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Trophic consistency of supraspecific taxa in belowground invertebrate communities

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Abstract

1. Animals that have similar morphological traits are expected to share similar ecological niches. This statement applies to individual animals within a species and thus species often serve as the functional units in ecological studies. Species are further grouped into higher-ranked taxonomic units based on their morphological similarity and thus are also expected to be ecologically similar. On the other hand, theory predicts that strong competition between closely related species can lead to differentiation of ecological niches. Due to a high diversity and limited taxonomic expertise, soil food webs are often resolved using supraspecific taxa such as families, orders or even classes as functional units.
2. Here we for the first time empirically tested the trophic consistency of supraspecific taxa across major lineages of temperate forest soil invertebrates: Annelida, Chelicerata, Myriapoda, Crustacea and Hexapoda. Published data on stable isotope compositions of carbon and nitrogen were used to infer basal resources and trophic level, and explore the relationship between taxonomic and trophic dissimilarity of local populations.
3. Genera and families had normal and unimodal distributions of isotope niches, suggesting that supraspecific taxa are trophically consistent. The isotopic niche of populations across different localities is better predicted by species than by supraspecific taxa. However, within the same genus, the effect of species identity on stable isotope composition of populations was not significant in 92% of cases. The link to basal resources, i.e. plants or detritus, was convergent in different lineages, while trophic levels followed the Brownian motion taxonomic model. Virtually none of the studied taxa showed pronounced trophic niche conservatism within a lineage.

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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 $\Delta^{13}C$ and $\Delta^{15}N$ 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

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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.

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Ecological similarity among related species usually is investigated in respect to morphology, physiology and behaviour of organisms, with behavioural adaptations being evolutionarily more labile (Blomberg, Garland, Ives, & Crespi, 2003; Böhning-Gaese & Oberrath, 1999). As a complex trait, trophic niches may either be similar or differ considerably among closely related taxa. Feeding habits of an organism are not strongly related to its taxonomic position since similar feeding strategies occur in many lineages (i.e., convergence in trophic positions). Pronounced trophic-niche differentiation between species was shown for dominant groups of soil detritivores (Chahartaghi, Langel, Scheu, & Ruess, 2005; Schneider et al., 2004). Nevertheless, supraspecific taxa often are used as trophic species (nodes) in soil food web models (Berg & Bengtsson, 2007; de Ruiter, Neutel, & Moore, 1994; de Vries et al., 2013). Despite trophic guilds conceptually are independent of taxonomy, taxonomically related species usually are included in the same trophic guild (Simberloff & Dayan, 1991). This assumption recently has received empirical support in freshwater (catfishes) and soil (springtails) detritivores, for which trophic niches were shown to differ between supraspecific taxa (Lujan, Winemiller, & Armbruster, 2012; Potapov, Semenina, Korotkevich, Kuznetsova, & Tiunov, 2016). Moreover, it has been argued that ecological links between species (e.g., via trophic interactions) often are related to their phylogenetic position (Gómez, Verdú, & Perfectti, 2010; Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007). In marine communities predators tend to consume phylogenetically related prey species and prey tend to be consumed by phylogenetically related predators (Eklöf & Stouffer, 2016). However, it remains unclear if this also holds true for taxa in terrestrial belowground communities with less pronounced size structure and high frequency of omnivorous species able to switch diet depending on its availability (Digel, Curtsdotter, Riede, Klarner, & Brose, 2014).

Three scenarios are suggested to explain the relationship between taxonomic relatedness of taxa and their dissimilarity in trophic niche. The ‘limiting similarity’ hypothesis suggests that morphological similarity of closely related taxa results in strong competition (Darwin, 1876;

