscope (Stemi, Zeiss, Jena, Germany). In total, 278 specimens were inspected, but twelve of them were strongly damaged and could not be reliably identified. These individuals were excluded from all calculations except total abundance of pseudoscorpions. Identification to family level was possible for all other 266 individuals and to morphospecies level for 131 adult individuals with the remaining 135 animals being juveniles. Morphospecies and their morphological traits were deposited in the database ecotaxonomy.org.

2.2 Stable isotope analysis

For stable isotope analysis, pseudoscorpions were first identified to morphospecies level and then analyzed individually. A maximum of three individuals (one for each subplot) of the same species were analyzed per plot. Overall, 53 specimens were chosen for the analysis. Tin capsules were washed with hexane, dried overnight at 60°C and then weighed. The specimens were transferred into the tin capsules, dried overnight at 60°C and weighed again. Stable isotope analysis was conducted at the 'Kompetenzzentrum Stabile Isotope' (KOSI) of the University of Göttingen. Stable isotope composition was expressed using the δ notation. For each subplot stable isotope values of the leaf litter material previously analyzed (Klarner et al. 2017) were used as baseline to calibrate stable isotope values of animals as $\Delta^{13}C_{animal} = \delta^{13}C_{animal} - \delta^{13}C_{litter}$ and $\Delta^{15}N_{animal} = \delta^{15}N_{animal} - \delta^{15}N_{litter}$. $\Delta^{13}C$ and $\Delta^{15}N$ values were used for statistical analyses.

2.3 Statistical analyses

Statistical analyses were carried out with R via RStudio (R Core Team 2018) using individual soil and litter samples as data points. First, density of riparian and non-riparian sites of the Harapan landscape were compared using generalized linear mixed-effects models with negative binomial distribution as implemented in the 'lme4' package (Bates et al. 2015). Of the non-riparian samples across both Bukit Duabelas and Harapan landscapes, both density (individuals / sample) and diversity (species / sample) were each analyzed by first fitting a model using 'glmer.nb' and further by using the {'Anova'} function from the 'car' package (Fox et al. 2020), which provided Wald chi-square tests for fixed effects in linear mixed-effects models. As abundance increases linearly with area, but species richness is saturating, recalculating to per square meter was not possible for richness. The fixed factors were land-use system (rainforest, rubber, oil palm), landscape (Bukit, Harapan) and soil layer (soil, litter). Plot was included as random factor to account for the interdependence of the litter and soil samples from the same plot. To estimate the regional species pool (gamma diversity) in each land-use system, we used the 'Bootstrap' parameter from the function {'specpool'} of the 'vegan' package (Oksanen et al. 2020).

To inspect differences between species in stable isotope composition linear models were fitted for each land-use system separately using the 'lm' function with either $\Delta^{13}C$ or $\Delta^{15}N$ the numeric response variable and species identity the linear predictor. In this analysis, only species with ≥ 3 replicates (Atemnidae sp.1, Atemnidae sp.2, *Hya minuta* and *Tyrannochthonius* sp.1) were included. Further, we used the function {'Anova'} to compute F-statistics of analyses of variance. Since only rainforest had enough replicates of multiple species to conduct this analysis, we refrained from analyzing the rubber and oil palm samples. To test for the effect of land-use system we also used the 'lm' function, but with land-use system as linear predictor. All 52 chosen individuals were included in this analysis and we ignored interspecific variability, but rather focused on community-level changes. A general linear hypothesis and pairwise comparison of the land-use systems was done using the {'glht'} function of the 'multcomp' package (Hothorn et al. 2021). To inspect if body length, body mass and $\Delta^{15}N$ or $\Delta^{13}C$ were correlated, we first log-transformed body length and body mass data and then used {'cor.test'} to acquire Pearson's product moment correlation coefficients (r). Results were displayed using the 'ggplot2' package (Wickham et al. 2020).

3. Results

3.1 Density

The density of pseudoscorpions in riparian sites (23 ± 34 ind./m²) was much lower than in non-riparian sites (266 ± 274 ind./m²) ($\chi^2_1 = 5.05$, p = 0.024). Among the non-riparian sites, the density of pseudoscorpions was highest in rainforest (307 ± 187 ind./m²), lower in rubber plantations (52 ± 56 ind./m²) and much lower in oil palm plantations (39 ± 67 ind./m²; $\chi^2_1 = 24.20$, p ≤ 0.001) (Fig. 2). However, the effect of land-use system varied with layer with the decline in density in plantations being more pronounced in the litter than in the soil layer (significant land use × soil layer interaction; $\chi^2_2 = 19.21$, $p \leq 0.001$). On average, litter hosted about 40% less animals than soil (97 ± 126 ind. m^{-2} *vs* 163 ± 140 ind. m^{-2}, respectively; $\chi^2_1 = 9.95$, $p = 0.0016$) and the density in the Harapan landscape was lower than in the Bukit Duabelas landscape (131 ± 145 ind. m^{-2} and 178 ± 161 ind. m^{-2}, respectively; $\chi^2_1 = 11.34$, $p \leq 0.001$).

3.2. Diversity

The number of species per sample did not vary significantly between land-use systems ($\chi^2_2 = 1.71$, $p = 0.42$) although it declined in the order rainforest (2.37 ± 0.74) > rubber (1.50 ± 0.84) > oil palm (1.25 ± 0.50). The number of species also did not differ significantly between the two landscapes ($\chi^1_1 = 0.573$, $p = 0.449$), but the estimated total number of species (gamma diversity) declined in the same order from rainforest (8.8 ± 0.8) to rubber (6.5 ± 0.6) to oil palm (3.0 ± <0.1) (Fig.3).

3.3 Community composition

Six of ten species did not occur in more than one land-use system, but four species did. Four of seven species found in rainforest belonged to the family Atemnidae Kishida, 1929, whereas especially rubber was colonized by species of the family Chthoniidae Daday, 1888 (the genera *Lagynochthonius* Beier, 1851 and *Tyrannochthonius* Chamberlin, 1929) (Table 1). The family Hyidae Chamberlin, 1930 was present with a single species (*Hya minuta* Tullgren, 1905) in rainforest and rubber of the Harapan landscape (Fig. 4). None of the species exclusively colonized oil palm, but one species was exclusive found in rubber and four in rainforest. One species (*Lagynochthonius* sp.3) was only found at a riparian site. No species was found across all land-use systems. Three of the five species present in monoculture plantations were not found in rainforest and only two out of ten species were found in both rainforest and monoculture plantations. Six out of the ten species were landscape-specific.

