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# UNIVERSITÀ DEGLI STUDI DI TORINO

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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 (1km<sup>2</sup> 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 1km<sup>2</sup> 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  $R^2_{\text{adj}}$  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).

434

435

436

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.

		<b>LW1</b>	<b>LW2</b>	<b>LW3</b>	<b>LW4</b>
<b>Landscape management</b>	Land-use	natural forest	managed forest	agro-forest	agro-forest
	Interventions	none	pruning	pruning/grazing	pruning/grazing
	Management level	none	low	low	medium
<b>N° of sampling plots</b>	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 <sup>2</sup> Cum	AdjR <sup>2</sup> 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).

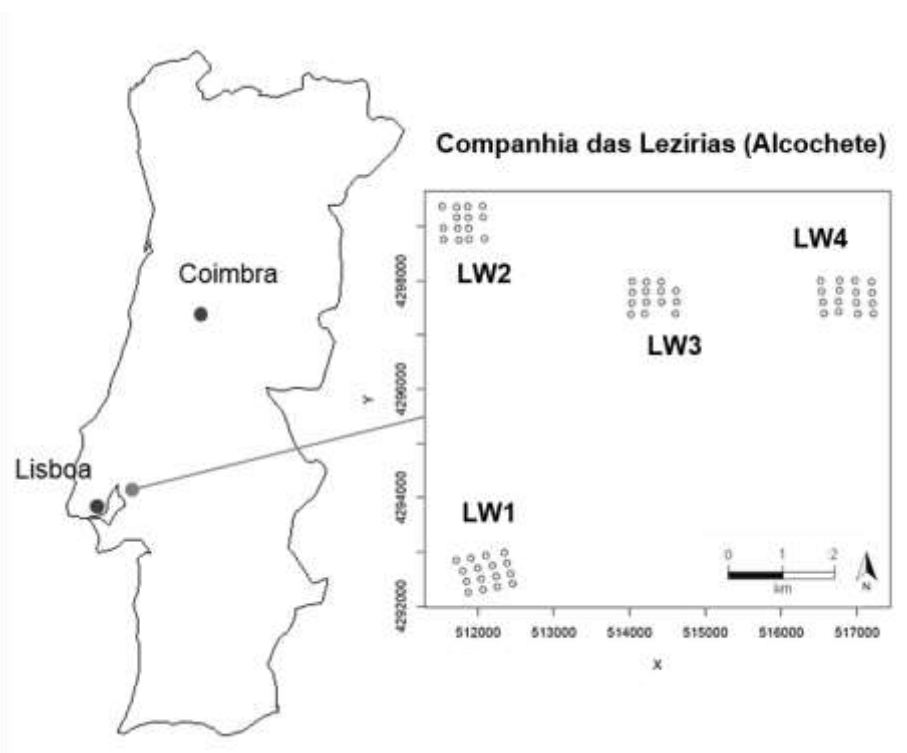
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525 **Figure 3.** Venn diagrams of variation partitioning for the environmental variables in the  
526 non-spatial model, considering habitat (“hab”) level, management (“man”) level and  
527 landscape (“lan”) level. Pure and shared effects of the 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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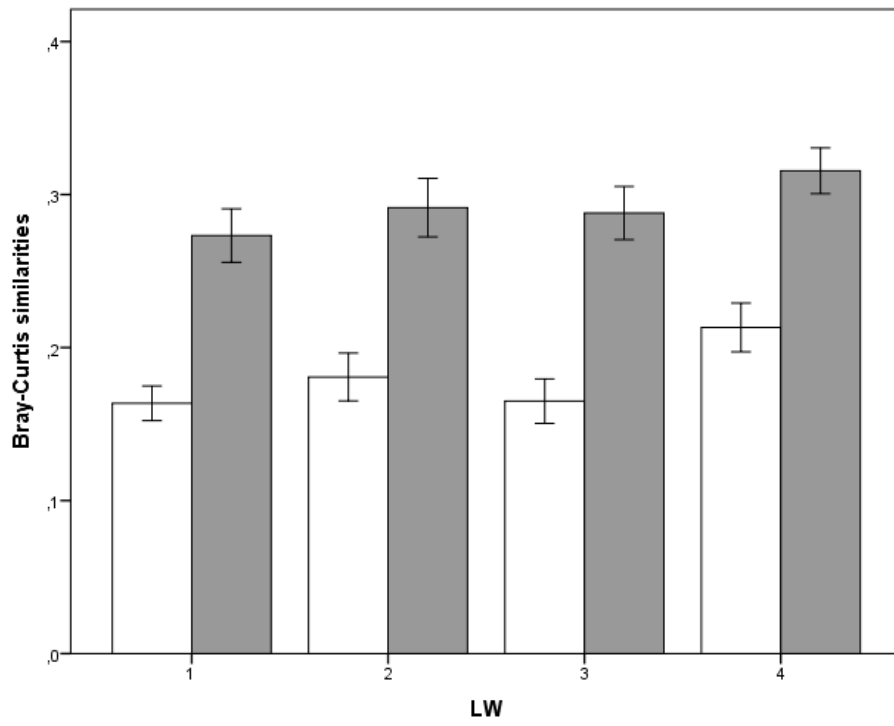
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544 **Figure 2:**



