1 **Trophic consistency of supraspecific taxa in belowground invertebrate communities**

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14 **Abstract**

15   1. Animals that have similar morphological traits are expected to share similar
16   ecological niches. This statement applies to individual animals within a species
17   and thus species often serve as the functional units in ecological studies. Species
18   are further grouped into higher-ranked taxonomic units based on their
19   morphological similarity and thus are also expected to be ecologically similar. On
20   the other hand, theory predicts that strong competition between closely related
21   species can lead to differentiation of ecological niches. Due to a high diversity
22   and limited taxonomic expertise, soil food webs are often resolved using
23   supraspecific taxa such as families, orders or even classes as functional units.

24   2. Here we for the first time empirically tested the trophic consistency of
25   supraspecific taxa across major lineages of temperate forest soil invertebrates:
26   Annelida, Chelicerata, Myriapoda, Crustacea and Hexapoda. Published data on
27   stable isotope compositions of carbon and nitrogen were used to infer basal
28   resources and trophic level, and explore the relationship between taxonomic and
29   trophic dissimilarity of local populations.

30   3. Genera and families had normal and unimodal distributions of isotope niches,
31   suggesting that supraspecific taxa are trophically consistent. The isotopic niche of
32   populations across different localities is better predicted by species than by
33   supraspecific taxa. However, within the same genus, the effect of species identity
34   on stable isotope composition of populations was not significant in 92% of cases.
35   The link to basal resources, i.e. plants or detritus, was convergent in different
36   lineages, while trophic levels followed the Brownian motion taxonomic model.
37   Virtually none of the studied taxa showed pronounced trophic niche conservatism
38   within a lineage.

39   4. Supraspecific taxa are meaningful as functional units in ecological studies, but the consistency varies among taxa and thus the choice of taxonomic resolution depends on the research question; generally, identification of taxa should be more detailed in more diverse taxonomic groups. We compiled a comprehensive list of mean Δ^{13}C and Δ^{15}N values of invertebrate taxa from temperate forest soils allowing to refine soil food-web models when identification to species level is not feasible.

Key words:

Arthropoda, niche conservatism, phylogenetic signal, soil food web, taxonomic sufficiency, taxonomic resolution, trophic niche

Introduction

Shared ancestry typically is associated with ecological similarity, with closely related species having similar traits and therefore similar ecological niches (Webb, 2000; Webb, Ackerly, McPeek, & Donoghue, 2002). Such similarity results from 'evolutionary inertia' and is referred to as phylogenetic signal (Blomberg & Garland, 2002). The inertia is likely supported by the ancestral constraint mechanisms, i.e. the property of a trait that, although possibly adaptive in the environment in which it originally evolved, acts to place limits on the evolution of new phenotypic variants (Blomberg & Garland, 2002; Pyron, Costa, Patten, & Burbrink, 2015). Notably, not only the trait itself can be conserved but also its potential to vary. This concept was formalized in the early 20th century by N. Vavilov in "*The law of homology series in genetical mutability*" (1935) and implies that related species tend to evolve similar phenotypic traits.

As a result of evolutionary inertia, taxonomically related species may respond similarly to environmental factors and perform similar ecosystem functions, since the organisms that share similar morphology are likely to share a similar ecological niche (Wainwright & Richard, 1995). Moreover, supraspecific taxa are suggested to behave as ecological units forming the structural parts of ecosystems (Chernov, 2008). The taxonomic level to which ecological characteristics of species can be extrapolated with a minimum loss of information, i.e. "taxonomic sufficiency", is an important question in basic and applied ecology (Ellis, 1985; Terlizzi, Bevilacqua, Fraschetti, & Boero, 2003). For instance, a moderate level of taxonomic aggregation (genera or even families) can be sufficient to indicate effects of environmental changes on the composition of benthic and soil invertebrates communities (Jiang et al., 2013; Minor, Ermilov, & Tiunov, 2017). Loss of information due to taxonomic aggregation likely is more pronounced in more diverse groups (Timms, Bowden, Summerville, & Buddle, 2013), but the ecological consistency of taxa at different taxonomic levels has never been tested empirically.

75   Ecological similarity among related species usually is investigated in respect to

76   morphology, physiology and behaviour of organisms, with behavioural adaptations being

77   evolutionarily more labile (Blomberg, Garland, Ives, & Crespi, 2003; Böhning-Gaese &

78   Oberrath, 1999). As a complex trait, trophic niches may either be similar or differ considerably

79   among closely related taxa. Feeding habits of an organism are not strongly related to its

80   taxonomic position since similar feeding strategies occur in many lineages (i.e., convergence in

81   trophic positions). Pronounced trophic-niche differentiation between species was shown for

82   dominant groups of soil detritivores (Chahartaghi, Langel, Scheu, & Ruess, 2005; Schneider et

83   al., 2004). Nevertheless, supraspecific taxa often are used as trophic species (nodes) in soil food

84   web models (Berg & Bengtsson, 2007; de Ruiter, Neutel, & Moore, 1994; de Vries et al., 2013).

85   Despite trophic guilds conceptually are independent of taxonomy, taxonomically related species

86   usually are included in the same trophic guild (Simberloff & Dayan, 1991). This assumption

87   recently has received empirical support in freshwater (catfishes) and soil (springtails)

88   detritivores, for which trophic niches were shown to differ between supraspecific taxa (Lujan,

89   Winemiller, & Armbruster, 2012; Potapov, Semenina, Korotkevich, Kuznetsova, & Tiunov,

90   2016). Moreover, it has been argued that ecological links between species (e.g., via trophic

91   interactions) often are related to their phylogenetic position (Gómez, Verdú, & Perfectti, 2010;

92   Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007). In marine communities predators

93   tend to consume phylogenetically related prey species and prey tend to be consumed by

94   phylogenetically related predators (Eklöf & Stouffer, 2016). However, it remains unclear if this

95   also holds true for taxa in terrestrial belowground communities with less pronounced size

96   structure and high frequency of omnivorous species able to switch diet depending on its

97   availability (Digel, Curtsdotter, Riede, Klarner, & Brose, 2014).

98   Three scenarios are suggested to explain the relationship between taxonomic relatedness

99   of taxa and their dissimilarity in trophic niche. The 'limiting similarity' hypothesis suggests that

100   morphological similarity of closely related taxa results in strong competition (Darwin, 1876;

101   Violle, Nemergut, Pu, & Jiang, 2011) and this may favour trophic niche divergence. Although

102   trophic niches of species may be dissimilar, shared ancestral morphology should lead to the

103   overlap of trophic niches of supraspecific taxa, such as genera and families (Fig. 1). The

104   'random' hypothesis suggests no changes in trophic-niche differentiation at different levels of

105   taxonomic resolution (i.e., morphological dissimilarity is not related to trophic niche

106   dissimilarity). The 'taxonomic signal' hypothesis suggests that closely related taxa have more

107   similar trophic niches than distantly related taxa. Accordingly, supraspecific taxa are expected to

108   occupy distinct trophic niches that reflect ancestral adaptations, while genera within families and

109   species within genera differ only little.

