Trophic niche differentiation and utilisation of food resources in Collembola is altered by rainforest conversion to plantation systems

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Conversion of tropical ecosystems is associated with major changes in ecological niches of species and communities, resulting in changes of ecosystem functioning. Collembola are among the most abundant soil arthropods sensitively responding to changes in vegetation and soil conditions at the community level. However, most of the studies to date were conducted in temperate ecosystems and focused on shifts in community composition or morphological traits, while parameters more closely linked to ecosystem functioning, such as trophic niches, received little attention. Here, we investigated changes in trophic structure of and use of food resources by Collembola after conversion of rainforest into rubber and oil palm plantations in Jambi province (Sumatra, Indonesia) using stable isotope analysis (^{13}C and ^{15}N). Across Collembola species $\Delta^{13}C$ values were highest in rainforest, suggesting more pronounced processing of litter resources by microorganisms in this system. Lower $\Delta^{13}C$ values, but high $\Delta^{13}C$ variation in Collembola in oil palm plantations indicated that Collembola shifted towards herbivory and used a wider range of resources in this system. Small range in $\Delta^{15}N$ values in Collembola species in monoculture plantations in comparison to rainforest indicated that conversion of rainforest into plantations is associated with simplification in the trophic structure of Collembola communities. Across the studied ecosystems, atmobiotic species (Symphypleona and Paronellidae) occupied the lowest, whereas euedaphic species occupied the highest trophic position, resembling patterns in temperate forests. Some species of Paronellidae in rainforest and jungle rubber had $\Delta^{15}N$ values below those of leaf litter suggesting algivory (*Salina* sp.1, *Callyntrura* sp.1 and *Lepidonella* sp.1), while *Pseudosinella* sp.1 had the

highest $\Delta^{15}N$ values in most of the land-use systems suggesting that this species at least in part lives as predator / scavenger. Overall, the results suggest that rainforest conversion into plantation systems is associated with marked shifts in the structure of trophic niches in soil and litter Collembola with potential consequences for ecosystem functioning and food-web stability.

TROPHIC NICHE DIFFERENTIATION AND UTILISATION OF FOOD RESOURCES IN COLLEMBOLA IS ALTERED BY RAINFOREST CONVERSION TO PLANTATION SYSTEMS

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ABSTRACT

Conversion of tropical ecosystems is associated with major changes in ecological niches of species and communities, resulting in changes of ecosystem functioning. Collembola are among the most abundant soil arthropods sensitively responding to changes in vegetation and soil conditions at the community level. However, most of the studies to date were conducted in temperate ecosystems and focused on shifts in community composition or morphological traits, while parameters more closely linked to ecosystem functioning, such as trophic niches, received little attention. Here, we investigated changes in trophic structure of and use of food resources by Collembola after conversion of rainforest into rubber and oil palm plantations in Jambi province (Sumatra, Indonesia) using stable isotope analysis (^{13}C and ^{15}N). Across Collembola species $\Delta^{13}C$

values were highest in rainforest, suggesting more pronounced processing of litter resources by microorganisms in this system. Lower $\Delta^{13}C$ values, but high $\Delta^{13}C$ variation in Collembola in oil palm plantations indicated that Collembola shifted towards herbivory and used a wider range of resources in this system. Small range in $\Delta^{15}N$ values in Collembola species in monoculture plantations in comparison to rainforest indicated that conversion of rainforest into plantations is associated with simplification in the trophic structure of Collembola communities. Across the studied ecosystems, atmobiotic species (Symphypleona and Paronellidae) occupied the lowest, whereas euedaphic species occupied the highest trophic position, resembling patterns in temperate forests. Some species of Paronellidae in rainforest and jungle rubber had $\Delta^{15}N$ values below those of leaf litter suggesting algivory (*Salina* sp.1, *Callyntrura* sp.1 and *Lepidonella* sp.1), while *Pseudosinella* sp.1 had the highest $\Delta^{15}N$ values in most of the land-use systems suggesting that this species at least in part lives as predator / scavenger. Overall, the results suggest that rainforest conversion into plantation systems is associated with marked shifts in the structure of trophic niches in soil and litter Collembola with potential consequences for ecosystem functioning and food-web stability.

Key words: rainforest, oil palm, rubber, land-use change, stable isotope analysis, trophic niches, springtail

Introduction

Agricultural intensification in Indonesia is associated with deforestation which increased strongly in the last 20 years (Koh & Ghazoul, 2010 ; Gatto *et al.*, 2015). Large parts of rainforest in lowland Sumatra have been converted into oil palm (16% of total area) and rubber plantations (12%) (Gatto *et al.*, 2015). The conversion of tropical rainforest into plantation systems is associated with major changes in ecological niches of animal species, loss of biodiversity, and thereby with changes in ecosystem functioning (Barnes *et al.*, 2014; Clough *et al.*, 2016; Fitzherbert *et al.*, 2008; Gilbert, 2012). These changes affect both the above- and belowground system. Complex and diverse microbial and animal communities in soil regulate important ecosystem functions and support aboveground life (Bardgett & Van Der Putten, 2014), but knowledge on effects of land-use change on soil live in the tropics is very limited.

Conversion of rainforest into oil palm and rubber plantations in Indonesia is associated with a decline in species diversity, population density, biomass and energy flux in litter macroinvertebrate communities by approximately 45% (Barnes *et al.,* 2014). However, this decline is uneven across size classes and trophic levels, altering the structure of soil food webs (Potapov *et al.*, 2019). Different basal resources available in different land-use systems result in changes in trophic niches of decomposer and predatory soil invertebrates, and results in reduced abundance of primary decomposers and in soil animals shifting their feeding habits towards herbivory (Klarner *et al.*, 2017; Krause *et al.*, 2019; Susanti *et al.*, 2019). Land-use change may also result in reduced trophic niche differentation among species in belowground communities (Korotkevich, Potapov, Tiunov, & Kuznetsova, 2018), but this has not been investigated in tropical ecosystems.

Collembola are among the most abundant soil decomposer invertebrates, inhabiting various organic substrates and using a wide range of food resources (Josef Rusek, 1998). Early studies on food resources of Collembola concluded that the majority of euedaphic and hemiedaphic species feed unselectively on a wide variety of food materials (Hopkin, 1997). However, stable isotope analysis showed pronounced trophic niche differentiation among Collembola species in temperate forests (Chahartagi *et al.*, 2005). This differentiation in large has been explained by the taxonomic identity and life forms of Collembola (Potapov *et al.*, 2016). Species, living aboveground and on the litter surface (atmobiotic and epedaphic life forms) are mainly phycophages, feeding on lichens, algae and pollen. Species, living in the litter (hemiedaphic life form) are decomposers which feed on saprotrophic microorganisms and litter. Species, living in soil (euedaphic life form) feed on soil organic matter, roots and fungi (Ponge, 2000; Potapov *et al.,* 2016). Further, food resources and trophic levels also vary among taxa with e.g., Poduromorpha occupying higher trophic positions than Entomobryomorpha and Symphypleona, suggesting evolutionary selection for microbivory in the former (Potapov *et al.,* 2016). To date, information on food resources and trophic niches of Collembola is based on studies from temperate ecosystems, whereas information from tropical ecosystems is virtually lacking.