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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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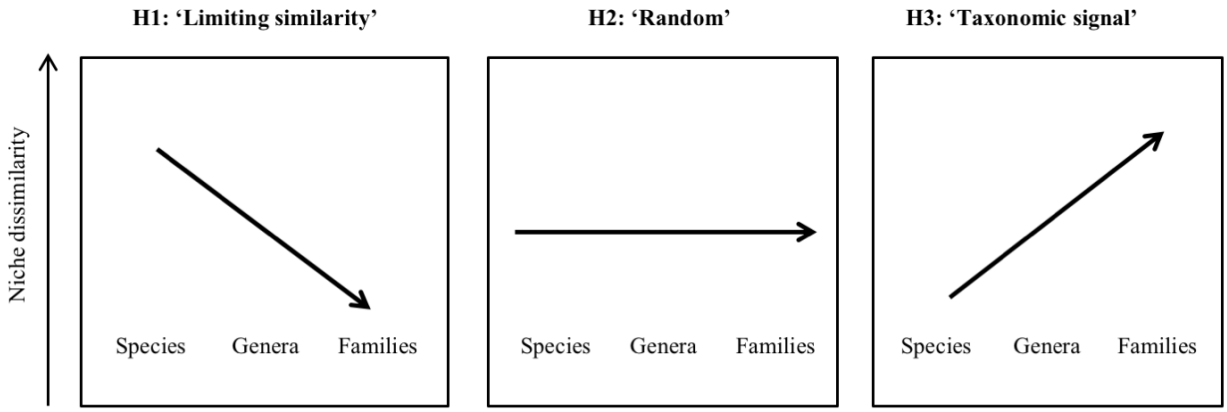

111

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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niche of species (Newsome, Martinez del Rio, Bearhop, & Phillips, 2007; Rodríguez & Herrera, 2013) and provide information on their basal resources and trophic level, respectively (Boecklen, Yarnes, Cook, & James, 2011; Martinez del Rio, Wolf, Carleton, & Gannes, 2009). In soil food webs ^{13}C concentrations increase with decomposition of plant material, while ^{15}N concentrations increase with trophic level (Potapov et al., 2018). Based on these findings, we used published data on stable isotope composition of carbon and nitrogen to explore the trophic niches of major belowground arthropod lineages at different taxonomic levels. The following main questions were addressed: (1) Is there evidence for trophic niche conservatism (*sensu* Losos, 2008) in soil animal taxa? (2) Are supraspecific taxa in soil communities trophically consistent? (3) How much information about basal resources and trophic level of soil animals do we lose by using supraspecific taxa instead of species?

Methods

The analysis was based on a large compilation of published data on stable isotope composition of soil invertebrates from temperate forests (Potapov et al., 2018). In the dataset, only records identified to species or genus level were included resulting in 415 species from 21 orders and 5 high-order taxa: Annelida, Chelicerata, Myriapoda, Crustacea and Hexapoda (Table S1). Each data record in the dataset comprised average stable isotope composition of species / taxa sampled at a local community with some species investigated at different localities / ecosystems resulting in a total of 961 local populations. Stable isotope compositions of carbon and nitrogen were normalized to the local leaf litter to account for inter-ecosystem variations and denoted as $\Delta^{13}C$ and $\Delta^{15}N$ values (Klarner et al., 2014). Further, each record was classified into the following taxonomic levels: Phylum, Subphylum, Class, Order, Family, Genus and Species, according to (Zhang, 2011). Although arbitrarily defined and varying between taxonomic groups, supraspecific taxa form a hierarchical system representing different levels of aggregation of species.

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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

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between taxonomic levels using Nemenyi test in package *PMCMR* (Pohlert, 2014) and general linear hypothesis for multiple comparisons in package *multcomp* (Hothorn, Bretz, & Westfall, 2008), respectively. Both tests showed similar results; only results of the former are presented.

To test the trophic consistency of supraspecific taxa we visually explored the distributions of $\Delta^{13}C$ or $\Delta^{15}N$ values of all taxa at different taxonomic levels. To analyse all taxa together, we first calculated mean $\Delta^{13}C$ and $\Delta^{15}N$ values for all taxa at all taxonomic levels. Next, we calculated offsets of $\Delta^{13}C$ and $\Delta^{15}N$ values for populations from the mean values for all parental taxa. For example, to construct data distribution for the 'family' level, offsets for all populations were calculated using the mean values of the corresponding 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.). Offsets were compared between taxonomic levels using general linear hypothesis for multiple comparisons in package *multcomp*.

To estimate how much information about basal resources and trophic level of soil animals is lost by using supraspecific taxa instead of species, we checked whether different species within the same parental taxon occupy significantly distinct trophic niches. For doing that, we inspected the effect of 'species identity' on the $\Delta^{13}C$ or $\Delta^{15}N$ values of populations using one-way ANOVAs. Only taxa with two or more nested taxa of the lower taxonomic level were included in the analysis. Thereafter, results of the ANOVA (effect of species / no effect of species as a binomial variable) were used to calculate percentage of taxa with significant species effect at different levels of taxonomic resolution.

