Trophic niche but not abundance of Collembola and Oribatida changes with drought and farming system

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Introduction

18 Soils in agricultural systems are not well buffered against changes in climate and therefore are

19 likely to undergo profound transformations in face of future climate change. For Central Europe,

20 the predicted climate changes include reduced precipitation during summer with consequent

21 higher frequency of summer droughts (EEA 2017; Samaniego et al. 2018). The resulting lower

22 soil moisture levels are not only relevant for the water supply of crops, but also for soil biota and

23 associated ecosystem functions, such as nutrient cycling and soil aggregate formation (Geng et

24 al. 2015; Spinoni et al. 2015; Zhang et al. 2018). Studies on the effect of drought on soil

25 microarthropods have focused on measures of diversity and abundance, and indicate either a

26 negative (Frampton et al. 2000; Blankinship et al. 2011; Karbol et al. 2011; Vestergård et al.

27 2015) or no response (Holmstrup et al. 2013; Krab et al. 2014).

28 One way to better understand the response of soil microarthropods to increased drought

29 conditions and to further connect them to processes such as nutrient cycling is to investigate

30 changes in their feeding behavior. Soil organisms interact with each other in a food web with

31 links of different strengths between the individual components (Scheu 1998; Hines et al. 2015;

32 Potapov et al. 2019). From the perspective of soil microarthropods, some of these links may be

33 particularly vulnerable to a decrease in soil moisture (Barreto et al. 2021). Bacteria and

34 nematodes, for example, need water films between soil particles to move, grow and survive

35 (Erktan et al. 2020), and thus are only available as a food resource for microarthropods at

36 sufficiently high soil moisture levels. Further, drought may reduce plant biomass and thereby

37 major basal resources of soil food webs such as leaf litter, roots and rhizodeposits (Jaleel et al.

38 2009; Scheunemann et al. 2015). Negative effects on these basal resources of soil food webs may

39 cascade up to higher trophic levels resulting in decreased abundance and changes in trophic

40 niches towards more drought-resistant resources like soil organic matter.

41 In agricultural systems trophic links are likely to vary with soil characteristics and management

42 practices. The availability of resources for microarthropods, such as soil organic matter and

43 microorganisms, differs substantially between management systems receiving organic or mineral

44 fertilizers (Mäder et al. 2002; Birkhofer et al. 2008). Organically managed fields are

45 characterized by higher abundances of microorganisms with a larger proportion of fungi

46 compared to systems receiving only mineral fertilizer (Haubert et al. 2009). These form an

47 important food resource for Collembola and Oribatida (Schneider et al. 2004; Chahartaghi et al.

48   2005; Pollierer and Scheu 2021). Such differences in resource availability are likely to change

49   the feeding behavior of microarthropods, which has been shown for several other compartments

50   of soil food webs before (Haubert et al. 2009; MacFadyen et al. 2009; Birkhofer et al. 2011).

51   However, the few studies that include Collembola and Oribatida species only documented subtle

52   or no niche shifts with changes in environmental conditions (Korotkevich et al. 2018; Krause et

53   al. 2019).

54   In this study we use stable isotope analysis to characterize trophic niches of abundant species of

55   Collembola and Oribatida in replicated plots of long-term conventional and organic farming

56   systems. The ratio of the stable isotopes of nitrogen allows insight into the trophic level of

57   consumers due to enrichment in ^{15}N in higher trophic levels, whereas the ratio of carbon stable

58   isotopes reflects the utilization of basal resources (Post 2002; Potapov et al. 2019). In previous

59   studies, stable isotope analysis has mainly been used to characterize the trophic structure of soil

60   animal communities of different habitats and to generally clarify the usage of basal resources by

61   certain taxonomic groups (Scheu and Falca 2000; Potapov et al. 2019). Only few studies

62   employed stable isotope analysis to investigate the response of the trophic structure of soil food

63   webs to different experimental treatments such as different farming systems (Haubert et al. 2009;

64   Birkhofer et al. 2011; Susanti et al. 2021) or track changes in trophic niches induced by changes

65   in environmental conditions (Birkhofer et al. 2016; Korotkevich et al. 2018; Krause et al. 2019).

66   Dry conditions were shown to increase δ^{15}N values of Oribatida in forests possibly due to trophic

67   shifts resulting from changes in microbial activity and community composition (Melguizo-Ruiz

68   et al. 2017). Further, drought is likely to increase periods of starvation due to lower availability

69   of resources that depend on high soil moisture. Starvation has been shown to increase δ^{13}C and

70   δ^{15}N values of the body tissue of animals in part as a result of metabolizing lipids, which are

71   depleted in ^{13}C (Adams and Sterner 2000; Oelbermann and Scheu 2002; Haubert et al. 2009).

72   Effects of drought on stable isotope ratios of microarthropods are likely to differ between

73   different farming systems which comprise differently structured soil food webs (Birkhofer et al.

74   2011). Additionally, a reduction in soil moisture can be buffered in organically managed fields

75   due to high soil organic carbon contents that result in more structured soils with a higher water

76   holding capacity (Lotter et al. 2003; Kundel et al. 2020). However, the interactive effects of

77   experimental drought and farming systems on the trophic behavior of microarthropods, to the

78   best of our knowledge, have not been investigated before.

79 Besides looking into mean values of stable isotope ratios of carbon and nitrogen separately, we

80 further include estimates of trophic niche sizes combining measurements of both isotopes in a

81 two-dimensional space (Bearhop et al. 2004; Jackson et al. 2011). Niche sizes are proposed to

82 become narrower in stable, deterministic environments due to more specialization (Giller 1996).

83 In line with this assumption empirical studies on trophic niches of soil animals suggest that

84 trophic niche sizes are smaller in undisturbed compared to disturbed habitats (Korotkevich et al.

85 2018). We, therefore, expected disturbances such as drought to enlarge the trophic niche of

86 Collembola and Oribatida. Likewise, regarding farming systems, we assumed that a conventional

87 system based on the input of mineral fertilizer without organic fertilizers to represent a more

88 disturbed system compared to an organically managed system receiving manure. Conditions in

89 the conventional system should hence force consumers to enlarge their trophic niche.

