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Soil fauna through the landscape window: factors shaping surface- and soil-dwelling communities across spatial scales in cork-oak mosaics

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15 **Abstract**

16 Context. The role of spatial and environmental processes governing community
17 structure are dependent on the spatial distances among local communities and the
18 degree of habitat heterogeneity at a given spatial scale. Also, they depend on the
19 dispersal ability of the targeted organisms collected throughout a landscape window.

20 Objectives. Here we assessed the relative importance of spatial and environmental
21 factors shaping edaphic (Collembola) and epigeous (Carabidae) communities at
22 different scales.

23 Methods. The sampling sites were four different landscape windows (1km² square each)
24 in a Mediterranean cork-oak landscape in Portugal. Variance partitioning methods were
25 used to disentangle the relative effects of spatial variables (MEMs, e.g. patch size, shape
26 and configuration) and environmental variables across spatial scales (habitat: data on %
27 of vegetation cover types; management: data on forestry and pasture interventions;
28 landscape: data on landscape metrics).

29 Results. The relative effects of environmental and spatial factors at different scales
30 varied between Collembola and Carabidae. The pure effect of the environmental
31 component was only significant for carabid beetles and explained a higher percentage of
32 their community variance compared to collembolan communities. The pure effects of
33 the spatial component were generally higher than the environmental component for both
34 groups of soil fauna. Carabid communities responded to landscape features related to
35 the patch connectivity of open areas (grasslands) as well as the shape of cork-oak
36 habitat patches integrating the agro-forest mosaic.

37 Conclusions. Community patterns of surface-dwelling soil fauna may be partly
38 predicted by some features of the landscape, while soil-dwelling communities require
39 ecological assessments at finer spatial scales.

40

41 **Keywords:** Community structure; Cork-oak landscape; Dispersal ability;
42 Environmental factors; Soil fauna; Spatial scale.

43

44 **Introduction**

45 Community structure within landscape mosaics is influenced by ecological processes
46 operating at a hierarchy of spatial scales, from local environmental filtering to the
47 regional movement of species among habitat patches (Ricklefs 1987; Myers et al.
48 2013). The relative influence of environmental and spatial processes may also depend
49 on the home range and dispersal ability of the targeted organisms (Cottenie 2005;
50 Thompson and Townsend 2006; van de Meutter et al. 2007; Heino 2013).

51 In terrestrial environments, only a limited number of ecological studies have
52 focused on soil fauna to test the relative effects of environmental and spatial factors,
53 mostly on epigeous beetles (e.g. Davies et al. 2009; Driscoll et al. 2010; Boieiro et al.
54 2013), but also a few studies on soil microarthropods, namely mites (Lindo and
55 Winchester 2009; Bowler and Benton 2011), collembolans (Aström and Bengtsson
56 2011; Martins da Silva et al. 2012), or both (Chisholm et al. 2011; Ingimarsdóttir et al.
57 2012). Soil fauna in fact comprise an interesting group to test this ecological question,
58 given their diverse array of dispersal abilities (Hopkin 1997; Ojala and Huhta 2001;
59 Ponge et al. 2006). Soil organisms are generally small, with a limited home range and
60 poor dispersal ability compared to aboveground organisms (Hedlund et al. 2004;
61 Rantalainen et al. 2005). However, large differences in terms of life-traits, such as the
62 vertical distributions in soils (life-forms), exist between different groups of soil
63 organisms and may underlie their movements and distributions throughout
64 heterogeneous landscapes (Lindberg and Bengtsson 2005; Ponge et al. 2006;
65 Vandewalle et al. 2010; Querner et al. 2013). For instance, a significant proportion of
66 carabid beetle species (Coleoptera, Carabidae) are epigeous and can fly (e.g. Desender
67 and Turin 1989; Lövei and Sunderland 1996), while collembolan communities
68 (Collembola) are generally dominated by eu-edaphic and hemi-edaphic species (soil

69 dwelling communities), and are very restricted in dispersal ability (e.g. Bengtsson et al.
70 1994).

71 Besides spatial limitation, the heterogeneity of habitat patches, their shape and
72 configuration within the landscape mosaic are perceived differently by species differing
73 in body size and vertical distribution in soils (Ettema and Wardle 2002; Chust et al.
74 2003a; Bardgett et al. 2005). Larger, epigeous organisms, especially predators,
75 generally need larger habitat areas to fulfill their niche requirements (Chust et al. 2003b;
76 Schuldt et al. 2013), and changes in their community structure may be related to habitat
77 fragmentation and landscape configuration at a broad spatial scale (e.g. Martins da Silva
78 et al. 2008; Diekötter et al. 2010; Woltz et al. 2012). The distribution of smaller, eu-
79 edaphic fauna, on the other hand, is more constrained by soil habitat heterogeneity at
80 finer-grained spatial scales due to their limited home range and dispersal ability
81 (Bengtsson et al. 1994; Ettema and Wardle 2002; Berg and Bengtsson 2007). Eu-
82 edaphic soil communities are then expected to exhibit a more patchy distribution in
83 comparison to epigeous communities (such as carabid beetles) occurring in the same
84 landscape mosaic. Nonetheless, recent studies have indicated the importance of broad-
85 scale landscape processes in governing soil fauna community structure (Querner et al.
86 2013), for instance by constraining local habitat conditions verified at finer spatial
87 scales (Martins da Silva et al. 2012; Heiniger et al. 2014).

88 Although researchers have increased their awareness of the fact that ecological
89 processes occur across a range of defined spatial scales (e.g. Sattler et al. 2010; Flohre
90 et al. 2011; Sarthou et al. 2014), the multi-scale effects of landscape complexity at a
91 broad scale and local habitat features at a fine-scale remain poorly understood. Also,
92 despite that the effects of spatial and environmental factors at different scales might
93 differ across taxonomic groups that vary in home range and dispersal ability, only a few

94 attempts at comparative studies have been carried out, mostly using aquatic fauna in
95 ponds and streams (e.g. Beisner et al. 2006; Thompson and Townsend 2006; van de
96 Meutter et al. 2007; Siqueira et al. 2012; Heino 2013).

