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

Winda Ika Susanti [Corresp., 1, 2] , **Rahayu Widyastuti** [2] , **Stefan Scheu** [1, 3] , **Anton Potapov** [1, 4]

[1] J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August Universität Göttingen, Göttingen, Germany

[2] Department of Soil Science and Land Resources, Bogor Institute of Agriculture, Bogor, Indonesia

[3] Center of Biodiversity and Sustainable Land Use, Göttingen, Germany

[4] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Rusia

Corresponding Author: Winda Ika Susanti
Email address: winda.ika-susanti@biologie.uni-goettingen.de

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 trophic structure of 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, and rubber and oil palm 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 $\Delta^{15}N$ 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 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**

5 *Winda Ika Susanti[1,2,*], Rahayu Widyastuti[2], Stefan Scheu[1,3], Anton Potapov[1,4]*

6 [1]J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August Universität Göttingen,

7 Göttingen, Germany

8 [2]Department of Soil Sciences and Land Resources, Bogor Institute of Agriculture, Bogor, Indonesia

9 [3]Centre of Biodiversity and Sustainable Land Use, Göttingen, Germany

10 [4]A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

12 Corresponding Author

13 Winda Susanti

14 Untere Karspüle 2, 37073 Goettingen, Germany

15 Email address: winda.ika-susanti@biologie.uni-goettingen.de

ABSTRACT

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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 trophic

26 structure of 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   and rubber and oil palm monoculture plantations). Across Collembola species $\Delta^{13}C$ values were

30   highest in rainforest, suggesting more pronounced processing of litter resources by

31   microorganisms and consumption of these microorganisms by Collembola in this system. Lower

32     $\Delta^{13}C$ values, but high $\Delta^{13}C$ variation in Collembola in oil palm plantations indicated that

33   Collembola shifted towards herbivory and used more variable resources in this system. Small

34   range in $\Delta^{15}N$ values in Collembola species in monoculture plantations in comparison to

35   rainforest indicated that conversion of rainforest into plantations is associated with simplification

36   in the trophic structure of Collembola communities. This was further confirmed by generally

37   lower isotopic niche differentiation among species in plantations. Across the studied ecosystems,

38   atmobiotic species (Symphypleona and Paronellidae) occupied the lowest, whereas euedaphic

39   Collembola species occupied the highest trophic position, resembling patterns in temperate

40   forests. Some species of Paronellidae in rainforest and jungle rubber had $\Delta^{15}N$ values below those

41   of leaf litter suggesting algivory (*Salina* sp.1, *Callyntrura* sp.1 and *Lepidonella* sp.1), while

42   *Pseudosinella* sp.1 had the highest $\Delta^{15}N$ values in most of the land-use systems suggesting that

43   this species at least in part lives as predator or scavenger. Overall, the results suggest that

44   rainforest conversion into plantation systems is associated with marked shifts in the structure of

45   trophic niches in soil and litter Collembola with potential consequences for ecosystem

46   functioning and food-web stability.

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

48   *springtail*

49

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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 (16% of total area) and rubber

55 plantations (12%) (Gatto *et al.*, 2015). These processes are driven by a high global demand for

56 agricultural products and positively affect income and employment for the local smallholders

57 (Grass *et al.*, 2020; Qaim *et al.,* 2020). At the same time, conversion of tropical rainforest into

58 plantation systems is associated with major changes in ecological niches of animal species, loss

59 of biodiversity, and thereby with changes in ecosystem functioning (Barnes *et al.*, 2014; Clough

60 *et al.*, 2016; Fitzherbert *et al.*, 2008; Gilbert, 2012). These changes affect both the above- and

61 belowground system. Complex and diverse microbial and animal communities in soil regulate

62 important ecosystem functions and support aboveground life (Bardgett & Van Der Putten, 2014),

63 but knowledge on effects of land-use change on soil life in the tropics is very limited.

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

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

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

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

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

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

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

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

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

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

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

75   tropical ecosystems.

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

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

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

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

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

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

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

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

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

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

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

87   2016). Further, food resources and trophic levels also vary among high-rank taxa with e.g.,

88   Poduromorpha occupying higher trophic positions than Entomobryomorpha and Symphypleona,

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

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

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

92   1982), they provide different ecological niches for Collembola, potentially resulting in a different

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

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

95   ecosystems is virtually lacking entirely.

