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## **Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages**

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3 **Environmental filtering vs. resource-based niche partitioning in diverse soil animal**

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7

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21 **Abstract**

22 Terrestrial invertebrates constitute most of described animal biodiversity and soil is a  
23 major reservoir of this diversity. In the classical attempt to understand the processes  
24 supporting biodiversity, ecologists are currently seeking to unravel the differential roles  
25 of environmental filtering and competition for resources in niche partitioning processes:  
26 these processes are in principle distinct although they may act simultaneously, interact  
27 at multiple spatial and temporal scales, and are often confounded in studies of soil  
28 communities. We used a novel combination of methods based on stable isotopes and  
29 trait analysis to resolve these processes in diverse oribatid mite assemblages at spatial  
30 scales at which competition for resources could in principle be a major driver. We also  
31 used a null model approach based on a general neutral model of beta diversity. A large  
32 and significant fraction of community variation was explainable in terms of linear and  
33 periodic spatial structures in the distribution of organic C, N and soil structure: species  
34 were clearly arranged along an environmental, spatially structured gradient. However,  
35 competition related trait differences did not map onto the distances separating species  
36 along the environmental gradient and neutral models provided a satisfying  
37 approximation of beta diversity patterns. The results represent the first robust evidence  
38 that in very diverse soil arthropod assemblages resource-based niche partitioning plays a  
39 minor role while environmental filtering remains a fundamental driver of species  
40 distribution.

41

42 **Keywords: stable isotopes, trophic niche, community structure, neutral theory, soil**  
43 **microarthropods, oribatid mites**

44

45 **1. Introduction**

46 The classical view of communities and the assembly processes forming them has  
47 historically been dominated by the approaches pioneered by the founders of niche  
48 theories. More recently classical theories have been rethought to include stochastic  
49 processes such as those related to stochastic demographic fluctuations and dispersal  
50 dynamics, which for example are the only mechanisms postulated in neutral theories  
51 (Bell, 2001; Hubbell, 2001). Stochastic processes have also been included in the more  
52 general framework of metacommunity theories (Cottenie, 2005; Leibold et al., 2004),  
53 which focus on the spatial nature of assembly processes and extend the principles of  
54 metapopulation dynamics to community ecology. For example, processes such as  
55 dispersal create spatial patterns in species distribution. These spatial patterns do not  
56 depend on spatial structure in the distribution of environmental variables although the  
57 processes generating these patterns may interact with environmentally driven processes  
58 (Smith and Lundholm, 2010). Biotic interaction, too, can create spatial patterns (e.g.,  
59 segregation of competing species in fairly homogeneous environments), regardless of  
60 other spatial processes (Gotelli, 2000; Gotelli et al., 2010). Environmental gradients  
61 determine spatial patterns in species distribution by sorting species according to their  
62 environmental requirements (e.g., dry-tolerant vs. moist tolerant species) and for a long  
63 time community ecology has been synonymous with studying species distributions  
64 along such gradients (Morin, 2011).

65 These various processes are entangled in nature at multiple spatial scales but a key  
66 general point we analyse in this paper is that environmental filtering is one component  
67 of niche partitioning dynamics, which might or might not involve resource based niche  
68 partitioning due to competition for shared resources (Adler et al., 2013;  
69 HilleRisLambers et al., 2012; Hubbell, 2005; Kraft et al., 2014). Interestingly, the point  
70 of possible independence of environmental filtering and resource-based niche

71 partitioning has been made both by niche (HilleRisLambers et al., 2012; Kraft et al.,  
72 2014) and neutral theorists (Hubbell, 2005) in spite of the fact that several ecologists in  
73 practice continue to see niches in the sense of Grinnell, that is to say in terms of species  
74 environmental requirements (Chase and Leibold, 2003).