97 In this study, we analyzed changes in community structure of collembolans (soil
98 dwelling, small-bodied, low dispersal ability) and carabid beetles (surface dwelling,
99 relatively large-bodied and high dispersal ability) in a typical Mediterranean landscape
100 mosaic of extensive managed pastures interspersed with cork-oak woodlands. Our first
101 hypothesis is that the relative importance of spatial processes differs between epigeous
102 and eu-edaphic fauna. We predict that distances separating cork-oak woodland habitats
103 have a higher effect on collembolans than on carabid beetles, due to the lower home
104 range and dispersal ability of the former. Our second hypothesis is that environmental
105 processes occurring at different spatial scales determine communities with different life-
106 forms. We predict that environmental factors at coarser spatial scales, namely patch
107 shape and configuration at the landscape scale, will more distinctly determine carabid
108 beetle community structure in relation to the eu-edaphic communities.

109

110 **Materials and methods**

111 *Study area and sampling design*

112 Field sampling was conducted in a typical Mediterranean cork-oak (*Quercus suber* L.)
113 agro-forest mosaic, located in the consolidated alluvial plain of the river Tagus, in
114 “Companhia das Lezírias” (Alcochete) - 20km east of Lisbon, Portugal (ca. 38° 53' N,
115 08° 52' W) in 2002. The sampling sites were four different landscape windows (LW,
116 1km² each), selected along a gradient of land-use management, from unmanaged
117 woodland (LW1) to areas subjected to traditional management practices, such as
118 forestry (LW2, LW3 and LW4) and pastures (LW3 and LW4). Thus, while LW1 and

119 LW2 were dominated by closed cork-oak woodlands, in LW3 and LW4 open
120 woodlands and pasture lands were predominant (Table 1, see for more details Sousa et
121 al., 2004). These landscape windows were selected in a former project (BIOASSESS:
122 <http://www.nbu.ac.uk/bioassess/>) to study the effects of land-use gradients on diversity
123 and ecological indicators. Sampling in each LW was carried out in a regular grid of 16
124 plots (4 by 4 plots) 200m apart (Fig. 1).

125 At each plot, collembolan communities were sampled by taking one soil core of
126 5 cm diameter in spring (May to June). Collembolans were extracted by the Macfadyen
127 extraction method (Sousa et al. 2004). Carabid beetles were sampled in spring and
128 autumn (September to October). They were collected using four unbaited pitfall traps
129 (filled with ethylene glycol to preserve the animals) at each plot, placed in a quadrat
130 with 5 m between each pitfall (Martins da Silva et al., 2008). Collembolan and carabid
131 species were identified to the species level using appropriate identification keys.

132

133 *Species data*

134 The total number of sampling points used in the analyses was 60 points of a potential
135 total of: $4 \times 4 \times 4 = 64$ points (from LW1, 2, 3 and 4). Four points (L3P5, L3P9, L4P13 and
136 L4P3) had no data for Collembola. As such, and in order to make the results even more
137 comparable, only the 60 points were used for both Collembola and Carabidae.

138 The species data were Hellinger transformed to make it suitable for the use of
139 linear ordination methods (Legendre and Gallagher 2001). Species data transformation
140 was calculated using the function “decostand” from the "vegan" package (Oksanen
141 2013) in R 3.0.1 software (R Core Team 2013).

142

143 *Environmental variables across scales*

144 The effects of environmental conditions in the local plots versus the importance of
145 distances separating cork-oak habitats across LWs, as well as the relative importance of
146 local habitat, patch management and aspects of landscape structure (landscape metrics)
147 on collembolan and carabid beetle community changes, were evaluated.

148 To analyze the relative importance of environmental factors at different scales,
149 we adopted the plot-patch-landscape approach according to Cushman and McGarigal
150 (2002). The concept was implemented and a dataset for each level was defined *a priori*
151 for this study.

152 At the plot-level (habitat dataset), plot variables were the percentage soil cover
153 by litter, lichens, mosses, herbs, low shrubs, tall shrubs and trees (Martins da Silva et
154 al., 2012; Table A1).

155 At the patch-level (management dataset), management type was measured by
156 several parameters of management intensity, namely forestry practices (e.g. cork-oak
157 area with cork production and time since last cork removal) and agricultural practices
158 (e.g. Cattle stock density and number of grazing days) (Table A1).

159 At the landscape level (landscape dataset), the landscape features were patch
160 composition and configuration metrics calculated for each patch type (cork-oak
161 woodland - F, shrub lands – S, pasture lands – G) in FRAGSTATS 3.3 (McGarigal et
162 al., 2002), which were extracted from aerial photographs using ArcView software
163 (version 3.x, ESRI, US). After exploratory factor analysis, performed to exclude highly
164 collinear landscape variables, we selected eight landscape metrics for each patch type
165 existing within each LW, namely four area/density metrics (total area - AREA, mean
166 patch area - AreaMN, number of patches – NP, and radius of gyration - GYRATE) and
167 four shape/configuration metrics (shape index – SHAPE, related circumscribing circle –

168 CIRCLE, contiguity index – CONTIG, and proximity index - PROX) (for a detailed
169 description of each metric see McGarigal et al. 2002 and Table A1).

170 Forward selection of the environmental variables was performed separately for
171 each dataset (i.e. habitat, management and landscape datasets), using double stopping
172 criteria (Blanchet et al. 2008). In this method, the forward selection stops when the
173 fixed threshold for the alpha significant level ($\alpha=0.05$) or the adjusted coefficient of
174 multiple determination (R^2_{adj}) of the full model is reached. The forward selection was
175 performed using the "packfor" package (Dray et al. 2013) in R 3.0.1 software (R Core
176 Team 2013).