90 Here, we investigated the trophic niches of individual species of Collembola and Oribatida as

91 affected by experimental drought and conventional versus organic farming. We hypothesized (1)

92 trophic niches to vary among species indicating the occupation of different trophic levels and the

93 utilization of different basal resources with intraspecific differences between the conventional

94 and the organic farming system. Further, we hypothesized (2) drought to change the trophic

95 ecology of the studied microarthropod species expressed by increased $\delta^{13}C$ and $\delta^{15}N$ values of

96 individual species with this being more pronounced in conventionally compared to organically

97 managed fields. We further hypothesized that (3) trophic niche sizes are larger in the

98 experimental drought treatments and the conventional farming system as more severely disturbed

99 systems.

100

101 **Materials & Methods**

102 Study site

103 The study was performed in 2017 in the DOK trial, an agricultural long-term field experiment

104 established in 1978 comparing different organic and conventional farming systems. The DOK

105 trial is located in Therwil, Switzerland, at 300 m above sea level on a Haplic Luvisol on deep

106 deposits of alluvial loess (Fließbach et al. 2007). The mean annual temperature over the last five

107 years was 10.5 °C and the mean annual precipitation was 842 mm (Krause et al. 2020). For this

108 study we used winter wheat fields with soybean as the previous crop. The experimental fields

109 were organized in four blocks each comprising a conventionally and an organically managed

110   field (factor farming system, CONMIN and BIODYN systems of the DOK trial, respectively).

111   Conventionally managed fields received mineral fertilizer (40 – 60 kg N/ha in March, April and

112   May), herbicides (0.1 l/ha of Husar OD, Bayer, Zollikofen, Switzerland, and 1 l/ha of Mondera,

113   Switzerland, once in March), insecticides (0.1 l/ha of Audienz, Omya, Oftringen, Switzerland, in

114   May) and fungicides (1.5 l/ha Pronto Plus in April and 1 l/ha AviatorXpro and Miros FL in May;

115   all Bayer) as well as plant growth regulators (1.5 l/ha Cycocel extra, Omya, in March).

116   Organically managed fields received only organic fertilizers (farmyard manure, compost and

117   slurry), biodynamic preparations and mechanical weed control (Krause et al. 2020; Kundel et al.

118   2020). All fields were ploughed up to a depth of 20 cm and seedbed preparation was done with a

119   tooth harrow to a depth of 10 cm. In both systems 415 grains/m² were sown. All fields followed

120   the same 7-year crop rotation with soybean as the preceding crop. On each field one drought

121   treatment and one control plot were established (factor drought). We simulated drought by using

122   experimental rainout-shelters that excluded 65% of the precipitation (for details on the shelter

123   construction see Kundel et al. 2018). On the control plots, we established a similar shelter

124   construction with the difference, that it did not reduce precipitation entering the plot. Thereby,

125   we accounted for possible side effects caused by the roof construction itself (Kundel et al. 2018).

126

127   Sampling

128   Samples were taken in May, eight weeks after the establishment of the experiment, with soil

129   cores of 5 and 20 cm diameter to a depth of 10 cm in the center of the plots (n = 16).

130   Microarthropods with high densities, in our case the Collembola *Mesaphorura* sp. and Oribatida,

131   were taken from the 5 cm cores. For the other Collembola, i.e. *Isotoma caerulea, Isotomurus*

132   *maculatus* and *Orchesella villosa*, abundances in the small cores were too low to obtain enough

133   material for stable isotope measurements, so we took them from the large soil cores that were

134   initially taken to extract macrofauna. Soil animals were extracted from intact soil cores by

135   gradually increasing the temperature from 25 to 55 °C over ten days (Macfadyen 1961; Kempson

136   et al. 1963), collected into a glycol-water solution (1:1) in canisters underneath the soil coresand

137   stored in 70% ethanol. We first sorted the extracted animals to order level under a

138   stereomicroscope (Stemi 2000; Zeiss). Thereafter, Collembola and Oribatida were identified to

139   species or genus level under the microscope (Axioplan; Zeiss). As slide-mounting medium we

140   used 70% ethanol, because other commonly used solutions like lactic acid may change stable

141   isotope compositions. We used keys by Hopkin (2007), Fjellberg (1998, 2007) and Weigmann

142   (2006).

143

144   Stable isotope analysis

145   The four most abundant Collembola taxa (*I. caerulea*, *I. maculatus*, *O. villosa* and *Mesaphorura*

146   sp.) and the two most abundant oribatid mite species (*Scheloribates laevigatus* and *Tectocepheus*

147   *sarekensis*) were chosen for stable isotope analysis. To achieve at least 10 µg of animal dry

148   weight per sample we used 1 - 14 individuals per sample. To have at least three values for every

149   species x drought x farming system combination we included pseudoreplicates in plots with

150   many individuals (Table 1). Animals were weighed into tin capsules and dried at 60°C for 24 h.

151   Wheat from every plot was dried, milled and weighed into tin capsules (ca. 1 mg per sample).

152   Stable isotope analysis of animals was done with a coupled setup of an elemental analyzer

153   (Eurovector, Milano, Italy) and a mass spectrometer (Delta Vplus, Thermo Fisher Scientific,

154   Bremen, Germany) adjusted for small sample sizes (Langel and Dyckmans 2014). Stable isotope

155   analysis of wheat was done with another set of elemental analyzer and mass spectrometer (Flash

156   2000 elemental analyser coupled to a DELTA Plus XP continuous-flow IRMS via a ConFlo IV

157   interface, Thermo Fisher Scientific, Bremen, Germany). Variations in stable isotope ratios

158   including baseline correction were expressed using the delta notation with

159    $\Delta X = (R_{SAMPLE} / R_{STANDARD}) / R_{STANDARD}$ x 1000 with X representing the target isotope (^{13}C, ^{15}N),

160   and R_{SAMPLE} and $R_{STANDARD}$ the ratios of the heavy to the light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of the

161   sample and the standard, respectively. As standard for ^{13}C PeeDee Belemnite and for ^{15}N

162   atmospheric air was used (Coplen et al. 2002). Acetanilide was used for internal calibration.

163

164   Statistical analyses

165   All statistical analyses were done in R version 4.0.2 (R Development Core Team 2020).

166   We calculated mean abundances for each species. Abundance data were analyzed with linear

167   mixed effects models (LMMs) for individual species with farming system and drought as fixed

168   factors, and field as random factor using the package nlme (Pinheiro et al. 2021).

169   Stable isotope data were baseline corrected using wheat stable isotope values of the respective

170   plot and analyzed with a LMM with farming system and drought as fixed factors, and plot as

171   random factor to account for differences in sample size. Because the interaction species x

172   drought as well as species x farming system was significant (Table 2), we ran individual LMMs

173   for each species to detect species-specific effects of drought and farming system. In these models

174   we again included drought and farming system and their interaction as fixed factors, and plot as

175   random factor.