75 Invertebrates constitute most of animal biodiversity and soil is a major reservoir of this  
76 diversity. Soil animal community ecologists, following other animal and plant  
77 ecologists (Dornelas et al., 2006; Hubbell, 2001; Ritchie, 2009), for a long time have  
78 addressed taxonomically defined assemblages such as oribatid mites, collembolans or  
79 nematodes to unravel the mechanisms that allow species coexistence in very diverse  
80 systems (Wardle, 2002). Recently, microarthropods have also been investigated within  
81 the niche-neutral debates or the more general framework of metacommunity theories  
82 (Caruso et al., 2012; Lindo and Winchester, 2009; Nielsen et al., 2010; Salmon and  
83 Ponge, 2012). However, in recent years studies based on stable isotopes and molecular  
84 genetics have clearly shown that assemblages such as oribatid mites or collembolans  
85 actually consist of species that can range in diet from being decomposers of low quality  
86 organic matter to being top predators of nematodes (Heidemann et al., 2011; Maraun et  
87 al., 2011; Schneider et al., 2004). This fact implies a strong bias of previous studies in  
88 terms of how observed patterns can inform on underlying mechanisms. For example, if  
89 we test neutral theories against niche partitioning theories, we should test these within  
90 trophic levels (Hubbell, 2005), which challenges previous studies (Caruso et al., 2012;  
91 Gao et al., 2014; Lindo and Winchester, 2009; Nielsen et al., 2010). In general, there is  
92 little theoretical and empirical support for the hypothesis that soil animal communities  
93 are structured by niche dynamics based on competition (Gao et al., 2014; Wardle,  
94 2006), although several studies have shown that microarthropod communities are sorted  
95 by environmental gradients (Auclerc et al., 2009; Lindo and Winchester, 2009; Salmon  
96 and Ponge, 2012).

97 We addressed this general point by focusing on diverse soil oribatid mite assemblages  
98 from a dry grassland using a spatially explicit sampling design that allowed us minimise  
99 dispersal processes and focus on environmental filtering and niche partitioning based on  
100 food resources. Instead of focusing on taxonomic assemblages, we used the stable  
101 isotopes ratios  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$ , and for the first time focus community analysis on  
102 trophic assemblages within which competition for shared resources could be a key  
103 process. To further characterise species in terms of traits that can be related to  
104 competition for resources, we quantified body size and depth distribution and then  
105 defined a trait matrix. We used these data to test the hypothesis that species that were  
106 closer in space and time were more dissimilar and vice-versa (limiting similarity  
107 concept) than expected by chance. The assumption is that limiting similarity and/or trait  
108 trade-offs should be observed if resource based niche partitioning is a mechanism  
109 through which species coexist locally while competing for shared resources. Still,  
110 resource-based niche partition and environmental filtering may act simultaneously.  
111 Thus, species could also be sorted along environmental gradients either in relation to the  
112 measured traits or not. In fact, environmental filtering and resource-based niche  
113 partition could also be decoupled if competition is not taking place or is of minor  
114 importance. The rationale behind the test of these hypotheses is that demonstrating a  
115 clear link between trait differences and environmental distance is a key premise to  
116 unravel the mechanisms that allow species coexistence in rich communities (Adler et  
117 al., 2013).

118

## 119 **2. Materials and Methods**

### 120 *2.1 Study area and sampling strategy*

121 This study was conducted in dry grassland in a natural reserve in Mallnow, Lebus,  
122 (Brandenburg, Germany,  $52^{\circ}27.778'$  N,  $14^{\circ}29.349'$  E). This reserve has been managed

123 by low-intensity sheep grazing for at least 500 years and is dominated by *Festuca*  
124 *brevipila* (Poaceae). There are areas where grazing may not occur for one year or longer  
125 and plant diversity can be very high locally (e.g., > 40 species in a 10 x 10 m plot)  
126 although grasses such as *Festuca* spp. dominate the assemblage. In these areas, in April  
127 and October 2012 we took soil core samples (local communities) within two  
128 undisturbed plots of 15 x 15 m along the slope of a hillside, with the two plots about 20  
129 m apart. The two plots represented spatial replicates of a steep soil textural gradient  
130 running from the sandy-loamy soil uphill to highly sandy soil downhill. Main soil  
131 parameters such as pH, water content, organic C and N varied along the gradient, in  
132 some case with remarkable variation (Supplementary Material, Table S1). Sampling  
133 was replicated in the two main seasons (spring and autumn). To standardise the local  
134 soil arthropod community, we took soil cores (5 cm diameter, 10 cm deep) centred on  
135 the grass *Festuca brevipila*, which was by far the most abundant species in the area (in  
136 some case cover > 70%). Twenty randomly positioned samples per plot were collected  
137 in each season (total of 80 local communities) and the position of each sample was  
138 recorded in the UTM system.