3.4. Trophic niches

Average $\Delta^{13}C$ values of the studied pseudoscorpions varied among land-use systems ($F_{2,49} = 28.08$, $p < 0.005$) and declined from rainforest (4.5 ± 1.3‰) to oil palm (3.9 ± 1.2‰) to rubber plantations (2.6 ± 0.5‰) (Fig. 5). By contrast, the $\Delta^{15}N$ values did not differ significantly between the land-use systems being on average 7.8 ± 1.9‰ ($F_{2,49} = 0.79$, $p = 0.458$). The $\Delta^{13}C$ values of the analyzed rainforest species (three or more replicates, see Methods) did not differ significantly ($F_{2,24} = 1.25$, $p = 0.34$). By contrast, the $\Delta^{15}N$ values differed significantly between species ($F_{2,24} = 11.63$, $p < 0.005$) and increased in the order *Hya minuta* < Atemnidae sp.2 < Atemnidae sp.1. In rubber and oil palm there were not enough replicates for analyzing differences in stable isotope values among species, however, $\Delta^{15}N$ values of species in rubber varied considerably (~5–10‰).

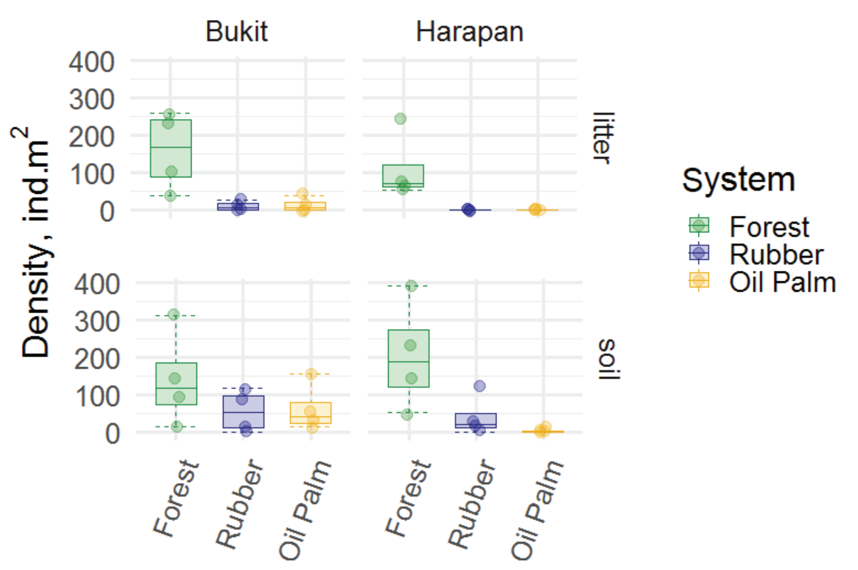

Figure 2. Density of pseudoscorpions in litter and soil of the three land-use systems studied (rainforest, rubber, oil palm) in the Bukit Duabelas and Harapan landscape. Each data point represents one sampling plot (three pooled subplot samples). Only non-riparian sites are shown.

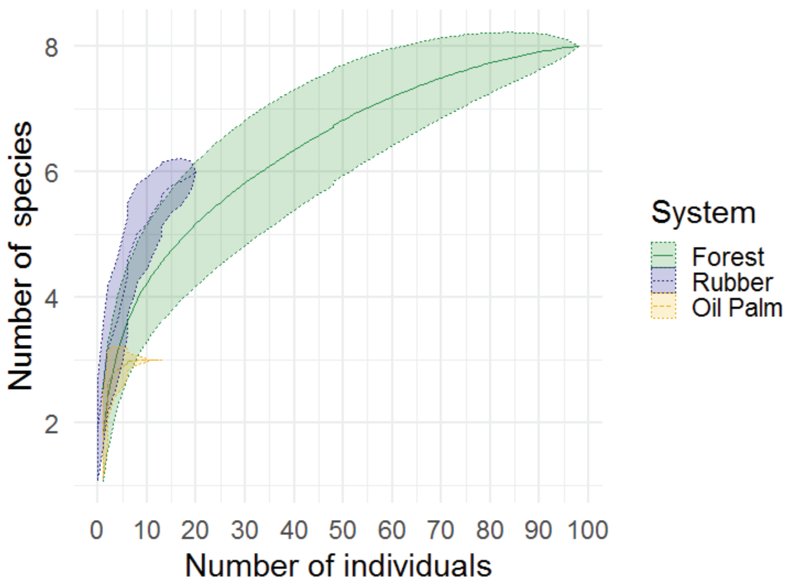

Figure 3. Bootstrap species accumulation curve based on the number of adult individuals in the studied land-use systems.

Table 1. Number of individuals from each morphospecies sampled in the three land-use systems studied (rainforest, rubber, oil palm), across both litter and soil as well as Harapan and Bukit Duabelas landscapes, and both riparian and non-riparian sites and their abbreviations. Juveniles were identified to family level only.

Morphospecies	**Abbreviation**	**Family**	**Rain-forest**	**Oil palm**	**Rubber**	**Total**
Atemnidae sp.1	Ate. sp.1	Atemnidae	57	5	0	62
Atemnidae sp.2	Ate. sp.2	Atemnidae	9	0	0	9
Atemnidae sp.3	Ate. sp.3	Atemnidae	2	0	0	2
Atemnidae sp.4	Ate. sp.4	Atemnidae	2	0	0	2
Atemnidae indet. (juveniles)		Atemnidae	85	9	5	99
Hya minuta	Hya	Hyidae	25	0	4	29
Hya indet. (juveniles)		Hyidae	10	0	0	10
Lagynochthonius sp.1	Lag. sp.1	Chthoniidae	0	0	3	3
Lagynochthonius sp.2	Lag. sp.2	Chthoniidae	0	0	3	3
Lagynochthonius sp.3	Lag. sp.3	Chthoniidae	1	0	0	1
Lagynochthonius sp.4	Lag. sp.4	Chthoniidae	2	0	1	3
Tyrannochthonius sp.1	Tyr	Chthoniidae	0	8	9	17
juveniles		Chthoniidae	8	7	11	26
Total			**201**	**29**	**36**	**266**

