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

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Intensively managed monoculture plantations are increasingly replacing natural forests across the tropics resulting in changes in ecological niches of species and communities, and in ecosystem functioning. Collembola are among the most abundant arthropods inhabiting the belowground system sensitively responding to changes in vegetation and soil conditions. However, most studies on the response of Collembola to land-use change 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 used stable isotope analysis (^{13}C and ^{15}N) to investigate changes in the trophic structure and use of food resources by Collembola in Jambi province (Sumatra, Indonesia), a region that experienced strong deforestation in the last decades. Isotopic values of Collembola from 32 sites representing four land-use systems were analyzed (rainforest, rubber agroforest, rubber (*Hevea brasiliansis*) and oil palm (*Elaeis guineensis*) monoculture plantations). Across Collembola species Δ^{13}C values were highest in rainforest suggesting more pronounced processing of litter resources by microorganisms and consumption of these microorganisms by Collembola in this system. Lower Δ^{13}C values, but high Δ^{13}C variation in Collembola in oil palm plantations indicated that Collembola shifted towards herbivory and used more variable resources in this system. Small range in Δ^{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. This was further confirmed by generally lower isotopic niche differentiation among species in plantations. Across the studied ecosystems, atmobiotic species

(Symphypleona and Paronellidae) occupied the lowest, whereas euedaphic Collembola species occupied the highest trophic position, resembling patterns in temperate forests.

Some species of Paronellidae in rainforest and jungle rubber had Δ^{15}N values below those of leaf litter suggesting algivory (*Salina* sp.1, *Callyntrura* sp.1 and *Lepidonella* sp.1), while

a dominant species, *Pseudosinella* sp.1, had the highest Δ^{15}N values in most of the land-use systems suggesting that this species at least in part lives as predator or 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.

1   **TROPHIC NICHE DIFFERENTIATION AND UTILISATION OF FOOD RESOURCES IN**

2   **COLLEMBOLA IS ALTERED BY RAINFOREST CONVERSION TO PLANTATION**

3   **SYSTEMS**

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17   **ABSTRACT**

18   Intensively managed monoculture plantations are increasingly replacing natural forests across

19   the tropics resulting in changes in ecological niches of species and communities, and in ecosystem

20   functioning. Collembola are among the most abundant arthropods inhabiting the belowground

21   system sensitively responding to changes in vegetation and soil conditions. However, most

22   studies on the response of Collembola to land-use change were conducted in temperate

23   ecosystems and focused on shifts in community composition or morphological traits, while

24   parameters more closely linked to ecosystem functioning, such as trophic niches, received little

25   attention. Here, we used stable isotope analysis (^{13}C and ^{15}N) to investigate changes in the trophic

26   structure and use of food resources by Collembola in Jambi province (Sumatra, Indonesia), a

27   region that experienced strong deforestation in the last decades. Isotopic values of Collembola

28   from 32 sites representing four land-use systems were analyzed (rainforest, rubber agroforest,

29   rubber (*Hevea brasiliansis*) and oil palm (*Elaeis guineensis*) monoculture plantations). Across

30   Collembola species $\Delta^{13}C$ values were highest in rainforest suggesting more pronounced

31   processing of litter resources by microorganisms and consumption of these microorganisms by

32   Collembola in this system. Lower $\Delta^{13}C$ values, but high $\Delta^{13}C$ variation in Collembola in oil palm

33   plantations indicated that Collembola shifted towards herbivory and used more variable

34   resources in this system. Small range in $\Delta^{15}N$ values in Collembola species in monoculture

35   plantations in comparison to rainforest indicated that conversion of rainforest into plantations is

36   associated with simplification in the trophic structure of Collembola communities. This was

37   further confirmed by generally lower isotopic niche differentiation among species in plantations.

38   Across the studied ecosystems, atmobiotic species (Symphypleona and Paronellidae) occupied

39   the lowest, whereas euedaphic Collembola species occupied the highest trophic position,

40   resembling patterns in temperate forests. Some species of Paronellidae in rainforest and jungle

41   rubber had $\Delta^{15}N$ values below those of leaf litter suggesting algivory (*Salina* sp.1, *Callyntrura* sp.1

42   and *Lepidonella* sp.1), while a dominant species, *Pseudosinella* sp.1, had the highest $\Delta^{15}N$ values

43   in most of the land-use systems suggesting that this species at least in part lives as predator or

44   scavenger. Overall, the results suggest that rainforest conversion into plantation systems is

45   associated with marked shifts in the structure of trophic niches in soil and litter Collembola with

46   potential consequences for ecosystem functioning and food-web stability.

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

48   *springtail*

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Introduction

51

52   Agricultural intensification in Indonesia is associated with deforestation which increased

53 strongly in the last 30 years (Koh & Ghazoul, 2010 ; Gatto *et al.*, 2015). Large parts of rainforest

54 in lowland Sumatra (Indonesia) have been converted into oil palm (*Elaeis guineensis*) (16% of

55 total area) and rubber plantations (*Hevea brasiliansis*) (12%) (Gatto *et al.*, 2015). These processes

56 are driven by the high global demand for agricultural products, and positively affect income and

57 employment of local smallholders (Grass *et al.*, 2020; Qaim *et al.,* 2020). At the same time,

58 conversion of tropical rainforest into plantation systems is associated with major changes in

59 ecological niches of animal species, loss of biodiversity, and thereby with changes in ecosystem

60 functioning (Barnes *et al.*, 2014; Clough *et al.*, 2016; Fitzherbert *et al.*, 2008; Gilbert, 2012). These

61 changes affect both the above- and belowground system. Complex and diverse microbial and

62 animal communities in soil regulate important ecosystem functions and support aboveground

63 life (Bardgett & Van Der Putten, 2014), but knowledge on effects of land-use change on soil life

64 in the tropics is very limited.

65   Studies from Sumatra showed that conversion of rainforest into oil palm and rubber

66 plantations is associated with a decline in species diversity, population density, biomass and

67 energy flux in litter macroinvertebrate communities by approximately 45% (Drescher *et al.,* 2016;

68 Grass et al., 2020). Uneven decline in energy flux across size classes and trophic levels was

69 documented for meso- and macrofauna soil communities leading to strong alterations in soil

70 food-web structure (Potapov *et al.*, 2019). Different basal resources available in different land-

71 use systems result in changes in trophic niches of decomposer and predatory soil invertebrates,

72 and results in reduced abundance of primary decomposers and in soil animals shifting their

73   feeding habits towards herbivory (Klarner *et al.*, 2017; Krause *et al.*, 2019; Susanti *et al.*, 2019).