177

178 *Spatial modelling*

179 The spatial coordinates (UTM coordinate system) were Euclidean-centered prior to the
180 spatial data analysis.

181 Moran's eigenvector maps (MEM) were used to detect and quantify the spatial
182 structure of the data. We follow the general framework described by Dray et al. (2006)
183 that define the spatial weighting matrix W as a Hadamard product of the connectivity
184 matrix B by the weighting matrix A . In our analysis, we used a binary (unweighted)
185 spatial matrix constructed using a connectivity matrix based on a Gabriel graph
186 (Legendre and Legendre 2012). Only the MEM eigenvectors that presented a
187 significantly spatial autocorrelation, calculated using Moran's I test (Moran 1948; Cliff
188 and Ord 1973), were selected for the analysis. Forward selection was performed on this
189 set of MEM eigenvectors using double stopping criteria (Blanchet et al. 2008) to
190 prevent incorrect variables from entering the model.

191 To evaluate the effect of the spatial scale, the spatial eigenfunction models were
192 divided into two sub-models, the broad-scale and the fine-scale sub-model. These two

193 sub-models are orthogonal to one another and consequently it is expected that the
194 shared explained variation will be zero. However, the current method of calculating the
195 variation partitioning based on R^2_{adj} creates small non-zero intersection values between
196 the two sub-models. The solution adopted to deal with this problem was to consider a
197 hierarchical partitioning of the shared fractions according to the different scales that
198 each sub-model represents (i.e. the broad-scale sub-model has priority over the fine-
199 scale sub-model) (Legendre et al. 2012).

200 Spatial eigenfunction models, namely MEM, were computed in R 3.0.1 software
201 (R Core Team 2013) using the "spdep" package (Bivand 2013) and the "spacemaker"
202 package (Dray 2013). Hierarchical variance partitioning was performed using the
203 function "varpart.MEM" (Legendre et al. 2012).

204

205 *Community similarity within and among LWs*

206 In order to check for differences in collembolan and carabid beetle' community
207 structure within and among LWs, we compared community similarities for the two
208 taxonomic groups using Bray-Curtis (BC) similarity indices (Bray and Curtis 1957). BC
209 similarity indices were calculated using PRIMER 5 for Windows (Version 5.2, Primer-
210 E, Ltd., Plymouth, UK). The magnitude of divergence between sampling plots for both
211 collembolan and beetle similarity matrices were estimated using Clarke's (1993) R
212 statistic (ranging from 0 to 1), and ANOSIM was used to estimate the significance of
213 differences between pairs of sampling plots, using 5000 permutations of the data
214 (Clarke 1993). For this analysis, BC similarity values were log-transformed.

215

216

217

218 *Variance partitioning along the land-use gradient*

219 The relative importance of spatial and environmental factors at different levels (habitat,
220 management, landscape) across taxonomic groups was analyzed by the method of
221 variance partitioning using partial RDA analyses. The variation partitioning analysis
222 was based on R^2_{adj} statistics, which has been proven to be an unbiased method to
223 calculate the fractions of the variation partitioning (Peres-Neto et al. 2006).

224

225 *Non-spatial model*

226 Variation partitioning techniques were first applied to the environmental variables in
227 order to decompose the variance of each of the predefined levels (i.e. habitat,
228 management and landscape) without considering the spatial component. The variation
229 partitioning was presented graphically using a Venn diagram, and through the use of
230 statistical tests (Monte Carlo permutations) we evaluated the significance of some of the
231 fractions of the variation partitioning.

232

233 *Space versus Environment*

234 The joint and independent (pure) effects of environmental and spatial factors were also
235 disentangled by the variance partitioning method. To extract the pure effects of spatial
236 and environmental components, we used the respective selected environmental and
237 spatial variables as co-variables, ruling out their relative influence on community
238 changes (Borcard et al. 1992; Cottenie 2005).

239 Previously, the variation partitioning of the environmental variables was
240 performed using the variables selected for each level (plot habitat, patch management
241 and landscape level). Here, the hierarchical variation partitioning of the spatial
242 component was also performed using two different spatial sub-models representing the

243 broad scale and the fine scale. Results were expressed through Venn diagrams and
244 Monte Carlo permutations as described above, for each fraction of the variation
245 partitioning, i.e. environmental (env), broad-scale (broad) and fine-scale (fine) spatial
246 components. .

247 The ordination analysis was performed using the "vegan" package (Oksanen
248 2013) in R 3.0.1 software (R Core Team 2013).

249

250 **Results**

251 *Overview on species richness and composition across LUs*

252 In total, 54 collembolan species were sampled across LWs (35, 24, 28 and 30 species in
253 LW1, LW2, LW3 and LW4, respectively), while 55 species of carabid beetles were
254 recorded (24, 20, 38 and 30 species in LW1, LW2, LW3 and LW4, respectively).

255 Overall, average dissimilarity among samples was greater among collembolan
256 communities compared to carabid communities (Fig. 2). A higher among-sample
257 divergence was found even within LWs (Fig. 2). However, differences in community
258 structure between LWs were generally stronger for carabid communities (more
259 significant R values from ANOSIM, Table 2). The exception was the pairwise
260 comparison between LW1 and LW2, showing that these two LWs were not dissimilar in
261 terms of carabid community composition and species relative abundances (Table 2).