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

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

98   (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

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

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

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

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

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

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

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

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

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

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

109   more detail we investigated the following hypotheses:

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

111   herbivory in plantation systems in comparison to rainforest.

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

113   Collembola is narrower in plantations in comparison to rainforest.

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

115   rainforest than in plantation systems.

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

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

118

119   **Material and Methods**

120   **Site description**

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

122   (*Hevea brasiliansis*) and oil palm (*Elaeis guineensis*) plantations, located in Jambi province,

123   southwest Sumatra, Indonesia. The study sites were located at a similar altitude varying between

124   50 and 100 m a.s.l. in two landscapes, the Harapan and Bukit Dua Belas landscape; each land-use

125   system was replicated four times per landscape, resulting in a total of 32 sites (for more details

126   see Drescher *et al.*, 2016). Lowland rainforest was used as reference, but represents secondary

127   rainforest, which has been logged once by taking out large trees some 30 years ago. Jungle rubber

128   represents a rubber agroforest system originating from rainforest enriched with rubber trees;

129   the age of rubber trees varied between 15-40 years (Kotowska, Leuschner, Triadiati, Meriem, &

130   Hertel, 2015). Rubber and oil palm plantations were intensively managed monocultures of an

131   average age of 7 to 16 and 8 to 15 years, respectively (Drescher e*t al.*, 2016), and were established

132   after logging, clearing, and burning of either rainforest or jungle rubber. Soils at the Harapan

133   landscape are loam Acrisols of low fertility, whereas in Bukit Dua Belas the major soil type is clay

134   Acrisol (Allen *et al*., 2015; Kotowska *et al.,* 2015). Management practices in these smallholder

135   monoculture plantations are described in more detail in Allen *et al.* (2015). Oil palm plantations

136   typically were fertilized once in the rainy season and once in the dry season. Typically, 300-500

137   kg NPK complete fertilizer, 300 kg KCl and 138 kg urea ($CO(NH_2)_2$) were added per hectare and

138   year. Rubber and oil palm plantations were weeded manually or chemically throughout the year.

139   The most commonly used herbicides were Gramoxone and Roundup; these were applied at an

140   average rate of 2 to 5 L ha^{-1} y^{-1} *(Allen et al., 2015; Clough et al., 2016; Kotowska et al., 2015).*

141

142   **Sampling procedure**

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

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

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

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

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

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

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

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

151   S.07/KKH-2/2013 issued by the Ministry of Forestry (PHKA). We thank the following persons and

152   organizations for granting us access to and use of their properties: village leaders, local plot

153   owners, PT Humusindo, PT Perkebunan Nusantara VI, Harapan Rainforest, and Bukit Duabelas

154   National Park.

155

156   **Species identification**

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

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

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

160   400× magnification. The checklist and keys for Indonesian Collembola by Suhardjono *et al.* (2012)

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

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

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

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

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

166   their   identification   characters   were   uploaded   to   Ecotaxonomy   database

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

168

169   **Bulk stable isotope analyses**

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

171   individuals on each plot (Supplementary Table S1). Dominant species were chosen for each plot

172   separately to represent the local 'functional community'. This selection procedure resulted in a

173   total of 30 out of 56 species being included in the analysis across all land-use systems. For stable

174   isotope measurements appropriate amounts of animal tissue (ranging from 0.003 to 1.268 mg)

175   were transferred into tin capsules and dried at 60°C for 24 h, weighed and stored in a desiccator

176   until analysis. Stable isotope ratios, and total C and N concentration were determined using a

177   coupled system consisting of an elemental analyzer (Eurovector, Milano, Italy) equipped with a

178   Blisotec autosampler (Blisotec, Jülich, Germany) and a Thermo Delta Vplus isotope ratio mass

179 spectrometer connected via a Conflo IV interface (both from Thermo Fisher Scientific, Bremen,

180 Germany) located at the Centre for Stable Isotope Research and Analysis, Göttingen, Germany

181 (Langel & Dyckmans, 2014). Isotope signatures were expressed using the δ notation as δX(‰) =