Over the last two decades, stable isotope analysis has become the most commonly used tool to assess trophic niches of soil animals (Potapov *et al.,* 2019). Two isotopic ratios, $^{13}C/^{12}C$ (i.e., $\delta^{13}C$ values) and $^{15}N/^{14}N$ (i.e., $\delta^{15}N$ values), typically are used in food-web studies. The trophic positions and the length of trophic chains can be assessed using $\delta^{15}N$ values, whereas the range of $\delta^{13}C$ values reflects the variability in the use of basal resources (Potapov, *et al.*, 2019).

The stable isotope composition of consumers follows that in food resources, thus allowing to reveal potential diet switching with land-use change (Klarner *et al.,* 2017; Krause *et al.,* 2019; Susanti *et al.*, 2019).

Here, we use stable isotope analysis to investigate trophic positions and food resources of soil and litter Collembola in four different land-use systems in Sumatra, Indonesia: rainforest, rubber agroforest ('jungle rubber'), and rubber and oil palm plantations. The study aimed at investigating how trophic positions and food resources of Collembola change after rainforest conversion into agricultural plantations, such as rubber and oil palm, and, for the first time, at exploring patterns in trophic niche differentiation among tropical Collembola species. In more detail we investigated the following hypotheses:

1) Analogous to other soil invertebrates, Collembola shift their trophic niches towards herbivory in plantations systems in comparison to rainforest.
2) Due to reduced food resources (poor litter layer), the trophic niche width of Collembola is lower in plantations in comparison to rainforest.
3) Trophic niche differentiation among species is more pronounced in rainforest than in disturbed plantation systems.
4) Trophic niche differentiation among families and life forms of Collembola in tropical ecosystems follows similar patterns as in ecosystems of the temperate zone.

Material and Methods

Site description

Soil and litter samples were taken in lowland rainforest, jungle rubber, rubber (*Hevea brasiliansis*) and oil palm (*Elaeis guineensis*) plantations, located in Jambi province, southwest Sumatra, Indonesia. The study sites are located at similar altitude varying between 50 and 100 m a.s.l. in two landscapes, the Harapan and Bukit Dua Belas landscape; each system was replicated four times (see Drescher *et al.*, 2016 for more details). Lowland rainforest was used as reference, but represents secondary rainforest which has been logged once by taking out large trees some 30 years ago. Jungle rubber represents rubber agroforests originating from rainforest enriched with rubber trees; the age of rubber trees varied between 15-40 years (Kotowska, Leuschner, Triadiati, Meriem, & Hertel, 2015). Rubber and oil palm plantations were intensively managed monocultures of an average age of 7 to 16 and 8 to 15 years, respectively (Drescher e*t al.*, 2016) and were established after logging, clearing, and burning of either rainforest or jungle rubber. Soils at the Harapan landscape are loam Acrisols of low fertility, whereas in Bukit Dua Belas the major soil type is clay Acrisol (Allen, Corre, Tjoa, & Veldkamp, 2015; Kotowska *et al.,* 2015). Management practices in these smallholder monoculture plantations are described in more detail in Allen *et al.* (2015). Oil palm plantations typically were fertilized once in the rainy season and once in the dry season. Typically, 300-500 kg NPK complete fertilizer, 300 kg KCl and 138 kg urea ($CO(NH_2)_2$) were added per hectare and year. Rubber and oil palm plantations were weeded manually or chemically throughout the year. The most commonly used herbicides were Gramoxone and Roundup; these were applied at an average rate of 2 to 5 L ha^{-1} y^{-1} *(Allen et al.*, 2015; Clough *et al.*, 2016; Kotowska *et al.,* 2015).

Sampling procedure

Samples were taken in October 2013 in three 5 x 5 m subplots within 50 x 50 m plots established at each study site (Drescher *et al.,* 2016). A total of 32 plots were investigated (2 landscapes x 4 land-use systems x 4 replicates). In each subplot soil samples of 16 x 16 cm were taken including the litter layer and the underlying top soil to a depth of 5 cm. Animals from both layers were pooled for stable isotope analysis to obtain sufficient amount of animal tissue for the analyses. Animals were extracted by heat (Kempson, Lloyd, & Gheraldi, 1963) during 6-8 days using glycerol : water mixture at a ratio of 1 : 1 as collection solution. After extraction animals were transferred into 70% ethanol. Sampling of animals used in this study was based on Collection permits No. S.07/KKH-2/2013 and No. 2841/IPH.1/KS.02.04/X/2016 issued by the Indonesian Ministry of Forestry (PHKA).

Species identification

Collembola were sorted in Petri dishes using a dissecting microscope. For (morpho)species identification, selected individuals were subsequently cleared in Nesbitt solution and mounted on slides with Hoyer solution. Collembola were identified under a compound light microscope at 400× magnification. The checklist and keys for Indonesian Collembola by Suhardjono *et al.* (2012) were used along with publications on Southeast Asian Collembola. Juvenile specimens in part were ascribed to morphospecies of adults or subadults present in the same sample or in samples from the same plot. After identification, all data on Collembola species and their identification characters were uploaded to Ecotaxonomy database

(http://ecotaxonomy.org). In total 56 species/morphospecies from 13 families and 27 genera were found.

Bulk stable isotope analyses

Stable isotope ratios were measured from dominant species representing at least 70% of the individuals on each plot. Dominant species were chosen for each plot separately to represent the local 'functional community'. This selection procedure resulted in a total of 30 out of 56 species being included in the analysis. For stable isotope measurements appropriate amounts of animal tissue (ranging from 0.003 to 1.268 mg) were transferred into tin capsules and dried at 60°C for 24 h, weighed and stored in a desiccator until analysis. Stable isotope and C-to-N ratios were determined using a coupled system consisting of an elemental analyzer (Eurovector, Milano, Italy) equipped with a Blisotec autosampler (Blisotec, Jülich, Germany) and a Thermo Delta Vplus isotope ratio mass spectrometer connected via a Conflo IV interface (both from Thermo Fisher Scientific, Bremen, Germany) located at the Centre for Stable Isotope Research and Analysis, Göttingen, Germany (Langel & Dyckmans, 2014). Isotope signatures are expressed using the δ notation as $\delta X(‰) = (R_{sample}–R_{standard})/R_{standard} \times 1000$, with X representing the target isotope and R the ratio of heavy to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). For $\delta^{15}N$ and $\delta^{13}C$ analyses, N in atmospheric air and Vienna PD Belemnite served as standards, respectively. Acetanilide (C_8H_9NO, Merck, Darmstadt) was used for internal calibration.