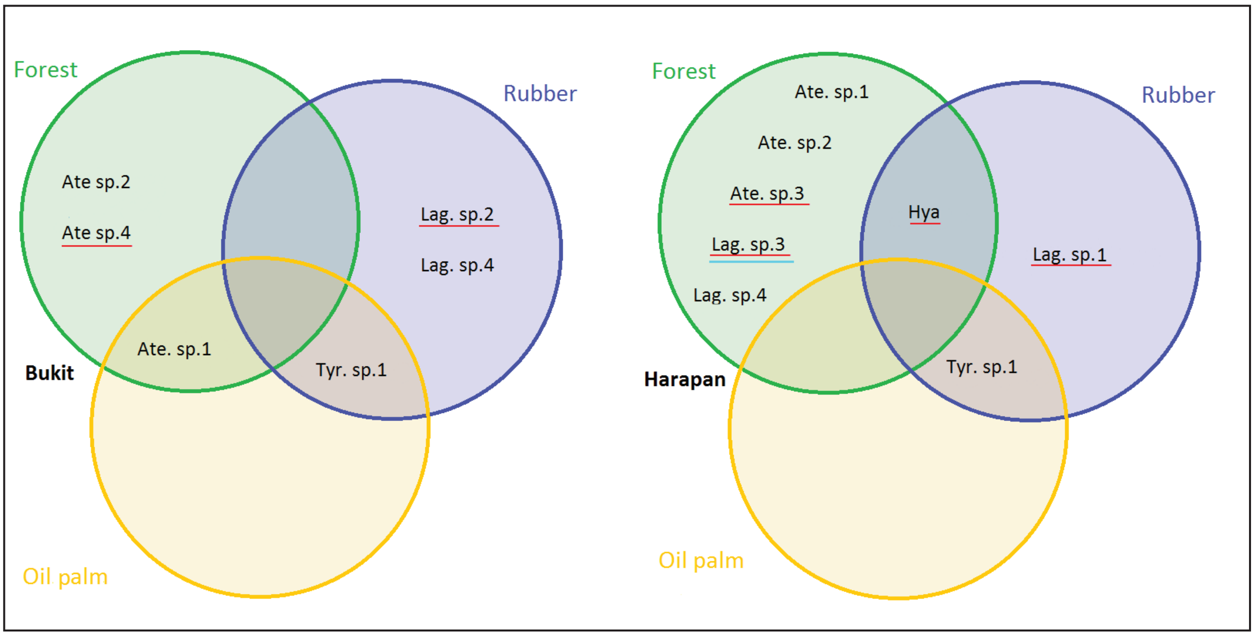

Figure 4. Venn diagram of the species composition in the three land-use systems studied (rainforest, rubber, oil palm) in the Bukit Duabelas (left) and Harapan landscape (right). Landscape-specific species are underlined in red. The riparian-specific species in Harapan is underlined in cyan. For abbreviations see Table 1.

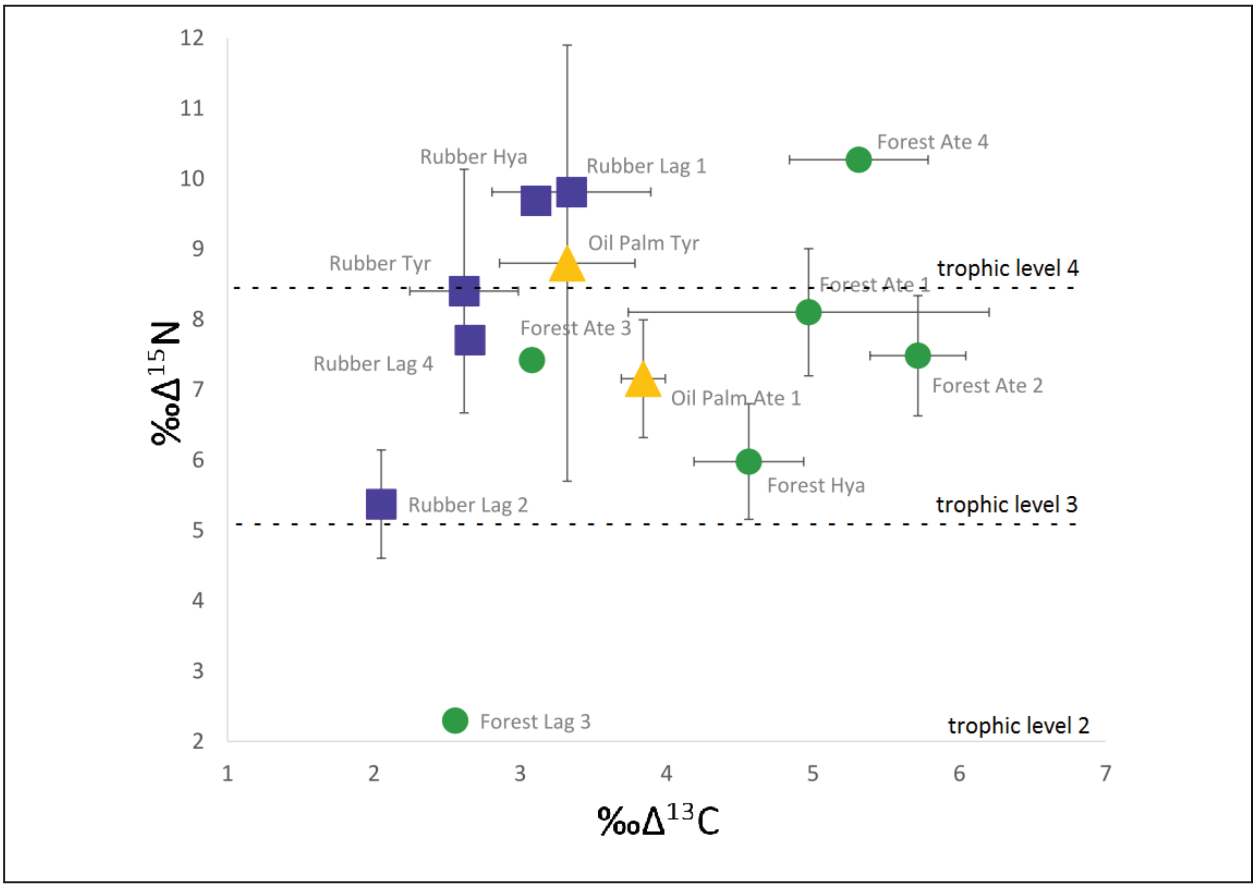

Figure 5. Stable isotope values of pseudoscorpion species in different land-use systems; means with standard deviation. Dashed horizontal lines represent estimated trophic level boundaries; trophic level 1 (plant material) not shown. Decomposers feeding on detritus (trophic level 2) were assumed to be enriched in ^{15}N by 1.7‰ compared to leaf litter, each following trophic level was assumed to span 3.4‰ (Post 2002; Potapov et al. 2019a). For abbreviations see Table 1.