262

263 *Variance partitioning: non-spatial model*

264 Environmental effects along the predefined levels (habitat, management and landscape)
265 were examined for both collembolan and carabid communities by means of (partial)
266 RDA analyses using the procedure of forward selection. A total of 5 and 7
267 environmental variables were selected for Collembola and Carabidae, respectively

268 (Table 3). The variables were selected independently for each one of the predefined
269 levels or subsets. Consequently, the habitat level was composed of 1 variable for both
270 Collembola and Carabidae (namely Herb), while the management and landscape levels
271 were composed by 2 variables for Collembola (management: Density, TimeCork;
272 landscape: G_NP, F_Contig) and 3 for Carabidae (management: AreaCork, TimeCork,
273 AreaCut; landscape: G_Shape, F_Shape, G_Prox) (Table 3).

274 The variation partitioning technique applied to the environmental variables
275 across scales showed different results between the two taxonomic groups. The pure
276 (independent) effect of each environmental variance component was not significant for
277 collembolan communities, while factors at the habitat and landscape scales significantly
278 explained carabid community changes across LWs (Venn diagram in Fig. 3). Moreover,
279 the percentage of collembolan community variance explained by environmental
280 variables was overall very low, in absolute terms and also in comparison with carabid
281 beetles (Fig. 3). The greater amount of community variation was explained by the
282 fraction of the shared effect between landscape structure and patch management (3%).
283 This same fraction also explained the higher amount of carabid community variance
284 (7.7%), followed by the joint effect of all variables (4.6%) and the pure effect of
285 landscape (3.3%) explaining the community changes. The most important landscape
286 factors determining carabid beetle communities were related to patch connectivity of
287 open areas (grasslands, G_Prox) as well as the shape of closed woodlands and more
288 open habitats (F_Shape and G_Shape, respectively) integrating the agro-forest mosaic
289 (Table 3).

290

291 *Spatial versus environmental effects across spatial scales*

292 In common with the environmental component, spatial variables were submitted to a
293 procedure of forward selection, resulting in 7 selected variables (MEMs) for each
294 taxonomic group, separated along broad-scale (Collembola: MEM's 1, 2, 3, 35;
295 Carabidae: MEM's 1, 2, 3, 11, 12, 18) and fine-scale sub-models (Collembola: MEM's
296 44, 47, 57; Carabidae: MEM 43).

297 The relative importance of environmental and spatial factors at different scales
298 varied between Collembola and carabid beetles. The effect of the environmental
299 component, after removing the effect of the space component, was only significant for
300 carabid beetles and explained a higher percentage of their community variance (5.34%,
301 $pseudo-F_{(6,46)}=1.626$, $P=0.003$) in relation to collembolan communities (1.12%, $pseudo-$
302 $F_{(5,47)}=1.134$, $P=0.203$) (Venn diagram in Fig. 4). The pure effects of the spatial
303 component were generally higher than the environmental component for both
304 taxonomic groups. Total effects of the pure space component explained 6.39% ($pseudo-$
305 $F_{(7,47)}=1.571$, $P=0.003$) of the collembolan species variance and 7.13% ($pseudo-$
306 $F_{(7,46)}=1.731$, $P=0.001$) of carabid species variance (Fig. 4). Considering the two subsets
307 of the spatial component, only the pure effects of the fine-scale sub-model significantly
308 explained collembolan species variance across LWs ($pseudo-F_{(3,47)}=1.997$, $P=0.001$),
309 while the independent effects of the broad-scale sub-model were not significant
310 ($pseudo-F_{(4,47)}=1.253$, $P=0.098$). Conversely, both spatial sub-models showed a
311 significant effect on carabid species variance (broad-scale: $pseudo-F_{(6,46)}=1.643$,
312 $P=0.002$; fine-scale: $pseudo-F_{(1,46)}=2.18$, $P=0.01$), and the broad-scale subset explained
313 a considerably higher percentage of community variance in relation to the fine-scale
314 model (Fig. 4).

315 In both taxonomic groups, the shared effects of environmental and broad-scale
316 spatial variables explained the highest amount of community variance (Collembola: 6%,

317 Carabidae: 14%), while a considerably higher percentage could not be explained by the
318 RDA axes (Collembola: 86.4%; Carabidae: 74%).

319

320 **Discussion**

321 Ecological studies analyzing the effects of land-use changes on local community
322 structure have traditionally focused on aboveground communities, belonging to the
323 same trophic level, and within a well-defined spatial scale (Chase and Bengtsson 2010).
324 However, spatial and ecological processes operate at a hierarchy of spatial scales
325 (Cushman and McGarigal 2002) and their relative influence depends on the spatial
326 range of the targeted organisms (Ettema and Wardle 2002; Berg 2010). Here, we have
327 analyzed changes in community structure across two groups of soil fauna, with a range
328 in body size, life-form and dispersal ability. On the one hand, the small-sized
329 collembolan communities, mainly eu-edaphic and with low dispersal ability, and on the
330 other hand, the carabid beetle communities, which are bigger than collembolans and
331 mainly epigeous, with a higher ability to disperse and colonize new areas.

332 We found that spatial processes were relevantly determining community
333 structure of both taxonomic groups. While carabid communities were spatially
334 structured at a broader scale, reflecting a LW effect, collembolan communities were
335 structured more at fine-grained spatial scales. However, in contrast with carabid
336 communities, both spatial and environmental factors explained only a relatively small
337 amount of community variance of soil eu-edaphic fauna. The effect of environmental
338 factors at different scales was small compared to spatial effects on collembolan
339 community variance. Conversely, environmental factors, especially at the landscape
340 scale, governed carabid community changes along the land-use gradient.

341 Our first hypothesis, that the relative importance of spatial processes differs
342 between soil arthropods with different dispersal ability, was therefore supported by the
343 observed data. Also, the fact that carabid beetles responded mainly to landscape features
344 across the agro-forest mosaics partly supports our second prediction that environmental
345 factors at coarser spatial scales, namely patch shape and configuration at the landscape
346 scale, more distinctly determine carabid beetle community structure in relation to the
347 eu-edaphic communities.