182 $(R_{sample} - R_{standard})/R_{standard}$, with X representing the target isotope and R the ratio of heavy to light

183 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 Pee Dee

184 Belemnite served as standards, respectively. We use IAEA CH6 (-10.43‰, Sucrose) and IAEA 600

185 (-27.7‰, Caffein) as C standards, and IAEA N1 (0.4‰) and IAEA N2 (20.3‰) for N (both are

186 Ammonium sulfates) for internal calibration.

187

188

189 **Statistical analysis**

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

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

192 $\Delta^{13}C = \delta^{13}C_{Collembola} - \delta^{13}C_{litter}$

193 $\Delta^{15}N = \delta^{15}N_{Collembola} - \delta^{15}N_{litter}$

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

195 sampling sites.

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

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

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

199 $\Delta^{15}N$ values of all measured Collembola individuals were tested using Linear Mixed Effect Models

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

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

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

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

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

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

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

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

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

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

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

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

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

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

214   function.

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

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

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

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

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

220   three measurements per land-use system were included.

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

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

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

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

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

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

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

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

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

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

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

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

233

234   **Results**

235   *Community-level changes with land use*

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

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

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

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

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

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

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

243   Supplementary Material Tables S6-S9).

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

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

246   15.0‰) and in jungle rubber (-7.5 to 16.0‰). Mean Δ^{15}N values of Collembola did not vary

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

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

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

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

251

252   *Niche differentiation among species*

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

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

255   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 =

256   0.370). In rainforest, Δ^{13}C values of *Pseudosinella* sp.1 were highest and differed significantly

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

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

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

260   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

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

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

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

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

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

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

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

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

269   Supplementary Material, Fig. 1).

270

271   *Differences among Collembola life forms and families*

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

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

274   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,

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

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

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

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

279   hemiedaphic species being intermediate.

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

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

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

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

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

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

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

287   approximately two times less variation in $\Delta^{15}N$ values than species identity with $R^2 = 0.29$ in

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

289

290   **Discussion**

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

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

293   associated with changes in basal resources ($\Delta^{13}C$ values) of Collembola, but does not significantly

294   affect their average trophic positions ($\Delta^{15}N$ values). These findings are in line with the results of

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

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

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

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

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

300   herbivory (i.e., lower ^{13}C enrichment). In rainforest and jungle rubber, $\delta^{13}C$ values of Collembola

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

302   forest ecosystems (Pollierer *et al.,* 2009). This "detrital shift" in $\delta^{13}C$ (Potapov *et al.,* 2019)

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

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

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

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

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

308   ^{13}C and ^{15}N in Collembola in temperate and tropical ecosystems suggest that Collembola rely little

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

310   general.

311   As indicated by $\Delta^{13}C$ values, Collembola species in oil palm plantations used food

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

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

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

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

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

317   The narrow range of $\Delta^{15}N$ values in oil palm plantations suggests similar trophic positions

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

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

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

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

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

323   (Krashevska *et al.,* 2019). Further, Klarner *et al.* (2017) found $\Delta^{15}N$ values of centipede species to

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

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

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

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

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

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

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

331   litter and soil, and, as indicated by Δ^{15}N values, occupied the highest trophic position among all

332   Collembola species studied. High Δ^{15}N values suggest that this species may either feed on

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

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

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

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

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

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

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

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

341

342   *Trophic differentiation among species*

343   Variations in Δ^{13}C values among Collembola species were more pronounced in rainforest

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

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

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

347   Collembola species studied Δ^{13}C values of *Pseudosinella* sp.1 in rainforest, and *Callyntrura* sp.1

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

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

350   species in the respective land-use system.

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

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

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

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

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

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

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

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

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

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

361   which is partly lost in plantation systems.

362

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

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

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

366   Symphypleona as well as Paronellidae are well adapted to aboveground live, both are large-sized

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

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

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

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

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

372   defines feeding preferences of Collembola across different p2hylogenetic lineages (see life form

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

402   forests is generally similar and this is partly explained by taxonomic affiliation and life form.

403

404   **Conclusion**

405   We showed that the conversion of rainforest into agricultural plantations, such as rubber and oil

406   palm, is associated with changes in trophic niches of Collembola. The use of food resources

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

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

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

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

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

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

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

414   species-level variation; atmobiotic species occupied the lowest and eudaphic species occupied

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

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

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

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

419   stability in plantations.