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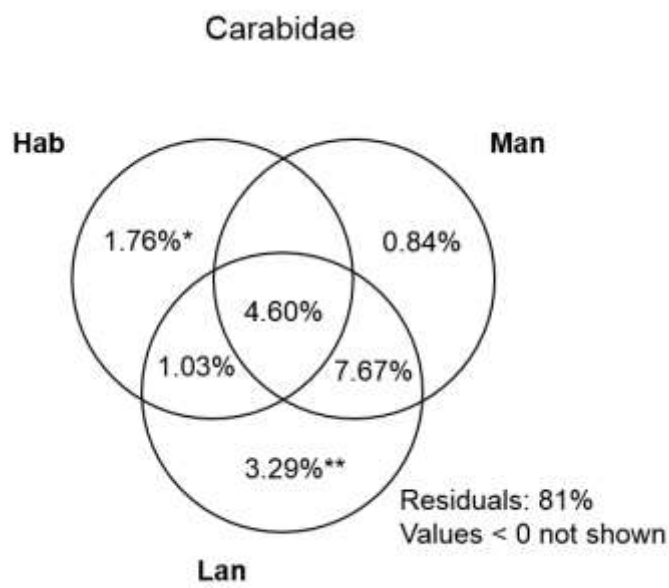
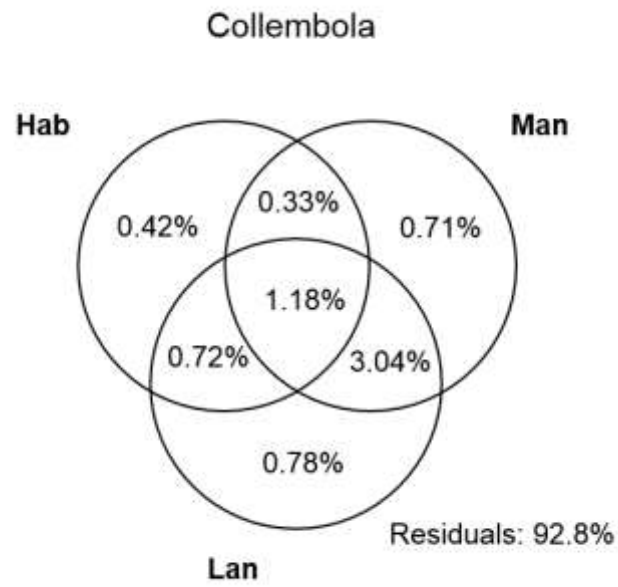
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550 **Figure 3:**



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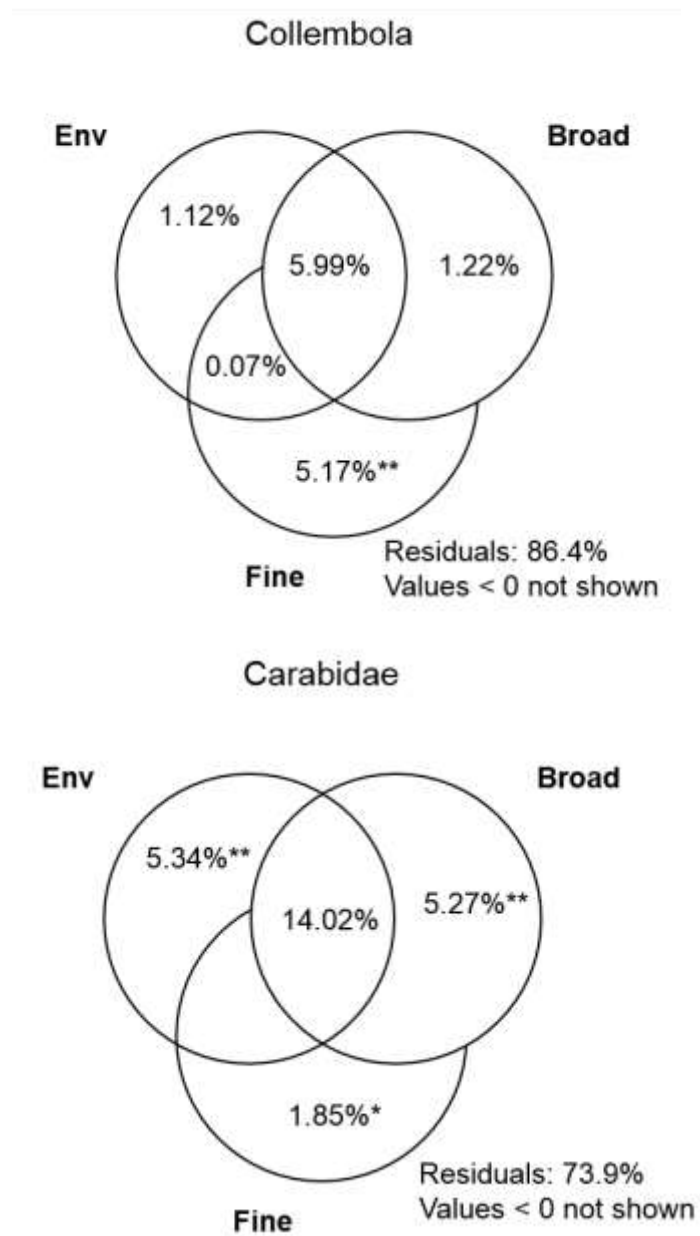
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558 **Figure 4:**