Statistical analysis

To compensate for inter-site variation in the isotopic baseline, all data were normalized to the local leaf litter using the following equations (Potapov *et al.*, 2019):

$\Delta^{13}C = \delta^{13}C_{Collembola} - \delta^{13}C_{litter}$

$\Delta^{15}N = \delta^{15}N_{Collembola} - \delta^{15}N_{litter}$

Stable isotope values of litter were taken from Klarner *et al.* (2017) who investigated the same sampling sites. Statistical analyses were performed using R v 3.5.2 (R Core Team, 2018) with R studio interface (R Studio, Inc.).

First, we analyzed the effect of land-use system on the isotopic composition of Collembola at the community level. Effects of land-use system on the $\Delta^{13}C$ and $\Delta^{15}N$ values of all measured Collembola individuals were tested using Linear Mixed Effect Models (LMM) with species identity as random effect. The analysis was conducted using the *lmer* function in the *lme4* package (Bates *et al*., 2015). Significance of fixed effects (factors) was tested using the *Anova* function from the package *car*. Significant differences in stable isotope values between land-use systems were tested using the *tukey te*st in the *emmeans* and *multicomp* packages. In addition, we analyzed the effect of land use only for one dominant species, present in sufficient replicates of each land-use systems (*Pseudosinella* sp.1) using analysis of variance implemented in the *aov* function. Additionally, the ranges of $\Delta^{13}C$ and $\Delta^{15}N$ values in each land-use system were visualized using the Kernel density estimation in the *ggplot 2* package using the *geom_violin* function.

Second, we assessed trophic niche differentiation among species using LMM. We used species identity as factor and either $\Delta^{13}C$ or $\Delta^{15}N$ values as response variables; sampling plot was included as random effect. The analysis was done separately for each land-use system (eight

197 analyses in total). In each case, only species with more than three measurements in the given
198 land-use system were included.

199 Third, we analyzed the effects of family identity and life form on stable isotope
200 composition using LMM. Here, we used both plot and land-use system as random effects.
201 Significant differences between families and life forms were tested using Tukey contrasts as
202 implemented in the *glth* function in the *multicomp* package. To display the isotopic niche space
203 of Collembola species, family and lifeform, standard ellipses were plotted using the
204 *standard.ellipses* function in the *siar* package, and visualized using the *ggplot* and *grepel*
205 packages. We also analyzed interactions between lifeform and family and land-use system with
206 species as random effects. In the analyses, we excluded Neanuridae and Onychiuridae as they
207 were only represented by a single species not present in each of the land-use systems.

208

209 **Results**

210 *Community-level changes with land use*

211 In rainforest $\Delta^{13}C$ values of Collembola ranged between 1.5 and 6.0‰ (4.5‰) and in oil
212 palm plantations between -1.5 and 8.5‰ (10.0‰), indicating that Collembola species in oil palm
213 plantations used a wider range of food resources compared to rainforest. In jungle rubber and
214 rubber plantations, the range of $\Delta^{13}C$ values was similar to rainforest (between 1.0 and 6.0 ‰).
215 Mean $\Delta^{13}C$ values in rainforest were significantly higher than in plantation systems ($F_{3,146}$ = 9.90,
216 p = 0.001; Fig. 1A, Supplementary Material Table S1,S2). All Collembola species were enriched in

217 $\delta^{13}C$ relative to leaf litter except for one individual of *Isotomiella* cf. *minor* in oil palm plantations
218 (Fig. 2; for details see Supplementary Material Table S5-S8).

219 In contrast to $\Delta^{13}C$, the range of $\Delta^{15}N$ values was largest in rainforest (-5.0 to 19.0‰),
220 lowest in oil palm plantations (-1.0 to 8.0‰) and intermediate in rubber plantations (-5.0 to
221 15.0‰) and in jungle rubber (-7.5 to 16.0‰). The mean $\Delta^{15}N$ values of Collembola did not vary
222 significantly among land-use systems ($F_{3,153} = 1.46$, $p = 0.228$; Fig. 1B, Supplementary Material
223 Table S3, S4). Stable isotope values of the most abundant Collembola species present in all land-
224 use systems, *Pseudosinella* sp.1, did not vary significantly among land-use systems both in $\Delta^{13}C$
225 ($F_{3,21} = 1.44$, $p = 0.260$) and $\Delta^{15}N$ ($F_{3,21} = 0.88$, $p = 0.467$).

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228 Figure 1. Variations in $\Delta^{13}C$ and $\Delta^{15}N$ values of Collembola among the studied land-use systems
229 (rainforest, jungle rubber, rubber and oil palm plantations). Violin plots show mirrored Kernel
230 density estimation, all individual measurements are displayed together, independently of the
231 taxonomic identity. *$\Delta^{13}C$ values in rainforest were significantly higher than in other three land-
232 use systems ($P < 0.05$).

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234

235 *Trophic niche differentiation among species*

236 $\Delta^{13}C$ values of the species analyzed (with at least three replicates per species; see
237 Methods) varied significantly in rainforest ($F_{4,12} = 6.34$, $p = 0.005$) and jungle rubber ($F_{5,17} = 3.67$,
238 $p = 0.020$), but not in rubber ($F_{5,19} = 1.39$, $p = 0.270$) and oil palm plantations ($F_{2,9} = 1.10$, $p =$
239 0.370). In rainforest $\Delta^{13}C$ values of *Pseudosinella* sp.1 were highest and differed significantly from
240 those of *Lepidocyrtus* sp.1 and *Pararrhopalites* sp.1, whereas in jungle rubber they were highest
241 in *Homidia cingula* and differed significantly from *Callyntrura* sp.1.

242 $\Delta^{15}N$ values of the species analyzed varied significantly in rainforest ($F_{4,14} = 5.00$, $p =$
243 0.010), jungle rubber ($F_{5,18} = 4.70$, $p = 0.006$) and oil palm plantations ($F_{2,9} = 23.59$, $p = 0.001$), but
244 not in rubber plantations ($F_{5,19} = 2.43$, $p = 0.072$) (Fig. 3; for details see Supplementary Material
245 Table S9-S12). In rainforest *Pseudosinella* sp.1 occupied the highest trophic position, followed by
246 *Isotomiella* cf. *minor*, whereas *Allacma* sp.1 occupied the lowest trophic position. Similar to
247 rainforest, in jungle rubber *Pseudosinella* sp.1 also occupied the highest trophic position, but
248 $\Delta^{15}N$ values were lowest in *Callyntrura* sp.1. Overall, *Pseudosinella* sp.1, the most dominant
249 species, occupied the highest trophic position across all species. Across all samples analyzed (20
250 species in rainforest, 17 species jungle rubber, 15 species in rubber plantations, and 13 species
251 in oil palm plantations) 3.0% had $\Delta^{15}N$ values below that of litter (see Supplementary Material,
252 Figure 1).