74   Land-use change may also result in reduced trophic niche differentiation among species in

75   belowground communities (Korotkevich *et al.*, 2018), but this has not been investigated in

76   tropical ecosystems.

77   Collembola are among the most abundant soil decomposer invertebrates, inhabiting

78   various organic substrates and using a wide range of food resources (Rusek, 1998). Early studies

79   on food resources of Collembola concluded that the majority of euedaphic and hemiedaphic

80   species feed unselectively on a wide variety of food materials (Hopkin, 1997). However, stable

81   isotope analysis showed pronounced trophic niche differentiation among Collembola species in

82   temperate forests (Chahartagi *et al.*, 2005). This differentiation in large has been explained by

83   the taxonomic identity and life forms of Collembola (Potapov *et al.*, 2016). Species, living

84   aboveground and on the litter surface (atmobiotic and epedaphic life forms) are mainly

85   phycophages, feeding on lichens, algae and pollen. Species, living in the litter (hemiedaphic life

86   form) are detritivores feeding on saprotrophic microorganisms and litter. Species, living in soil

87   (euedaphic life form) feed on soil organic matter, roots and fungi (Ponge, 2000; Potapov *et al.,*

88   2016). Further, food resources and trophic levels also vary among high-rank taxa with e.g.,

89   Poduromorpha occupying higher trophic positions than Entomobryomorpha and Symphypleona,

90   suggesting evolutionary selection for microbivory in the former (Potapov *et al.,* 2016). Since

91   lowland tropical forest ecosystems often have a less pronounced organic layer and different plant

92   and animal community composition than temperate forest ecosystems (Petersen and Luxton,

93   1982), they provide different ecological niches for Collembola, potentially resulting in a different

94   trophic structure of communities. To date, information on food resources and trophic niches of

95   Collembola is based on studies from temperate ecosystems, whereas information from tropical

96   ecosystems is virtually lacking entirely.

97   Over the last two decades, stable isotope analysis has become the most commonly used

98   tool to assess trophic niches of soil animals (Potapov *et al.,* 2019). Two isotopic ratios, $^{13}C/^{12}C$

99   (i.e., $\delta^{13}C$ values) and $^{15}N/^{14}N$ (i.e., $\delta^{15}N$ values), typically are used in food-web studies. Trophic

100   positions and length of trophic chains can be assessed using $\delta^{15}N$ values, whereas the range of

101   $\delta^{13}C$ values reflects variability in the use of basal resources (Potapov *et al.*, 2019). Stable isotope

102   composition of consumers follows that in food resources, thus allowing to reveal potential diet

103   switching with land-use change (Klarner *et al.,* 2017; Krause *et al.,* 2019; Susanti *et al.*, 2019).

104   Here, we use stable isotope analysis to investigate trophic positions and food resources

105   of soil and litter Collembola in four different land-use systems in Sumatra, Indonesia: rainforest,

106   rubber agroforest ('jungle rubber'), and monoculture rubber and oil palm plantations. The study

107   aimed at investigating how trophic positions and food resources of Collembola change after

108   rainforest conversion into agricultural plantations, such as rubber and oil palm, and, for the first

109   time, at exploring patterns in trophic niche differentiation among tropical Collembola species. In

110   more detail we investigated the following hypotheses:

111   1) Analogous to other soil invertebrates, Collembola shift their trophic niches towards

112   herbivory in plantation systems in comparison to rainforest.

113   2) Due to reduced food resources (poor litter layer), the trophic niche width of

114   Collembola is narrower in plantations in comparison to rainforest.

115   3) Trophic niche differentiation among Collembola species is more pronounced in

116   rainforest than in plantation systems.

117   4) Trophic niche differentiation among families and life forms of Collembola in tropical

118   ecosystems follows similar patterns as in ecosystems of the temperate zone.

119

120   **Material and Methods**

121   **Site description**

122   Four land-use systems were investigated: lowland rainforest, jungle rubber, rubber and

123   oil palm plantations, located in Jambi province, southwest Sumatra, Indonesia. The study sites

124   were located at a similar altitude varying between 50 and 100 m a.s.l. in two landscapes, the

125   Harapan and Bukit Dua Belas landscape; each land-use system was replicated four times per

126   landscape, resulting in a total of 32 sites (for more details see Drescher *et al.*, 2016). Lowland

127   rainforest was used as reference, but represents secondary rainforest, which has been logged

128   once by taking out large trees some 30 years ago. Jungle rubber represents a rubber agroforest

129   system originating from rainforest enriched with rubber trees; the age of rubber trees varied

130   between 15-40 years (Kotowska, Leuschner, Triadiati, Meriem, & Hertel, 2015). Rubber and oil

131   palm plantations were intensively managed monocultures of an average age of 7 to 16 and 8 to

132   15 years, respectively (Drescher e*t al.*, 2016), and were established after logging, clearing, and

133   burning of either rainforest or jungle rubber. Soils at the Harapan landscape are loam Acrisols of

134   low fertility, whereas in Bukit Dua Belas the major soil type is clay Acrisol (Allen *et al*., 2015;

135   Kotowska *et al.,* 2015). Management practices in these smallholder monoculture plantations are

136   described in more detail in Allen *et al.* (2015). Oil palm plantations typically were fertilized once

137   in the rainy season and once in the dry season. Typically, 300-500 kg NPK complete fertilizer, 300

138   kg KCl and 138 kg urea ($CO(NH_2)_2$) were added per hectare and year. Rubber and oil palm

139   plantations were weeded manually or chemically throughout the year. The most commonly used

140   herbicides were paraquat and glyphosate; these were applied at an average rate of 2 to 5 L ha^{-1}

141   y^{-1} *(Allen et al.*, 2015; Clough *et al.*, 2016; Kotowska *et al.,* 2015).

142

143   **Sampling procedure**

144   Samples were taken in October 2013 in three 5 x 5 m subplots within 50 x 50 m plots

145   established at each study site (Drescher *et al.,* 2016). In each subplot soil samples of 16 x 16 cm

146   were taken including the litter layer and the underlying top soil to a depth of 5 cm. Animals from

147   both layers were pooled for stable isotope analysis to obtain sufficient amount of animal tissue

148   for the analyses. Animals were extracted by heat (Kempson *et al.*, 1963) until the substrate was

149   completely dry (6-8 days) using glycerol : water mixture at a ratio of 1 : 1 as collection solution.

150   Field collection was conducted under the research permit No. 389/SIP/FRP/SM/X/2013 issued by

151   the State Ministry of Research and Technology of Indonesia (RISTEK) with collection permit No.