$\Delta^{13}C$ values correlated significantly with body length in rubber (p=0.020) and marginally in rainforest (p=0.050). Further, they correlated significantly with body mass in rubber (p=0.025) and oil palm plantations (p=0.043). By contrast, neither body length nor body mass correlated significantly with $\Delta^{15}N$ values in any of the land-use systems.

4. Discussion

4.1 Density

The results support our first hypothesis and previous studies showing detrimental effects of the conversion of rainforest into plantations on soil invertebrate communities (Barnes et al. 2014, Mumme et al. 2015). In rainforest the density of pseudoscorpions exceeded that in rubber plantations by a factor of six and that in oil palm plantations by a factor of eight. The decline in the density of pseudoscorpions with the conversion of rainforest into plantations therefore parallels that of other arthropod predators, including centipedes and spiders (Klarner et al. 2017, Potapov et al. 2020). This decline has been associated with an increase in soil pH and earthworm density in plantations (Potapov et al. 2019b) and these factors, as well as the higher herbicide input and the reduction of the litter layer in oil palm plantations (Clough et al. 2016; Potapov et al. 2020), may also have contributed to the decline in the density of pseudoscorpions. As suggested earlier, energy in monocultures is channeled to large decomposers such as earthworms thereby reducing the channeling of energy to higher trophic levels (Potapov et al. 2019b). The density was also significantly lower in riparian areas which could be explained by our sampling being conducted just a few weeks before flooding. According to Adis (1981), certain Amazonian soil inhabiting pseudoscorpion species have been found to migrate upwards, to the trunk and into the canopy of trees four to six weeks before flooding during the rainy season. The flooding of riparian areas at our study sites during the rainy season lasted approximately from October until February, i.e. starting in the weeks around our sampling campaign, which lasted from October until November. The steadily rising soil moisture probably caused the significantly lower abundance in riparian areas as pseudoscorpions migrated out of the area or died, although this needs to be confirmed in future studies. In future surveys in riparian regions the density of pseudoscorpions should be determined at the beginning of the dry season as well.

Despite the presence of a well-established litter layer, in rainforest most of the pseudoscorpions colonized the soil layer. This was even more pronounced in plantations with less developed litter layers, as habitat for the few litter-favouring pseudoscorpions was scarce. In fact, small soil predators have been shown to be more severely affected by the conversion of rainforest into plantations compared to larger, mostly litter-dwelling predators, such as centipedes and spiders (Klarner et al. 2017, Potapov et al. 2020). The significantly higher density of pseudoscorpions in soil compared to litter, even in rainforest, suggests that pseudoscorpions in tropical lowlands of Indonesia prefer to colonize soil rather than litter. Notably, this contrasts other abundant meso-predators at the study sites such as mesostigmatid mites, which are much more abundant in litter than in soil (D.A. Prameswari, unpublished data). This points to vertical partitioning of prey between the two predatory groups, underlining the importance of vertical dimensions for soil arthropod species distribution and community composition (Basset et al. 2015).

Interestingly, the density of pseudoscorpions in litter in plantations of the Bukit Duabelas landscape was considerably higher than in the Harapan landscape, especially in oil palm plantations. The generally low density of pseudoscorpions in the Harapan landscape might be related to the higher fertilizer application in this less fertile region (Allen et al. 2015, Kotowska et al. 2016) as fertilization has been shown to detrimentally affect pseudoscorpion density (Yang et al. 2007). Previous studies also found pseudoscorpion density to be negatively affected by thin litter layers and scarce vegetation cover, which points to the usefulness of pseudoscorpions as sensitive bioindicators for anthropogenic change (Yamamoto et al. 2001, Lencinas et al. 2015). Potentially, higher earthworm biomass in the Harapan than in the Bukit Duabelas landscape also contributed to the low density of pseudoscorpions in the former (Potapov et al. 2021). Earthworms have been shown to detrimentally affect the density of springtails (Eisenhauer 2010, Ferlian et al. 2018), which serve as major prey of pseudoscorpions (Bilde et al. 2000). Thus, bottom-up effects may impact pseudoscorpions in our study region.

4.2 Diversity

The extrapolated species richness of pseudoscorpions was reduced by 26% in rubber and by 66% in oil palm plantations compared to rainforest. These findings are in line with previous studies showing a loss in species richness of soil invertebrates, especially predators, after conversion of rainforest into rubber and oil palm plantations (Klarner et al. 2017, Nazarreta et al. 2020, Potapov et al. 2020). However, more than 80% of the individuals of the ten recorded species belonged to only three species. This resembles earlier studies on pseudoscorpions, e.g. a large scale study assessing the pseudoscorpion fauna of eastern Germany including 23,000 specimens of which 82 % of the 38 species belonged to only five species (Drogla & Lippold 2004). In our study all species but one (*Lagynochthonius* sp.2; found at a riparian site) were sampled more than once. In total, six species were recorded in riparian areas, compared to seven in non-riparian areas of Harapan. However, since abundance in riparian areas was five times lower, this suggests that the riparian zones do not negatively impact biodiversity. Rather, riparian pseudoscorpions likely migrated to more favourable sites prior to flooding (Paoletti et al. 2018). Our diversity estimates suggest that we sampled the majority of pseudoscorpion species in each of the land-use systems studied except in oil palm, in which the species accumulation curve did not saturate. Data on the diversity of pseudoscorpions are scarce, but other studies in tropical forest ecosystems, such as forests in the Amazon and in Colombia, found six and three litter dwelling species, respectively (Adis & Mahnert 1985, Villarreal et al. 2019). This is similar to temperate forests in Germany, where seven species were found (Muster & Blick 2015). These numbers put our extrapolated species richness for forests at the high end of existing estimates and that of plantations at an intermediate to low position. Notably, the extrapolated species richness in rubber was higher than that in oil palm plantations, where it varied strongly among sites suggesting that environmental conditions, such as a thin litter layer or low total vegetation cover, detrimentally affect colonization by pseudoscorpion species.