176   The size of the isotopic niches of each species in the two farming systems and in the two drought

177   treatments was calculated and visualized with the R package SIBER (Jackson et al. 2011).

178   Standard ellipse areas with a correction for small sample sizes (SEAc) based on maximum

179   likelihood were estimated and used to visualize isotopic niches of all species in the two farming

180   systems and drought treatments. To compare isotopic niche widths between farming systems and

181   drought treatments within species, Bayesian multivariate normal distributions were fitted to the

182   two levels of the factor farming system and drought, with prior settings of length, number and

183   iterations of sampling chains, and distribution parameters as recommended by Jackson (2019).

184   Based on these probability distributions Bayesian standard ellipse areas were calculated and

185   plotted using the function siberDensityPlot() including 50%, 75% and 95% credible intervals.

186   For statistical comparison of isotopic niche sizes of the farming systems and the drought

187   treatments for individual species, we compared probability distributions from the Bayesian

188   standard ellipses with 95% credible intervals.

189
190   **Results**
191   Soil characteristics

192   Water holding capacity, pH and total carbon were higher in organically compared to

193   conventionally managed fields (Supplementary Table 1). Total carbon at our study site is

194   equivalent to total organic carbon, because the soil is free of carbonates. Soil water content was

195   decreased by experimental drought by 4.23 % and was generally higher in organically compared

196   to conventionally managed fields (Supplementary Figure 1; see Meyer et al. 2021).

197
198   Abundance
199   Based on their mean abundance the six mesofauna taxa could be separated into two groups of

200   high and low abundance with abundances of the former being 23 to 73 times higher than that of

201   the latter. Highly abundant taxa included *S. laevigatus, T. sarekensis* and *Mesaphorura* sp.

202   (overall average of 7648 ± 1528, 7392 ± 1286 and 5312 ± 1734 ind. m⁻², respectively; mean ±

203   SE). Species with low abundances included *I. caerulea, I. maculatus* and *O. villosa* (106.8 ±

204   32.7, 105.0 ± 29.3 and 227.5 ± 49.8 ind. m⁻², resepectively). Generally, abundances of individual

205   species did not change significantly with drought treatment or farming system (Table 3,

206   Supplementary Figure 2).

207

208   Isotope values

209   Mean stable isotope values were significantly different between species, spanning over two δ

210   units for ^{13}C and over four δ units for ^{15}N (Figure 1, Table 2). The Δ^{13}C values of the two

211   oribatid mite species were three to four δ units higher than those of the three Collembola species.

212   Mean Δ^{15}N values spanned over four δ units with the values of *S. laevigatus* exceeding those of

213   the other species by three to four δ units.

214   The Δ^{13}C but not Δ^{15}N values differed significantly among the studied mesofauna species

215   between the drought treatments (Table 2), with this pattern being driven by a significant

216   reduction in the Δ^{13}C values of *S. laevigatus* under drought; Δ^{13}C values of the other species

217   were not significantly affected by drought (Figure 2, Table 3). By contrast, both Δ^{13}C and Δ^{15}N

218   values of mesofauna species varied significantly with farming system (significant species ×

219   farming system interaction; Table 2). In organically managed fields the Δ^{13}C value of *T.*

220   *sarekensis* and the Δ^{15}N values of *I. caerulea* and *O. villosa* significantly exceeded those in

221   conventionally managed fields (Figure 3, Table 3).

222   Drought significantly reduced the isotopic niche width of *S. laevigatus* ($P = 0.016$), *I. caerulea*

223   ($P = 0.003$) and *I. maculatus* (P = 0.032) (Figure 4), with isotopic niches of *S. laevigatus* partly

224   overlapping between the two drought treatments, whereas in *I. caerulea* and *I. maculatus* they

225   overlapped in full (Figure 5). Further, the isotopic niche space of *I. caerulea* and *I. maculatus*

226   was significantly smaller in organically compared to conventionally managed fields, with

227   isotopic niches of *I. caerulea* partly overlapping between the two farming systems, whereas

228   those of *I. maculatus* overlapped in full (Figure 6).

229
230   **Discussion**

231   The species studied were selected based on two criteria: sufficiently high abundance combined

232   with sufficiently high biomass for stable isotope analyses, and therefore can be considered as the

233   most important Collembola and Oribatida species of the system regarding energy flux and

234   functioning. Interestingly, the farming system and the experimental drought did not affect the

235   abundances of the studied species significantly, but affected their trophic niches as indicated by

236   stable isotope analyses.

237

238   Trophic positions

239   Overall, stable isotope values of the studied microarthropods spanned two δ units in ^{13}C and four

240   δ units in ^{15}N, indicating the utilization of different C resources and the representation of at least

241   two trophic levels, assuming an enrichment of about 3 δ units per trophic level (Post 2002).

242   Based on the Δ^{13}C and Δ^{15}N values of the individual species, the studied taxa can be separated

243   into three groups, the three Collembola species, the Oribatida species *T. sarekensis* and the

244   Oribatida species *S. laevigatus.*

245   The three Collembola species *I. caerulea*, *I. maculatus* and *O. villosa* had Δ^{15}N values close to

246   zero, indicating they are closely linked to wheat plants and suggesting that they live as primary

247   decomposers that are little enriched in ^{15}N (-0.05 ‰, -0.12 ‰, 1.23 ‰, respectively). Earlier

248   studies also found large epi- and hemiedaphic Collembola species, such as the ones we studied,

249   to predominantly feed on plant-derived resources in both agroecosystems and forests (Pollierer et

250   al. 2009; Birkhofer et al. 2016; Potapov et al. 2016). Ngosong et al. (2009) further found plant

251   rather than fungal resources to be incorporated by Collembola in agricultural systems, and results

252   of the study of Li et al. (2020) suggest that root-derived carbon is a major resource.

253   Isotope values of ^{13}C of both Oribatida species exceeded those of the three Collembola species

254   by one to two δ units, indicating that both are linked to resources enriched in ^{13}C. However, their

255   Δ^{15}N values indicated that they occupy different trophic levels with *T. sarekensis* living as

256   primary decomposer and *S. laevigatus* as secondary decomposer or predator, similar to what has

257   been previously suggested (Schneider et al. 2004; Haynert et al. 2017). The average δ^{13}C value

258   of *T. sarekensis* being 4.55 ‰ higher than plant litter indicates that *T. sarekensis* is linked to

259   older carbon resources, probably soil organic matter in deeper soil layers (Potapov et al. 2019).