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565 **References**

566

567 Aström J, Bengtsson J (2011) Patch size matters more than dispersal distance in a  
568 mainland–island metacommunity. *Oecologia* 167:747-757

569

570 Baars MA (1979) Catches in pitfall traps in relation to mean densities of carabid beetles.  
571 *Oecologia* 41:25-46

572

573 Barbaro L, van Halder I (2009) Linking bird, carabid beetle and butterfly life-history  
574 traits to habitat fragmentation in mosaic landscapes. *Ecography* 32:321-333

575

576 Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to  
577 linking aboveground and belowground ecology. *Trends Ecol Evol* 20:634-641

578

579 Beisner B, Peres-Neto P, Lindstro E, Barnett A, Longhi ML (2006) The role of  
580 environmental and spatial processes in structuring lake communities from bacteria to  
581 fish. *Ecology* 87:2985–2991

582

583 Bengtsson G, Hedlund K, Rundgren S (1994) Food- and density-dependent dispersal:  
584 evidence from a soil collembolan. *J Anim Ecol* 63:513-520

585

586 Berg MP (2010) Spatio-temporal structure in soil communities and ecosystem  
587 processes. In: Verhoef HA and Morin PJ (eds) *Community Ecology*. Oxford University  
588 Press, Oxford, pp 69-80

589

590 Berg MP, Bengtsson J (2007) Temporal and spatial variability in soil food web  
591 structure. *Oikos* 116:1789-1804  
592

593 Berg MP, Kiers ET, Driessen G, van Der Heijden M, Kooi BW, Kuenen F, Liefjing M,  
594 Verhoef HA, Ellers J (2010) Adapt or disperse: understanding species persistence in a  
595 changing world. *Glob Change Biol* 16:587–598  
596

597 Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, Blanchet G,  
598 Blankmeyer E, Carvalho M, Christensen B, Chun Y, Dormann C, Dray S, Gómez-  
599 Rubio V, Halbersma R, Krainski E, Legendre P, Lewin-Koh N, Li H, Ma J, Millo G,  
600 Mueller W, Ono H, Peres-Neto P, Piras G, Reder M, Tiefelsdorf M, Yu D (2013) spdep:  
601 Spatial dependence: weighting schemes, statistics and models. R package version 0.4-56  
602 (<http://cran.r-project.org/>)  
603

604 Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables.  
605 *Ecology* 89:2623-2632  
606

607 Boieiro M, Carvalho JC, Cardoso P, Aguiar CAS, Rego C, Faria e Silva I, Amorim I,  
608 Pereira R, Azevedo FEB, Borges PAV, Serrano ARM (2013) Spatial factors play a  
609 major role as determinants of endemic ground Beetle Beta diversity of Madeira Island  
610 Laurisilva. *PLOS One* 8:1-10  
611

612 Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of  
613 ecological variation. *Ecology* 73:1045–1055  
614

615 Bowler DE, Benton TG (2011) Testing the interaction between environmental variation  
616 and dispersal strategy on population dynamics using a soil mite experimental system.  
617 *Oecologia* 166:111-119  
618

619 Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern  
620 Wisconsin. *Ecol Monogr* 27:325-349  
621

622 Brose U (2003) Bottom-up control of carabid beetle communities in early successional  
623 wetlands: mediated by vegetation structure or plant diversity? *Oecologia* 135:407–413  
624