To mitigate the negative effects of monoculture plantations on both diversity and abundance of pseudoscorpions and other soil arthropods, biodiversity-friendly agricultural practices may be applied. Herbicide use may be reduced especially in oil palm plantations, since there have been little indications of competition between oil palms and understory vegetation (Ashton-Butt et al. 2018). Instead, manual removal of plants or additional mulching to increase soil carbon input should be encouraged. We further suggest enhancing understory vegetation, especially in new oil palm plantations, to reduce erosion and fertilizer use, increase total vegetation cover and possibly yield (Guillaume et al. 2015; Darras et al. 2019; Khasanah et al. 2020; Marsden et al. 2020).

4.3 Community composition

The large decline in density was also associated with a very strong community turnover. Only 20 % (11 individuals) of the specimens of the family Chthoniidae (53 individuals in total) were found in rainforest, where Atemnidae (155 individuals) and Hyidae (35 individuals) dominated, while in both rubber and oil palm Chthoniidae dominated with 27 and 15 individuals, respectively. Atemnidae are widespread and diverse in the tropics (Harvey 2011), where many species live in soil habitats or under tree bark and in higher vegetation, whereas Hyidae exclusively live in soil (Harvey 1992). Our results indicate that the Chthoniidae might be better adapted to disturbed ecosystems such as plantations. Notably, Chthoniidae were on average smaller (1.04 ± 0.14 mm) than Hyidae (1.28 ± 0.18 mm) and Atemnidae (1.64 ± 0.56 mm), which may have facilitated colonization of the mineral soil in plantations, thereby reducing the danger of predation by surface living macro-predators (Potapov et al. 2020). Dominance of Atemnidae and Hyidae in rainforest and scarcity in plantations indicate that species of these families are vulnerable to changes in environmental factors associated with land-use change. Six out of ten species were exclusive to a given landscape and this may be related to different soil types between landscapes (Allen et al. 2015) or, alternatively, poor dispersal in some of these taxa (Hille Ris Lambers et al. 2012). Unfortunately, virtually nothing is known about the biology of the species found in our study region and we cannot test these hypotheses. Overall, however, our results support our second hypothesis that only few rainforest species are present in monoculture plantations.

4.4 Trophic niches

The range in $\Delta^{13}C$ values was largest in rainforest (5.1 ‰), suggesting that pseudoscorpions in rainforest feed on prey species using a wide range of basal resources. By contrast, the narrow range in $\Delta^{13}C$ values of pseudoscorpions in oil palm (1.4 ‰) and rubber plantations (1.9 ‰) indicates that the prey species in these systems used a narrow spectrum of basal resources. Soil invertebrates linked to the detrital channel are enriched in ^{13}C compared to living plants and leaf litter, and this 'detrital shift' presumably is due to the differential use of plant litter compounds and ^{13}C fractionation by microorganisms (Potapov et al. 2019a). Thus, the low ^{13}C enrichment of pseudoscorpions in plantations indicates that they are more closely linked to the plant-based rather than the detritus-based channel, e.g. by more intensively feeding on herbivores, and this supports our third hypothesis that trophic niches of pseudoscorpions are shifted from detrivore prey in rainforest to more herbivore prey in plantation systems as well as a more narrow range of trophic levels in plantations. A similar shift has been observed for centipedes at our study sites (Klarner et al. 2017) and the pattern in fact may apply to a wide range of soil invertebrate predators. Interestingly, $\Delta^{13}C$ values were positively correlated with body mass of pseudoscorpions in rubber and oil palm plantations; potentially, larger animals are more closely associated with the detrius-based energy channel in plantations. As soil organisms of all size classes are linked to either the plant- or detrius-based channel, there is no such correlation in the rainforest samples. We may also speculate that small-sized detritivores were more abundant in rainforest, allowing pseudoscorpions to get energy from both the plant- and detrius-based channel irrespective of their body size. In contrast to $\Delta^{13}C$ values, $\Delta^{15}N$ values did not correlate with body mass supporting the conclusion that in terrestrial food webs body mass and trophic level are not closely related (Potapov et al. 2019c). Further, the trophic level of pseudoscorpions was not shifted in plantations compared to rainforest. However, the wide variation in $\Delta^{15}N$ values indicates that pseudoscorpions are feeding on prey of different trophic levels and this includes other predators, i.e. in part they are functioning as intraguild predators, as is widespread in other arachnid groups such as spiders (Potapov et al. 2019a)

5. Conclusions

Overall, the results indicate that soil-dwelling pseudoscorpions react strongly to the conversion of rainforest into plantation systems, with the decline in density being more pronounced than in other arthropod predators such as spiders and centipedes. Similar to density, the diversity of pseudoscorpions was at a maximum in rainforest. The decline in diversity was associated with a strong species turnover with land-use change, pointing to the possibility of the loss of species and the sensitivity of pseudoscorpions to anthropogenic changes and their usefulness as bioindicators. Species richness in riparian-areas was comparable to that in non-riparian areas while abundance was five times lower, potentially pseudoscorpions migrated out of the area at the beginning of the rainy season prior to flooding. Despite the overall negative effect of plantations, about half of the species found in plantations were not found in rainforest, indicating that at the landscape scale plantations may contribute to the diversity of pseudoscorpions. Differences in community composition of pseudoscorpions between the two studied landscapes indicate dispersal limitation or association of species with different soil types. Stable isotope values of pseudoscorpions in rainforest indicated association to a wider range of basal resources and a closer link to the decomposer system than in plantations. By contrast, pseudoscorpions in plantations were more closely associated with the plant-based energy channel. High trophic level of pseudoscorpions across land-use systems underlined their position as high-level predators in tropical soil food webs despite their small body size. We showed a high vulnerability of pseudoscorpions to land-use changes and to mitigate these effects, biodiversity-friendly agricultural practices, such as the reduction of herbicide and fertilizer use, and the implementation of schemes favoring understory vegetation and the formation of a litter layer, e.g. by manual weeding and mulching, appears advisable.

6. Acknowledgements

This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project number 192626868 – SFB 990 in the framework of the collaborative German - Indonesian research project CRC990. We thank the State Ministry of Research and Technology of Indonesia (RISTEK), the Indonesian Institute of Sciences (LIPI), Ministry of Forestry (PHKA) and Restoration Ecosystem Indonesia Harapan for the support of the project. The study was conducted under the collection permit No. 2841/IPH.1/KS.02.04/X/2016 issued by the Indonesian Ministry of Forestry (PHKA). We thank Indonesian organizations and farmers for granting access to the sampling plots and use of their properties. Furthermore, we thank the staff of the Kompetenzzentrum Stabile Isotope Göttingen (KOSI) for measurement of stable isotopes.