260   The average δ^{15}N value of *S. laevigatus* being 3.77 ‰ higher than that of plant litter indicates a

261   mixed diet consisting of mainly microorganisms, but in part also microbial feeders such as

262   nematodes.

263

264   Farming system

265   Our second hypothesis was partly supported by the significantly higher isotope values of *T.*

266   *sarekensis, I. caerulea* and *O. villosa* in the organic compared to the conventional farming

267   system. However, we did not find differences for the other taxa, which is in line with earlier

268   studies comparing different agricultural systems (Haubert et al. 2009; Birkhofer et al. 2011;

269   Lagerlöf et al. 2017). The higher isotope values of *T. sarekensis, I. caerulea* and *O. villosa* in the

270   organic farming system likely are related to the higher soil organic carbon content that was found

271   in this system. The higher Δ^{13}C values of *T. sarekensis* in organically compared to

272   conventionally managed fields indicate that they more intensively feed on old carbon resources

273   in the organic system, which is richer in soil organic matter due to long-term input of farmyard

274   manure and compost (Mäder et al. 2002). In *I. caerulea* and *O. villosa* Δ^{15}N values were higher

275   in organically compared to conventionally managed fields, pointing to a higher proportion of

276   microorganisms in their diet in the organic system. In fact, previous studies conducted in the

277   same long-term experiment as the present study found higher microbial biomass in the

278   organically than the conventionally managed fields indicating a higher availability of microbes

279   as food resource (Esperschütz et al. 2007; Fließbach et al. 2007). This is likely to be a

280   consequence of higher soil water content and soil organic carbon in the organically managed

281   fields. This effect might further be enhanced by higher δ^{15}N values of the organic fertilizer

282   (farmyard manure) compared to the inorganic fertilizer in the conventional system (Birkhofer et

283   al. 2011). Higher stable isotope values in the organic system may additionally be caused by

284   stable isotope enrichment of soil organic matter due to stronger internal nutrient cycling (Vervaet

285   et al. 2002; Hobbie and Ouimette 2009).

286   Besides the comparison of mean stable isotope values, additional information on trophic shifts of

287   species can be obtained by comparing trophic niche width and trophic niche space (Behan-

288   Pelletier 1999; Bearhop et al. 2004). Our hypothesis on changes in trophic niche width with

289   farming system was based on the assumption that in less disturbed habitats consumers would

290   have a greater range of potentially available food resources, from which species could select

291   according to their preferences. By contrast, in more severely disturbed systems, preferred

292   resources may not be available, forcing consumers to feed on a wider range of resources

293   resulting in broader trophic niches. Our data support this hypothesis only partly for the two

294   farming systems and, interestingly, in some species showed the opposite pattern for the drought

295   treatment (see below). Variations in Δ^{13}C values in *I. caerulea* and *I. maculatus* were small in the

296   organic farming system indicating a diet consisting of fresh litter or root exudates, whereas in the

297   conventional farming system diets varied more widely. This suggests the utilization of a wider

298   range of resources including old litter and microorganisms resulting in increased $\delta^{13}C$ values

299   (Potapov et al. 2019) or algae resulting in decreased $\delta^{13}C$ values (Tozer et al. 2005). In the

300   conventional system, the amount of litter input is low and limited to plant residues from the crop

301   plant, i.e., mainly roots, whereas in the organic system plant residues in the organic fertilizer

302   provide additional food resources. Further, the amount of rhizodeposits in the conventional

303   system is likely to be lower than in the organic system, thereby providing fewer resources to the

304   belowground food web (Jones et al. 2001; Li et al. 2016; Wang et al. 2016). The lower

305   availability of preferred food resources in the conventional compared to the organic farming

306   system may force soil invertebrates to broaden their trophic niche. Further, in the conventional

307   farming system more algae may be present due to the scarcity of weeds (Meyer et al. 2021)

308   providing additional food resources that are not equally available in organic farming systems.

309

310   Drought

311   Drought significantly decreased soil moisture in both farming systems. However, contradicting

312   our second hypothesis, drought did not affect stable isotope values of most taxa and there was no

313   significant interaction with farming system. Only *S. laevigatus* had lower $\Delta^{13}C$ and constantly

314   high $\Delta^{15}N$ values in the drought treatment indicating prey switching. Assuming that *S.*

315   *laevigatus,* at least in part, feeds on nematodes, this might represent a switch from microbial-

316   feeding to plant-feeding nematodes, due to microbial-feeding nematodes being heavily stressed

317   under dry conditions due to reduced microbial activity (Kundel et al. 2020). In contrast to

318   conventional farming and contrasting our second hypothesis, drought decreased the trophic niche

319   width in some species (*S. laevigatus, I. caerulea* and *I. maculatus*). For *S. laevigatus* this was

320   caused by lower $\Delta^{13}C$ values in the drought treatment, probably due to prey switching (see

321   above). In the two Collembola species the decreased trophic niche width was due to decreased

322   variation in $\Delta^{13}C$ values, but not lower mean $\Delta^{13}C$ values, indicating more restricted

323   consumption of plant-derived resources rather than algae and microorganisms. Accessibility of

324   algae and microorganisms is likely to decrease at low soil moisture, whereas the availability of

325   (higher) plant-derived resources may be less affected. In fact, plant-related variables, including

326   root biomass, shoot biomass and grain yield, did not differ between the drought treatments in this

327   experiment (Kundel et al. 2020). For *I. caerulea*, additionally, the smaller variation in $\Delta^{15}N$

328   values, but no changes in mean $\Delta^{15}N$ values, in the drought treatment supports the conclusion of

329   narrower trophic niches due to more pronounced feeding on plant material.

330

331   **Conclusions**

332   Drought did not significantly affect mean stable isotope values of most of the studied mesofauna

333   species, but trophic niche width and space changed significantly, highlighting the relevance of

334   these trophic niche characteristics for tracking effects of changes in environmental factors on soil

335   food webs. Our results provide further evidence that in agricultural fields both plant litter and

336   root-derived carbon play an important role as food resource for soil microarthropods. Overall,

337   our data indicate that short-term drought as well as organic farming reduces the diversity of the

338   resources used by soil microarthropods and favors the use of plants as basal resource for

339   Collembola and Oribatida instead of microorganisms and algae. At the same time, the

340   abundances of Collembola and Oribatida were not affected, suggesting that a flexible usage of

341   resources may buffer negative effects of drought conditions on microarthropod communities in

342   agricultural fields.