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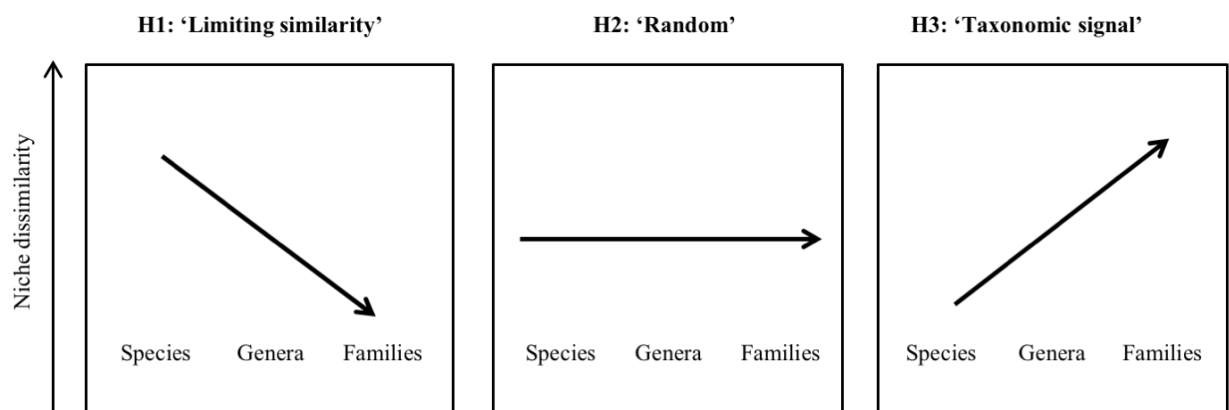
112   **Figure 1.** Contrasting scenarios of niche differentiation among closely-related taxa. Hypothesis 1

113   ('limiting similarity') suggests strong competition and trophic-niche divergence among closely-

114   related taxa. Hypothesis 2 ('random') hypothesis suggests no relationship between taxonomic

115   and trophic-niche dissimilarity. Hypothesis 3 ('taxonomic signal') suggests that closely related

116   taxa have more similar trophic niches than distantly related taxa and that niche differentiation is

117   increasing with increasing taxonomic level.

118

119   The limitations of measuring trophic-niche dimensions *in situ* were partly overcome with

120   the introduction of stable isotope analysis in ecological studies (Peterson & Fry, 1987). Natural

121   variations in stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) reflect the trophic

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122   niche of species (Newsome, Martinez del Rio, Bearhop, & Phillips, 2007; Rodríguez & Herrera,

123   2013) and provide information on their basal resources and trophic level, respectively (Boecklen,

124   Yarnes, Cook, & James, 2011; Martinez del Rio, Wolf, Carleton, & Gannes, 2009). In soil food

125   webs ^{13}C concentrations increase with decomposition of plant material, while ^{15}N concentrations

126   increase with trophic level (Potapov et al., 2018). Based on these findings, we used published

127   data on stable isotope composition of carbon and nitrogen to explore the trophic niches of major

128   belowground arthropod lineages at different taxonomic levels. The following main questions

129   were addressed: (1) Is there evidence for trophic niche conservatism (*sensu* Losos, 2008) in soil

130   animal taxa? (2) Are supraspecific taxa in soil communities trophically consistent? (3) How

131   much information about basal resources and trophic level of soil animals do we lose by using

132   supraspecific taxa instead of species?

133

134   **Methods**

135   The analysis was based on a large compilation of published data on stable isotope

136   composition of soil invertebrates from temperate forests (Potapov et al., 2018). In the dataset,

137   only records identified to species or genus level were included resulting in 415 species from 21

138   orders and 5 high-order taxa: Annelida, Chelicerata, Myriapoda, Crustacea and Hexapoda (Table

139   S1). Each data record in the dataset comprised average stable isotope composition of species /

140   taxa sampled at a local community with some species investigated at different localities /

141   ecosystems resulting in a total of 961 local populations. Stable isotope compositions of carbon

142   and nitrogen were normalized to the local leaf litter to account for inter-ecosystem variations and

143   denoted as $\Delta^{13}C$ and $\Delta^{15}N$ values (Klarner et al., 2014). Further, each record was classified into

144   the following taxonomic levels: Phylum, Subphylum, Class, Order, Family, Genus and Species,

145   according to (Zhang, 2011). Although arbitrarily defined and varying between taxonomic

146   groups, supraspecific taxa form a hierarchical system representing different levels of aggregation

147   of species.

148   Statistical analyses were performed in R 3.4.0 with R studio interface (R Core Team,

149   2017). To test if stable isotope composition of soil invertebrates is distributed non-randomly on

150   the taxonomic tree, we analysed $\Delta^{13}C$ and $\Delta^{15}N$ values using Blomberg's K criterion in the

151   package *phytools* (Revell, 2012). This criterion was developed to test for significance of

152   phylogenetic signal, i.e. its non-random distribution on a phylogenetic tree, and allows

153   comparisons of phylogenetic signal across traits and phylogenetic trees (Blomberg et al., 2003).

154   Data were transformed to a tree using *as.phylo* in package *ape* (Paradis, Claude, & Strimmer,

155   2004). The empirical Blomberg's K criteria were compared with 999 Brownian motion

156   simulations (*fastBM*) in package *phytools*. Due to a positive skewness of the distribution, the

157   95% confidence interval for simulated K criteria was calculated after log-transformation and was

158   estimated as 0.62-1.81. K values below 0.62 indicate trophic-niche convergence among taxa

159   (similar isotopic composition is observed in different lineages), while values above 1.81 indicate

160   trophic-niche conservatism (different lineages have different isotopic composition; Losos, 2008).