7. References

Adis, J. U. (1981): Comparative ecological Studies of the terrestrial arthropod fauna in Central Amazonian Inundation-Forests. – Amazoniana: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas, AMAZONIA **7**(2): 87–173.

Adis, J. U. & V. Mahnert (1985): On the natural history and ecology of Pseudoscorpiones (Arachnida) from an Amazonian blackwater inundation forest. – Amazoniana: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas 9/3: 297–314.

Allen, K., M. D. Corre, A. Tjoa & E. Veldkamp (2015): Soil nitrogen-cycling responses to conversion of lowland forests to oil palm and rubber plantations in Sumatra, Indonesia. – PLoS ONE **10**/7 [https://doi.org/10.1371/journal.pone.0133325].

Ashton-Butt, A., A. A. K. Aryawan, A. S. C. Hood, M. Naim, D. Purnomo, Suhardi, R. Wahyuningsih, S. Willcock, G. M.Poppy, J.-P. Caliman, E. C. Turner, W. A. Foster,

K. S.-H. Peh & J. L. Snaddon (2018): Understory Vegetation in Oil Palm Plantations Benefits Soil Biodiversity and Decomposition Rates. – Frontiers in Forests and Global Change **1** [https://doi.org/10.3389/ffgc.2018.00010].

Barnes, A. D., M. Jochum, S. Mumme, N. F. Haneda, A. Farajallah, T. H. Widarto & U. Brose (2014): Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. – Nature Communications **5**/1: 5351 [https://doi.org/10.1038/ncomms6351].

Basset, Y., L. Cizek, P. Cuénoud, R. K. Didham, V. Novotny, F. Ødegaard, T. Roslin, A. K. Tishechkin, J. Schmidl, N. N. Winchester & et al (2015): Arthropod Distribution in a Tropical Rainforest: Tackling a Four Dimensional Puzzle. – PLOS ONE **10**/12: e0144110 [https://doi.org/10.1371/journal.pone.0144110].

Bates, D., M. Mächler, B. Bolker & S. Walker (2015): Fitting Linear Mixed-Effects Models Using {lme4}. – Journal of Statistical Software **67**/1 [https://doi.org/10.18637/jss.v067.i01].

Battirola, L. D., G. G. Brizzola dos Santos, E. Meurer, A. C. C Castilho, V. Mahnert, A. D. Brescoyit & M. I. Marques (2017): Soil and canopy Pseudoscorpiones (Arthropoda, Arachnida) in a monodominant forest of *Attalea phalerata* Mart. (Arecaceae) in the Brazilian Pantanal, – Studies on Neotropical Fauna and Environment **52**/2: 87–94 [https://doi.org/10.1080/01650521.2017.1282210].

Beier, M. (1932): Das Tierreich: Pseudoscorpionidea I: Subord. Chthoniinea et Neobisiinea. – De Gruyter **254**/57: 89–96.

Bilde, T., J. A. Axelsen & S. Toft (2000): The value of Collembola from agricultural soils as food for a generalist predator. – Journal of Applied Ecology **37**/4: 672–683 [https://doi.org/10.1046/j.1365-2664.2000.00527.x.].

Briones, M. J. I. (2018): The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. – Frontiers in Environmental Science **6** [https://doi.org/10.3389/fenvs.2018.00149].

Brose, U. & S. Scheu (2014): Into darkness: unravelling the structure of soil food webs. – Oikos **123**/10: 1153–1156 [https://doi.org/10.1111/oik.01768].

Clough, Y., V. V. Krishna, M. D. Corre, K. Darras, L. H. Denmead, A. Meijide, S. Moser, O. Musshoff, S. Steinebach, E. Veldkamp & et al. (2016): Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. – Nature Communications **7**/1 [13137. https://doi.org/10.1038/ncomms13137].

Cullen, K. & M. Harvey (2008): Short-range endemism in hypogean environments: The pseudoscorpion genera Tyrannochthonius and Lagynochthonius (Pseudoscorpiones: Chthoniidae) in the semiarid zone of Western Australia. – Invertebrate Systematics **22**: 259–293 [https://doi.org/10.1071/IS07025].

Darras, K. F. A., M. D. Corre, , G. Formaglio, A. Tjoa, A. Potapov, F. Brambach, K. T. Sibhatu, I. Grass, A. Rubiano, D. Buchori & et al. (2019): Reducing Fertilizer and Avoiding Herbicides in Oil Palm Plantations — Ecological and Economic Valuations. – Frontiers in Forests and Global Change **2** [https://doi.org/10.3389/ffgc.2019.00065].

Dennis, P., M. R. Young & C. Bentley (2001): The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of Nardus stricta grassland in upland Scotland. – Agriculture, Ecosystems & Environment **86**/1: 39–57 [https://doi.org/10.1016/S0167-8809(00)00263-2].

Digel, C., A. Curtsdotter, J. Riede, B. Klarner & U. Brose (2014): Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. – Oikos, **123**/10: 1157–1172 [https://doi.org/10.1111/oik.00865].

Drescher, J., K. Rembold, K. Allen, P. Beckschäfer, D. Buchori, Y. Clough, H. Faust, A. M. Fauzi, D. Gunawan, D. Hertel & et al. (2016): Ecological and socio-economic functions across tropical land use systems after rainforest conversion. – Philosophical Transactions of the Royal Society B: Biological Sciences **371**/1694: 20150275 [https://doi.org/10.1098/rstb.2015.0275].

Drogla, R. & K. Lippold (2004): Zur Kenntnis der Pseudoskorpion-Fauna von Ostdeutschland (Arachnida, Pseudoscorpiones). – Arachnologische Mitteilungen **27/28**: 1–54 [https://doi.org/10.5431/aramit2701].

Eisenhauer, N. (2010): The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. – Pedobiologia **53**/6: 343–352 [https://doi.org/10.1016/j.pedobi.2010.04.003].

FAO (2020): (Food Agric. Organ.). 2020. Crops. FAOSTAT statistical database, Rome, updated September 14, 2020 [http://www.fao.org/faostat/en/#data/QC. – Retrieved October 13, 2020, from http://www.fao.org/faostat/en/#data/QC].