152   S.07/KKH-2/2013 issued by the Ministry of Forestry (PHKA) and support from the following

153   persons and organizations who granting us to access and use their properties: village leaders,

154   local plot owners, PT Humusindo, PT Perkebunan Nusantara VI, Harapan Rainforest, and Bukit

155   Duabelas National Park.

156

157   **Species identification**

158   Collembola were sorted in Petri dishes using a dissecting microscope. For species-level

159   identification, selected individuals were subsequently cleared in Nesbitt solution and mounted

160   on slides with Hoyer solution. Collembola were identified under a compound light microscope at

161   400× magnification. The checklist and keys for Indonesian Collembola by Suhardjono *et al.* (2012)

162   were used along with publications on Southeast Asian Collembola. Due to a relatively poorly

163   described fauna, in many cases we had to assign individuals to morphospecies without Linnaean

164   names (in total 72% of all identified species); for simplicity, we refer to both as 'species'. When

165   possible, juvenile specimens were ascribed to species of adults or subadults present in the same

166   sample or in samples from the same plot. After identification, all data on Collembola species and

167   their   identification   characters   were   uploaded   to   Ecotaxonomy   database

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

169

170   **Bulk stable isotope analyses**

171   Stable isotope ratios were- measured from dominant species representing at least 70% of the

172   individuals on each plot (Supplementary Table S1). A number of rare species were observed only

173   on few sites and such data would be not suitable for a proper analysis of the species and land-

174   use effects and also for analytical facilities in the laboratory. Dominant species were chosen for

175   each plot separately to represent the local 'functional community'. This selection procedure

176   resulted in a total of 30 out of 56 species being included in the analysis across all land-use

177   systems. For stable isotope measurements appropriate amounts of animal tissue (ranging from

178   0.003 to 1.268 mg) were transferred into tin capsules and dried at 60°C for 24 h, weighed and

179   stored in a desiccator until analysis. Stable isotope ratios, and total C and N concentration were

180   determined using a coupled system consisting of an elemental analyzer (Eurovector, Milano,

181   Italy) equipped with a Blisotec autosampler (Blisotec, Jülich, Germany) and a Thermo Delta Vplus

182   isotope ratio mass spectrometer connected via a Conflo IV interface (both from Thermo Fisher

183   Scientific, Bremen, Germany) located at the Centre for Stable Isotope Research and Analysis,

184   Göttingen, Germany (Langel & Dyckmans, 2014). Isotope signatures were expressed using the δ

185   notation as $\delta X(‰) = (R_{sample} – R_{standard})/R_{standard}$, with X representing the target isotope and R the

186   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

187   air and Vienna Pee Dee Belemnite served as standards, respectively. We use IAEA CH6 (-10.43‰,

188   Sucrose) and IAEA 600 (-27.7‰, Caffein) as C standards, and IAEA N1 (0.4‰) and IAEA N2

189   (20.3‰) for N (both are Ammonium sulfates) for internal calibration.

190

191

192   **Statistical analysis**

193   To compensate for inter-site variation in the isotopic baseline, prior to the analysis all data were

194   normalized to the local leaf litter using the following equations (Potapov *et al.*, 2019):

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

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

197   Stable isotope values of litter were taken from Klarner *et al.* (2017) who investigated the same

198   sampling sites.

199   Statistical analyses were performed using R v 3.5.2 (R Core Team, 2018) with R studio

200   interface (R Studio, Inc.). First, we analyzed the effect of land-use system on the isotopic

201   composition of Collembola at the community level. Effects of land-use system on the $\Delta^{13}C$ and

202 $\Delta^{15}N$ values of all measured Collembola individuals were tested using Linear Mixed Effect Models

203 (LMM) with species identity as random effect. Species identity was coded as random effect for

204 the following reasons: (1) In this first analysis we were not interested in variations in $\Delta^{13}C$ and

205 $\Delta^{15}N$ values among species but still wanted to account for it, (2) species presence was uneven

206 across plots and land-use systems preventing the analysis of land-use effects, and (3) including

207 species as fixed factor would have compromised the analysis of land-use effects on $\Delta^{13}C$ and $\Delta^{15}N$

208 values of Collembola by reducing error degrees of freedom. The analysis was conducted using

209 the *lmer* function in the *lme4* package (Bates *et al.*, 2015). Significance of fixed effects (factors)

210 was tested using the *Anova* function in the *car* package. Significant differences in stable isotope

211 values between land-use systems were tested using the *tukey te*st in the *emmeans* and

212 *multicomp* packages. We also analyzed the effect of land use only for one dominant species,

213 present in sufficient replicates in each land-use system (*Pseudosinella* sp.1) using analysis of

214 variance implemented in the *aov* function. Additionally, the ranges in $\Delta^{13}C$ and $\Delta^{15}N$ values in

215 each land-use system were calculated as difference between minimum and maximum values and

216 visualized using the Kernel density estimation in the *ggplot 2* package using the *geom_violin*

217 function.

218   Second, we assessed trophic niche differentiation among species by assessing the effect

219 of species identity on stable isotope composition of Collembola with LMM. We used species

220 identity as factor and either $\Delta^{13}C$ or $\Delta^{15}N$ values as response variables; sampling plot was included

221 as random effect to account for site-specific differences in trophic niches. The analysis was done

222 separately for each land-use system (eight analyses in total). Only species allowing more than

223 three measurements per land-use system were included.

224   Third, we analyzed the effects of family identity and life form on stable isotope

225   composition of Collembola using LMM. Here, we used both plot and land-use system as random

226   effects. Significant differences between families and life forms were tested using Tukey contrasts

227   as implemented in the *glth* function in the *multicomp* package. To display the isotopic niche space

228   of Collembola species, family, and lifeform, ellipses denoting 60% intervals were plotted using

229   the *standard.ellipse* function in the *siar* package, and visualized using the *ggplot* and *ggrepel*

230   packages. We also analyzed interactions between land-use system and life form and between

231   land-use system and family with plot as random effect. In the analyses, we excluded Neanuridae

232   and Onychiuridae as they were only represented by a single species not present in each of the

233   land-use systems. In addition, we also analyzed R square values between species, family, and

234   lifeform to identify the most important factor. Here, we used plot as random effect The analysis

235   was done using the *r.squaredGLMM* function in the *lme4* and *MuMin* packages.