161   According to the abovementioned hypotheses, we explored the relationship between

162   isotopic dissimilarity and taxonomic dissimilarity of taxa at different taxonomic levels. Isotopic

163   dissimilarity (as a proxy of trophic niche dissimilarity) was measured as Euclidean distance

164   between populations' $\Delta^{13}C$ and $\Delta^{15}N$ values. Taxonomic dissimilarity was ranked from 1 to 8,

165   with 1 denoting different populations of the same species, 2 denoting populations of different

166   species of the same genus, 3 – populations of different genera of the same family, 4 –

167   populations of different families of the same order, 5 – populations of different orders of the

168   same class, 6 – populations of different classes of the same subphylum, 7 – populations of

169   different subphyla of the same phylum, and 8 – populations of different phyla. Matrixes for

170   isotopic and taxonomic dissimilarities were calculated using *daisy* in package *cluster* (Maechler,

171   Rousseeuw, Struyf, Hubert, & Hornik, 2017). Subsequently, isotopic and taxonomic

172   dissimilarity matrixes were correlated using Mantel test with 999 permutations (package *ade4*;

173   (Dray, Dufour, & others, 2007). Medians and means of isotopic dissimilarity were compared

174   between taxonomic levels using Nemenyi test in package *PMCMR* (Pohlert, 2014) and general

175   linear hypothesis for multiple comparisons in package *multcomp* (Hothorn, Bretz, & Westfall,

176   2008), respectively. Both tests showed similar results; only results of the former are presented.

177   To test the trophic consistency of supraspecific taxa we visually explored the

178   distributions of $\Delta^{13}C$ or $\Delta^{15}N$ values of all taxa at different taxonomic levels. To analyse all taxa

179   together, we first calculated mean $\Delta^{13}C$ and $\Delta^{15}N$ values for all taxa at all taxonomic levels.

180   Next, we calculated offsets of $\Delta^{13}C$ and $\Delta^{15}N$ values for populations from the mean values for all

181   parental taxa. For example, to construct data distribution for the 'family' level, offsets for all

182   populations were calculated using the mean values of the corresponding parental families. Only

183   taxa with two or more nested taxa of the lower taxonomic level were included in the analysis

184   (i.e., species with ≥ 2 populations, genera with ≥ 2 species, families with ≥ 2 genera etc.). Offsets

185   were compared between taxonomic levels using general linear hypothesis for multiple

186   comparisons in package *multcomp*.

187   To estimate how much information about basal resources and trophic level of soil

188   animals is lost by using supraspecific taxa instead of species, we checked whether different

189   species within the same parental taxon occupy significantly distinct trophic niches. For doing

190   that, we inspected the effect of 'species identity' on the $\Delta^{13}C$ or $\Delta^{15}N$ values of populations using

191   one-way ANOVAs. Only taxa with two or more nested taxa of the lower taxonomic level were

192   included in the analysis. Thereafter, results of the ANOVA (effect of species / no effect of

193   species as a binomial variable) were used to calculate percentage of taxa with significant species

194   effect at different levels of taxonomic resolution.

195   Lastly, we inspected mean $\Delta^{13}C$ and $\Delta^{15}N$ values for individual subphyla, classes and

196   orders across three major lineages of soil arthropods that were well represented in the dataset, i.e.

197   Chelicerata, Myriapoda and Hexapoda. In this analysis we used the expanded dataset of 1146

198   populations including those not identified to species level (Table S1).

199

200   **Results**

201   Based on the entire dataset both $\Delta^{13}C$ and $\Delta^{15}N$ values showed taxonomic signal, i.e.

202   closely related taxonomic units shared basal resources and trophic levels more often than

203   expected by random distribution (p = 0.001 for both). Comparisons based on the Brownian

204   motion model showed that trophic niches are not taxonomically conserved with $\Delta^{13}C$ values

205   being convergent among taxa (Blomberg's K = 0.50) and $\Delta^{15}N$ values distributed following the

206   Brownian motion model (K = 0.87).

207   Mean isotopic dissimilarity between populations in $\Delta^{13}C$ values only slightly increased

208   with taxonomic dissimilarity (Mantel test: R = 0.006, simulated p = 0.245); by contrast, isotopic

209   dissimilarity in $\Delta^{15}N$ values increased steadily from the population to the class level but

210   decreased thereafter (R = 0.065, p = 0.001; Fig. 2). Whereas populations of different species

211   within a genus differed by 1.3‰ (a median), populations from different classes within a

212   subphylum differed by 3.9‰.

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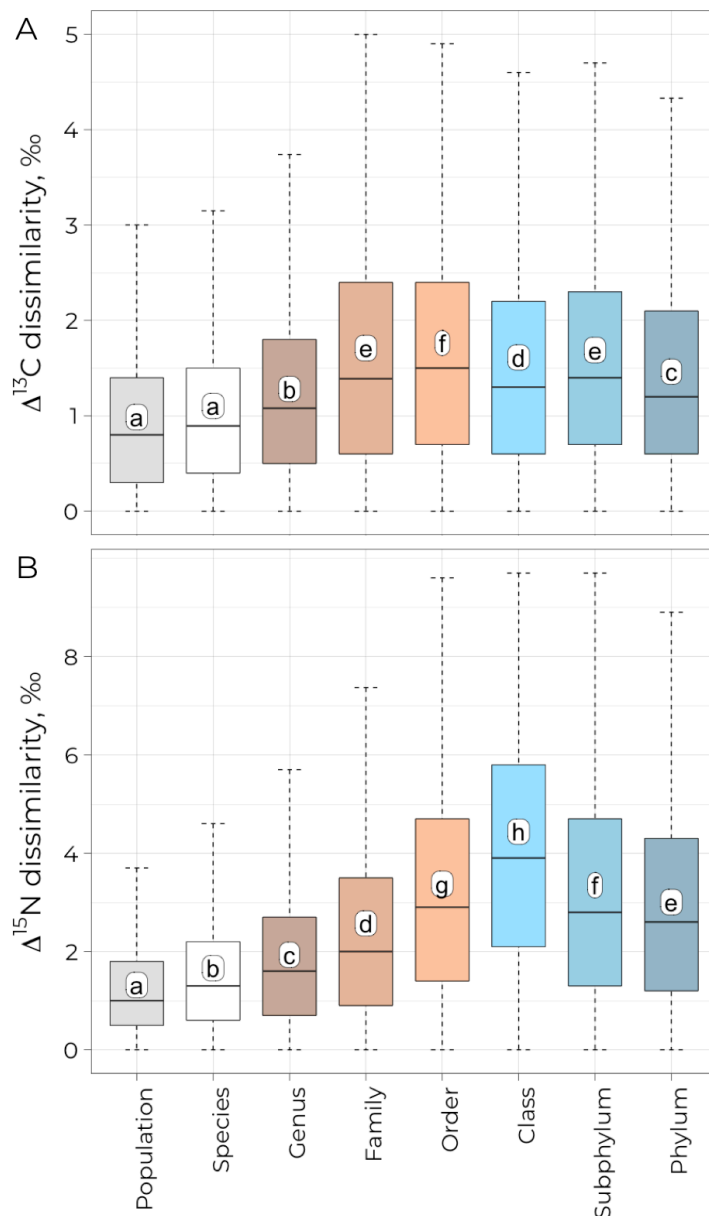
Figure 2. Isotopic dissimilarity as related to taxonomic dissimilarity in soil invertebrates.
Isotopic dissimilarity was measured as Euclidean distance in $\Delta^{13}C$ or $\Delta^{15}N$ values between populations. Taxonomic dissimilarity is reflected by eight levels of taxonomic resolution: For instance, 'Population' represents differences between populations of the same species, 'Species' represents differences between populations from different species of the same genus, 'Genus' represents differences between populations from different genera of the same family, etc. Distances within groups are illustrated using boxplots with horizontal lines representing medians; long upper tails in few cases were cut for clarity (2% of records for both $\Delta^{13}C$ and $\Delta^{15}N$). Means are indicated by white circles; letters refer to median comparison (Nemenyi test):