343

344   **Acknowledgements**

345   We thank Guido Humpert for help with field work and Barbara Wozniak for help with sorting of

346   animals. We gratefully acknowledge support by the Open Access Publication Funds of the

347   University Göttingen. We further thank the Physiological Plant Ecology Group led by Ansgar

348   Kahmen at the University of Basel for the measurement of stable isotopes in wheat plants.

349

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Figure 1

Stable isotope values of Collembola and Oribatida

Mean (± standard deviation) Δ^{13}C and Δ^{15}N values of two species of Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarakensis*) and three species of Collembola (*Isotoma viridis*, *Isotomurus maculatus*, *Orchesella villosa*); data are calibrated against stable isotope values of wheat in the respective plot.

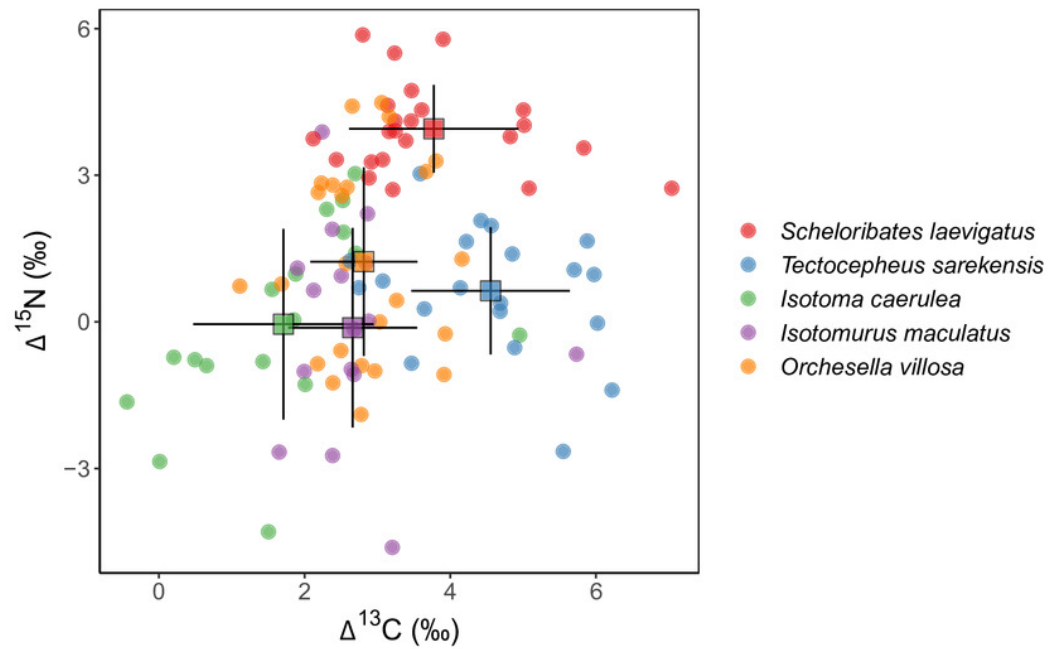



Figure 2

Stable isotope values of Collembola and Oribatida in drought and control treatment

Mean (± 95% confidence interval) Δ^{13}C values in control and drought treatments (roof) for two species of Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarakensis*) and four Collembola taxa (*Isotoma caerulea*, *Isotomurus maculatus*, *Orchesella villosa*, *Mesaphorura* sp.); for statistical analysis see Table 3.

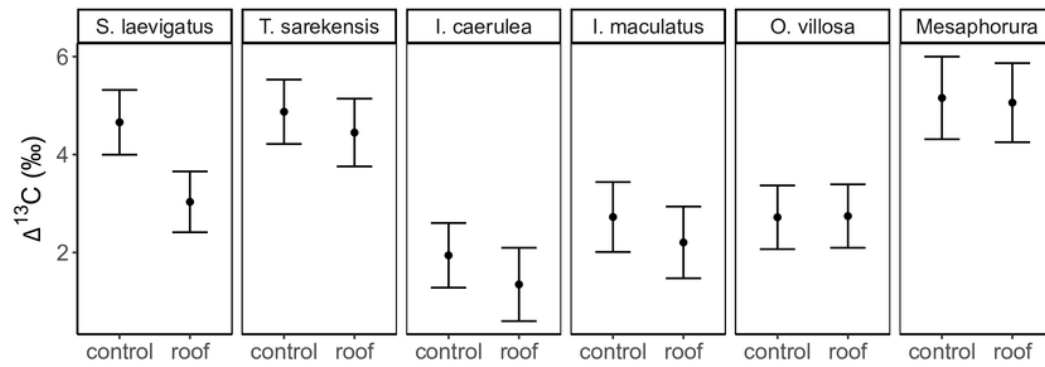



Figure 3

Stable isotope values of Collembola and Oribatida in two farming systems

Mean (± 95% confidence interval) Δ^{13}C (upper panel) and Δ^{15}N values (lower panel) of two oribatid mite (*Scheloribates laevigatus*, *Tectocepheus sarakensis*) and four Collembola species (*Isotoma caerulea, Isotomurus maculatus, Orchesella villosa, Mesaphorura* sp.) in conventional (conv) and organic (org) farming systems; note that for *Mesaphorura* sp. only Δ^{13}C values are shown. For statistical analysis see Table 3.