139

## 140 *2.2 Sample processing and analysis*

141 Each soil core was cut into five 2 cm slices to quantify species depth distribution.  
142 However, the soil core was the main unit of analysis and we defined the local assemblage  
143 as the species inhabiting this unit. Eventually, each species was assigned a depth score  
144 based on the weighted average of its depth distribution and depth was treated as a species  
145 trait. The soil fauna was extracted in a Macfadyen apparatus for two weeks. All  
146 arthropods were preserved in 70% ethanol and the adult oribatids morphologically  
147 determined to species level (Weigmann, 2006). Body lengths were measured for each  
148 individual under a dissecting microscope (Leica M 165, Wetzlar, Germany) using the

149 software LAS. Each species was assigned a size score based on the average length  
150 obtained from a number of replicated measurements (mean number of measurements per  
151 species = 85; median number of measurements per species = 30). Soil water content was  
152 measured as the difference between the weights of fresh vs. dried soil (soil dry weight,  
153 SWD), with samples collected at field capacity. Soil pH was measured in a soil-water  
154 suspension, where 3 g of soil and 15 ml distilled H<sub>2</sub>O were mixed and stirred. The  
155 measurement was conducted in the supernatant until the value remained constant.  
156 Organic carbon (C) and total nitrogen (N) were measured by direct combustion of 30 mg  
157 of soil in a Euro EA Element Analyzer (HEKAtech GmbH, Wegberg, Germany). Mean  
158 weight diameter (MWD) was calculated as the weighted sum of the proportion of soil  
159 particles and aggregates in each size class (2-4 mm, 1-2 mm, 0.5-1 mm and 0.2-0.5 mm),  
160 determined by dry sieving of the soil.

161

### 162 *2.3 Stable isotope analysis*

163 Specimens were transferred into tin capsules. Rare (e.g. *Carabodes willmanni*) or smaller-  
164 sized species (e.g. *Micropopia minus*) required the pooling of several individuals to reach  
165 the biomass necessary to the analysis. After drying at 60°C for at least 12 h, samples were  
166 reweighed and stored in a desiccator until further analysis. The same procedure was used  
167 to prepare samples of nematodes, extracted from fresh soil by using a modified Baermann  
168 funnel method. Soil, mosses, lichens, roots, and plant material were ground and subjected  
169 to the same procedure (root and plant material 1.0 - 1.5 mg, soil 34.1 - 35.3 mg). We  
170 analysed these organisms and material to obtain baseline values of different potential food  
171 sources for oribatid mites (Supplementary Material). A coupled system of an elemental  
172 analyzer (Euro EA 3000, Euro Vector S.p.A.: Milano, Italy) and a mass spectrometer  
173 (Delta V Plus Thermo Electron; Bremen, Germany) was used to analyze the <sup>13</sup>C/<sup>12</sup>C and  
174 <sup>15</sup>N/<sup>14</sup>N ratios (Reineking et al., 1993). The primary standard for <sup>15</sup>N was atmospheric



175 nitrogen whereas acetanilide (C<sub>8</sub>H<sub>9</sub>NO, Merck, Darmstadt, Germany) served for internal  
176 calibration. Vienna Pee Dee Belemnite (V-PDB) was used as a primary standard for <sup>13</sup>C.  
177 See also Fischer et al. (2010), Maraun et al. (2011), Pollierer et al. (2009), and Schneider  
178 et al. (2004) for further details.

179

#### 180 *2.4 Data analysis*

181 We used stable isotopes to focus on a diverse but narrowly defined trophic assemblage.

182 We based the definition of ‘relatively narrow trophic assemblage’ on the concentration  
183 of <sup>15</sup>N, which increases from food sources to consumers (Deniro and Epstein, 1981;

184 Peterson and Fry, 1987; Scheu, 2002). The enrichment of <sup>15</sup>N varies with diet,

185 especially in generalists, but despite this variation, an average enrichment of 3.4‰ is

186 commonly used to define trophic groups (Post, 2002). The concentration of <sup>13</sup>C is

187 usually associated with the analysis of <sup>15</sup>N because <sup>13</sup>C reflects the basal food source

188 (Deniro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002). The variance of stable

189 isotope signatures reflects the dietary niche width of consumers (Bearhop et al., 2004),

190 which led some authors to define the concept of isotopic niche (Newsome et al., 2007).

191 Eventually (see results) we could define a set of 18 species that potentially competed for

192 fungal resources, and we focused our analysis on this assemblage.

193 In order to visualise and quantitatively summarise the multivariate covariation of

194 environmental variables (Organic C, N, C:N, Water, pH, Mean Weight Diametre of soil

195 particles) and major gradients, we performed a Principal Component Analysis (PCA) on

196 the correlation matrix of the variables (Legendre and Legendre 1998; Gotelli and

197 Ellison 2004). We used PCA axes as environmental correlates of species distribution to

198 eliminate collinearity in predictors (Gotelli and Ellison 2004).