Ferlian, O., N. Eisenhauer, M. Aguirrebengoa, M. Camara, I. Ramirez-Rojas, F. Santos, K. Tanalgo & M. P. Thakur (2018): Invasive earthworms erode soil biodiversity: A meta-analysis. – Journal of Animal Ecology **87**/1: 162–172 [https://doi.org/10.1111/1365-2656.12746].

Grass, I., C. Kubitza, V. V. Krishna, M. D. Corre, O. Mußhoff, P. Pütz, J. Drescher, K. Rembold, E. S. Ariyanti, A. D. Barnes & et al. (2020): Trade-offs between multifunctionality and profit in tropical smallholder landscapes. – Nature Communications **11**/1: 1186. https://doi.org/10.1038/s41467-020-15013-5.

Guillaume, T., M. Damris & Y. Kuzyakov (2015): Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by δ13C. – Global Change Biology **21**/9: 3548–3560 [https://doi.org/10.1111/gcb.12907].

Harvey, M. S. (1988): The systematics and biology of pseudoscorpions – In: Austin, A. D. & N. W. Heather (eds): Australian Arachnology, Miscellanious Publication No.5 - The Australian Entomological Society, Brisbane: 75–85. – Australian Enthomological Society.

Harvey, M. S. (1992): The phylogeny and classification of the Pseudoscorpionida (Chelicerata : Arachnida). – Invertebrate Systematics **6**/6: 1373–1435 (CSIRO PUBLISHING) [https://doi.org/10.1071/it9921373].

Harvey, M. S. & E. Volschenk (2007): Systematics of the Gondwanan pseudoscorpion family Hyidae (Pseudoscorpiones : Neobisioidea): new data and a revised phylogenetic hypothesis. – Invertebrate Systematics **21**: 365–406 [https://doi.org/10.1071/IS05030].

Harvey, M. S. (2011): Pseudoscorpions of the World, version 1.2. Western Australian Museum, Perth [http://www.museum.wa.gov.au/catalogues/pseudoscorpions (Retrieved November 27, 2019)].

Haubert, D., M. M. Häggblom, R. Langel, S. Scheu & L. Ruess (2006): Trophic shift of stable isotopes and fatty acids in Collembola on bacterial diets. – Soil Biology and Biochemistry **38**/7: 2004–2007 [https://doi.org/10.1016/j.soilbio.2005.11.031].

Hille Ris Lambers, J., P. B. Adler, W. S. Harpole, J. M. Levine & M. M. Mayfield (2012): Rethinking community assembly through the lens of coexistence theory. – Annual Review of Ecology, Evolution, and Systematics **43**/1: 227–248 [https://doi.org/10.1146/annurev-ecolsys-110411-160411].

Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister & S. Scheibe (2021): multcomp: Simultaneous Inference in General Parametric Models. – Biometrical Journal **50**/3: 346–363 [http://doi.wiley.com/10.1002/bimj.200810425].

Huang, C.-Y., K. L. Tully, D.A. Clark, S. F. Oberbauer & T. P. McGlynn (2012): The $\delta^{15}N$ signature of the detrital food web tracks a landscape-scale soil phosphorus gradient in a Costa Rican lowland tropical rain forest. – Journal of Tropical Ecology **28**/4: 395–403 [https://doi.org/10.1017/S0266467412000284].

Khasanah, N., M. van Noordwijk, M. Slingerland, M. Sofiyudin, D. Stomph, A. F. Migeon & K. Hairiah (2020): Oil Palm Agroforestry Can Achieve Economic and Environmental Gains as Indicated by Multifunctional Land Equivalent Ratios. – Frontiers in Sustainable Food Systems **3** [https://doi.org/10.3389/fsufs.2019.00122].

Kempson, D., M. Lloyd & R. Ghelardi (1963): A new extractor for woodland litter. – Pedobiologia **3**/1: 1–21.

Klarner, B., H. Winkelmann, V. Krashevska, M. Maraun, R. Widyastuti & S. Scheu (2017): Trophic niches, diversity and community composition of invertebrate top predators (Chilopoda) as affected by conversion of tropical lowland rainforest in Sumatra (Indonesia). – PLOS ONE **12**/8: e0180915 [https://doi.org/10.1371/journal.pone.0180915].

Kotowska, M. M., C. Leuschner, T. Triadiati & D. Hertel (2016): Conversion of tropical lowland forest reduces nutrient return through litterfall, and alters nutrient use efficiency and seasonality of net primary production. – Oecologia **180**/2: 601–618 [https://doi.org/10.1007/s00442-015-3481-5].

Krashevska, V., E. Malysheva, B. Klarner, Y. Mazei, M. Maraun, R. Widyastuti & S. Scheu (2018): Micro-decomposer communities and decomposition processes in tropical lowlands as affected by land use and litter type. – Oecologia **187**/1: 255–266 [https://doi.org/10.1007/s00442-018-4103-9].

Krause, A., D. Sandmann, S. L. Bluhm, S. Ermilov, R. Widyastuti, N. F. Haneda, S. Scheu & M. Maraun (2019): Shift in trophic niches of soil microarthropods with conversion of tropical rainforest into plantations as indicated by stable isotopes (15N, 13C). – PLOS ONE **14**/10: e0224520 [https://doi.org/10.1371/journal.pone.0224520].

Lencinas, M. V., G. Kreps, R. Soler, P. L. Peri, A. Porta, M. Ramírez & G. M. Pastur (2015): Neochelanops michaelseni (Pseudoscorpiones: Chernetidae) as a potential bioindicator in managed and unmanaged Nothofagus forests of Tierra del Fuego. – The Journal of Arachnology **43**/3: 406–412 [https://doi.org/10.1636/0161-8202-43.3.406]

Maraun, M., G. Erdmann, B. M. Fischer, M. M. Pollierer, R. A. Norton, Schneider, K. & S. Scheu (2011): Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology. – Soil Biology and Biochemistry **43**/5: 877–882 [https://doi.org/10.1016/j.soilbio.2011.01.003].

Margono, B. A., S. Turubanova, I. Zhuravleva, P. Potapov, A. Tyukavina, A. Baccini, S. Goetz & M. C. Hansen (2012): Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. – Environmental Research Letters **7**/3: 034010 [https://doi.org/10.1088/1748-9326/7/3/034010].

Marsden, C., A. Martin-Chave, J. Cortet, M. Hedde & Y. Capowiez (2020): How agroforestry systems influence soil fauna and their functions - a review. – Plant and Soil **453**/1: 29–44 [https://doi.org/10.1007/s11104-019-04322-4].