Lastly, we inspected mean $\Delta^{13}C$ and $\Delta^{15}N$ values for individual subphyla, classes and orders across three major lineages of soil arthropods that were well represented in the dataset, i.e. Chelicerata, Myriapoda and Hexapoda. In this analysis we used the expanded dataset of 1146 populations including those not identified to species level (Table S1).

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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‰.

213

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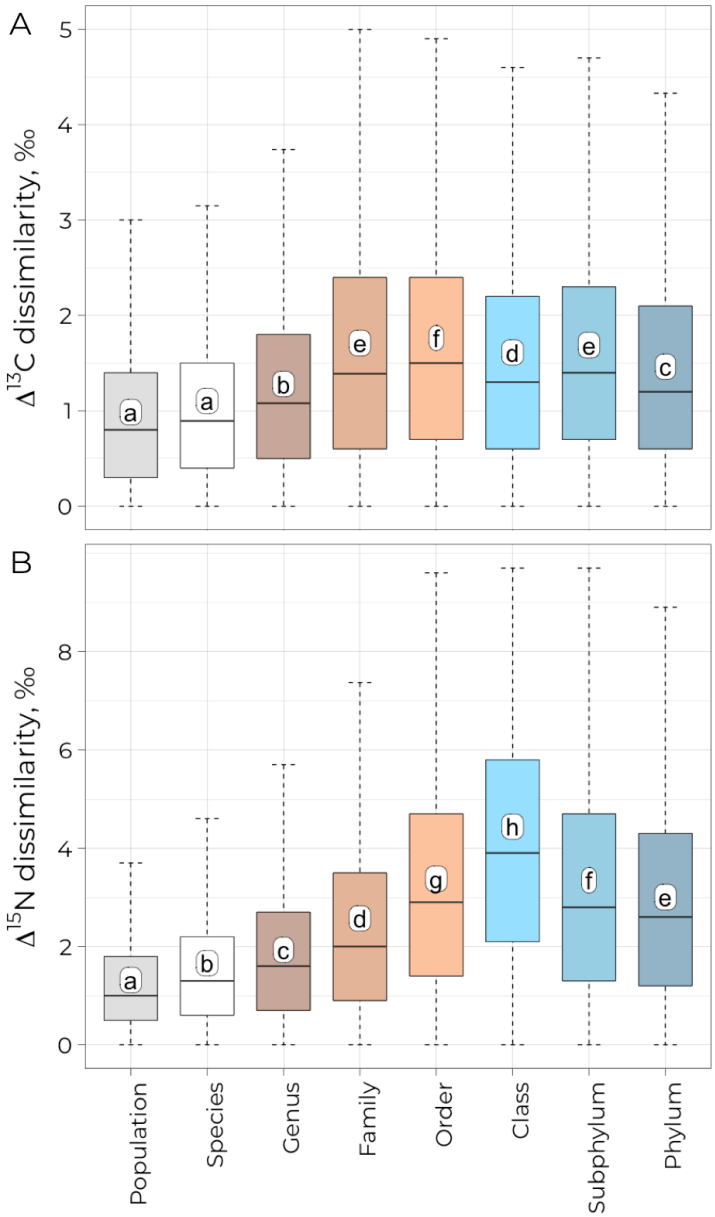

Figure 2. Isotopic dissimilarity as related to taxonomic dissimilarity in soil invertebrates. Isotopic dissimilarity was measured as Euclidean distance in $\Delta^{13}C$ or $\Delta^{15}N$ values between populations. Taxonomic dissimilarity is reflected by eight levels of taxonomic resolution: For instance, '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):

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224 groups sharing the same letter are not significantly different. Isotopic and taxonomic
225 dissimilarity were significantly correlated for $\Delta^{15}N$ but not for $\Delta^{13}C$ values (see text).
226
227 The variability of both $\Delta^{13}C$ and $\Delta^{15}N$ values increased continuously with decreasing
228 level of taxonomic resolution. However, taxa from species to family level for $\Delta^{15}N$ and from
229 species to order level for $\Delta^{13}C$ 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 $\Delta^{13}C$ and $\Delta^{15}N$ values, respectively (Fig. 3C, D). Average
233 absolute offsets of $\Delta^{13}C$ values were 0.6‰ for species and 0.8‰ for families; average offsets of
234 $\Delta^{15}N$ values were 0.9‰ for species and 1.3‰ for families.
235