199 Given the small scale of the study and all else being equal, we used a modelling strategy

200 consisting of several steps to test the general hypothesis that species closer in space and

201 time were more dissimilar in terms of traits related to competition for resources  
202 (limiting similarity concept): if resource based niche partitioning is a mechanism  
203 through which species coexist locally while competing for shared resources, then  
204 limiting similarity or trait trade-offs should be observed (HilleRisLambers et al., 2012;  
205 Adler et al. 2013). In order to test this hypothesis, we first used a multivariate regression  
206 approach based on RDA (Borcard et al., 2004, 1992; Legendre and Legendre, 1998) to  
207 empirically define the spatial and temporal niches of each species. We Hellinger  
208 transformed raw data to meaningfully apply RDA, which is PCA-based (Euclidean  
209 space), and ensure no inflation of the weights of rare species (Legendre and Gallagher,  
210 2001). The spatially explicit and seasonal sampling design together with the  
211 measurement of several crucial environmental variables allowed us to model species  
212 distribution as a function of both spatial and environmental factors, and changes  
213 between the two sampled seasons. We used the well-established method of principal  
214 coordinate analysis of neighbour matrices (PCNM; Borcard and Legendre, 2002) to  
215 define a set of spatial factors that parsimoniously accounted for patterns in species  
216 distribution. The final set of PCNM vectors was defined using a multivariate extension  
217 of the Akaike information criterion (AIC; Dray et al., 2006). Environmental factors  
218 were soil water content (% dry weight), pH, organic C, total N, the C:N ratio, and the  
219 mean weight diameter of soil aggregates, used as a proxy for soil structure (Caruso et  
220 al., 2011). We used the species scores of the statistically significant axes of the RDA  
221 model to define species niches: by definition, the Euclidean distance between any two  
222 species in the vectorial space defined by RDA axes reflects predicted distances in space,  
223 seasons, and environmental conditions: the further apart any two species are in the RDA  
224 space the further apart these species are in space, time, and average environmental  
225 characteristics of the patches they colonise. We also used permutational tests to test for  
226 the effects of spatial and environmental factors, including partial effects (i.e. testing for

227 one factor while statistically controlling for other factors). Once we defined the RDA  
228 model-based spatial, temporal and environmental position of species (Grinnellian  
229 niche), we used body size and depth distribution together with the  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$   
230 signature to define a species trait matrix. After data standardization and calculation of  
231 Euclidean distance, a trait distance matrix of species was obtained. We finally used a  
232 Mantel test to test the hypothesis of a negative correlation between the trait distance  
233 matrix and the distance matrix based on space, season, and environment: we expected a  
234 negative correlation under the limiting similarity hypothesis because the more similar  
235 species are in traits involved in competition the more distant species should be in their  
236 Grinnellian niche. In practice, species minimise spatial and temporal coexistence to  
237 avoid competition and at the same time can coexist locally if they differ in key traits.  
238 Conversely, the closer species are in terms of spatial, temporal and environmental  
239 position the less similar they should be in terms of traits involved in competition. We  
240 used the R packages `vegan`, `spacemakeR` and `ade4` for all multivariate analyses  
241 (Chessel et al., 2004.; Dray et al., 2006; Oksanen et al., 2009).

242 We completed our analysis with a neutral model, based on the null assumption that  
243 trophically similar species are not involved in resource-based niche partitioning when  
244 they come together to form assemblages. To fit a general neutral model, we used the  
245 formula for multiple samples and a PARI/GP code (Etienne, 2007) to estimate neutral  
246 model parameters  $\theta$  (diversity) and  $I$  (immigration rate). Afterwards, we used the  
247 PARI/GP function `urn2.gp` (Etienne, 2007) to create 4999 neutral communities based on  
248 the estimate parameters. We applied this approach to the following datasets: all species  
249 across all trophic levels (spring and autumn, respectively), and just fungal feeders  
250 (spring and autumn, respectively). The simulated communities were used to build a null  
251 distribution of beta diversity values. We quantified beta diversity (BD) following  
252 Legendre and De Cáceres (2013): the sum of species variances in the species by site

253 matrix (with usual correction terms for unbiased estimates of variance). Data were  
254 Hellinger-transformed (Legendre and Gallagher 2001). The observed value of BD was  
255 compared to the null distribution: if observed BD was within the 95% interval of the  
256 simulated data sets, the neutral model could not be rejected at  $p < 0.05$  (Maaß et al.,  
257 2014).