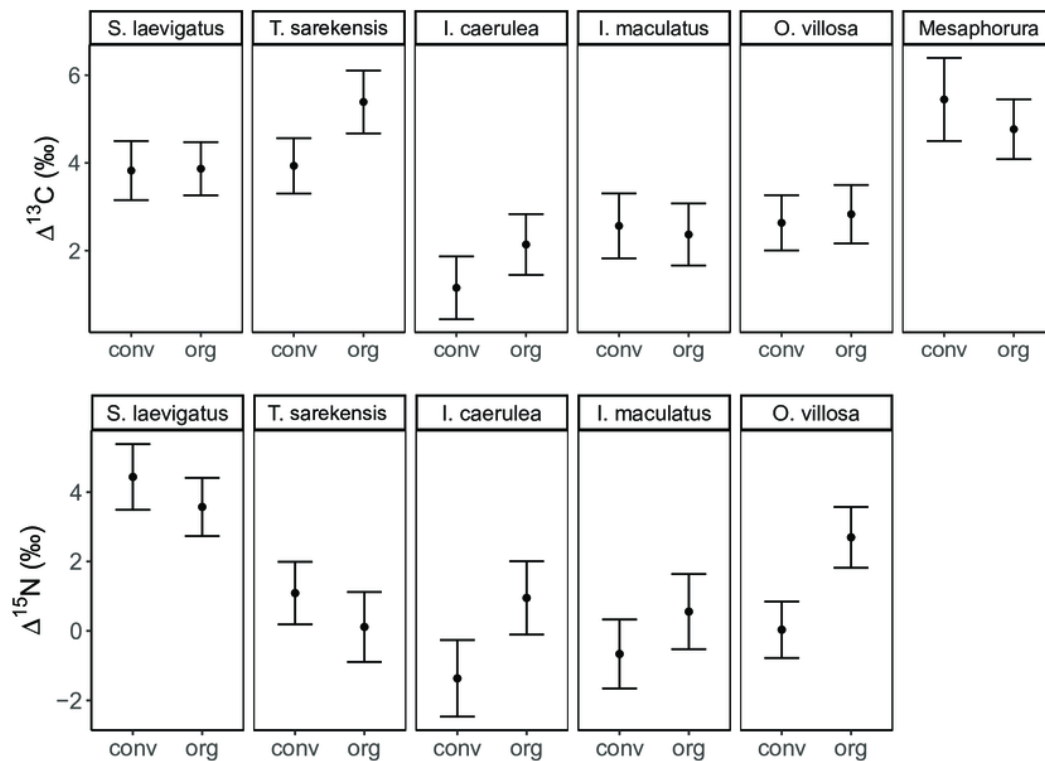



Figure 4

Isotopic niche sizes in drought and control plots and in two different farming systems

Probability distribution of the sizes of isotopic niches of five microarthropod species (*Scheloribates laevigatus, Tectocepheus sarakensis, Isotoma caerulea, Isotomurus maculatus, Orchesella villosa*) in the drought (roof) and the control treatment (upper panel), and in conventional (conv) and organic (org) farming systems (lower panel). Points show posterior estimates of the Bayesian standard ellipse area with 50%, 75% and 95% credible intervals (from dark to light gray).

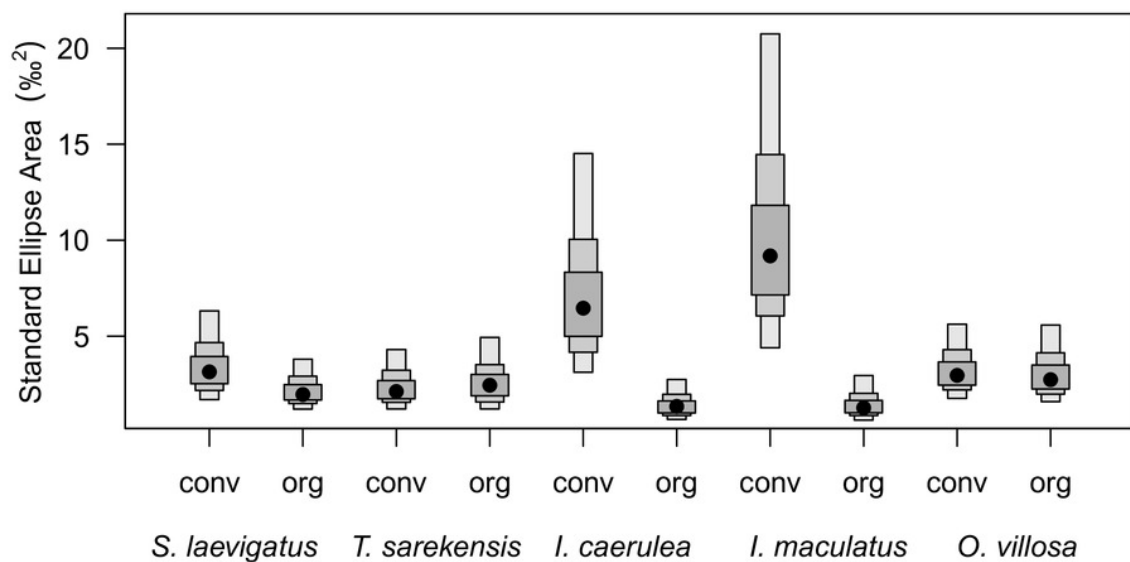
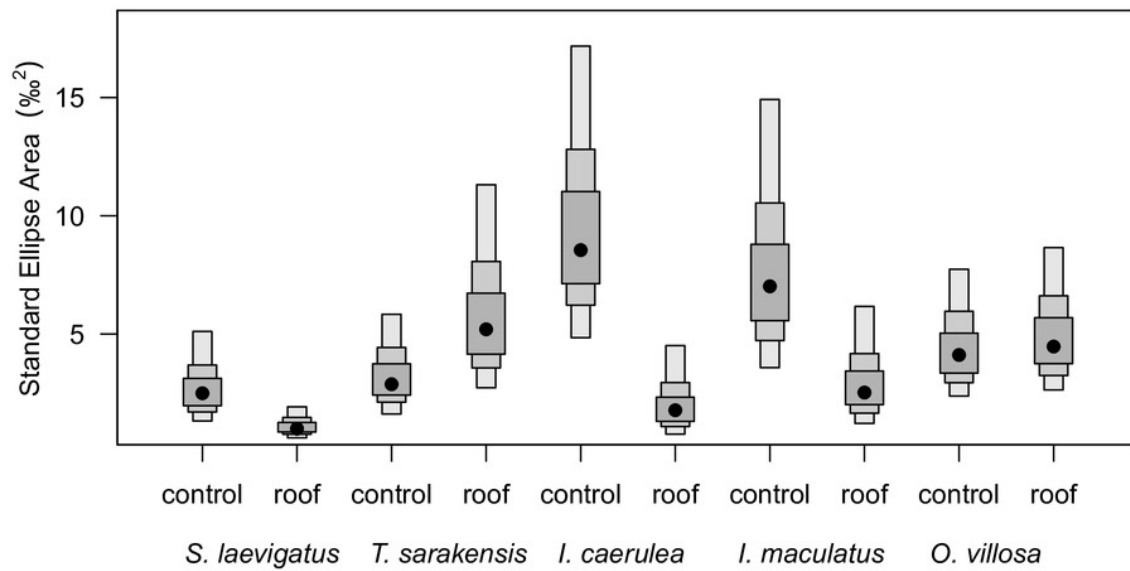



Figure 5

Isotopic niche space of Collembola and Oribatida in drought and control treatment

Isotopic niche space of two oribatid mite (*Scheloribates laevigatus*, *Tectocepheus sarakensis*) and three Collembola species (*Isotoma caerulea, Isotomurus maculatus, Orchesella villosa*) in the drought (roof, orange) and the control (turquoise) treatment. Standardized ellipses (SEAc) account for different sample sizes between taxa and small sample sizes per taxon and encompass approximately 95% of the data; see Methods.