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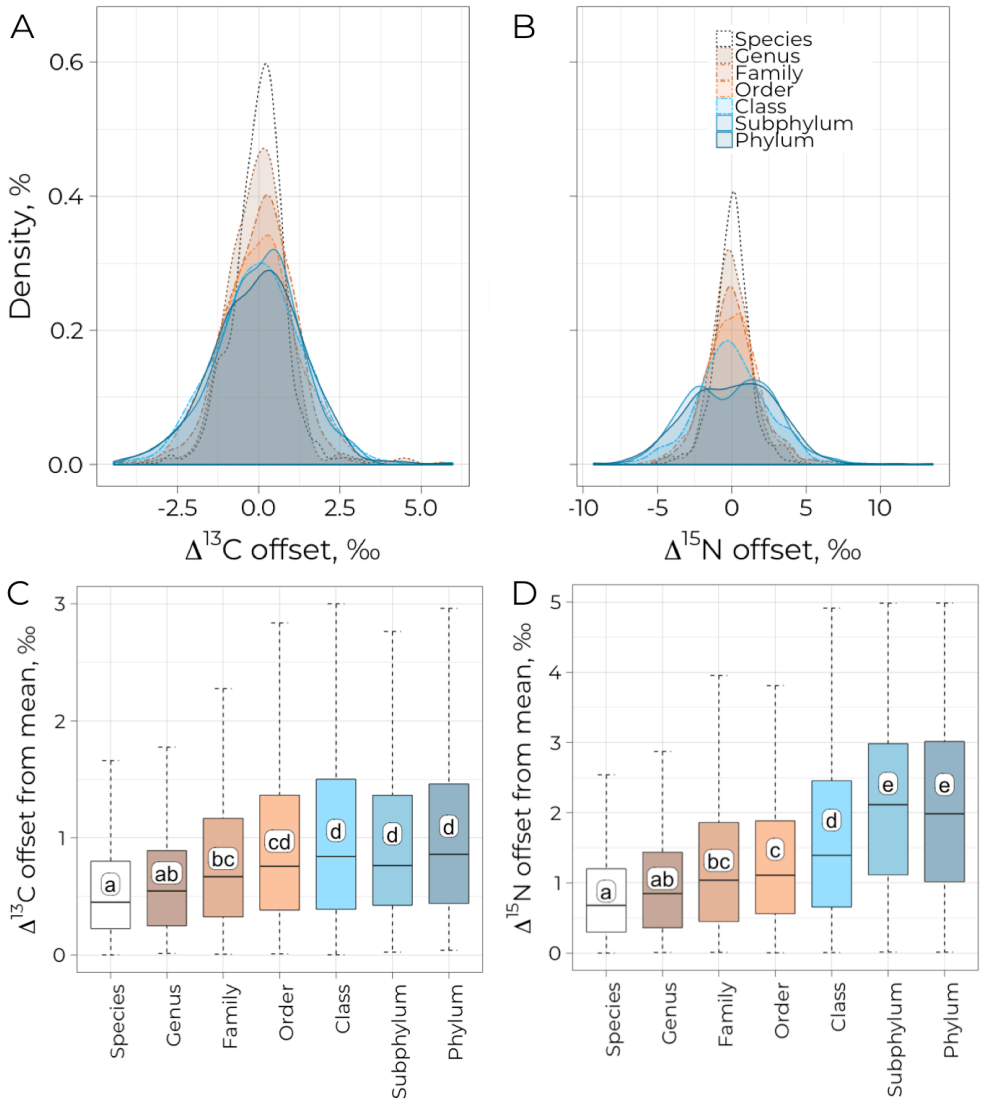

Figure 3. Offsets in stable isotope composition of populations from means of parental taxa of different taxonomic level. Offsets were calculated as mean $\Delta^{13}C$ (A, C) and $\Delta^{15}N$ values (B, D) for populations minus the mean value for parental taxonomic units, all data are plotted together. 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.