258

### 259 **3. Results**

#### 260 *3.1 Environmental variation*

261 PCA of environmental variables (Fig. 1) summarised more than three quarters of total  
262 variation in the first two axes. Although all variables have some effect on all PCA axes,  
263 PC1 (53%) described a main gradient mostly due to organic matter (organic C and total  
264 N) and soil structure (Mean Weight Diameter, MWD) while PC2 (24%) mostly  
265 accounted for a negative covariation between water content and C:N ratio. Consistently  
266 with the construction of our sampling strategy, the gradients were maximised along the  
267 up- to down-hill direction, with some variation between the two sampling plots  
268 (Supplementary Material, Table S1): the gradient in organic matter and soil structure  
269 was more pronounced in Plot 1 while the negative correlation between water and C:N  
270 was more pronounced in Plot 2. There was no significant difference between spring and  
271 autumn samples for either plots (Supplementary Material, Fig. S1). Absolute variation  
272 in individual soil variables was remarkable in some case: for example, organic C  
273 content ranged from 0.15 to 3.49%, total N from 0.01 to 0.26%, and pH from 4.8 to 8.9,  
274 and these ranges were comparable between the two plots.

275

#### 276 *3.2 Oribatid mite assemblage and isotopes*

277 In total, we collected 2,397 adult Oribatids of 33 species belonging to 18 families. The  
278 most abundant species in both seasons were *Liebstadia pannonica*, *Punctoribates*

279 *punctum* and *Peloptulus phaenotus*. There were five species (*Achipteria coleoptrata*,  
280 *Carabodes willmanni*, *Trichoribates novus*, *Galumna obvia*, and *Minunthozetes*  
281 *semirufus*) that were present with few individuals (1 to 4) only in one of the two  
282 seasons. Rarefaction curves (not shown) confirmed that the sampling effort was  
283 sufficient to describe the overall richness of the oribatid community. We obtained  $^{15}\text{N}$   
284 and  $^{13}\text{C}$  data for 28 species (Supplementary Material, Fig. S2 and Table S3). *Microppia*  
285 *minus* and *Porobelba spinosa* showed the highest  $^{15}\text{N}$  signatures whereas *Carabodes*  
286 *willmanni* had the lowest  $^{15}\text{N}$  signature. Three species (*M. semirufus*, *T. vel. sarekensis*,  
287 *S. sculptus*) had very similar  $^{15}\text{N}$  signatures comparable with the root signatures while  
288 mosses, lichens, and nematodes were about one trophic level below their potential  
289 consumers/predators (Supplementary Material, Fig. S2 and Table S1).

290 Overall, the stable isotope analysis and relevant literature (Fischer et al., 2010; Maraun  
291 et al., 2011; Pollierer et al., 2009; Schneider et al., 2004) allowed us to group the  
292 oribatid mite community into five trophic groups (predators, fungal feeders/secondary  
293 decomposers, decomposers, lichen feeders and species with endophagous  
294 juveniles/tunnelers, see Supplementary Material). However, for *T. novus*, *Passalozetes*  
295 *perforates* and *M. semirufus*, the group affiliation was not clear. We consider *P.*  
296 *perforates* to be a mycophagous species and *M. semirufus* a moss feeder but definitive  
297 evidence is missing. The feeding preferences of *T. novus* remain unclear.

298 Based on these data, we defined a group of 18 species (Table 1; Supplementary  
299 Material, Table S2) in the broad category fungal feeder/secondary decomposers: several  
300 of these species can in principle compete for shared resources. We focused our  
301 modelling and hypothesis testing on this assemblage.

302

303 *3.3 Hypothesis testing*

304 The RDA showed that PCNM-based spatial factors and environmental factors (PC1 and  
305 PC2 from PCA of environmental variables, see Fig. 1) could account for 31% of total  
306 community variation, the total effect of these factors being statistically significant at  $p <$   
307  $0.01$  following a permutational test. However, variance partitioning showed that 21% of  
308 this variation was attributable to spatial patterns in the environmental variables while  
309 10% were accounted for by statistically significant (partial RDA,  $p < 0.05$ ) spatial  
310 patterns not related to environmental variation. Less than 1% of variation was  
311 explainable in terms of environmental variation that was not spatially structured and this  
312 variation was not statistically significant. A RDA based just on environmental factors  
313 (i.e. implicitly including spatial structures) accounted for 22% of total variation, the  
314 effect of the environment being significant at  $p < 0.01$ . To test for the factor season, we  
315 extracted the residuals of the first, main RDA model and submitted these to a  
316 PERMANOVA test, which showed a significant effect of season ( $F_{1, 78} = 4.17$ ,  $p <$   
317  $0.01$ ).