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254

255 Figure 2. $\Delta^{13}C$ values of Collembola species in different land-use systems (rainforest, jungle
256 rubber, rubber and oil palm plantations); model-estimated means (lsmeans) with standard
257 deviation. Horizontal stripes represent individual measurements. Only species with more than
258 three replicates per land-use system were analyzed (see Methods). Isotope values of each species
259 in each land-use system with the same letter are not significantly different according to Tukey's
260 honestly significant difference test ($p > 0.05$).

Figure 3. Differences of $\Delta^{15}N$ values of Collembola in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations); model-estimated means (lsmeans) with standard deviation. Horizontal stripes represent individual measurements. Only species with more than three replicates per land-use system were analyzed (see Methods). Isotope values of each species in each land-use system with the same letter are not significantly different according to Tukey's honestly significant difference test ($p > 0.05$).

Stable isotope niches of Collembola life forms and families

$\Delta^{15}N$ values of Collembola varied among life forms ($F_{24,126} = 1.82$, $p = 0.018$), but this was not the case for $\Delta^{13}C$ values ($F_{24,126} = 1.19$, $p = 0.260$), with the interaction between lifeform and land-use system neither being significant for $\Delta^{15}N$ ($F_{9,131.60} = 0.87$, $p = 0.556$) nor for $\Delta^{13}C$ ($F_{9,135.05} = 0.79$, $p = 0.619$). Differences between life forms were more pronounced in rainforest and jungle rubber and less in rubber and oil palm plantations (Figure 4). Euedaphic species were generally most enriched in ^{15}N, whereas atmobiotic species on average occupied the lowest trophic position (except in rubber plantations), often having $\Delta^{15}N$ values below 5.0‰, with epedaphic and hemiedaphic species being intermediate.

$\Delta^{15}N$ ($F_{24,128.87} = 2.19$, $p = 0.002$) but not $\Delta^{13}C$ values ($F_{24,127.86} = 1.01$, $p = 0.470$) of Collembola also varied significantly among families (Figure 5), with the interaction between family and land-use system neither being significant for $\Delta^{15}N$ ($F_{8,121.94} = 0.34$, $p = 0.945$) nor for $\Delta^{13}C$ ($F_{8,120.67} = 1.84$, $p = 0.075$). Across all land-use systems Isotomidae and Entomobryidae occupied the highest trophic positions, but in rainforest and oil palm plantations Symphypleona occupied the lowest trophic position, whereas in jungle rubber and rubber plantations the lowest trophic position was occupied by Paronellidae.

Figure 4. Stable isotope niches of four Collembola life forms in rainforest, jungle rubber, rubber and oil palm plantations. Ellipses denote 60% confidence intervals, different life forms are shown with colors (eudaphic = dark blue, epedaphic = grey, hemiedaphic = dark goldenrod, atmobiotic = forest green). Large colored dots represent means of land-use systems, small points represent individual measurements.

Figure 5. Stable isotope niche of Collembola families in rainforest, jungle rubber, rubber and oil palm plantations. Ellipses denote 60% intervals, different families are shown with colors (Paronellidae = blue, Isotomidae = green, Symphypleona = purple, Entomobryidae = light red; Symphypleona comprises the families Sminthuridae, Sminthirididdidae, Dycirtomidae and Katiannidae). Large colored dots represent means of land-use systems, small points represent individual measurements.

Discussion

Variations in trophic niches with land-use system

Results of the present study indicate that rainforest conversion into agricultural plantations is associated with changes in basal resources ($\Delta^{13}C$ values) of Collembola, but does not significantly affect their average trophic positions ($\Delta^{15}N$ values). These findings are in line with the results of the study of Krause *et al.* (2019) investigating oribatid mites at the same study sites and showing that the shift in trophic niches to be mainly due to changes in the use of basal resources rather than trophic levels. Similar to previous studies on centipedes, oribatid mites and other soil animal taxa (Klarner *et al.,* 2017; Susanti *et al.,* 2019; Krause e*t al.*, 2019), we also found the conversion of rainforest into plantations to be associated in Collembola with a shift from detritivory towards herbivory (i.e. lower ^{13}C enrichment). In rainforest and jungle rubber,

Collembola were enriched in $\delta^{13}C$ by about 2.0-5.0‰ compared to leaf litter, which resembles the shift observed in temperate forest ecosystems (Pollierer *et al.,* 2009). This "detrital shift" in $\delta^{13}C$ (Potapov *et al.,* 2019) presumably is due to acquiring C from saprotrophic fungi and bacteria (Potapov *et al*., 2013). High $\delta^{13}C$ enrichment in most of the studied Collembola species in the two more natural ecosystems (rainforest and jungle rubber) suggests that they predominantly rely on microorganisms decomposing organic matter rather than on fresh plant material as the food source (Potapov *et al.,* 2019). Overall, similar enrichment in ^{13}C and ^{15}N in Collembola in temperate and tropical ecosystems suggest that Collembola rely little on fresh plant material or mycorrhizal fungi in both and this may well apply to the soil food web in general.

As indicated by $\Delta^{13}C$ values, Collembola species in oil palm plantations used the widest range of food resources compared to the other land-use systems studied, but occupied a narrower range of trophic positions. The wide range in food resources in oil palm plantations may be attributed to the large variety of management practices of the smallholder systems studied (Clough *et al.*, 2016), potentially associated with different organic inputs depending on weeding and fertilization practices. The narrow range of trophic positions in oil palm plantations was due to both the absence of high (predators, scavengers) and low trophic level species (primary decomposers, specialized lichen feeders). This may reflect trophic generalization in the disturbed and unstable habitat of oil palm plantations (Korotkevich *et al.*, 2018). In fact, among the studied land-use systems nematode communities were shown to be most unstable in monoculture plantations (Krashevska, *et al.,* 2019). Further, Klarner *et al.* (2017) showed that certain species of centipedes had lower $\Delta^{15}N$ values in oil palm compared to jungle rubber and rubber

335 plantations suggesting that trophic chains in oil palm plantations are shorter than in the other
336 land-use systems studied.