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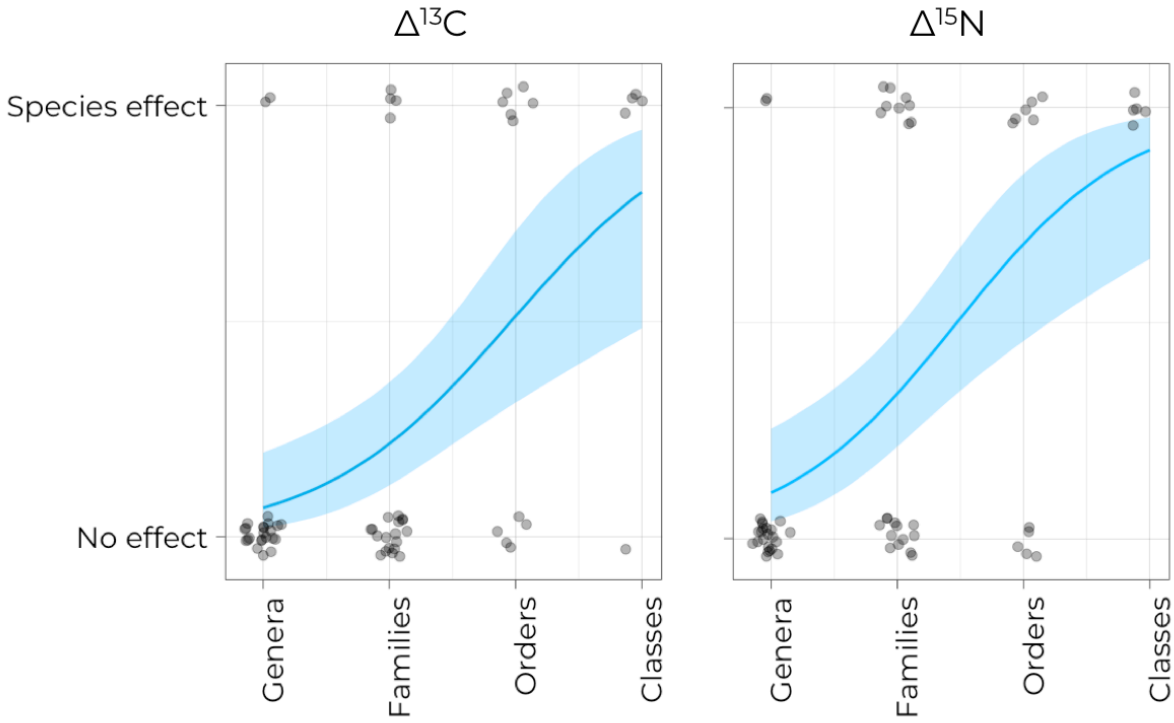
248 To estimate, to what extent information is lost by using supraspecific taxa instead of
249 species, we tested for the effect of species on $\Delta^{13}C$ and $\Delta^{15}N$ values within each supraspecific
250 taxa from genus to class level. Within genera, the effect of species was not significant 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).