236

237   **Results**

238   *Community-level changes with land use*

239   In rainforest Δ^{13}C values of Collembola ranged between 1.5 and 6.0‰ (total range 4.5‰),

240   and in oil palm plantations between -1.5 and 8.5‰ (10.0‰), indicating a wider range of Δ^{13}C

241   values in food resources in the latter. In jungle rubber and rubber plantations, the range of Δ^{13}C

242   values was similar to rainforest (between 1.0 and 6.0 ‰). Mean Δ^{13}C values in rainforest were

243   significantly higher than in plantation systems ($F_{3,146}$ = 9.90, p = 0.001; Fig. 1A, Supplementary

244   Material Tables S2, S3). All δ^{13}C values of Collembola species exceeded those of leaf litter except

245   for one individual of *Isotomiella* cf. *minor* in oil palm plantations (Fig. 2; for details see

246   Supplementary Material Tables S6-S9).

247   In contrast to Δ^{13}C, the range of Δ^{15}N values was largest in rainforest (-5.0 to 19.0‰),

248   lowest in oil palm plantations (-1.0 to 8.0‰), and intermediate in rubber plantations (-5.0 to

249   15.0‰) and in jungle rubber (-7.5 to 16.0‰). Mean Δ^{15}N values of Collembola did not vary

250   significantly among land-use systems ($F_{3,153}$ = 1.46, p = 0.228; Fig. 1B, Supplementary Material

251   Tables S4, S5). Stable isotope values of the most abundant Collembola species present in all land-

252   use systems, *Pseudosinella* sp.1, did not vary significantly among land-use systems both in Δ^{13}C

253   ($F_{3,21}$ = 1.44, p = 0.260) and Δ^{15}N ($F_{3,21}$ = 0.88, p = 0.467).

254

255   *Niche differentiation among species*

256   Δ^{13}C values across abundant species (represented by at least three measurements, see

257   Methods) varied significantly in rainforest ($F_{4,12}$ = 6.34, p = 0.005) and jungle rubber ($F_{5,17}$ = 3.67,

258   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 =

259   0.370). In rainforest, Δ^{13}C values of *Pseudosinella* sp.1 were highest and differed significantly

260   from those of *Lepidocyrtus* sp.1 and *Pararrhopalites* sp.1, whereas in jungle rubber they were

261   highest in *Homidia cingula* and differed significantly from *Callyntrura* sp.1.

262   Δ^{15}N values across abundant species varied significantly in rainforest ($F_{4,14}$ = 5.00, p =

263   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

264   not in rubber plantations ($F_{5,19}$ = 2.43, p = 0.072) (Fig. 3; for details see Supplementary Material

265   Tables S10-S13). In rainforest *Pseudosinella* sp.1 occupied the highest trophic position, followed

266   by *Isotomiella* cf. *minor*, whereas *Allacma* sp.1 occupied the lowest trophic position. Similar to

267   rainforest, in jungle rubber *Pseudosinella* sp.1 also occupied the highest trophic position, but

268    $\Delta^{15}N$ values were lowest in *Callyntrura* sp.1. Overall, *Pseudosinella* sp.1, the most dominant

269   species, occupied the highest trophic position across all species. Across all samples analyzed (20

270   species in rainforest, 17 species jungle rubber, 15 species in rubber plantations, and 13 species

271   in oil palm plantations) 3% of the measurements had $\Delta^{15}N$ values below that of litter (see

272   Supplementary Material, Fig. 1).

273

274   *Differences among Collembola life forms and families*

275   The $\Delta^{15}N$ values of Collembola varied among life forms ($F_{24,126}$ = 1.82, p = 0.018), but this was not

276   the case for $\Delta^{13}C$ values ($F_{24,126}$ = 1.19, p = 0.260), with the interaction between lifeform and land-

277   use system neither being significant for $\Delta^{15}N$ ($F_{9,132}$ = 0.87, p = 0.556) nor for $\Delta^{13}C$ ($F_{9,135}$ = 0.79,

278   p = 0.619). Differences between life forms were more pronounced in rainforest and jungle rubber

279   and less in rubber and oil palm plantations (Fig. 4). Euedaphic species were generally most

280   enriched in ^{15}N, whereas atmobiotic species on average occupied the lowest trophic position

281   (except in rubber plantations), often having $\Delta^{15}N$ values below 5.0‰, with epedaphic and

282   hemiedaphic species being intermediate.

283   Similar to results of the life form analysis, the $\Delta^{15}N$ ($F_{24,129}$ = 2.19, p = 0.002) but not $\Delta^{13}C$

284   values ($F_{24,128}$ = 1.01, p = 0.470) of Collembola varied significantly among families (Fig. 5), with the

285   interaction between family and land-use system neither being significant for $\Delta^{15}N$ ($F_{8,122}$ = 0.34,

286   p = 0.945) nor for $\Delta^{13}C$ ($F_{8,121}$ = 1.84, p = 0.075). Isotomidae and Entomobryidae occupied the

287   highest trophic positions across land-use systems, Symphypleona occupied the lowest trophic

288   position in rainforest and oil palm plantations, whereas in jungle rubber and rubber plantations

289   the lowest trophic position was occupied by Paronellidae. Family and lifeform identity explained

290   approximately two times less variation in Δ^{15}N values than species identity with R^2 = 0.29 in

291   models based on species, and R^2 = 0.13 in both models based on families and life forms.

292

293   **Discussion**

294   *Variations in trophic niches with land-use system*

295   Results of our study indicate that rainforest conversion into agricultural plantations is

296   associated with changes in basal resources (Δ^{13}C values) of Collembola, but does not significantly

297   affect their average trophic positions (Δ^{15}N values). These findings are in line with the results of

298   the study of Krause *et al.* (2019) investigating oribatid mites at the same study sites and showing

299   that the shift in trophic niches to be mainly due to changes in the use of basal resources rather

300   than trophic levels. Similar to previous studies on centipedes, oribatid mites and other soil animal

301   taxa (Klarner *et al.,* 2017; Susanti *et al.,* 2019; Krause e*t al.*, 2019), we also found the conversion

302   of rainforest into plantations to be associated in Collembola with a shift from detritivory towards

303   herbivory (i.e., lower ^{13}C enrichment). In rainforest and jungle rubber, δ^{13}C values of Collembola

304   were 2.0-5.0‰ higher compared to leaf litter, which resembles the shift observed in temperate

305   forest ecosystems (Pollierer *et al.,* 2009). This "detrital shift" in δ^{13}C (Potapov *et al.,* 2019)

306   presumably is due to acquiring C from saprotrophic fungi and bacteria (Potapov *et al.*, 2013) that

307   preferentially use ^{13}C-rich plant compounds (Pollierer *et al.,* 2009). High ^{13}C enrichment in most

308   of the studied Collembola species in more natural ecosystems (rainforest and jungle rubber)

309   suggests that they predominantly rely on microorganisms decomposing organic matter rather

310   than on fresh plant material as food source (Potapov *et al.,* 2019). Overall, similar enrichment in

311   ^{13}C and ^{15}N in Collembola in temperate and tropical ecosystems suggest that Collembola rely little

312   on fresh plant material or mycorrhizal fungi in both, and this may well apply to soil food webs in

313   general.