337 The most dominant Collembola species at our study sites, *Pseudosinella* sp.1, occupied a
338 similar trophic niche in each of the land-use systems studied, suggesting that its diet changes
339 little with the conversion of rainforest into plantation systems. *Pseudosinella* sp.1 colonized both
340 litter and soil, and, as indicated by $\Delta^{15}N$ values, occupied the highest trophic position among all
341 Collembola species studied. High $\Delta^{15}N$ values suggest that this species may either feed on
342 mycrorrhizal fungi, which are enriched in ^{15}N (Potapov & Tiunov, 2016), and / or on nematodes,
343 which are similarly abundant across the land-use systems studied (Krashevska *et al.*, 2019).
344 Conversion of rainforest may have little affected the mineral soil- and root-based resources and
345 this may explain the high abundance of *Pseudosinella* sp.1 in plantations. Similarly, Krause *et al.*
346 (2019*)* found the trophic niche of some dominant species of oribatid mites to change little with
347 the conversion of rainforest into plantations.

348

349 *Trophic differentiation among species*

350 Variations in $\Delta^{13}C$ values among Collembola species were more pronounced in rainforest
351 and jungle rubber than in rubber and oil palm plantations. Korotkevich *et al.* (2018) also found
352 the interspecific (in contrast to intraspecific) variation in trophic niches of Collembola
353 communities to be higher in natural (forest and meadows) than in disturbed habitats (pastures
354 and lawns). Among the Collembola species studied $\Delta^{13}C$ values of *Pseudosinella* sp.1 in rainforest
355 and *Callyntrura* sp.1 and *Sphyroteca* sp.1 in jungle rubber differed significantly from those of the

356 other species indicating that these species are able to exploit resources not available to the other
357 Collembola species in the respective land-use system.

358 Similar to $\Delta^{13}C$ values, Collembola species in each of the land-use system studied, except
359 rubber plantations, also differed in $\Delta^{15}N$ values. *Callyntrura* sp.1 in jungle rubber was most
360 depleted in $\delta^{15}N$ among the studied Collembola species indicating that this species occupied the
361 lowest trophic position. *Pseudosinella* sp. 1 in rainforest was most enriched in $\delta^{15}N$ values
362 compared the litter substrate and followed by *Isotomiella cf. minor* and *Acrocyrtus* sp. Overall,
363 based on $\Delta^{13}C$ and $\Delta^{15}N$ values, trophic niche differentiation among species was most
364 pronounced in rainforest, presumably due to the availability of a wider spectrum of food
365 resources and more stable environmental conditions. This is likely to result in more efficient food-
366 web functioning in natural ecosystems due to species complementarity (Loreau and Hector
367 2001), which is partly lost in plantation systems.

368

369 *Variations in isotopic niches of Collembola taxa and life forms with land-use systems*

370 Collembola taxa such as Symphypleona and Paronellidae typically had low $\Delta^{15}N$ values,
371 indicating that these taxa feed on algae or lichens (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2018).
372 Symphypleona as well as Paronellidae are well adapted to living above the ground, both are large
373 and possess well-developed visual systems. Such 'atmobiotic' Collembola have been assumed to
374 live at least in part as herbivores on vascular plants or algae (Rusek, 2007) and this is in line with
375 studies from temperate forests investigating variations in stable isotope ratios in Symphypleona
376 (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2016). Paronellidae predominantly occur in tropical

regions and also are adapted to living above the ground. Entomobryidae and Isotomidae occupied high trophic positions and this also is consistent with earlier studies based on variations in stable isotope ratios suggesting that they predominantly feed on litter as well as microorganisms colonizing decomposing litter materials (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2016). However, some species of these two families also occupied very high trophic positions resembling those of Onychiuridae and Neanuridae in temperate ecosystems suggesting that at least in part they live as predators / scavengers presumably including nematodes as prey (Heidemann *et al.*, 2014). Since Onychiuridae and Neanuridae were extremely rare on our sampling sites, species from other families might have been able to occupy their trophic niches.

Trophic niches of Collembola also varied with life form as shown previously for temperate ecosystems (Ponge, 2000; Potapov *et al.*, 2016). Conform to the patterns in Collembola families, the results suggest that atmobiotic and epedaphic species occupied the lowest trophic position across land-use systems, whereas eudaphic species such as *Pseudosinella* sp.1 occupied the highest trophic position. This is in line with the results of the study of Potapov *et al*. (2016) indicating that species inhabiting deeper soil layers (hemiedaphic and euedaphic) are more enriched in $\delta^{15}N$ than those living in litter and above the ground (epedaphic and atmobiotic). Possibly, high $\delta^{15}N$ values resulted from feeding on ectomycorrhizal fungi which are enriched in $\delta^{15}N$ (see above; Potapov and Tiunov, 2016), however, this unlikely applies to tropical forests where trees predominantly form mutualistic interactions with arbuscular mycorrhizal fungi. Low $\delta^{15}N$ values in epedaphic and atmobiotic Collembola were attributed to algae or lichen feeding. This is widespread in Collembola in temperate forests (Potapov et al., 2018), but in our study only few species had $\delta^{15}N$ values below those of litter. This contradicts results based on fatty acid

399 analysis suggesting that Collembola feed more on algae in tropical than in temperate ecosystems
400 (Susanti *et al.,* 2019). To clarify the contribution of algae in soil food webs in tropical and
401 temperate ecosystems, more data on stable isotope composition of various food resources in
402 tropical forests, or direct experimentation, are needed. Overall, the results suggest that similar
403 to oribatid mites (Tsurikov, Ermilov, & Tiunov, 2019) the trophic niche structure in Collembola
404 communities is generally similar in temperate and tropical forests and this is partly explained by
405 taxonomic affiliation and life form.

406

407 **Conclusion**

408 We showed that the conversion of rainforest into agricultural plantations, such as rubber and oil
409 palm, is associated with changes in trophic niches of Collembola. We observed a shift in the use
410 of food resources towards herbivory, with the range of food resources of Collembola in oil palm
411 plantations being the highest, likely due to the heterogeneity in management. By contrast, the
412 range of trophic positions in oil palm plantations was low suggesting simplified trophic structure.
413 This is further supported by the less pronounced trophic niche differentiation among species in
414 monoculture plantations. Trophic niche variation of Collembola life forms and families was
415 generally in line with data from temperate forests (although less pronounced), with atmobiotic
416 species occupying the lowest and eudaphic species occupying the highest trophic position.
417 Overall, the results document that the conversion of rainforest into plantation systems not only
418 is associated with shifts in Collembola community composition, but also in shifts in the trophic

organization of Collembola communities and species, potentially compromising ecosystem functions and food-web stability in plantations.

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Figure 1

Variations in $\Delta^{13}C$ and $\Delta^{15}N$ values of Collembola among the studied land-use systems (rainforest, jungle rubber, rubber and oil palm plantations).

Variations in $\Delta^{13}C$ and $\Delta^{15}N$ values of Collembola among the studied land-use systems (rainforest, jungle rubber, rubber and oil palm plantations). Violin plots show mirrored Kernel density estimation, all individual measurements are displayed together, independently of the taxonomic identity. *$\Delta^{13}C$ values in rainforest were significantly higher than in other three land-use systems ($P < 0.05$).