254

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,

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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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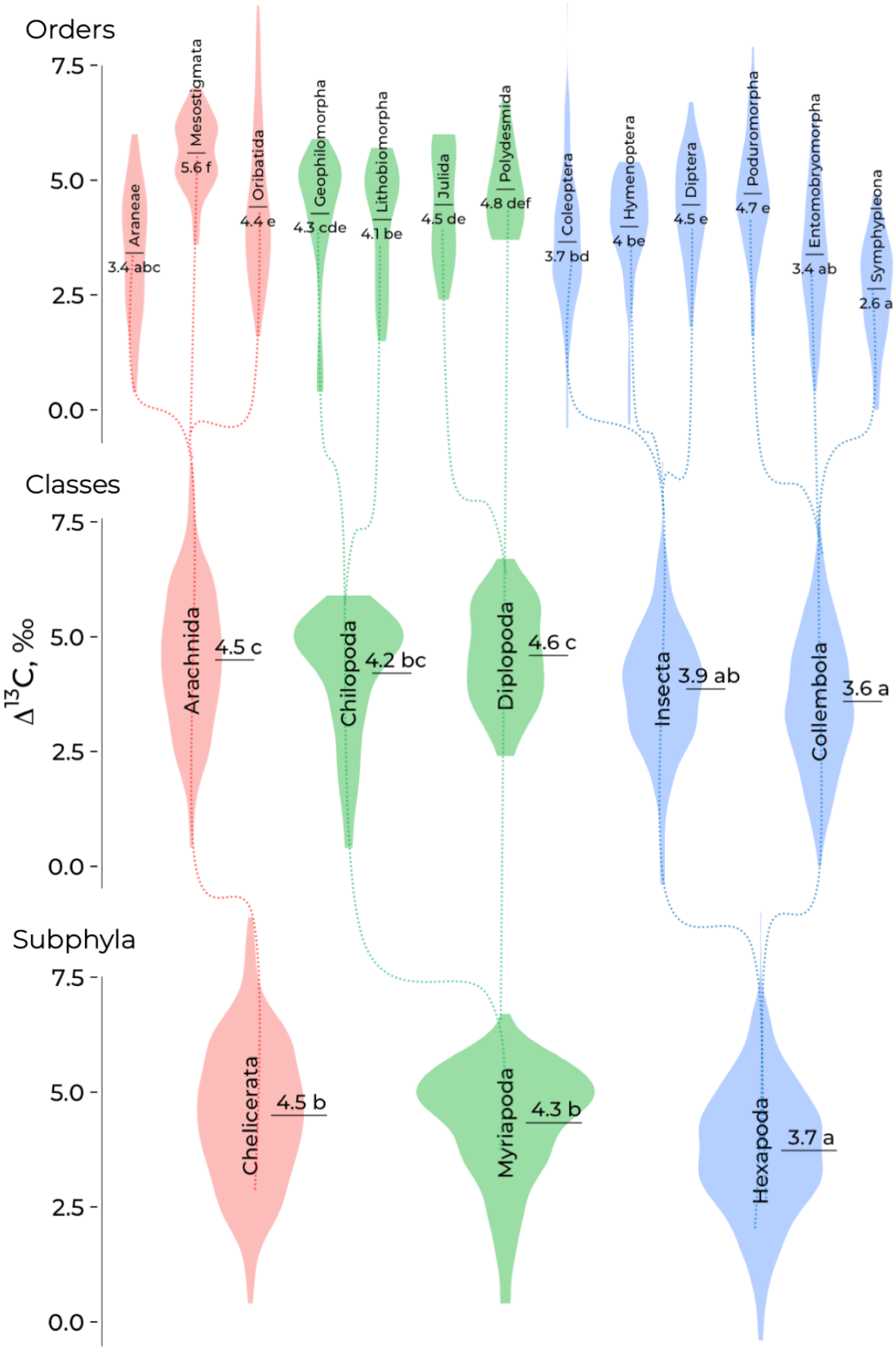

Figure 5. **$\Delta^{13}C$ values of subphyla, classes and orders in three main lineages of soil arthropods, Chelicerata, Myriapoda and Hexapoda.** Data on populations are presented in the form of violin plots (mirrored Kernel density estimation). Mean values are shown with

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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.