318 Introducing the season factor in the RDA increased total explained variation to 44%. A  
319 permutation test showed that the first five RDA axes were significant at  $p < 0.01$  and  
320 these axes were therefore retained to define the niche space (i.e., based on spatial and  
321 temporal distance, which we, given our result, basically understand as the  
322 environmental or Grinnellian component of a species niche). A plot of the first two  
323 RDA axes (Fig. 2) and the main environmental gradients (based on PCA of  
324 environmental variables) showed that the first RDA axis is driven by a gradient in  
325 organic matter and soil structure. This gradient is associated with a certain species set  
326 while the second axis is driven by a second gradient due to the negative covariation of  
327 soil water and C:N. This second gradient is associated to a species set other than that  
328 associated to the first gradient. Size and the  $^{15}\text{N}$  signature were negatively and  
329 significantly correlated with each other but scarcely correlated with the major

330 environmental gradients, although a positive and significant correlation was detected  
331 between  $^{15}\text{N}$  and RDA1 (Fig. 3). After standardization, a Euclidean distance matrix was  
332 calculated from the Grinnellian niche space and correlated to the species trait distance  
333 matrix (based on  $^{15}\text{N}$ ,  $^{13}\text{C}$ , size and depth distribution) via a Mantel test: no significant  
334 correlation was found (Fig. 4), which is inconsistent with the limiting similarity  
335 hypothesis.

336 None of the tested assemblages differed significantly from a neutral model for beta  
337 diversity (Supplementary Information, Fig. S3; whole assemblage, spring:  $p = 0.10$ ;  
338 whole assemblage autumn:  $p = 0.16$ ; fungal feeders spring:  $p = 0.07$ ; fungal feeders  
339 autumn:  $p = 0.10$ , see Table S4 for the estimate of neutral model parameters). However,  
340 in all cases we observed assemblages with beta diversity higher than expected under  
341 neutrality (Fig. S3), and this trend was more pronounced in the fungal feeder group.

342

#### 343 **4. Discussion**

##### 344 *4.1 Differences between environmental filtering and competition*

345 In recent works investigating the role of deterministic and stochastic drivers of soil  
346 organism community structure (Beck et al., 2015; Caruso et al., 2012; Dumbrell et al.,  
347 2010; Gao et al., 2014; Lindo and Winchester, 2009; Nielsen et al., 2010) researchers  
348 contrasted environmental filtering, typically equated to niche dynamics, with spatial  
349 factors not dependent on patterns of environmental variation, sometimes called ‘pure’  
350 spatial factors. These spatial factors are often understood as the effect of dispersal  
351 and/or demographic fluctuations in neutral assembly processes; but several ecologists,  
352 including those cited above, also recognise that these factors do not necessarily  
353 represent stochastic spatial factors (Anderson et al., 2011; Caruso et al., 2012; Smith  
354 and Lundholm, 2010). Besides the problem of the interpretation of spatial factors, a key  
355 but not often addressed aspect of this central topic is that environmental filtering may

356 imply competition for resources but does not necessarily imply resource-based niche  
357 partitioning dynamics: this is a point on which niche and neutral theorists may agree  
358 (HilleRisLambers et al., 2012; Hubbell, 2005), although from very different  
359 perspectives. At certain scales environmental filtering is compatible with neutral  
360 processes because in neutral dynamics competition for resources between species is not  
361 a driver of community structure while individuals, regardless of the species they belong  
362 to, must still exploit resources and fit their environment (Hubbell 2005). Different  
363 species can therefore come together into a local community if they are adapted to the  
364 environmental conditions of the locale, and in this sense the environment will tend to  
365 select for similar species (e.g., shade-tolerant species in shaded environments).. A  
366 neutrally assembled local community can therefore be environmentally filtered at  
367 certain scales while being neutral at scales at which competition among species has  
368 classically been postulated to structure communities (Etienne, 2007; Hubbell, 2005). It  
369 is in this general framework that we interpret our results: when biotic interactions start  
370 to be a fundamental driver and predictor of community structure neutral theories should  
371 be abandoned. Specifically, neutral theories directly contrast with resource-based niche  
372 partitioning processes. A first consideration is therefore that not all biological  
373 interactions should be considered, especially multitrophic interactions, which, apart  
374 from possible future developments, are usually outside the realm of application of  
375 neutral theories (Hubbell, 2005, 2001). For the first time, we have focused on a soil  
376 animal assemblage that was trophically defined by the use of stable isotopes of N and C.  
377 In doing so, we could start from the empirically validated assumption that competition  
378 for resources is a fairly valid possibility within the analysed assemblage. The small  
379 scale of the study also allowed us to assume that dispersal limitation, while still a  
380 possible factor given the size of our animals (Ettema and Wardle, 2002), should play a  
381 minor role. As shown by the analysis of the soil, communities were sampled along steep