11

224   groups sharing the same letter are not significantly different. Isotopic and taxonomic

225   dissimilarity were significantly correlated for Δ^{15}N but not for Δ^{13}C values (see text).

226

227   The variability of both Δ^{13}C and Δ^{15}N values increased continuously with decreasing

228   level of taxonomic resolution. However, taxa from species to family level for Δ^{15}N and from

229   species to order level for Δ^{13}C fitted normal and unimodal distribution (Fig. 3A, B), suggesting

230   trophic consistency of taxa at these taxonomic levels. The offset of individual populations from

231   the mean values of parental taxa continuously increased with decreasing taxonomic resolution

232   until class and subphylum levels for Δ^{13}C and Δ^{15}N values, respectively (Fig. 3C, D). Average

233   absolute offsets of Δ^{13}C values were 0.6‰ for species and 0.8‰ for families; average offsets of

234   Δ^{15}N values were 0.9‰ for species and 1.3‰ for families.

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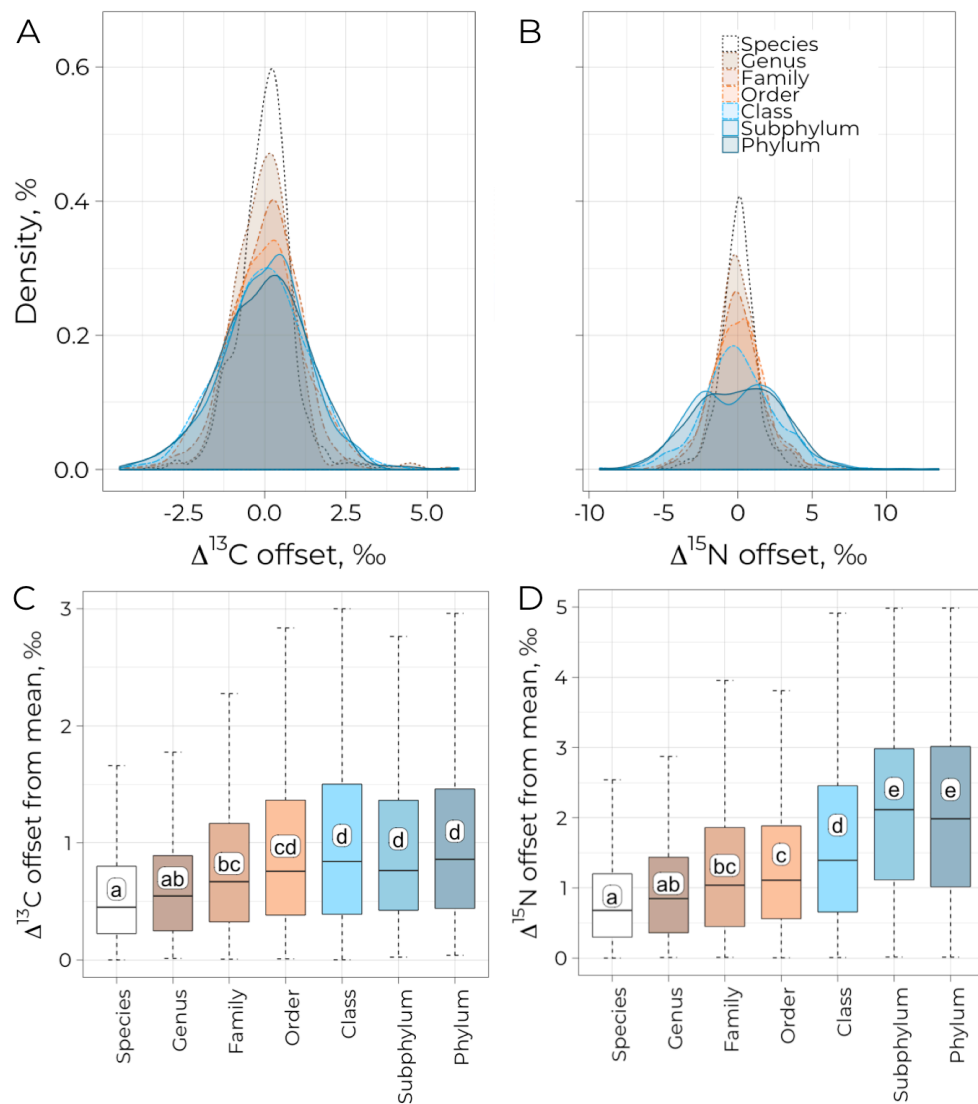
Figure 3. Offsets in stable isotope composition of populations from means of parental taxa of different taxonomic level. Offsets were calculated as mean $\Delta^{13}C$ (A, C) and $\Delta^{15}N$ values (B, D) for populations minus the mean value for parental taxonomic units, all data are plotted together. E.g. 'Family' stands for offsets of individual populations from the mean of parental families. Only taxa with two or more nested taxa of the lower taxonomic level were included in the analysis (i.e., species with ≥ 2 populations, genera with ≥ 2 species, families with ≥ 2 genera etc.). A and B: Offsets are displayed as the Kernel density estimation. C and D: Absolute offsets are displayer as boxplots with horizontal lines representing medians. Means are indicated by white circles; letters refer to median comparison (Nemenyi test): groups sharing the same letter are not significantly different.