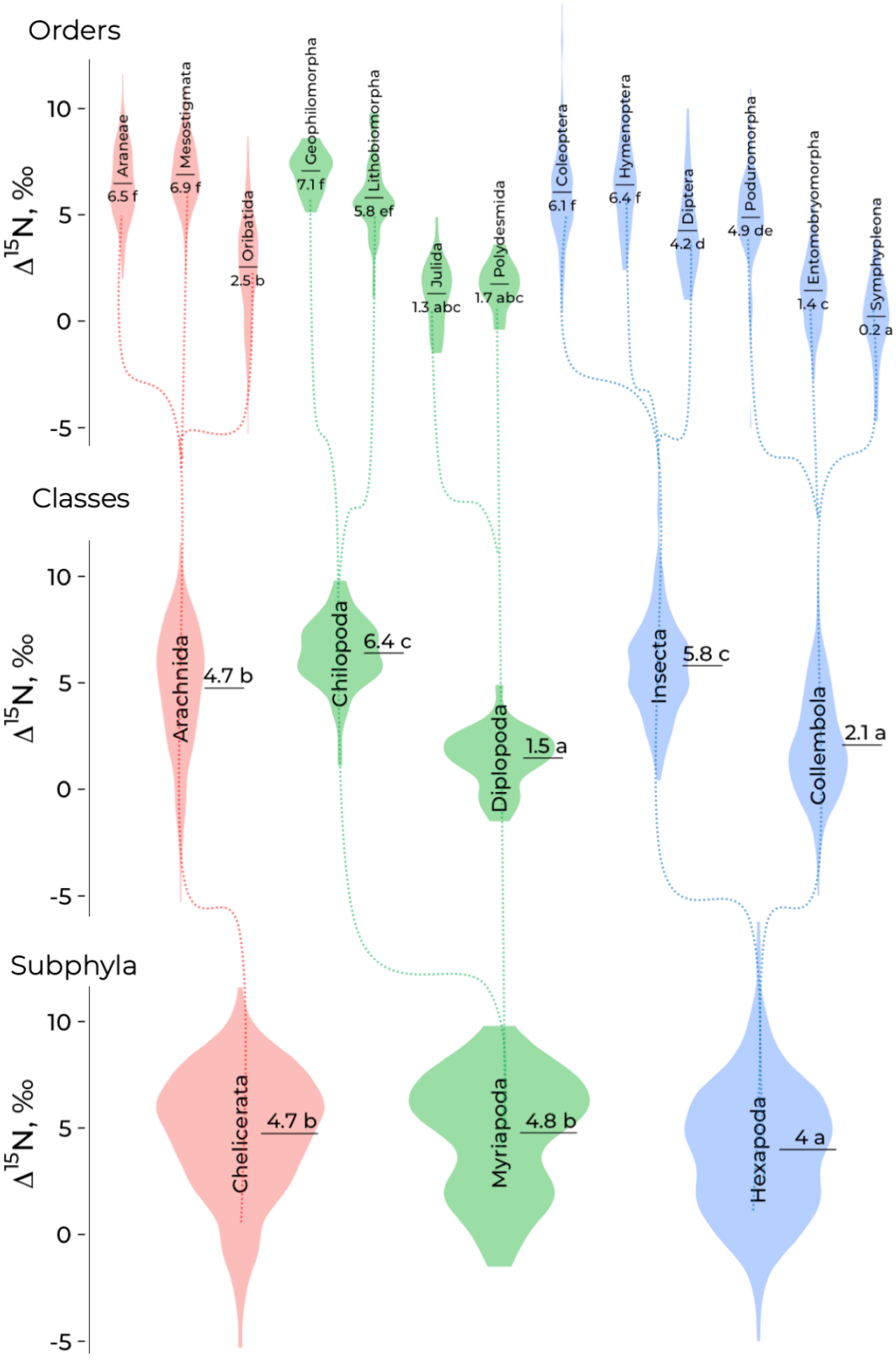

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Figure 6. **Δ^{15}N values of subphyla, classes and orders in three main lineages of soil arthropods, Chelicerata, Myriapoda and Hexapoda.** Data on populations are presented in the form of violin plots (mirrored Kernel density estimation). Mean values are shown with horizontal segments and numbers; mean values sharing the same letter within a taxonomic level are not significantly different (general linear hypothesis for multiple comparisons). Colours denote different lineages, dotted lines denote taxon hierarchy.

Discussion

Supraspecific taxa are often assumed to comprise species that perform similar ecological function. However, this assumption has not been formally tested. Using stable isotope analysis we found strong support that dissimilarity in trophic level in soil invertebrates is related to taxonomic dissimilarity, supporting the 'taxonomic signal' hypothesis. Trophic level (as indicated by Δ^{15}N values) was well reflected by taxonomic units, which was mainly due to the fact that high-order taxa (i.e., class and order level) encompass either detritivores or predators. The pattern in Δ^{13}C values supported 'random' hypothesis, indicating that similar basal resources can be utilized by various taxonomic groups with different types of body organisation.

The distribution of Δ^{13}C and Δ^{15}N values in supraspecific taxa, at least for genera and families, were on average unimodal and close to normal, indicating that supraspecific taxa are trophically consistent. Depending on the research question, our finding validates the usage of supraspecific taxa as functional units in ecological studies if identification to species level is not feasible. As expected low-rank taxonomic units provide a higher precision and a lower chance of information loss. Still, due to a high variability within species, the effect of species identity on Δ^{13}C and Δ^{15}N values of populations was not significant in 92% of the tested genera.