348

349 *Effect of space across groups of soil fauna*

350 Our results showed that epigeous carabid beetles (sampled by pitfalls), were less
351 affected by distances among habitat patches than eu-edaphic and hemi-edaphic
352 collembolan communities (collected with soil cores). These were still affected by the
353 smallest distances between neighboring plots within landscape windows (LWs). These
354 results suggested that, for collembolans, the distances among neighboring habitat plots,
355 a minimum of 200 meters apart, were already working as a spatial barrier. Presumably
356 the spatial scale of the sampling design of this study was too wide for *Collembola* (see
357 for example, Aström and Bengtsson 2011). The 4x4 grid of sampling points was not
358 able to capture the real effects spatial and environmental factors determining
359 collembolan community changes, as they show high variability at very fine-grain spatial
360 scales. In fact, the spatial range of edaphic fauna is tuned by high spatial and temporal
361 variation in microhabitat conditions and resource availability at smaller spatial scales
362 (Bengtsson et al. 1994; Chust et al. 2003b; Hedlund et al. 2004). So it is not surprising
363 that home range and dispersal ability of soil-dwelling fauna is much more limited than
364 dispersal ability of surface-dwelling communities (Hedlund et al. 2004; Berg et al.
365 2010). In line with previous studies (e.g. Thompson and Townsend 2006; van de

366 Meutter et al. 2007; Siqueira et al. 2012) we found that the relative influence of spatial
367 and environmental factors, at a specific spatial scale set up in the sampling design,
368 depends on the spatial range and dispersal ability of the studied taxonomic groups. This
369 outcome should be considered in studies testing the effects of multi-scale ecological
370 processes on multiple taxa within a landscape mosaic, namely ecological studies based
371 on a metacommunity approach (Leibold et al. 2004), weighting the relative effect of
372 spatial and environmental factors at a fixed spatial scale.

373 Even for soil-dwelling communities, the relative importance of spatial distances
374 among local communities might depend on the degree of habitat heterogeneity and
375 complexity within the landscape (Kneitel and Chase 2004). In a previous study using
376 collembolan communities, sampled not only in woodland habitats but also in open areas
377 (mostly agricultural fields) along the land-use gradient, we found a decrease in the
378 importance of spatial factors relative to environmental factors (Martins da Silva et al.
379 2012) due to the striking contrasting situations such as forest habitats vs. agricultural
380 habitats.

381 The importance of abiotic and biotic conditions for the structuring of soil fauna
382 has been shown in previous works (e.g. Rantalainen et al. 2005; Heiniger et al. 2014).
383 Thus, both spatial distances between patches and the degree of habitat heterogeneity
384 play a role in determining the community structure of soil fauna, although in this study
385 spatial factors ruled out environmental factors because the sampled community
386 assemblages were too distant from each other. Also, the environmental component
387 could have been underestimated simply by missing those environmental variables most
388 relevant to eu-edaphic fauna. Indeed, Collembolan communities are deemed to be
389 structured by strong species sorting across a gradient of soil moisture and organic
390 content, although these variables were not explicitly measured in this study (Hopkin

391 1997). This limitation should also be taken into account in this comparison between
392 soil-dwelling and surface-dwelling communities, regarding the relative importance of
393 spatial and environmental components.

394

395 *Effect of environmental factors at different spatial scales*

396 Contrary to collembolans, many carabid beetles have the ability to fly (Lövei and
397 Sunderland 1996) or disperse over relatively long distances by active walking (Baars
398 1979; Niemelä et al. 1992). Spatial distances among sampling plots, within each LW,
399 were not too high to hamper the environmental effects on carabid community changes
400 along the land-use gradient. Still, the importance of shared and pure effects of space at
401 broader scales showed that carabid communities were spatially structured, which could
402 be reflecting an LW effect, i.e., distances among LWs were in part confounded with
403 environmental factors (e.g. management types and landscape configurations of each
404 LW) due to the effect of spatial autocorrelation (Borcard et al. 1992; Smith and
405 Lundholm 2010).

406 Both spatial and non-spatial models revealed that changes in carabid beetle
407 community structure were mainly governed by environmental conditions at a coarser
408 spatial scale, namely to changes in the arrangement of the landscape mosaic along the
409 land-use gradient. As surface-living communities comprise in general species with a
410 larger body size and wider spatial range, they naturally require broader habitat areas and
411 perceive the habitat differently to soil-dwelling communities (Chust et al. 2003a). For
412 instance, the effects of habitat fragmentation, by creating a more complex configuration
413 of the landscape mosaic, may have a stronger effect on carabid community structure
414 than finer scale changes in local vegetation cover within the same land-use type (e.g.
415 cork-oak habitats). The importance of landscape features on carabid activity, density,

416 species richness and community composition has been the focus of recent studies (e.g.
417 Barbaro and Halder 2009; Nabe-Nielsen et al. 2010; Sattler et al. 2010; Woodcock et al.
418 2010; Flohre et al. 2011; Jonason et al. 2013; Lemessa et al. 2014; Puech et al. 2014),
419 although landscape metrics such as patch shape of different land-use types have hardly
420 been addressed. In this study we found that the shape of habitat patches interspersed in
421 the landscape mosaic may provide a clearer understanding about the ecological
422 processes underlying community dynamics and species trade-offs in agro-forest
423 landscapes. For instance, the proportion of good dispersers to poor dispersers, as well as
424 the predominance of generalists over habitat specialist species, may depend on how
425 narrow and convoluted habitat patches are within the landscape mosaic (Hamazaki
426 1996; Tanner 2003). In this sense, further insight may be gained with studies including
427 community traits related to dispersal power (e.g. macropterous vs. brachypterous
428 species), body size (active versus passive dispersal) or degree of habitat specialization
429 (e.g. Ribera et al. 2001; Brose 2003; Kotze and O'Hara 2003; Niemelä and Kotze
430 2009). By identifying general patterns of community responses to landscape features,
431 we could have a more comprehensive view on how community assemblages and
432 functional groups are effectively distributed, and to predict how they will cope with
433 current and future land-use changes (Kotze et al. 2011).