Mumme, S., M. Jochum, U. Brose, N. F. Haneda & A. D. Barnes (2015): Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. – Biological Conservation **191**: 750–758 [https://doi.org/10.1016/j.biocon.2015.08.033].

Muster, C. & T. Blick (2015): Pseudoscorpions (Arachnida: Pseudoscorpiones) in strict forest reserves in Hesse (Germany). – Arachnologische Mitteilungen **50**: 37–50 [https://doi.org/10.5431/aramit5006].

Nazarreta, R., T. R. Hartke, P. Hidayat, S. Scheu, B. Damayanti & J. Drescher (2020): Rainforest conversion to smallholder plantations of rubber or oil palm leads to species loss and community shifts in canopy ants (Hymenoptera: Formicidae). – Myrmecological News **30**: 175–186 [https://doi.org/10.25849/MYRMECOL.NEWS_030:175].

Oelbermann, K. & S. Scheu (2010): Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}N/^{14}N$). – Bulletin of Entomological Research **100**/5: 511–520 [https://doi.org/10.1017/S0007485309990587].

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos & et al. (2020): vegan: Community Ecology Package.

Paoletti, A., K. Darras, H. Jayanto, I. Grass, M. Kusrini & T. Tscharntke (2018): Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest. – Global Ecology and Conservation **16**: e00492 [https://doi.org/10.1016/j.gecco.2018.e00492].

Pollierer, M. M., R. Langel, C. Körner, M. Maraun & S. Scheu (2007): The underestimated importance of belowground carbon input for forest soil animal food webs. – Ecology Letters **10**/8: 729–736 [https://doi.org/10.1111/j.1461-0248.2007.01064.x].

Pollierer, M. M., R. Langel, S. Scheu & M. Maraun (2009): Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). – Soil Biology and Biochemistry **41**/6: 1221–1226 [https://doi.org/10.1016/j.soilbio.2009.03.002].

Post, D. M. (2002): Using stable isotopes to estimate trophic position: Models, methods, and assumptions. – Ecology **83**/3: 703–718 [https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2].

Potapov, A. M., A. V. Tiunov & S. Scheu (2019a): Uncovering trophic positions and food resources of soil animals using bulk natural stable isotope composition. – Biological Reviews **94**/1: 37–59 [https://doi.org/10.1111/brv.12434].

Potapov, A. M., B. Klarner, D. Sandmann, R. Widyastuti & S. Scheu (2019b): Linking size spectrum, energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. – Journal of Animal Ecology **88**/12: 1845–1859. [https://doi.org/10.1111/1365-2656.13027].

Potapov, A. M., U. Brose, S. Scheu & A. V. Tiunov (2019c): Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. – The American Naturalist **194**/6: 823–839 [https://doi.org/10.1086/705811].

Potapov, A. M., N. Dupérré, M. Jochum, K. Dreczko, B. Klarner, A. D. Barnes, V. Krashevska, K. Rembold, H. Kreft, U. Brose, R. Widyastuti, D. Harms & S. Scheu (2020): Functional losses in ground spider communities due to habitat structure degradation under tropical land-use change. – Ecology **101**/3: e02957 [https://doi.org/10.1002/ecy.2957].

Potapov, A. M., I. Schaefer, M. Jochum, R. Widyastuti, N. Eisenhauer & S. Scheu (2021): Oil palm and rubber expansion facilitates earthworm invasion in Indonesia. – Biological Invasions [https://doi.org/10.1007/s10530-021-02539-y].

R Core Team (2018): R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [https://www.R-project.org/. – *httg://www.R-project.org/.* Retrieved February 25, 2020, from https://www.r-project.org/].

Riede, J. O ., U. Brose, B. Ebenman, U. Jacob, R. Thompson, C. R. Townsend & T. Jonsson (2011a): Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. – Ecology Letters **14**/2: 169–178 [https://doi.org/10.1111/j.1461-0248.2010.01568.x].

Rooney, N., K. McCann, G. Gellner & J. C. Moore (2006): Structural asymmetry and the stability of diverse food webs. – Nature **442**/7100: 265–269 [https://doi.org/10.1038/nature04887].

Sahner, J., S. W. Budi, H. Barus, N. Edy, M. Meyer, M. D. Corre & A. Polle (2015): Degradation of root community traits as indicator for transformation of tropical lowland rain forests into oil palm and rubber plantations. – PLOS ONE **10**/9: e0138077 [https://doi.org/10.1371/journal.pone.0138077].

Scheu, S. (2002): The soil food web: structure and perspectives. – European Journal of Soil Biology **38**/1: 11–20 [https://doi.org/10.1016/S1164-5563(01)01117-7].

Sodhi, N. S., L. P. Koh, B. W. Brook & P. K. L. Ng (2004): Southeast Asian biodiversity: an impending disaster. – Trends in Ecology & Evolution **19**/12: 654–660 [https://doi.org/10.1016/j.tree.2004.09.006].

Susanti, W. I., M. W. Pollierer, R. Widyastuti, S. Scheu & A. Potapov (2019): Conversion of rainforest to oil palm and rubber plantations alters energy channels in soil food webs. – Ecology and Evolution **9**/16: 9027–9039 [https://doi.org/10.1002/ece3.5449].

Villarreal, E., N. Martínez & C. Romero-Ortiz (2019): Diversity of Pseudoscorpiones (Arthropoda: Arachnida) in two fragments of dry tropical forest in the colombian Caribbean region. – Caldasia **41**/1: 139–151 [https://doi.org/10.15446/caldasia.v41n1.72189].

Weygoldt, P. (1969): The biology of Pseudoscorpions. – 168 pp. (Harvard University Press).

Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, D. Dunnington & RStudio (2020): ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics.

Yamamoto, T., N. Nakagoshi & Y. Touyama (2001): Ecological study of pseudoscorpion fauna in the soil organic layer in managed and abandoned secondary forests: Pseudoscorpions and forest management. – Ecological Research **16**/3: 593–601 [https://doi.org/10.1046/j.1440-1703.2001.00422.x].

Yang, X., M. Warren & X. Zou (2007): Fertilization responses of soil litter fauna and litter quantity, quality, and turnover in low and high elevation forests of Puerto Rico. – Applied Soil Ecology **37**/1–2: 63–71 [https://doi.org/10.1016/j.apsoil.2007.03.012].