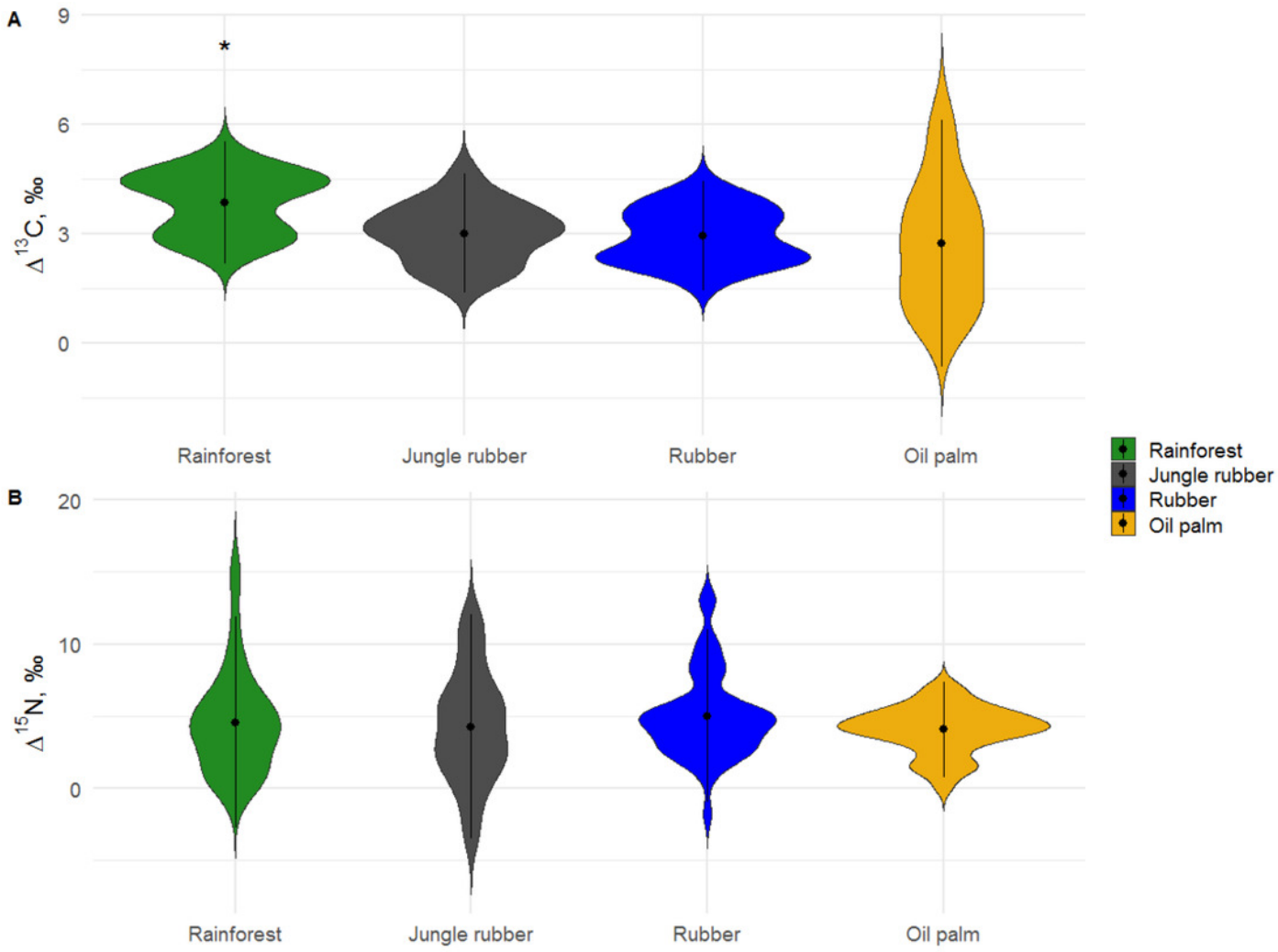


Figure 2

$\Delta^{13}C$ values of Collembola species in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations)

$\Delta^{13}C$ values of Collembola species in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations); model-estimated means (lsmeans) with standard deviation. Horizontal stripes represent individual measurements. Only species with more than three replicates per land-use system were analyzed (see Methods). Isotope values of each species in each land-use system with the same letter are not significantly different according to Tukey's honestly significant difference test ($p > 0.05$).