382 environmental gradients in a very short distance. Accordingly, we observed a strong,  
383 spatially structured correlation between environmental gradients and the structure of the  
384 species assemblage. We can therefore conclude that the assemblage was subjected to  
385 environmental filtering. This result might imply that species living in different  
386 environmental patches spatially segregate to avoid competition locally. However, by no  
387 means can this result in itself be considered evidence of resource-based niche  
388 partitioning, which should also explain coexistence locally. This is an observational  
389 study: in order to reject non-neutral dynamics and find strong evidence of resource-  
390 based niche partitioning, we should have rejected neutral prediction of beta diversity  
391 and detected patterns consistent with the limiting similarity hypothesis along the  
392 environmental gradient, including the local scale of the assemblage inhabiting  
393 individual soil cores. Instead, neither could we reject neutral predictions of beta  
394 diversity nor could we find patterns consistent with the limiting similarity hypothesis.  
395 Observed beta diversity of the assemblage was higher than neutral predictions, as  
396 usually expected under environmental filtering (Caruso et al., 2012; Dornelas et al.,  
397 2006), but not significantly higher, with fairly high p-values in all cases but one.  
398 Species more similar in terms of spatial and seasonal distribution were not more  
399 dissimilar in terms of isotopic signature, size, and depth distribution. In theory, size  
400 could here be related to competition if we make the classical assumption that species at  
401 similar trophic positions avoid competition by differing in size: in this way competing  
402 species have access to similar resources in different places (i.e., colonization of  
403 differently sized soil pores; Weis-Fogh, 1948; Ritchie, 2009; Turnbull et al., 2014). The  
404 local community of our study is the cylindrical soil core used as sampling unit. In this  
405 relatively small locale, species that feed on similar resources and have similar size could  
406 still partition space by dwelling at different average depths but species weighed mean  
407 average depth was not a trait that could explain coexistence.

408

409 *4.2 Niche partitioning mechanisms and competition*

410 In spite of all the efforts we made to identify the possible dimensions along which  
411 competing species could partition their niches, none of these dimensions or their  
412 combination provided us with evidence of limiting similarities indicative of resource-  
413 based niche partitioning. In fact, the only pattern we have found is a slightly positive  
414 correlation between trophic position ( $\delta^{15}\text{N}$  value) and the major environmental gradient  
415 along which the community is structured. However, the correlation seems made up by  
416 three low  $\delta^{15}\text{N}$  values and one high  $\delta^{15}\text{N}$  value, with the other points scattered in a fairly  
417 random manner. In any case, even if we accepted the validity of this correlation, this  
418 result would not support the limiting similarity hypothesis. We observed a significant  
419 fraction of spatial variation that was not related to environmental gradients. This  
420 variation can be due to stochastic but spatial factors such as dispersal, or it could be due  
421 to biotic interactions such as predation or competition. Predation can mediate  
422 competition by controlling the population of the more competitive species (Chase and  
423 Leibold, 2003): predators may spatially structure their prey but in the case of oribatid  
424 mites, and differently from collembolans, there is strong evidence that predation is not a  
425 strong factor controlling populations (Peschel et al., 2006). Competition and resource  
426 based niche partitioning could still play some role because we measured the traits that  
427 were most logically expected to be key traits for coexistence, but in fact we could have  
428 missed some important aspects. For example, there are limitations in the stable isotope  
429 markers we employed: the  $^{13}\text{C}$  signature of animal fatty acids has now been  
430 demonstrated to be a finer marker for a detailed differentiation of fungal feeders  
431 (Pollierer et al., 2012; Ruess and Chamberlain, 2010) while with the method we  
432 employed we have been able to isolate a narrowly defined trophic assemblage (i.e.  
433 guild) but we might not have been able to differentiate trophic differences within this