314   As indicated by Δ^{13}C values, Collembola species in oil palm plantations used food

315   resources of a wide range of ^{13}C values, which was not the case in the other land-use systems

316   studied. Variations in ^{13}C values of food resources in oil palm plantations may be attributed to

317   the variety of management practices of the smallholder systems studied (Clough *et al.*, 2016).

318   Potentially, variations in organic inputs due to differences in weeding, herbicide, and fertilization

319   practices, resulted in an overestimation of the trophic niche width in oil palm plantations

320   The narrow range of Δ^{15}N values in oil palm plantations suggests similar trophic positions

321   of Collembola species in this land-use system. Notably, the narrow range was due to both the

322   lack of high trophic level (predators, scavengers) and low trophic level species (primary

323   decomposers, specialized lichen feeders). This may reflect the dominance of generalist species in

324   the disturbed habitat of oil palm plantations (Korotkevich *et al.*, 2018). Nematode communities

325   also indicated oil palm plantations to be the most disturbed of the four land-use systems studied

326   (Krashevska *et al.,* 2019). Further, Klarner *et al.* (2017) found Δ^{15}N values of centipede species to

327   be lower in oil palm compared to jungle rubber and rubber plantations suggesting that trophic

328   chains in oil palm plantations are shorter than in the other land-use systems studied. Overall,

329   these findings suggest that the structure of soil food-webs in monoculture plantations, especially

330   oil palm, is simplified due to reduced number of trophic levels.

331   The most dominant Collembola species at our study sites, *Pseudosinella* sp.1, occupied a

332   similar trophic niche in each of the land-use systems studied, suggesting that its diet changes

333   little with the conversion of rainforest into plantation systems. *Pseudosinella* sp.1 colonized both

334   litter and soil, and, as indicated by $\Delta^{15}N$ values, occupied the highest trophic position among all

335   Collembola species studied. High $\Delta^{15}N$ values suggest that this species may either feed on

336   mycrorrhizal fungi, which are enriched in ^{15}N (Hobbie *et al.*, 2001; Potapov & Tiunov, 2016), and

337   / or live as predators feeding e.g., on nematodes, which are similarly abundant across the land-

338   use systems studied (Krashevska *et al.*, 2019). Conversion of rainforest may have less affected

339   the mineral soil- and root-based resources than litter resources, and this may explain the high

340   abundance of euedaphic *Pseudosinella* sp.1 in plantations. Similarly, Krause *et al.* (2019*)* found

341   the trophic niche of dominant species of oribatid mites to change little with the conversion of

342   rainforest into plantations. This suggests that trophic niches of certain species may be little

343   affected by land-use change despite strong changes in the overall food-web structure.

344

345   *Trophic differentiation among species*

346   Variations in $\Delta^{13}C$ values among Collembola species were more pronounced in rainforest

347   and jungle rubber than in rubber and oil palm plantations. Korotkevich *et al.* (2018) also found

348   the interspecific (in contrast to intraspecific) variation in trophic niches of Collembola to be higher

349   in natural (forest and meadows) than in disturbed habitats (pastures and lawns). Among the

350   Collembola species studied $\Delta^{13}C$ values of *Pseudosinella* sp.1 in rainforest, and *Callyntrura* sp.1

351   and *Sphyroteca* sp.1 in jungle rubber differed significantly from those of other Collembola species

352 indicating that these species are able to exploit resources not available to the other Collembola

353 species in the respective land-use system.

354   Similar to $\Delta^{13}C$ values, Collembola species in each land-use system, except rubber

355 plantations, also differed in $\Delta^{15}N$ values. In jungle rubber *Callyntrura* sp.1 was most depleted in

356 $\delta^{15}N$ among the studied Collembola species indicating that this species occupied the lowest

357 trophic position pointing to phycophagy (Potapov *et al.,* 2018). In rainforest *Pseudosinella* sp.1

358 had the highest $\delta^{15}N$ values followed by *Isotomiella* cf. *minor* and *Acrocyrtus* sp. suggesting that

359 these species are as microbivores in undisturbed ecosystems. Overall, based on $\Delta^{13}C$ and $\Delta^{15}N$

360 values, trophic niche differentiation among species was most pronounced in rainforest,

361 presumably due to the availability of a wider spectrum of food resources and more stable

362 environmental conditions than in plantations. This is likely to result in more efficient food-web

363 functioning in natural ecosystems due to species complementarity (Loreau and Hector 2001),

364 which is partly lost in plantation systems.

365

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

367   Collembola taxa such as Symphypleona and Paronellidae typically had low $\Delta^{15}N$ values,

368 indicating that these taxa feed on algae or lichens (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2018).

369 Symphypleona as well as Paronellidae are well adapted to aboveground life, both are large-sized

370 and possess well-developed visual systems. Such 'atmobiotic' Collembola have been assumed to

371 live at least in part as herbivores on vascular plants or algae (Rusek, 2007). This suggestion is in

372 line with studies from temperate forests investigating variations in stable isotope ratios in

373   Symphypleona (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2016). Paronellidae predominantly occur

374   in tropical regions also living above the ground suggesting that the microhabitat they live in

375   defines feeding preferences of Collembola across different phylogenetic lineages (see life form

376   discussion below). Entomobryidae and Isotomidae occupied high trophic positions and this also

377   is consistent with earlier studies based on variations in stable isotope ratios suggesting that they

378   predominantly feed on microorganisms colonizing decomposing litter materials (Chahartaghi *et*

379   *al.*, 2005; Potapov *et al.*, 2016). Some species of these two families occupied very high trophic

380   positions resembling those of Onychiuridae and Neanuridae in temperate ecosystems suggesting

381   that at least in part they live as predators or scavengers, presumably including nematodes as prey

382   (Heidemann *et al.*, 2014). Since Onychiuridae and Neanuridae were rare at our study sites,

383   species from other families might have been able to occupy their trophic niches.