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437 *Implications for fundamental and applied ecology*

438 Soil-dwelling and surface-living communities responded differently to spatial distances
439 among cork-oak habitats along the land-use gradient, and were affected differently by
440 environmental factors acting at different spatial scales. While most soil-dwelling

441 communities require ecological assessments at the local plot scale, community patterns
442 of epigeous soil fauna, especially of predatory taxa, may be predicted by some features
443 of the landscape, including the shape of forest and open habitat patches interspersed in
444 the agro-forest mosaic. We believe these findings add important insights into recent
445 ecological frameworks, particularly the metacommunity concept (Leibold et al. 2004),
446 which incorporates the relative importance of spatial and environmental processes to
447 explain community patterns in fragmented landscapes. Based on the present results, we
448 suggest that studies testing ecological models should take into account the spatial range
449 of the targeted taxa - not only their dispersal ability, but also the proper spatial scale at
450 which the organisms perceive habitat heterogeneity and respond to changes in local
451 conditions (Chust et al. 2004). The need for multiscale analyses in order to adequately
452 characterize landscape heterogeneity has been highlighted in previous work in the field
453 of landscape ecology (e.g. Wu 2004; Costanza et al. 2011). This notion gains even more
454 importance considering that habitat heterogeneity and landscape patterns might be
455 differently perceived by surface and soil-dwelling organisms, depending on the focal
456 spatial scale of a specific study.

457 This aspect has also important implications for landscape management and
458 conservation plans in Mediterranean agro-forest mosaics. Particular features of the
459 landscape resulting from traditional management may contribute to determine
460 community structure of different taxonomic groups, and hence monitoring programs for
461 conservation purposes should be scaled at the level of the targeted taxa or functional
462 group. This is in line with previous studies that have suggested that different
463 conservation strategies are needed to protect biodiversity, depending on the particular
464 taxonomic group (e.g. Yaacobi et al. 2007; Lemessa et al. 2014).

465 In conclusion, our results support that in both theoretical and applied ecological
466 studies with regards to the effects of spatial and environmental processes governing
467 community structure in landscape mosaics, the fields of community and landscape
468 ecology should be integrated. Indeed, the trans-disciplinary nature of landscape ecology
469 has been emphasized by relevant authors in this field (see Wu and Hobbs 2002) and a
470 multiscale approach, as well as the combination of hierarchy concepts (*sensu* Wu and
471 Loucks 1995; Turner et al. 2001) with community ecological frameworks (*sensu*
472 Leibold et al. 2004; Cottenie 2005) could help to improve the ability to predict changes
473 in community structure over space and time.

474

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484

485

486 **Table 1.** Characterization of the land-use windows (LW1, LW2, LW3 and LW4)
487 selected for this study. At the regional scale, the landscape structure reflected by the
488 main types of land-use and management practices caused different patterns of

489 vegetation cover among LWs, i.e. higher numbers of closed habitats within LW1 and
 490 LW2 in relation to LW3 and LW4.

		LW1	LW2	LW3	LW4
Landscape management	Land-use	natural forest	managed forest	agro-forest	agro-forest
	Interventions	none	pruning	pruning/grazing	pruning/grazing
	Management level	none	low	low	medium
N° of sampling plots	Closed woodland	8	9	3	4
	Open woods	3	3	8	6
	Grass/Shrubland	5	3	5	6

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494 **Table 2.** R and P-values derived from ANOSIM pairwise comparisons of collembolan
 495 and carabid community composition values using the Bray-Curtis similarity index.

	Collembola		Carabidae	
	R	P-values	R	P-values
LW1 vs. LW2	0.196	0.008	0.037	1
LW1 vs. LW3	0.094	0.271	0.236	0.002
LW1 vs. LW4	0.194	0.005	0.281	0.002
LW2 vs. LW3	0.184	0.021	0.327	<0.001
LW2 vs. LW4	0.237	0.005	0.317	<0.001
LW3 vs. LW4	0.132	0.064	0.311	0.002
Total	0.175	<0.001	0.247	<0.001

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499 **Table 3.** Selected environmental variables (at plot-patch-landscape levels) obtained
500 from the RDA forward selection procedure performed for each taxonomic group.
501 Detailed descriptions of each variable are provided in Supplementary material Table A1
502 (“Herb” - percentage coverage of herbaceous vegetation; “Density” – “cattle density”,
503 “Area Cork” - area with cork production, “Time Cork” - time since last cork removal,
504 “Area Cut” – forest area harvested; “G_NP” –number of grassland patches, “F_Contig”
505 - spatial connectedness, or contiguity, of forest patches, “F_Shape” and “G_Shape” -
506 shape index of cork-oak patches in forest and grassland habitats, respectively, “G_Prox”
507 - proximity of all grassland patches).

		Variables	Order	R ² Cum	AdjR ² Cum	F	P values
Collembola	Hab	1 Herb	5	0.004	0.003	2.607	0.004
		1 Density	5	0.051	0.035	3.128	0.001
	Man	2 TimeCork	3	0.085	0.053	2.089	0.006
		1 G_NP	10	0.051	0.035	3.106	0.001
	Lan	2 F_Contig	7	0.089	0.057	2.400	0.006
		1 Herb	5	0.088	0.072	5.586	0.001
Carabidae	Man	1 AreaCork	2	0.089	0.073	5.635	0.001
		2 TimeCork	3	0.143	0.113	3.636	0.001
		3 AreaCut	1	0.174	0.129	2.056	0.027
	Lan	1 G_Shape	13	0.101	0.085	6.503	0.001
		2 F_Shape	5	0.179	0.150	5.414	0.001
		3 G_Prox	16	0.208	0.166	2.090	0.029

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513 **Figures captions:**

514 **Figure 1.** Sampling points (spatial coordinates) of the selected landscape windows
515 (LWs1-4) along the consolidated alluvial plain of the river Tagus (Alcochete). LW1 –
516 unmanaged cork-oak woodland, LW2 – managed closed woodlands, LW3 – managed
517 agro-forest dominated by open woodlands, LW4 - managed agro-forest dominated by
518 open woodlands and pastures (see Table A1 for details on landscape structure among
519 the different LWs).