13

248   To estimate, to what extent information is lost by using supraspecific taxa instead of

249   species, we tested for the effect of species on $\Delta^{13}C$ and $\Delta^{15}N$ values within each supraspecific

250   taxa from genus to class level. Within genera, the effect of species was not significant in 92% of

251   the cases for both $\Delta^{13}C$ and $\Delta^{15}N$ values (Supplementary Table S2). Within families, orders, and

252   classes the effect of species on $\Delta^{13}C$ values was not significant in 82, 45, and 20% of cases,

253   respectively. The respective values for $\Delta^{15}N$ values were 59, 45, and 0% (Fig. 4).
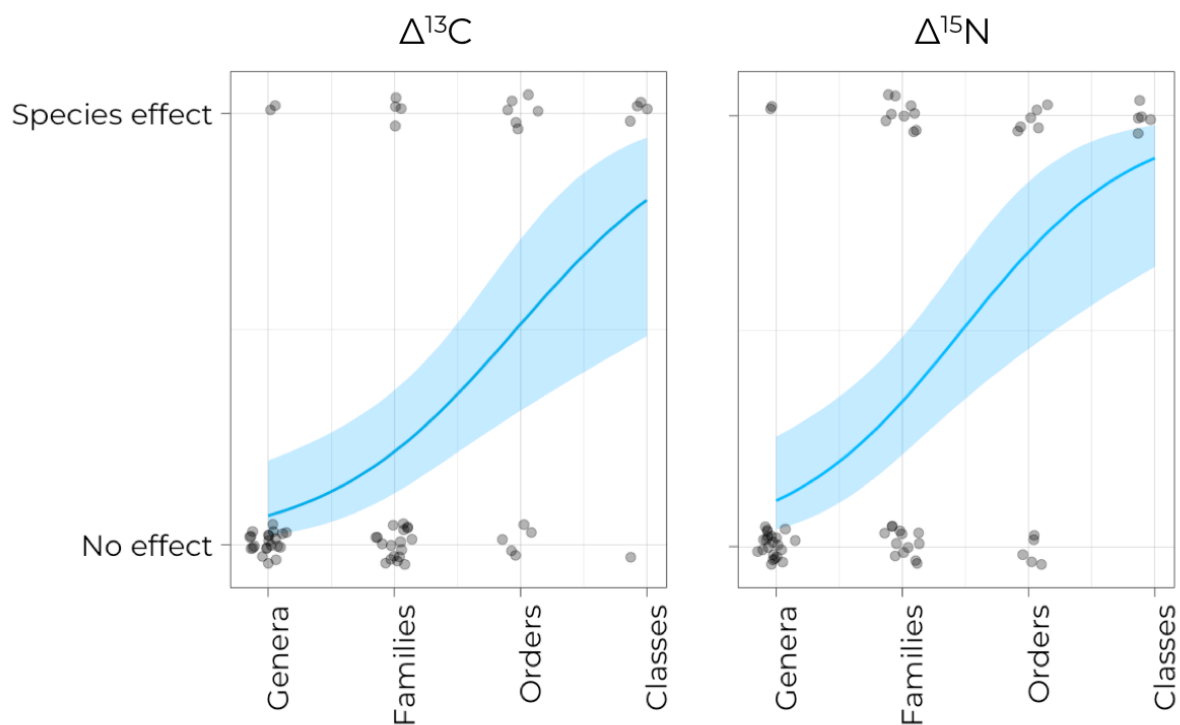
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255   **Figure 4. Effect of species identity on $\Delta^{13}C$ and $\Delta^{15}N$ values at different taxonomic levels.**

256   Significant effects of species on population stable isotope composition within the parental taxon

257   were inspected using ANOVA (Table S3). Only taxa with two or more nested taxa of the lower

258   taxonomic level were included in the analysis (i.e., species with ≥ 2 populations, genera with ≥ 2

259   species, families with ≥ 2 genera etc.). Probability of significant effect is illustrated with

260   binomial smoother; shaded areas show 95% confidence intervals.

261

262   More detailed analysis of high-rank taxa showed that at the level of subphyla, Chelicerata

263   and Myriapoda were on average enriched in both ^{13}C and ^{15}N as compared to Hexapoda (Figs 5,

264   6). There were no differences in $\Delta^{13}C$ values between classes within subphyla, but classes within

265   Myriapoda and Hexapoda were distinct in $\Delta^{15}N$ values (Chilopoda vs. Diplopoda and Insecta vs.

266   Collembola). Further, $\Delta^{13}C$ values differed between orders within Arachnida, Insecta and

267   Collembola, but not within Chilopoda and Diplopoda. $\Delta^{15}N$ values clearly differed between

268   predominantly predatory orders (Mesostigmata, Araneae, Geophilomorpha, Lithobiomorpha,

269   Coleoptera and Hymenoptera) and predominantly detritivore orders (Oribatida, Julida,

270   Polydesmida, Entomobryomorpha and Symphypleona). Diptera and Poduromorpha had

271   intermediate $\Delta^{15}N$ values. Significant differences were also found at the family and genus level

272   of taxonomic resolution (Supplementary materials, Fig. S1-S3).