420

421   **Acknowledgements**

422   We thank the State Ministry of Research and Technology of Indonesia (RISTEK), the Indonesian

423   Institute of Sciences (LIPI), Ministry of Forestry (PHKA) and Restoration Ecosystem Indonesia

424   Harapan. We also thank the following persons and organizations: village leaders, local plot

425   owners, PT Humusindo, PT Perkebunan Nusantara VI, Harapan Rainforest, and Bukit Duabelas

426   National Park. We acknowledge support of the Open Access Publication Funds of the University

427   of Göttingen.

428

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Figure 1

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

Variations in Δ^{13}C and Δ^{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 Δ^{13}C values in rainforest were significantly higher than in the other three land-use systems ($P < 0.05$)
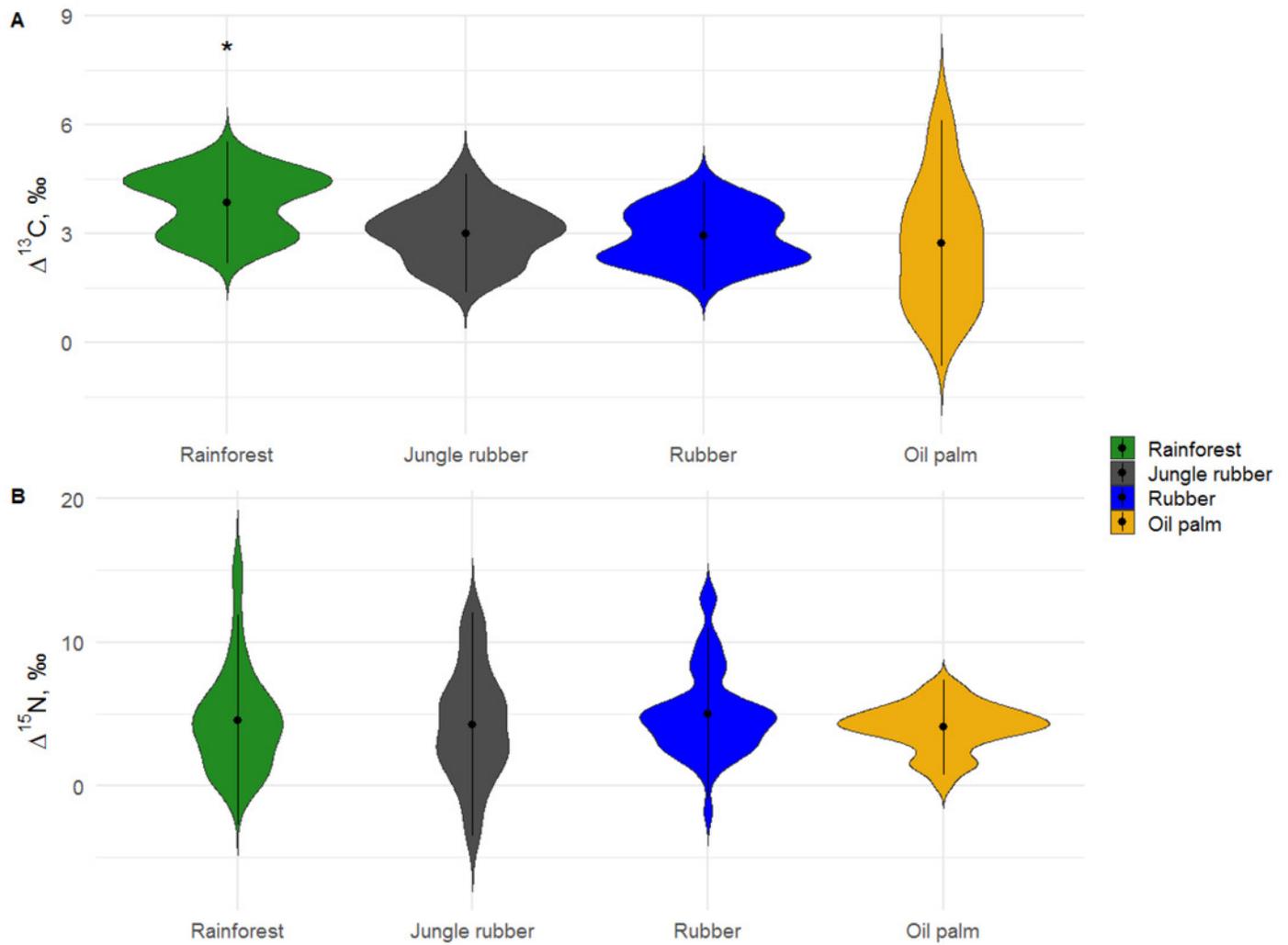
Figure 2