520

521 **Figure 2.** Average (and SE) of Bray-Curtis similarity values between sampling plots
522 within LWs for the two taxonomic groups (Collembola: white bars; Carabidae: grey
523 bars).

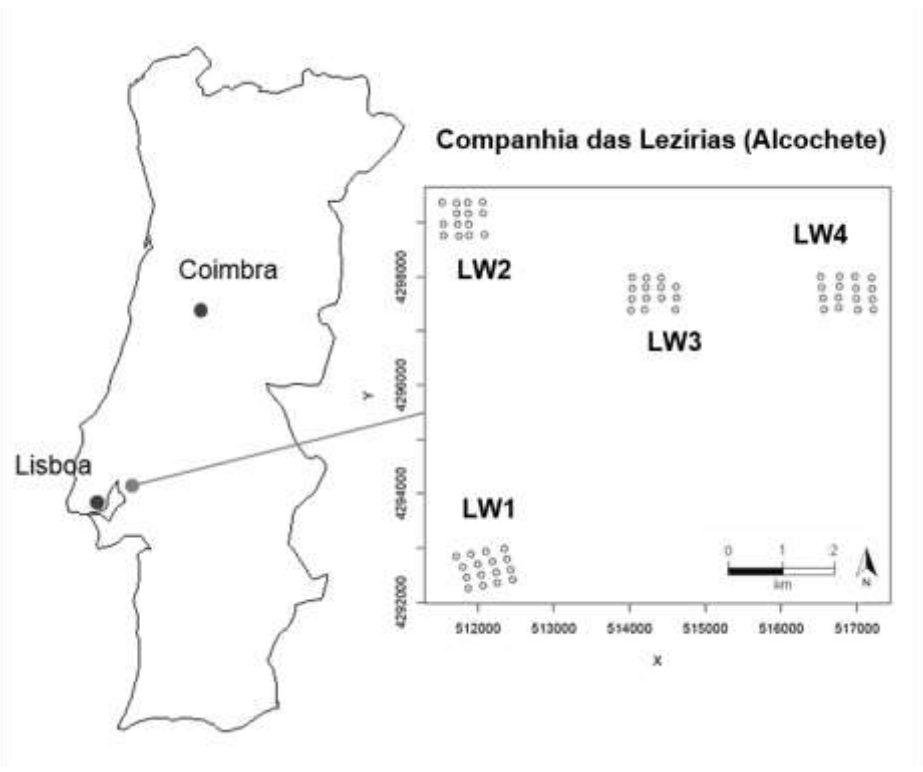
524

525 **Figure 3.** Venn diagrams of variation partitioning for the environmental variables in the
526 non-spatial model, considering habitat (“hab”) level, management (“man”) level and
527 landscape (“lan”) level. Pure and shared effects of the explained % of variance in
528 collembolan and carabid beetle community structure along the land-use gradient. “*”
529 and “**” correspond to the significance levels ($P < 0.05$ and $P < 0.01$) of the percentage
530 explained by the different environmental predictors.

531

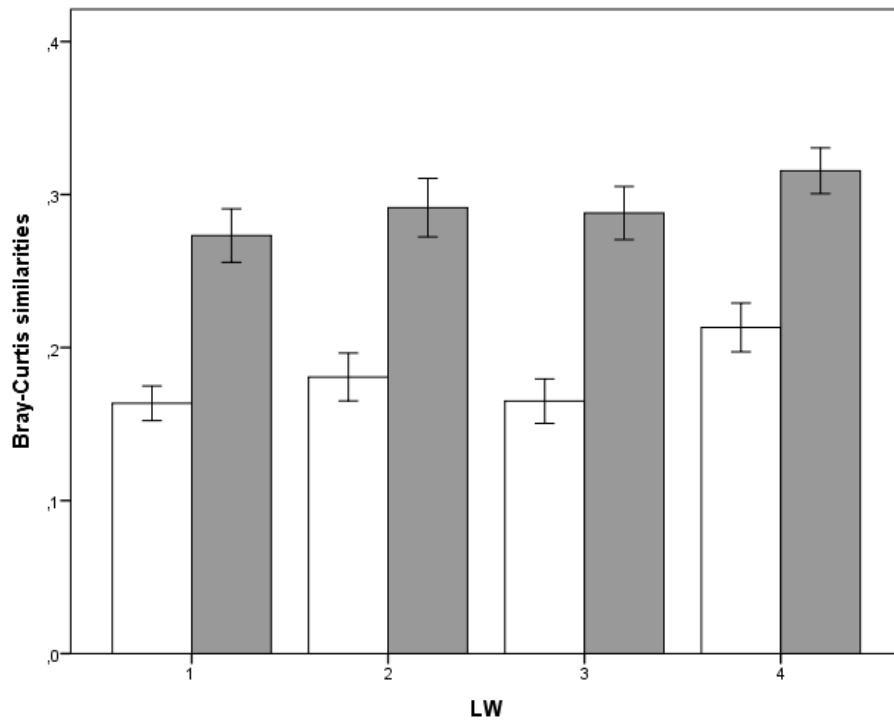
532 **Figure 4.** Venn diagrams of the variation partitioning between the environmental
533 component (“env”), broad-scale and fine-scale space component. Pure and shared
534 effects of the explained % of variance in collembolan and carabid beetle community
535 structure along the land-use gradient. “*” and “**” correspond to the significance levels
536 ($P < 0.05$ and $P < 0.01$) of the percentage explained by the different spatial (MEMs) and
537 environmental predictors.