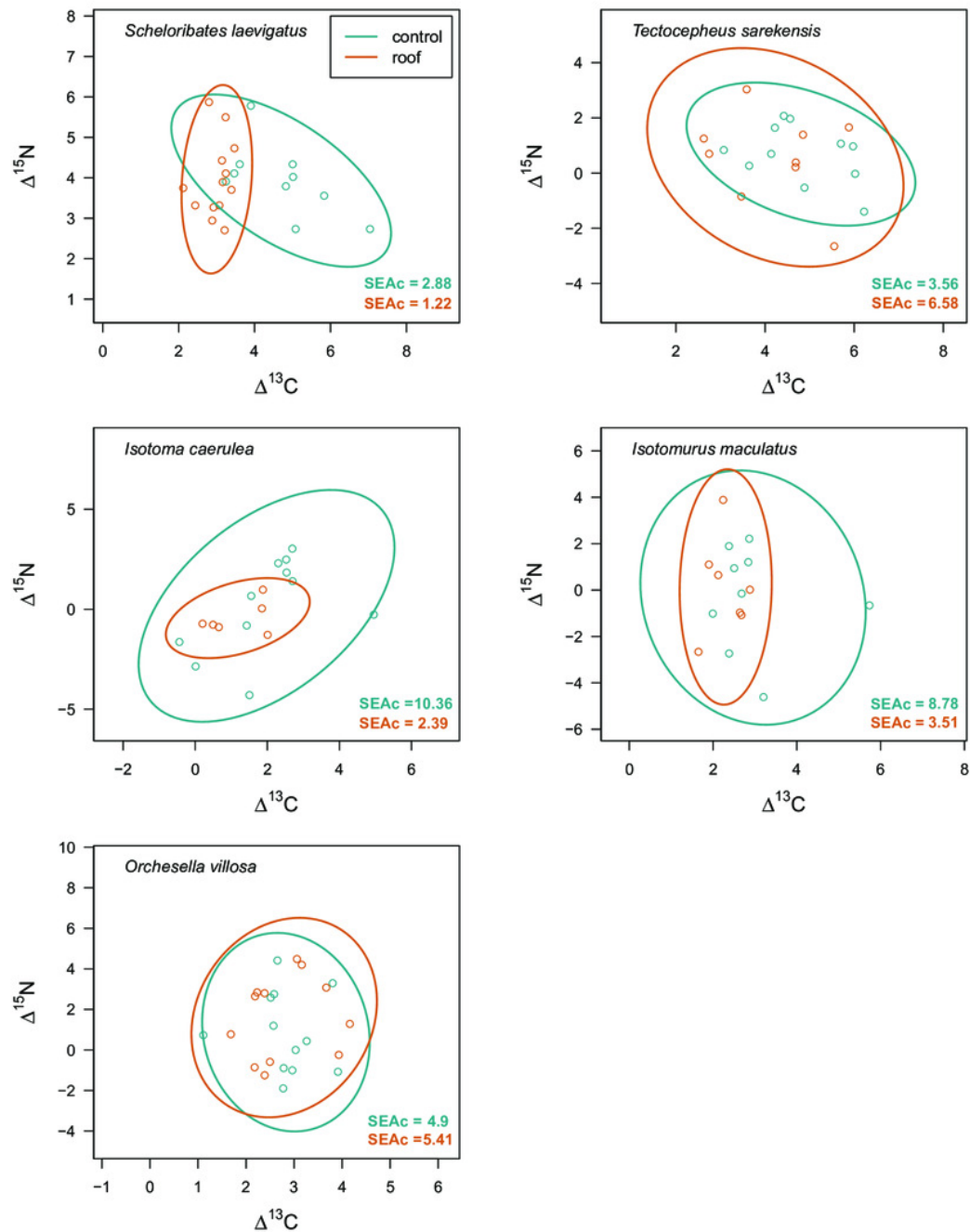
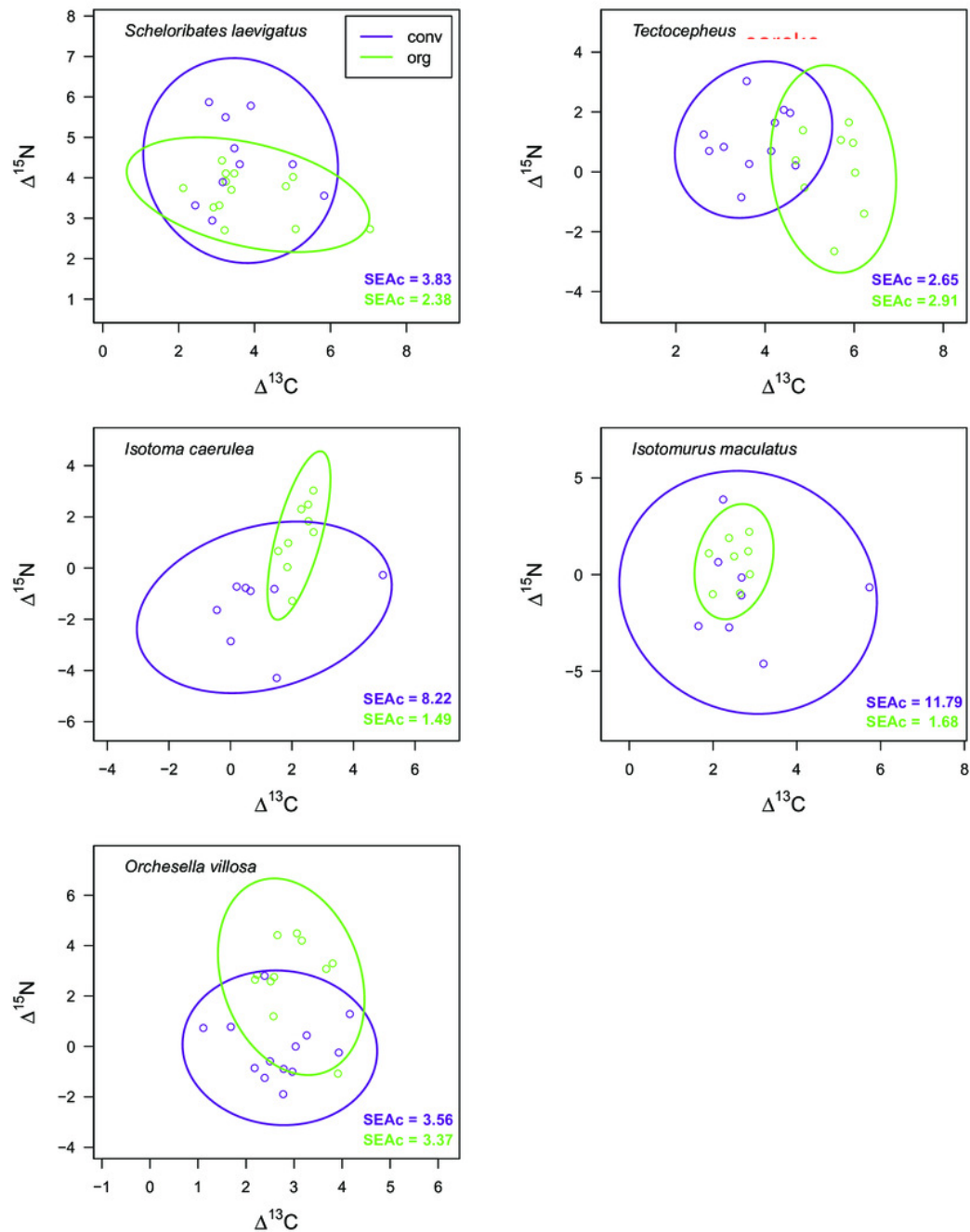