384   Trophic niches of Collembola in our study varied with life form as shown previously for

385   temperate ecosystems (Ponge, 2000; Potapov *et al.*, 2016). Conform to the patterns in

386   Collembola families, the results suggest that atmobiotic and epedaphic species occupied the

387   lowest trophic position across land-use systems, whereas euedaphic species such as

388   *Pseudosinella* sp.1 occupied the highest trophic position. This is in line with the results of the

389   study of Potapov *et al*. (2016) indicating that species inhabiting deeper soil layers (hemiedaphic

390   and euedaphic) are more enriched in ^{15}N than those living in litter and above the ground

391   (epedaphic and atmobiotic). High δ^{15}N values may result from feeding on ectomycorrhizal fungi

392   which are enriched in ^{15}N (see above; Hobbie et al., 2001; Potapov and Tiunov, 2016), however,

393   this unlikely applies to tropical forests where trees predominantly form mutualistic interactions

394   with arbuscular mycorrhizal fungi. We attributed low δ^{15}N values in epedaphic and atmobiotic

395   Collembola to algae or lichen feeding, which is widespread in Collembola in temperate forests

396   (Potapov et al., 2018), but in our study only few species had δ^{15}N values below those of litter.

397   This contradicts results based on fatty acid analysis suggesting that Collembola feed more on

398   algae in tropical than in temperate ecosystems (Susanti *et al.,* 2019). To clarify the contribution

399   of algae in soil food webs in tropical and temperate ecosystems, more data on stable isotope

400   composition of various food resources in tropical forests, or direct experimentation, are needed.

401   Differences between life forms were more pronounced in rainforest and jungle rubber and less

402   in plantation systems, which may reflect the more pronounced litter layer in the former than the

403   latter (Krashevska et al. 2015). Overall, the results suggest that similar to oribatid mites (Tsurikov

404   *et al*., 2019) the trophic niche structure in Collembola communities in temperate and tropical

405   forests is generally similar and this is partly explained by 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. The use of food resources

410   shifted towards herbivory, with the range of food resources of Collembola in oil palm plantations

411   being the highest, likely due to the heterogeneity in management. By contrast, the range of

412   trophic positions in oil palm plantations was low suggesting that the trophic structure is simplified

413   lacking high but also low trophic levels. This is further supported by the less pronounced trophic

414   niche differentiation among species in monoculture plantations. Similar to the pattern in oribatid

415   mites (Tsurikov *et al.*, 2019), the structure of trophic niches in tropical Collembola communities

416   resembled that in temperate forests. Life form and family identity explained about half of the

417   species-level variation; atmobiotic species occupied the lowest and euedaphic species the

418   highest trophic position, but the difference was less pronounced in plantations. Overall, the

419   results document that changes in community composition associated with the conversion of

420   rainforest into plantation systems are followed by shifts in the trophic structure and trophic

421   niches in Collembola communities, potentially compromising ecosystem functions and food-web

422   stability in plantations.

423

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431

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543

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: (A) rainforest, (B) jungle rubber, (C) rubber and (D) oil palm plantations. Violin plots show frequency distribution of values (mirrored Kernel density estimation), all individual measurements are displayed together independent of taxonomic identity. *Average $\Delta^{13}C$ values in rainforest were significantly higher than in the other three land-use systems ($P < 0.05$)
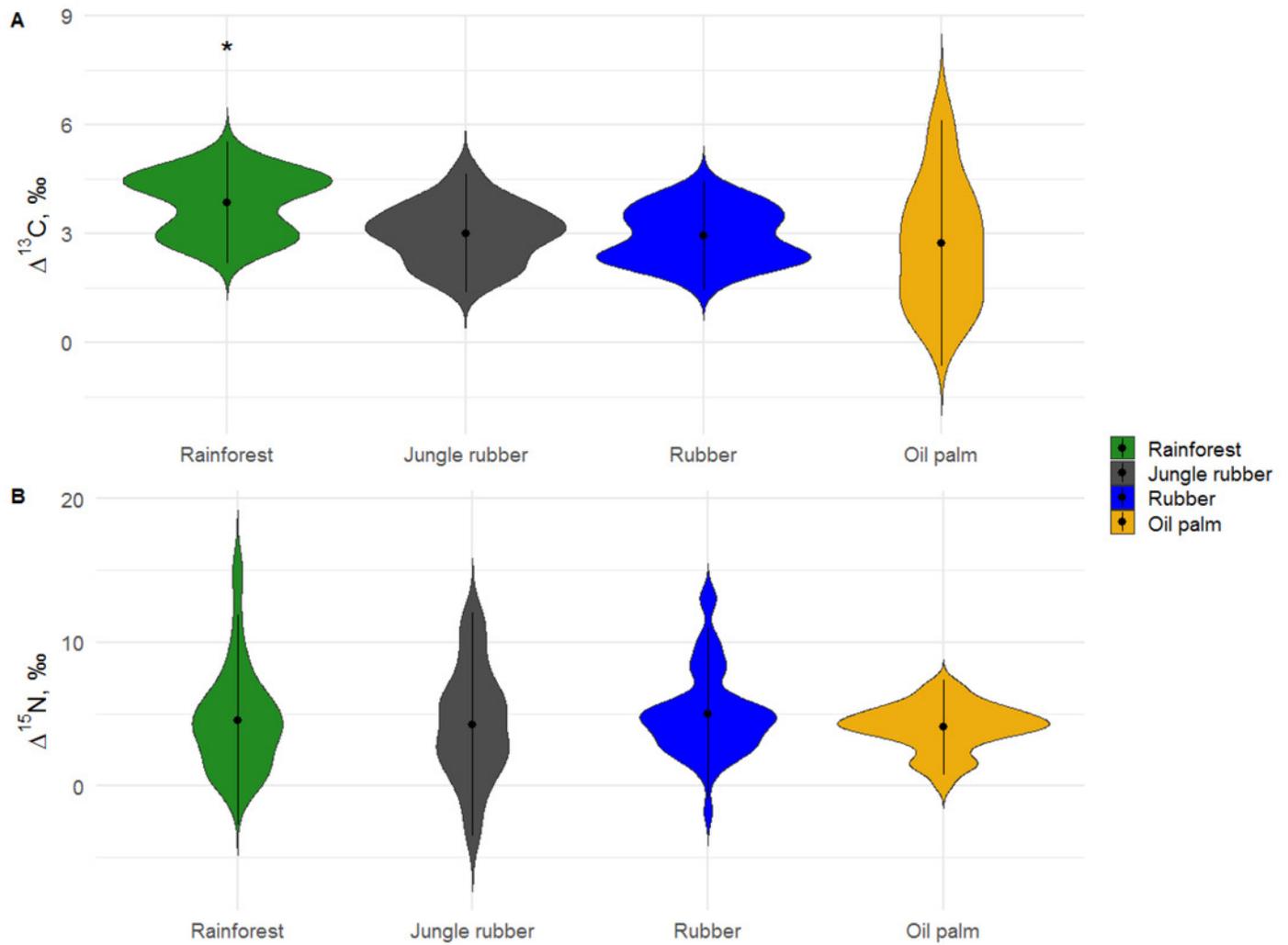
Figure 2