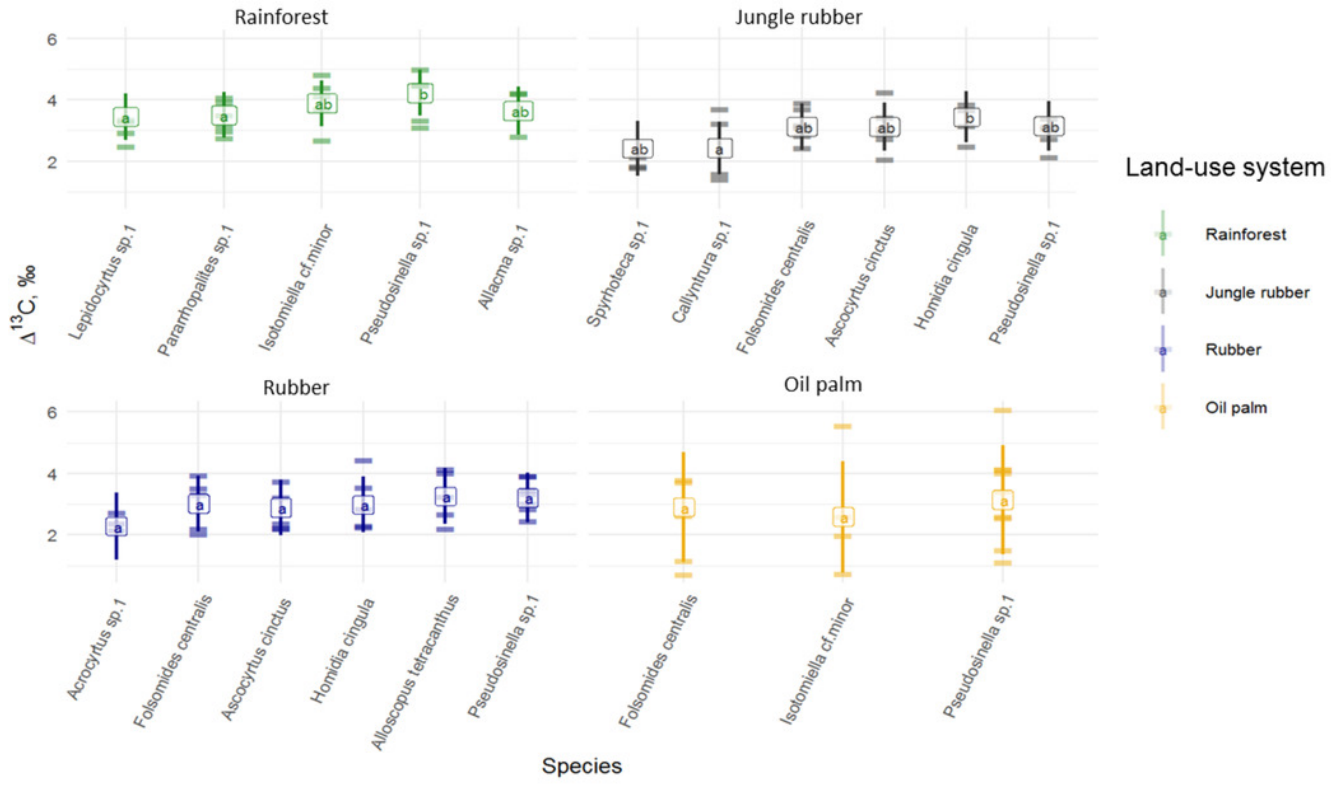


Figure 3

Differences of $\Delta^{15}N$ values of Collembola in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations)

Differences of $\Delta^{15}N$ values of Collembola in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations); model-estimated means (lsmeans) with standard deviation. Horizontal stripes represent individual measurements. Only species with more than three replicates per land-use system were analyzed (see Methods). Isotope values of each species in each land-use system with the same letter are not significantly different according to Tukey's honestly significant difference test ($p > 0.05$).

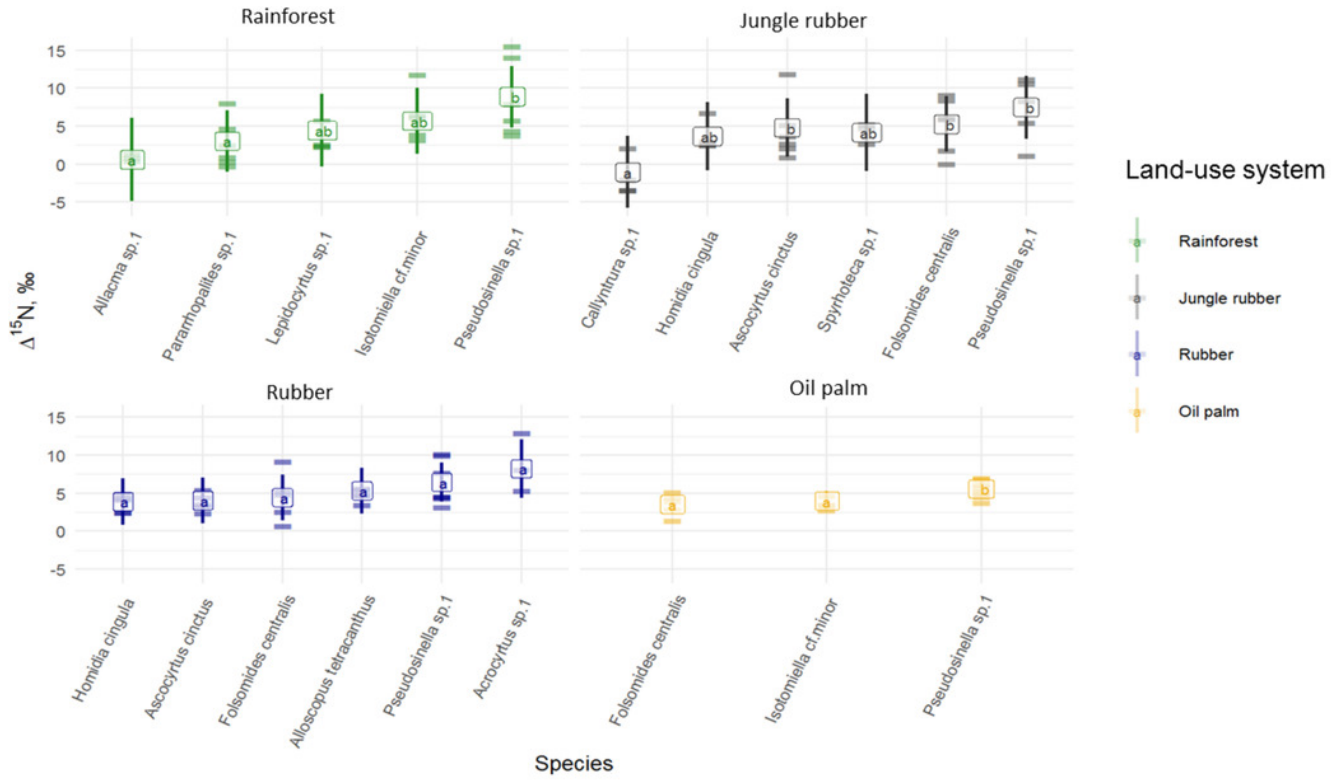


Figure 4

Stable isotope niches of four Collembola life forms in rainforest, jungle rubber, rubber and oil palm plantations.

Stable isotope niches of four Collembola life forms in rainforest, jungle rubber, rubber and oil palm plantations. Ellipses denote 60% confidence intervals, different life forms are shown with colors (eudaphic = dark blue, epedaphic = grey, hemiedaphic = dark goldenrod, atmobiotic = forest green). Large colored dots represent means of land-use systems, small points represent individual measurements.