538 **Figure 1:**



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544 **Figure 2:**



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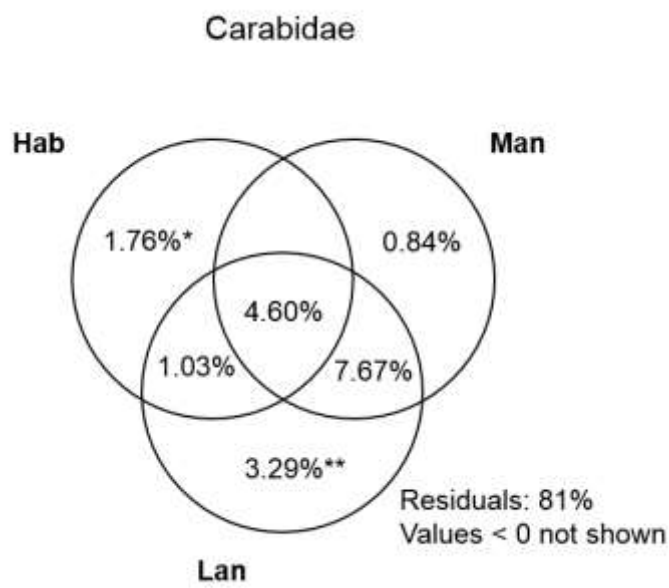
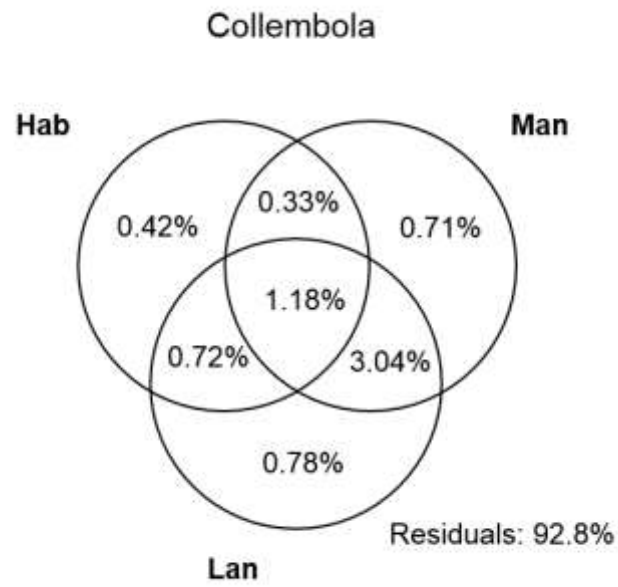
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550 **Figure 3:**



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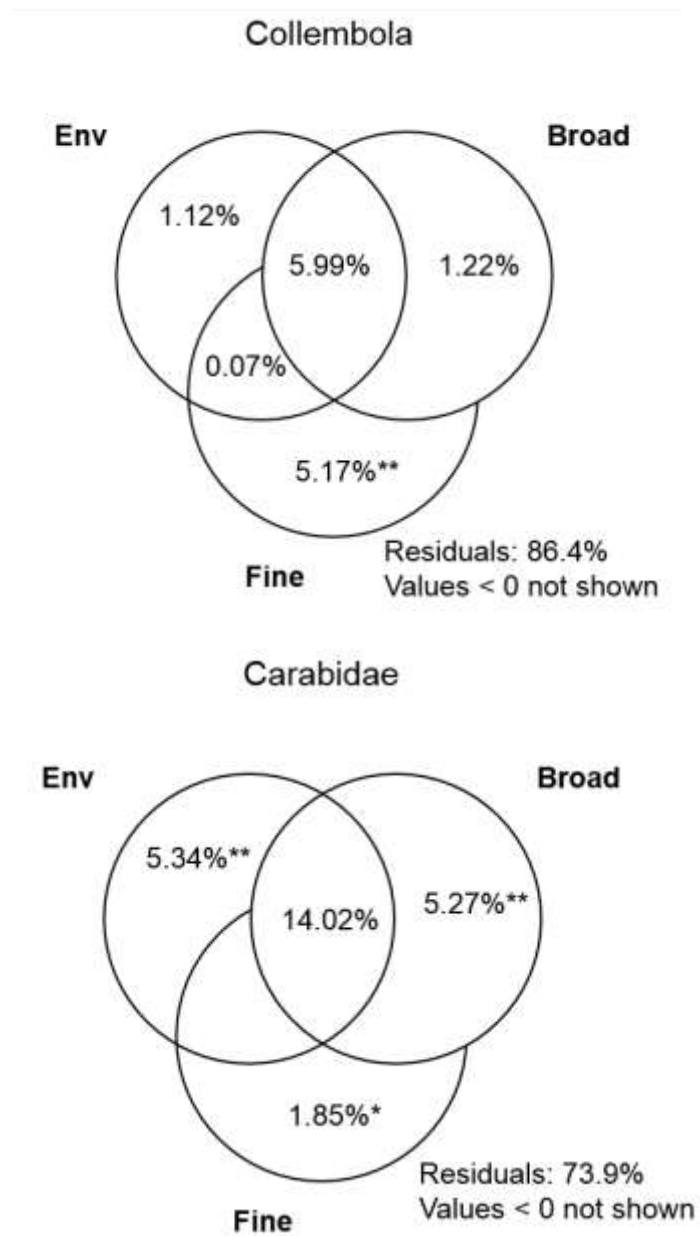
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558 **Figure 4:**



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