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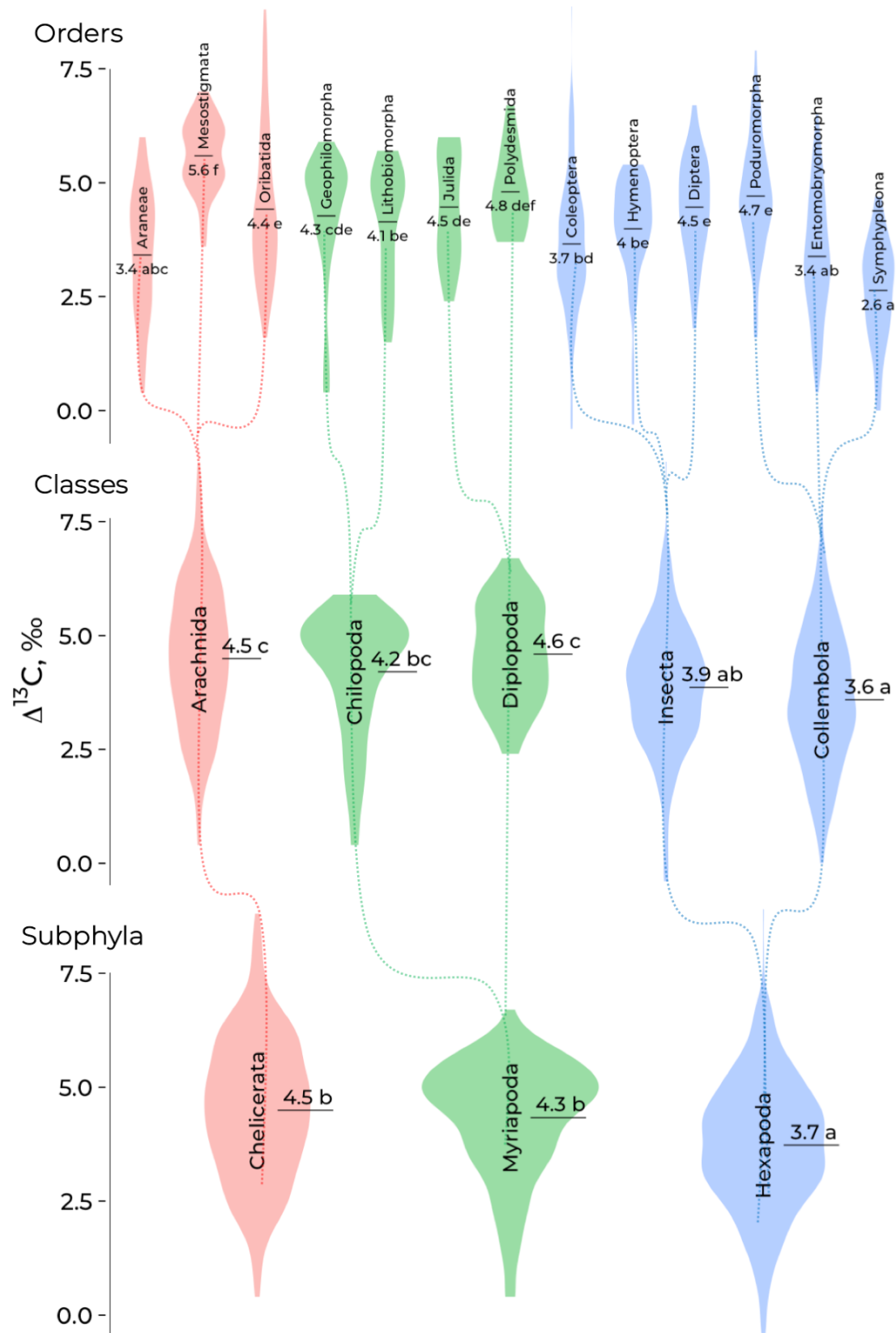
Figure 5. **Δ^{13}C values of subphyla, classes and orders in three main lineages of soil arthropods, Chelicerata, Myriapoda and Hexapoda.** Data on populations are presented in the form of violin plots (mirrored Kernel density estimation). Mean values are shown with

277   horizontal segments and numbers; mean values sharing the same letter within a taxonomic level

278   are not significantly different (general linear hypothesis for multiple comparisons). Colours

279   denote different lineages, dotted lines denote taxon hierarchy.
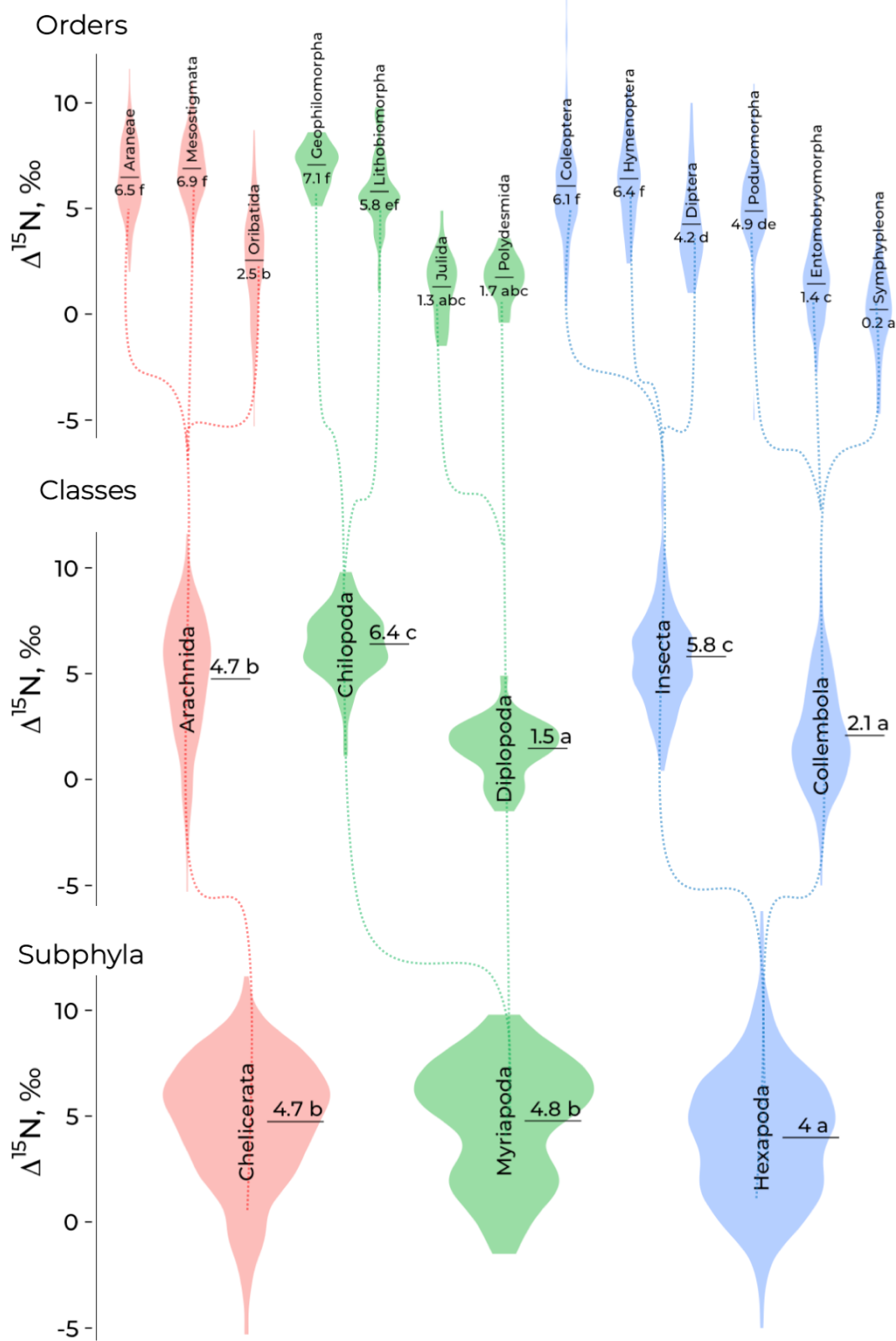

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281   **Figure 6**. **Δ^{15}N values of subphyla, classes and orders in three main lineages of soil**

282   **arthropods, Chelicerata, Myriapoda and Hexapoda.** Data on populations are presented in the

283   form of violin plots (mirrored Kernel density estimation). Mean values are shown with

284   horizontal segments and numbers; mean values sharing the same letter within a taxonomic level

285   are not significantly different (general linear hypothesis for multiple comparisons). Colours

286   denote different lineages, dotted lines denote taxon hierarchy.