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

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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,

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which complicates selective feeding on specific food resources. 'Convergence' in $\Delta^{13}C$ values in different taxa suggests that different types of organic compounds (plant tissues or microbially processed detritus; Potapov et al., 2018) are utilized by an array of different lineages of consumers resulting in functional redundancy. Resource specialization such as feeding on different organic matter compounds, therefore is unlikely to drive evolutionary adaptations in soil invertebrates, suggesting that it is relatively easy to switch between herbivory and detritivory or between preying on herbivores and decomposers. Such switches have been shown e.g., for species of Collembola (Endlweber, Ruess, & Scheu, 2009), Chilopoda (Klarner et al., 2017) and Elateridae (Samoylova & Tiunov, 2017).

The stronger taxonomic signal in $\Delta^{15}N$ as compared to $\Delta^{13}C$ values suggests that switching between prey of different trophic levels is evolutionary difficult resulting in taxa being conserved within their trophic level. Despite there are examples of predatory species in detritivore lineages such as Collembola (Hopkin, 1997; Potapov et al., 2016) and Oribatida (Heidemann et al., 2014; Maraun et al., 2011), they likely represent only a minority of the species of these groups. Notably, isotopic dissimilarity increased steadily from the species to the class level, but decreased thereafter, suggesting that the differences in trophic level between taxa were established early in the evolution of these lineages, i.e. during the colonisation of land by the major arthropod lineages, and diversification within these lineages was associated by refinement of trophic niches (Rota-Stabelli et al., 2013; Schaefer, Norton, Scheu, & Maraun, 2010).

Taxonomic sufficiency in soil food-web studies

Species is a keystone but one of the most debated concepts in biology. For instance, the increasing recognition of cryptic species challenges morphology as the criterion for species delineation (Fišer, Robinson, & Malard, 2018). However, virtually all animal and plant taxa are described based on morphology (Cook, Edwards, Crisp, & Hardy, 2010). Taxonomists delineate

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supraspecific taxa from each other in order to establish a system of morphologically consistent units. Normal and unimodal distributions of isotopic niches of genera and even families, suggest that the taxonomic system developed for soil invertebrates is consistent also in ecological functions and thus may be used in ecological studies. This, however, needs to be done with caution since each question addressed may deserve its own level of taxonomic resolution (Bhusal, Kallimanis, Tsiafouli, & Sgardelis, 2014; Timms et al., 2013). To facilitate selection of the adequate taxonomic level for respective research questions we provide a list of mean $\Delta^{13}C$ and $\Delta^{15}N$ values of soil invertebrates from temperate forests from species to class level of taxonomic resolution and classified the records according to their reliability and trophic flexibility in the Appendix (Tables S1-S4).

Among taxa, maximum information on the structure of trophic niches is obtained at the species level of taxonomic resolution. Nevertheless, our data suggest that species identity in soil communities provides little additional information relative to the respective genera. In 92% of cases stable isotope composition of congeneric species was not significantly different and the mean offset of populations within genera was only 0.1‰ higher than that of populations within species. For instance, trophic niches in congeneric species of Chilopoda and Lumbricidae were shown to be similar (Ferlian, Scheu, & Pollierer, 2012; Schmidt, Curry, Dyckmans, Rota, & Scrimgeour, 2004). Also, congeneric species of Collembola and Oribatida typically have similar stable isotope composition, although there are exceptions (Potapov et al., 2016; Schneider et al., 2004). The cases in which the stable isotope composition of congeneric species differed significantly (8%) were distributed across a variety of taxa including Oribatida, Collembola and Formicidae (see Table S2). Niche differentiation among congeneric species may in part be explained by morphological variability within genera, pointing to the need to disclose relationships between morphological traits and feeding habits of soil invertebrates in future studies (Malcicka, Berg, & Ellers, 2017; Potapov et al., 2016).

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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

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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

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consistency of these supraspecific taxa. Supraspecific taxa can serve as meaningful functional units in ecological studies, but the choice of taxonomic resolution needs to be adopted based on the particular research question and taxonomic group. In particular, diverse groups, such as Oribatida, Collembola and Coleoptera, deserve higher taxonomic resolution. Further studies need to explore how and why trophic radiation varies between lineages. The compiled list of mean $\Delta^{13}C$ and $\Delta^{15}N$ values of taxa can be combined with other literature data in order to infer feeding habits of soil invertebrates and move towards more realistic soil food-web models.

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Author contributions statement

AP analysed the data and worked on the drafts. AP, AT and SS conceived and refined the ideas. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility statement

Should the manuscript be accepted, the data supporting the results will be archived in a public repository and the data DOI will be included at the end of the article.

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