434 assemblage. Natural variability in isotopic signatures may also suggest high  
435 intraspecific variability in feeding strategies. This could be especially true for different  
436 developmental stages. We are aware of data at this level for one species only (Schneider  
437 et al. 2004) and these data suggest small differences between adults and nymphs but  
438 other species could definitely vary their diet depending on developmental stage. The  
439 interesting point is that high intraspecific variability can imply broad interspecific niche  
440 overlaps at the species level, opening the way to neutral assembly processes. The same  
441 arguments apply to temporal variation in species soil depth and may imply a theoretical  
442 scenario for which levels of competition vary in space (both horizontally and vertically)  
443 and time as a function of fluctuations in population densities.

444 Another limit of our study is that we might not have included all the species relevant to  
445 the analysed assemblage. We focused on fungal feeder/secondary decomposer oribatid  
446 mites, which is by far the most diverse and abundant group of microarthropods together  
447 with collembolans. However, there are other fungal feeders/secondary decomposers in  
448 soil, for example collembolan species. We cannot exclude that competition for  
449 resources would have been a strong driver of an assemblage that included all the species  
450 competing for a limited set of resources.

451 Finally, our multivariate analysis suggested that seasonal variation is potentially a key  
452 niche dimension although our study is deficient in terms of temporal replication.

453 Species competing for similar resources could peak at different times of the year to  
454 avoid competition, basically for the same principle for which competing species may  
455 segregate spatially. Nevertheless, only future studies will tell whether the observed  
456 temporal patterns depend on a temporal form of environmental filtering (e.g.  
457 seasonality) or resource based niche partitioning mediated by temporal fluctuations in  
458 resources and population densities, or both.

459 Overall, our results indicate that environmental filtering and resource-based niche  
460 partitioning can be decoupled in soil animal assemblages while the burden of the proof  
461 of resource-based niche partitioning in soil community still remains with the ecologist.

462

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469

### 470 **Data Accessibility**

471 All data (species abundances, environmental and geographical data, isotopic data, trait  
472 data) are uploaded as Supporting Information

473

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643 **Fig. Legends**

644 **Fig. 1** Principal Component Analysis (PCA) of the correlation matrix (z-scores) of  
645 environmental variables: 77% of total variance can be summarized in the first two axes.  
646 PC1 (53%) described a main gradient in organic matter (organic C and total N) and soil  
647 structure (Mean Weight Diameter, MWD); PC2 (24%) described a negative covariation  
648 between water content and the C:N ratio. The vectors associated with the variables are  
649 based on PCA eigenvectors (i.e. variables loadings on PCA axes).

650

651 **Fig. 2** First two RDA axes based on a model including spatial vectors, environmental  
652 gradient and seasons. Only species points are displayed to show which species are  
653 associated with the two environmental gradients. See Table 1 for species labels. This  
654 RDA model accounted for 44% of total species matrix. The RDA axis 1 is driven by a  
655 gradient of organic matter and soil structure (PC1 of Fig. 1). RDA axis 2 by a contrast  
656 between water content and C:N ratio (PC2 of Fig. 1);

657

658 **Fig. 3** a) correlation between size (x-axis) and species trophic position ( $^{15}\text{N}$ , y-axis) is  
659 negative and statistically significant; b and c), correlation between species scores of  
660 RDA 1 (y-axis; see Fig. 2) and size (panel b) or  $^{15}\text{N}$  (panel c), on the x-axis. RDA1 is a  
661 proxy for the environmental, spatial and temporal (seasonality in this case) components  
662 of niche. No or weak correlation is observed in panel c and d respectively. Similar  
663 figures were drawn (but now shown here) for the first five RDA axes, with the same  
664 result. Each data point represents a species.

665

666 **Fig. 4** Niche distance between species is based on the species scores of the statistically  
667 significant axes of an RDA (spatial vectors, seasons, and environmental variables). The  
668 Euclidean distance between any two species in the vectorial space defined by RDA axes

669 reflects predicted spatial, temporal and environmental distances: the further apart any  
670 two species are in this space the further apart these species are in terms of their niche.  
671 This RDA-based Euclidean distance matrix was correlated to the species trait distance  
672 matrix (based on  $^{15}\text{N}$ ,  $^{13}\text{C}$ , size and depth distribution) via a Mantel test: the Fig. and test  
673 show a remarkable lack of correlation, which is inconsistent with the limiting similarity  
674 hypothesis.