287

288   **Discussion**

289   Supraspecific taxa are often assumed to comprise species that perform similar ecological

290   function. However, this assumption has not been formally tested. Using stable isotope analysis

291   we found strong support that dissimilarity in trophic level in soil invertebrates is related to

292   taxonomic dissimilarity, supporting the 'taxonomic signal' hypothesis. Trophic level (as

293   indicated by Δ^{15}N values) was well reflected by taxonomic units, which was mainly due to the

294   fact that high-order taxa (i.e., class and order level) encompass either detritivores or predators.

295   The pattern in Δ^{13}C values supported 'random' hypothesis, indicating that similar basal resources

296   can be utilized by various taxonomic groups with different types of body organisation.

297   The distribution of Δ^{13}C and Δ^{15}N values in supraspecific taxa, at least for genera and

298   families, were on average unimodal and close to normal, indicating that supraspecific taxa are

299   trophically consistent. Depending on the research question, our finding validates the usage of

300   supraspecific taxa as functional units in ecological studies if identification to species level is not

301   feasible. As expected low-rank taxonomic units provide a higher precision and a lower chance of

302   information loss. Still, due to a high variability within species, the effect of species identity on

303   Δ^{13}C and Δ^{15}N values of populations was not significant in 92% of the tested genera.

304

305   *Basal-resource and trophic-level conservatism in soil food webs*

306   Since we analysed a taxonomic rather than a phylogenetic tree, our conclusions about

307   evolutionary aspects of trophic niche conservatism are limited. However, the taxonomic tree that

308   we used reflects well the basic distinction between the main invertebrate lineages/high-rank taxa

309   (Misof et al., 2014; Rehm et al., 2011; Rota-Stabelli, Daley, & Pisani, 2013). Thus, the

310   prominent differences in trophic niches for high-rank taxa (orders, classes) suggest that early

311   evolutionary adaptations played a crucial role in shaping the niches of soil invertebrates.

312   Similarly, in arbuscular mycorrhizal fungi different colonization and resource exploitation

313   strategies evolved early during diversification (Powell et al., 2009).

314   Phylogenetic inertia constrain the evolution of ecological niches, but this can be very

315   different for different niche dimensions. For instance, behavioural adaptations in vertebrates are

316   quite labile, while morphological adaptations are often evolutionary conserved (Blomberg et al.,

317   2003; Böhning-Gaese & Oberrath, 1999). The concept of evolutionary conservatism was refined

318   by Losos (2008) who emphasized that ecological niches are often related to phylogeny and the

319   question is whether they are more or less conserved than expected by the Brownian motion

320   model. Both $\Delta^{13}C$ and $\Delta^{15}N$ values were distributed on the taxonomic tree in a non-random way,

321   however, we found no evidence that trophic niches are more conserved than expected by

322   Brownian motion. $\Delta^{13}C$ values (reflecting the link to basal resources) were likely evolutionary

323   convergent in different lineages. $\Delta^{15}N$ values (reflecting the trophic level) followed the

324   Brownian motion.

325   It has been suggested that niche conservatism is reinforced by stabilizing selection due to

326   the presence of sympatric species which occupy adjacent ecological niches (Ackerly, 2003;

327   Losos, 2008). Despite soil is one of the most densely populated habitats on Earth, trophic niche

328   conservatism is not evident. Presumably, the heterogeneous nature of soil provides an array of

329   microhabitats varying in space, size and time, and therefore reduces competitive interactions

330   between species (Maaß, Maraun, Scheu, Rillig, & Caruso, 2015; Nielsen et al., 2010). Besides,

331   the soil environment limits mobility and sensing of chemical cues by predators / consumers,

332   which complicates selective feeding on specific food resources. 'Convergence' in Δ^{13}C values in

333   different taxa suggests that different types of organic compounds (plant tissues or microbially

334   processed detritus; Potapov et al., 2018) are utilized by an array of different lineages of

335   consumers resulting in functional redundancy. Resource specialization such as feeding on

336   different organic matter compounds, therefore is unlikely to drive evolutionary adaptations in

337   soil invertebrates, suggesting that it is relatively easy to switch between herbivory and detritivory

338   or between preying on herbivores and decomposers. Such switches have been shown e.g., for

339   species of Collembola (Endlweber, Ruess, & Scheu, 2009), Chilopoda (Klarner et al., 2017) and

340   Elateridae (Samoylova & Tiunov, 2017).

341   The stronger taxonomic signal in Δ^{15}N as compared to Δ^{13}C values suggests that

342   switching between prey of different trophic levels is evolutionary difficult resulting in taxa being

343   conserved within their trophic level. Despite there are examples of predatory species in

344   detritivore lineages such as Collembola (Hopkin, 1997; Potapov et al., 2016) and Oribatida

345   (Heidemann et al., 2014; Maraun et al., 2011), they likely represent only a minority of the

346   species of these groups. Notably, isotopic dissimilarity increased steadily from the species to the

347   class level, but decreased thereafter, suggesting that the differences in trophic level between taxa

348   were established early in the evolution of these lineages, i.e. during the colonisation of land by

349   the major arthropod lineages, and diversification within these lineages was associated by

350   refinement of trophic niches (Rota-Stabelli et al., 2013; Schaefer, Norton, Scheu, & Maraun,

351   2010).

352

353   *Taxonomic sufficiency in soil food-web studies*

354   Species is a keystone but one of the most debated concepts in biology. For instance, the

355   increasing recognition of cryptic species challenges morphology as the criterion for species

356   delineation (Fišer, Robinson, & Malard, 2018). However, virtually all animal and plant taxa are

357   described based on morphology (Cook, Edwards, Crisp, & Hardy, 2010). Taxonomists delineate

358   supraspecific taxa from each other in order to establish a system of morphologically consistent

359   units. Normal and unimodal distributions of isotopic niches of genera and even families, suggest

360   that the taxonomic system developed for soil invertebrates is consistent also in ecological

361   functions and thus may be used in ecological studies. This, however, needs to be done with

362   caution since each question addressed may deserve its own level of taxonomic resolution

363   (Bhusal, Kallimanis, Tsiafouli, & Sgardelis, 2014; Timms et al., 2013). To facilitate selection of

364   the adequate taxonomic level for respective research questions we provide a list of mean Δ^{13}C

365   and Δ^{15}N values of soil invertebrates from temperate forests from species to class level of

366   taxonomic resolution and classified the records according to their reliability and trophic

367   flexibility in the Appendix (Tables S1-S4).