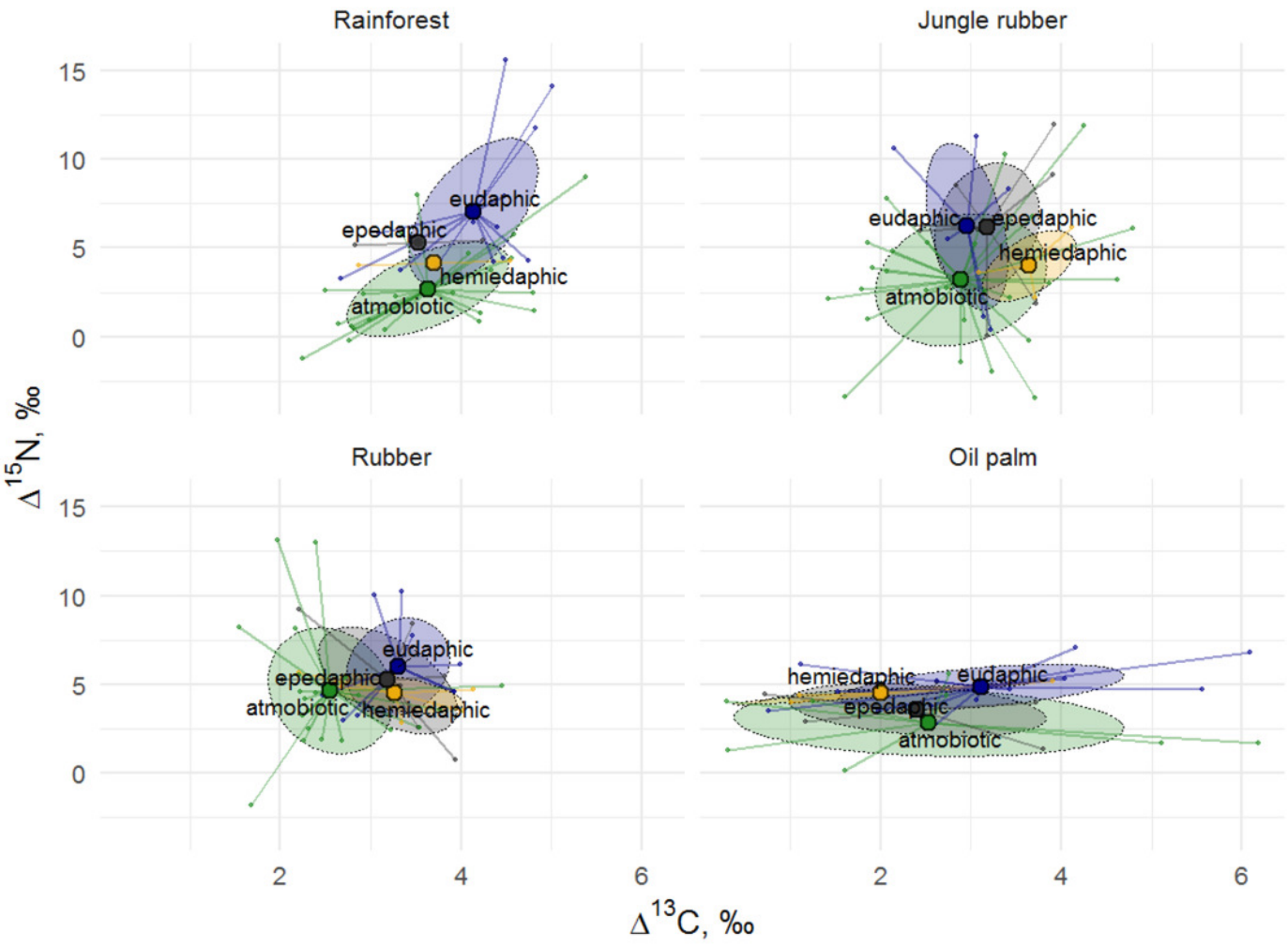
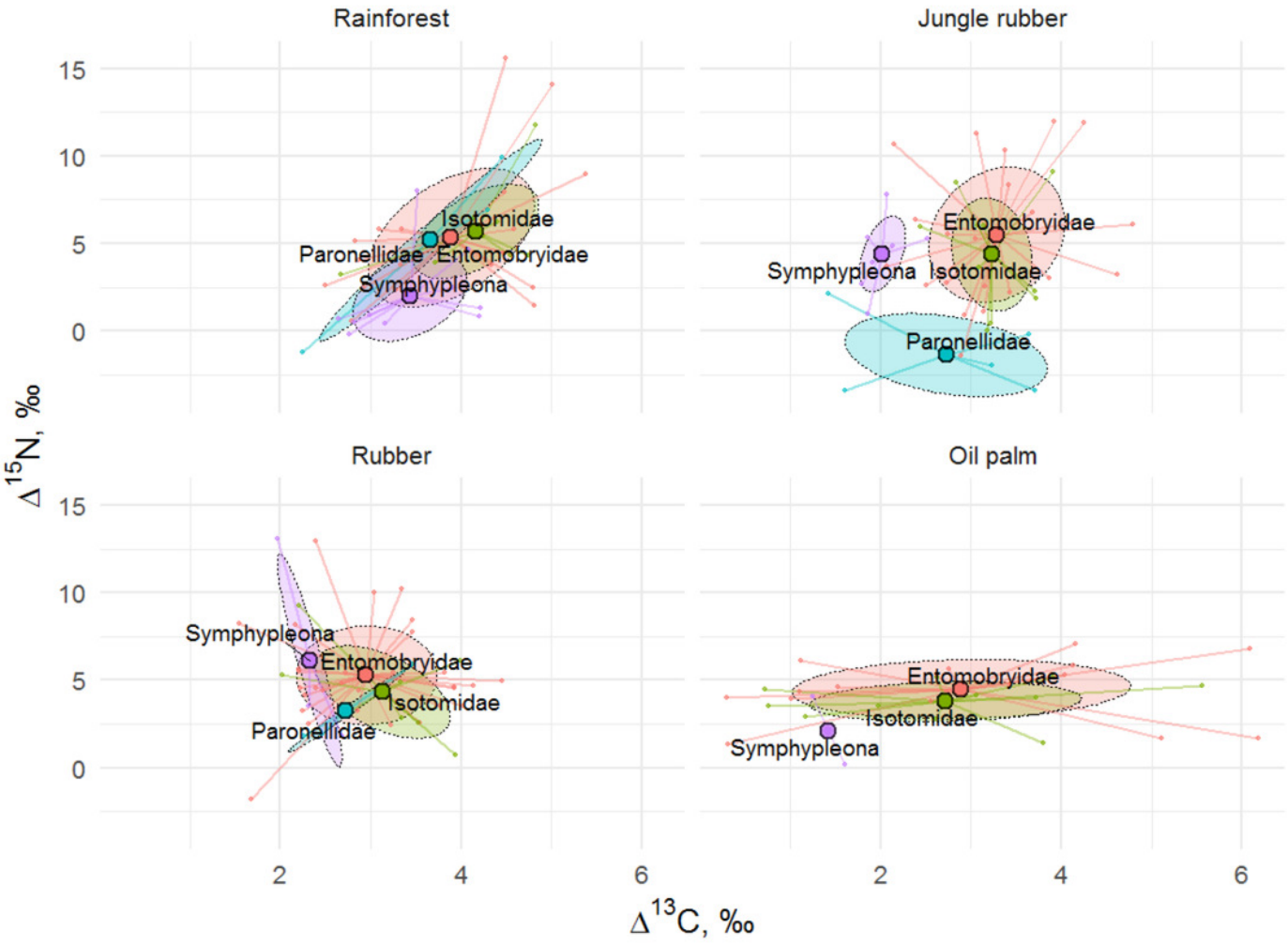


Figure 5

Stable isotope niche of Collembola families in rainforest, jungle rubber, rubber and oil palm plantations.

Stable isotope niche of Collembola families in rainforest, jungle rubber, rubber and oil palm plantations. Ellipses denote 60% intervals, different families are shown with colors (Paronellidae = blue, Isotomidae = green, Symphypleona = purple, Entomobryidae = light red; Symphypleona comprises the families Sminthuridae, Sminthirididdidae, Dycirtomidae and Katiannidae). Large colored dots represent means of land-use systems, small points represent individual measurements.