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

Differences of $\Delta^{13}C$ values of Collembola species in different land-use systems: (A) rainforest, (B) jungle rubber, (C) rubber and (D) 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 ($p > 0.05$)
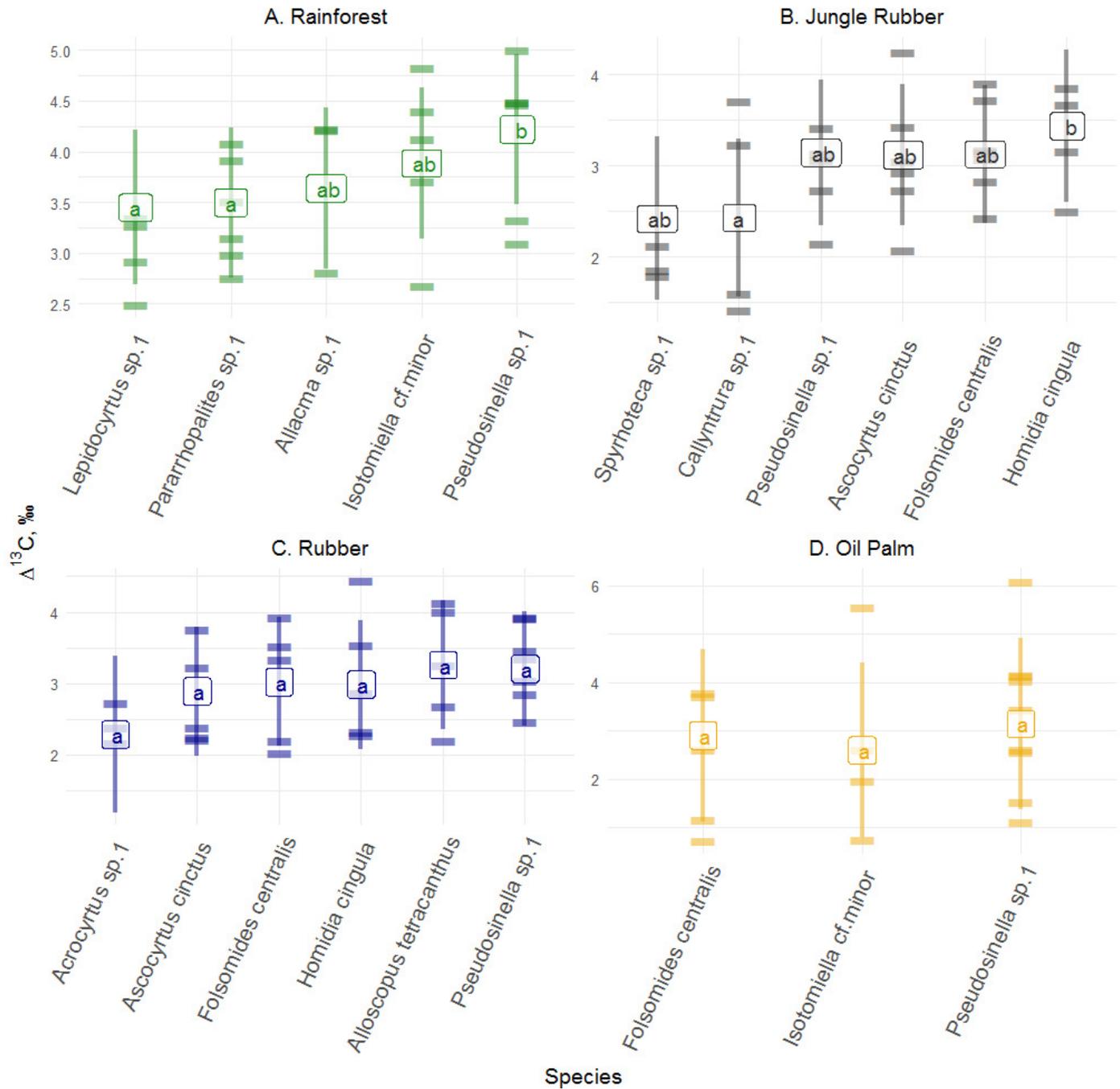
Figure 3

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

Differences of Δ^{15}N values of Collembola in different land-use systems: (A) rainforest, (B) jungle rubber, (C) rubber and (D) oil palm plantation; 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 ($p > 0.05$)