Figure 6

Isotopic niche space of Collembola and Oribatida in two different farming systems

Isotopic niche space of two oribatid mite (*Scheloribates laevigatus*, *Tectocepheus sarakensis*) and three Collembola species (*Isotoma caerulea, Isotomurus maculatus, Orchesella villosa*) in conventionally (conv, purple) and organically (org, green) managed fields. Standardized ellipses (SEAc) account for different sample sizes between taxa and small sample sizes per taxon and encompass approximately 95% of the data; see Methods.

Number of replicates for stable isotope measurements.

Per farming system (conventional, conv; organic, org) and drought treatment (control, roof).

Species	Farming system	Drought	number of replicates	
			δ¹³C	δ¹⁵N
Isotoma caerulea	conv	control	5	5
		roof	4	3
	org	control	6	6
		roof	4	3
Isotomurus maculatus	conv	control	4	5
		roof	4	4
	org	control	5	5
		roof	4	3
Orchesella villosa	conv	control	6	7
		roof	7	7
	org	control	6	6
		roof	5	6
Scheloribates laevigatus	conv	control	4	4
		roof	6	6
	org	control	7	6
		roof	7	7
Tectocepheus sarekensis	conv	control	6	6
		roof	6	5
	org	control	5	5
		roof	4	4

Results of LMMs on the effects of drought and farming system on the abundance, $\Delta^{13}C$ and $\Delta^{15}N$ values of abundant species of the mesofauna.

Significant effects are given in bold.

	$\Delta^{15}N$			$\Delta^{13}C$		
	df	F	P	df	F	P
Drought (D)	1,12	2.74	0.124	1,12	3.09	0.104
Farming system (F)	**1,12**	**13.84**	**0.003**	1,12	3.02	0.108
Species (S)	**4,71**	**32.56**	**<0.001**	**5,83**	**43.02**	**<0.001**
D x F	1,12	2.19	0.164	1,12	0.04	0.844
D x S	4,71	0.72	0.58	**5,83**	**2.92**	**0.018**
F x S	**4,71**	**10.11**	**<0.001**	**5,83**	**4.30**	**0.002**
D x F x S	4,71	2.39	0.059	5,83	1.49	0.203

Results of LMM on the effects of drought, farming system and species identity on the abundance, $\Delta^{13}C$ and $\Delta^{15}N$ values of the studied mesofauna species

Significant effects ($P < 0.05$) are given in bold.

	Scheloribates laevigatus			Tectocepheus sarekensis			Isotoma caerulea			Isotomurus maculatus			Orchesella villosa			Mesaphorura sp.		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Abundance																		
Drought (D)	1,6	0.01	0.943	1,6	2.68	0.153	1,6	0.88	0.384	1,6	3.06	0.131	1,6	1.05	0.344	1,6	0.53	0.495
Farming system (F)	1,6	1.80	0.228	1,6	0.01	0.910	1,6	0.83	0.396	1,6	0.13	0.728	1,6	1.63	0.249	1,6	1.79	0.229
D x F	1,6	0.84	0.394	1,6	0.42	0.540	1,6	1.51	0.266	1,6	0.49	0.510	1,6	0.09	0.779	1,6	4.56	0.077
d13C																		
Drought (D)	**1,6**	**17.08**	**0.001**	1,6	1.16	0.310	1,6	0.54	0.485	1,6	2.51	0.157	1,6	0.01	0.922	1,6	0.10	0.766
Farming system (F)	1,6	<0.01	0.960	**1,6**	**14.11**	**0.005**	1,6	1.16	0.312	1,6	0.88	0.379	1,6	0.36	0.562	1,6	0.43	0.536
D x F	1,6	0.07	0.798	1,6	0.04	0.851	1,6	0.19	0.676	1,6	2.68	0.145	1,6	0.13	0.726	1,6	0.75	0.419
d15N																		
Drought (D)	1,6	0.03	0.867	1,6	0.04	0.845	1,6	0.10	0.759	1,6	0.21	0.663	1,6	1.44	0.261	-	-	-
Farming system (F)	1,6	4.30	0.062	1,6	2.82	0.132	**1,6**	**15.47**	**0.008**	1,6	2.69	0.145	**1,6**	**15.90**	**0.003**	-	-	-
D x F	1,6	0.09	0.771	1,6	0.22	0.649	1,6	3.92	0.095	1,6	2.22	0.180	1,6	0.04	0.855	-	-	-