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

Δ^{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 ($p > 0.05$)
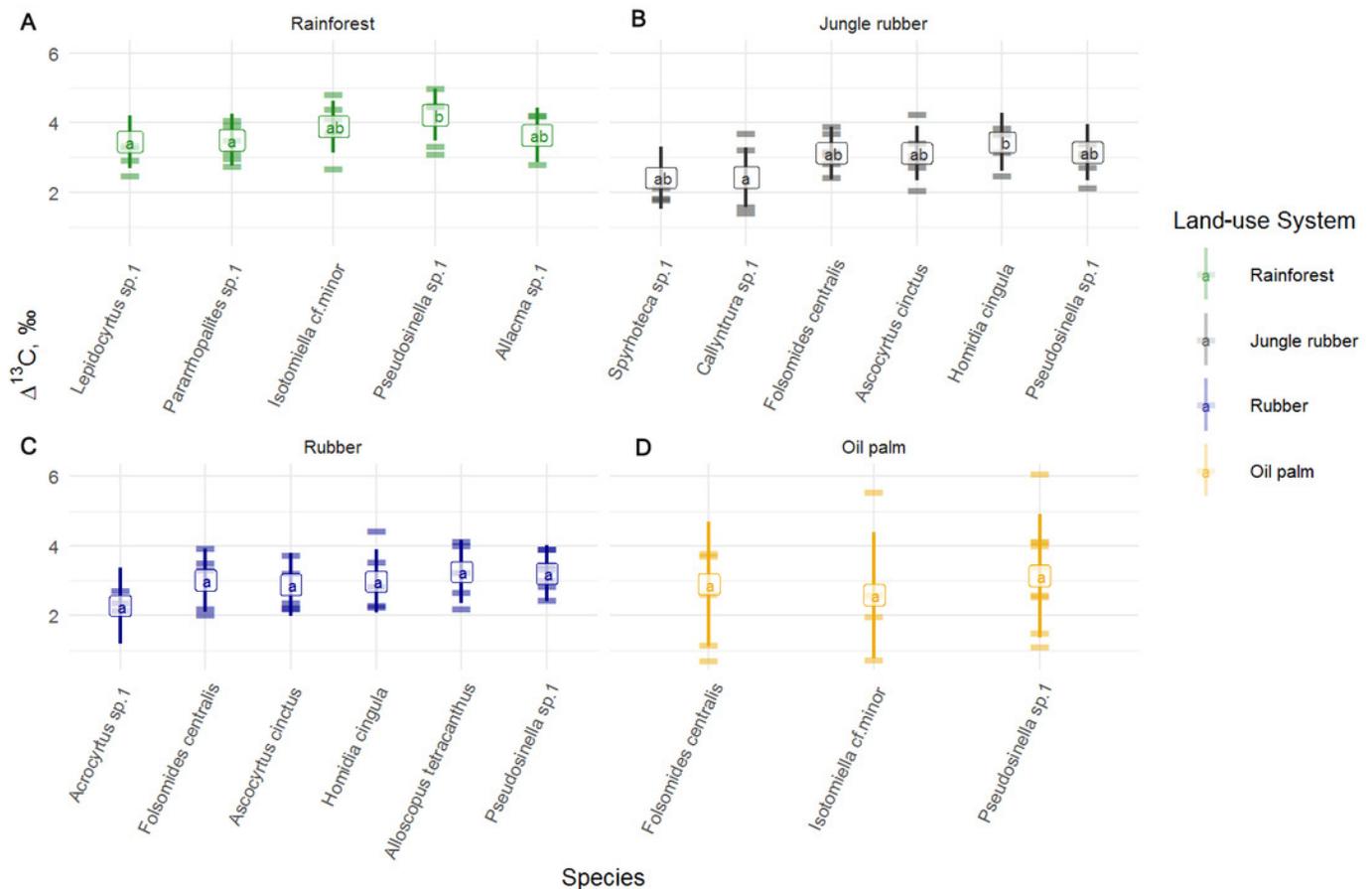
Figure 3