A. Rainforest

B. Jungle Rubber

C. Rubber

D. Oil Palm

Δ^{15}N, ‰

Species
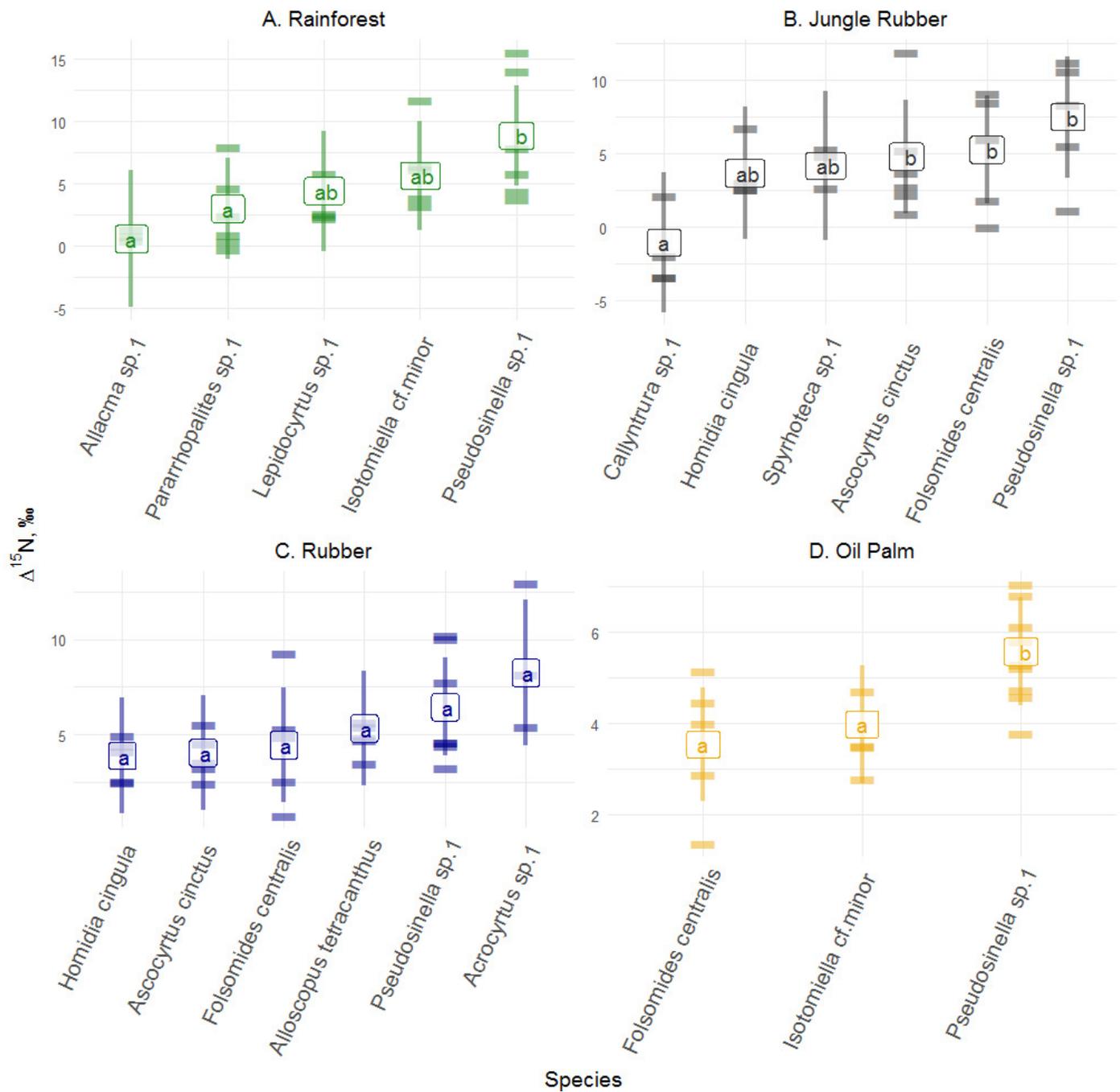
Figure 4

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 (A) rainforest, (B) jungle rubber, (C) rubber, and (D) oil palm plantations. Ellipses denote 60% confidence intervals, different life forms are shown in color (eudaphic = blue, epedaphic = grey, hemiedaphic = yellow, atmobiotic = green). Large colored dots represent means of land-use systems, small points represent individual measurements
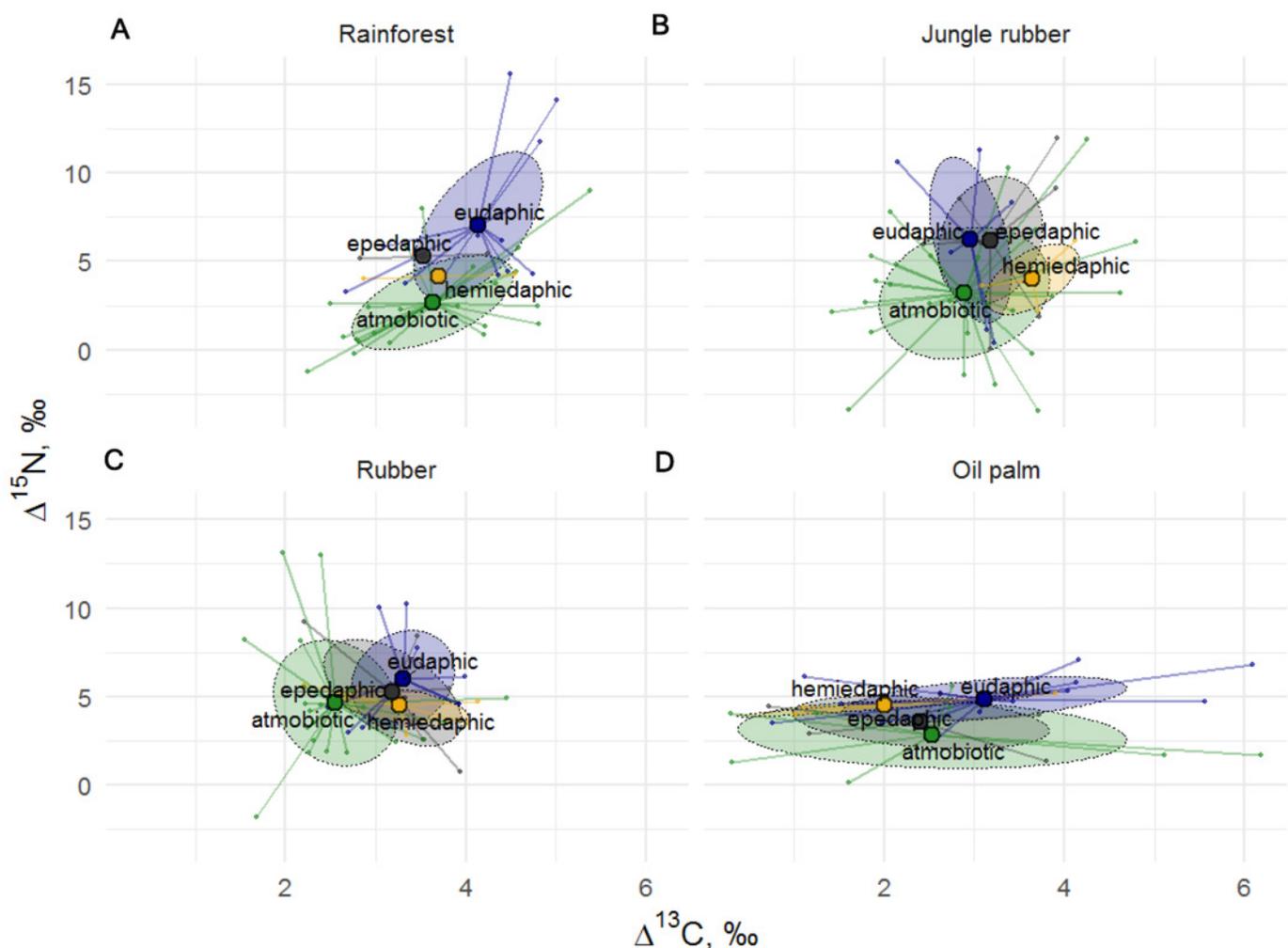
Figure 5

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

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