368   Among taxa, maximum information on the structure of trophic niches is obtained at the

369   species level of taxonomic resolution. Nevertheless, our data suggest that species identity in soil

370   communities provides little additional information relative to the respective genera. In 92% of

371   cases stable isotope composition of congeneric species was not significantly different and the

372   mean offset of populations within genera was only 0.1‰ higher than that of populations within

373   species. For instance, trophic niches in congeneric species of Chilopoda and Lumbricidae were

374   shown to be similar (Ferlian, Scheu, & Pollierer, 2012; Schmidt, Curry, Dyckmans, Rota, &

375   Scrimgeour, 2004). Also, congeneric species of Collembola and Oribatida typically have similar

376   stable isotope composition, although there are exceptions (Potapov et al., 2016; Schneider et al.,

377   2004). The cases in which the stable isotope composition of congeneric species differed

378   significantly (8%) were distributed across a variety of taxa including Oribatida, Collembola and

379   Formicidae (see Table S2). Niche differentiation among congeneric species may in part be

380   explained by morphological variability within genera, pointing to the need to disclose

381   relationships between morphological traits and feeding habits of soil invertebrates in future

382   studies (Malcicka, Berg, & Ellers, 2017; Potapov et al., 2016).

383   The rather small loss of information on trophic niches when using genera instead of

384   species in large was due to the high variability in stable isotope composition among populations

385   within species, which was emphasized before (Lehmitz & Maraun, 2016; Tillberg, McCarthy,

386   Dolezal, & Suarez, 2006; Zalewski et al., 2014). A recent study based on molecular gut content

387   analysis of three morphologically similar species of Collembola showed high diversity and

388   temporal variability in their fungal diet, but no significant differences in feeding habits were

389   found between species across locations and seasons (Anslan, Bahram, & Tedersoo, 2018).

390   Clearly, the trophic niche of species / taxa in a given community will always depend on the

391   biotic and abiotic environment and it is preferable to explicitly study the trophic niches of

392   species of the community investigated.

393         $\Delta^{13}C$ and $\Delta^{15}N$ values of species within families were not different in 80 - 60% of the

394   cases indicating that trophic niches of species are not well represented using families as

395   functional units as suggested e.g., for Mesostigmata in grasslands (Walter & Ikonen, 1989). The

396   trophic differentiation of species / taxa showed different trends in the three major lineages of soil

397   arthropods. Chelicerata (represented by Arachnida) and Myriapoda were enriched in ^{13}C and ^{15}N

398   as compared to Hexapoda, with the enrichment being on average 0.8‰ for both $\Delta^{13}C$ and $\Delta^{15}N$

399   values. However, large variations in ^{13}C and ^{15}N values suggest large variability in trophic niches

400   in each of the three lineages. Myriapoda in our dataset comprised two classes, i.e. Diplopoda and

401   Chilopoda feeding on very different resources, i.e. dead organic matter and animal prey,

402   respectively. Arachnida in our dataset comprised Oribatida, predominantly living as detritivores

403   and fungal feeders, and Mesostigmata and Araneae living as predators. In Hexapoda the trophic

404   niche varied between classes (Insecta vs. Collembola) and also between orders. Presumably, this

405   is related to the high diversity of Hexapoda exceeding that of Arachnida and Myriapoda (Zhang,

406   2011). Notably, the $\Delta^{13}C$ and $\Delta^{15}N$ values of species-rich taxa such as Coleoptera varied

407   markedly due to including taxa of very different trophic position such as Carabidae living mainly

408   as predators and Tenebrionidae living mainly as detritivores (Table S1). This supports the notion

22

409   that species- and genus-rich families need to be resolved at higher taxonomic resolution to

410   adequately represent their trophic position (Jiang et al., 2013; Timms et al., 2013). A wider range

411   of niches in species-rich taxa illustrates a close link between morphological and ecological

412   diversification. The diversification of lineages is driven primarily by the occupation of new niche

413   space (Gavrilets & Losos, 2009; Mahler, Revell, Glor, & Losos, 2010). During the long

414   evolutionary history of old lineages, some lineages, such as Insecta, managed to exploit novel

415   resources / prey species thereby radiating markedly, whereas other lineages, such as Diplopoda

416   and Chilopoda, remained confined to their trophic niche and remained less species rich.

417   Therefore, using supraspecific taxa as functional units in ecological studies needs to consider the

418   degree of ecological diversification of the different lineages rather than using a uniform

419   taxonomic level across the taxa studied. Including $\Delta^{13}C$ and $\Delta^{15}N$ values as continuous variables

420   allows to refine classic food-web models based on discrete trophic levels and to include

421   omnivory and intraguild predation which are of significant importance for food web dynamics in

422   soil (Digel et al., 2014).

423

424   **Conclusions**

425   Soil animals that are sharing similar taxonomic affiliation and therefore morphology are

426   also sharing similar trophic niches. Blomberg's K criteria suggest that feeding on different basal

427   resources (plants or detritus) is 'convergent' across different lineages of soil invertebrates

428   whereas the occupation of different trophic levels followed the Brownian-motion taxonomic

429   model. We found no evidence for strict trophic niche conservatism in soil invertebrates.

430   Although higher taxonomic resolution provides more information on feeding habits, in

431   92% of the cases stable isotope values of congeneric species of soil invertebrates did not differ

432   significantly. This small loss of information was due to the high variability in stable isotope

433   composition between populations within species. Nevertheless, trophic niches of populations

434   within genera and families fitted normal and unimodal distributions, suggesting trophic

435 consistency of these supraspecific taxa. Supraspecific taxa can serve as meaningful functional

436 units in ecological studies, but the choice of taxonomic resolution needs to be adopted based on

437 the particular research question and taxonomic group. In particular, diverse groups, such as

438 Oribatida, Collembola and Coleoptera, deserve higher taxonomic resolution. Further studies need

439 to explore how and why trophic radiation varies between lineages. The compiled list of mean

440 Δ^{13}C and Δ^{15}N values of taxa can be combined with other literature data in order to infer feeding

441 habits of soil invertebrates and move towards more realistic soil food-web models.

442

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447

Author contributions statement

449 AP analysed the data and worked on the drafts. AP, AT and SS conceived and refined the ideas.

450 All authors contributed critically to the drafts and gave final approval for publication.

451

Data accessibility statement

453 Should the manuscript be accepted, the data supporting the results will be archived in a public

454 repository and the data DOI will be included at the end of the article.

455

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