Differences of Δ¹⁵N 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: (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 ($p > 0.05$)
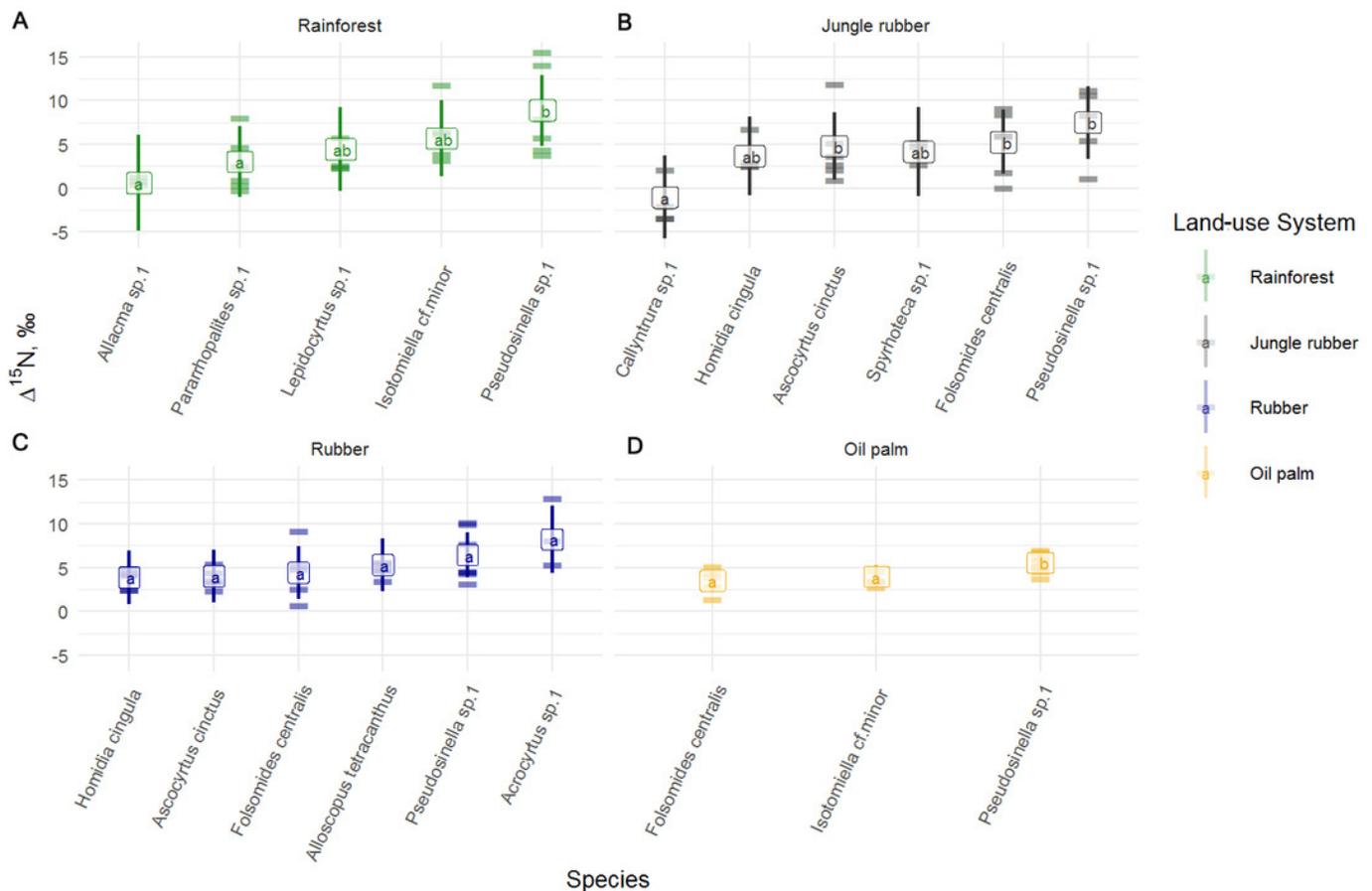
Figure 4

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
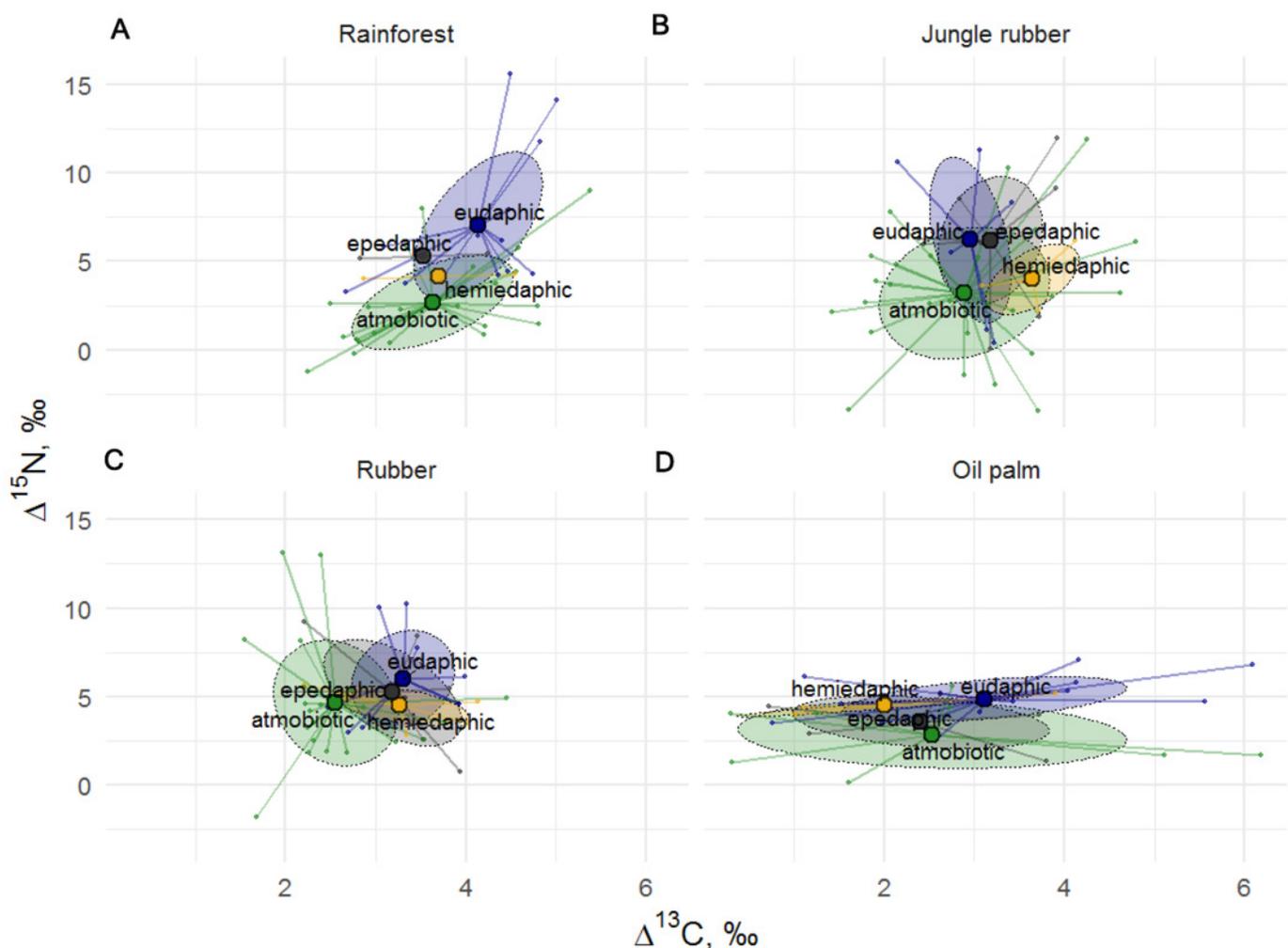
Figure 5

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