625 Chase JM, Bengtsson J (2010) Increasing spatio-temporal scales: meta-community  
626 ecology. In: Verhoef HA and Morin PJ (eds) *Community Ecology*. Oxford University  
627 Press, Oxford, pp 57-68  
628

629 Chisholm C, Lindo Z, Gonzalez A (2011) Metacommunity diversity depends on  
630 connectivity and patch arrangement in heterogeneous habitat networks. *Ecography* 34:  
631 415-424  
632

633 Chust G, Pretus JL, Ducrot D, Bedos A, Deharveng L (2003a) Identification of  
634 landscape units from an insect perspective. *Ecography* 26:257-268  
635

636 Chust G, Pretus JL, Ducrot D, Bedos A, Deharveng L (2003b) Response of soil fauna to  
637 landscape heterogeneity: Determining optimal scales for biodiversity modeling.  
638 *Conserv Biol* 17:1712-1723  
639

640 Chust G, Pretus JL, Ducrot D, Ventura D (2004) Scale dependency of insect  
641 assemblages in response to landscape pattern. *Landscape Ecol* 19:41–57  
642  
643 Clarke KR (1993) Nonparametric multivariate analyses of changes in community  
644 structure. *Aust J Ecol* 18:117-143  
645  
646 Cliff A, Ord J (1973) *Spatial Autocorrelation*. Pion press, London  
647  
648 Cottenie K (2005) Integrating environmental and spatial processes in ecological  
649 community dynamics. *Ecol Lett* 8:1175-1182  
650  
651 Costanza JK, Moody A, Peet RK (2011) Multi-scale habitat heterogeneity as a predictor  
652 of plant species richness. *Landscape Ecol* 26:851–864  
653  
654 Cushman SA, McGarigal K (2002) Hierarchical, multi-scale decomposition of species-  
655 environment relationships. *Landsc Ecol* 17:637–646  
656  
657 Davies KF, Holyoak M, Preston KA, Offeman VA, Lum Q (2009) Factors controlling  
658 community structure in heterogeneous metacommunities. *J Anim Ecol* 78:937–944  
659  
660 Desender K, Turin H (1989) Loss of habitat and changes in the composition of the  
661 ground and tiger beetle fauna in four West European countries since 1950 (Coleoptera:  
662 Carabidae, Cicindelidae). *Biol Conserv* 48:277–294  
663

664 Diekötter T, Wamser S, Wolters V, Birkhofer K (2010) Landscape and management  
665 effects on structure and function of soil arthropod communities in winter wheat. *Agric*  
666 *Ecosyst Environ* 137:108-112  
667

668 Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive  
669 framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol*  
670 *Model* 196:483-493  
671

672 Dray S (2013) SpacemakeR: Spatial modelling. R package version 0.0–5/r101  
673 (<http://cran.r-project.org/>)  
674

675 Dray S, Legendre P, Blanchet FG (2007) packfor: R package for forward selection with  
676 permutation. R package version 0.0-7.h (<http://cran.r-project.org/>)  
677

678 Driscoll DA, Kirkpatrick JB, McQuillan PB, Bonham KJ (2010) Classic  
679 metapopulations are rare among common beetle species from a naturally fragmented  
680 landscape. *J Anim Ecol* 79:294–303  
681

682 Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends Ecol Evol* 17:177-183  
683

684 Flohre A, Fischer C, Aavik T, Bengtsson J, Berendse F, Bommarco R, Ceryngier P,  
685 Clement LW, Dennis C, Eggers S, Emmerson M, Geiger F, Guerrero I, Hawro V,  
686 Inchausti P, Liira J, Morales MB, Oñate JJ, Pärt T, Weisser WW, Winqvist C, Thies C,  
687 Tschantke T (2011) Agricultural intensification and biodiversity partitioning in  
688 European landscapes comparing plants, carabids, and birds. *Ecol Appl* 21:1772–1781

689

690 Hamazaki T (1996) Effects of patch shape on the number of organisms. *Landsc Ecol*  
691 11:299-306

692

693 Hedlund K, Griffiths B, Christensen S, Scheu S, Setälä H, Tscharrntke T, Verhoef H  
694 (2004) Trophic interactions in changing landscapes: responses of soil food webs. *Basic*  
695 *Appl Ecol* 5:495-503

696

697 Heiniger C, Barot S, Ponge JF, Salmon S, Botton-Divet L, Carmignac D, Dubs F (2014)  
698 *Pedobiologia* 57:103-117

699

700 Heino J (2013) Environmental heterogeneity, dispersal mode and co-occurrence in  
701 stream macroinvertebrates. *Ecol Evol* 3:344–355

702

703 Hopkin SP (1997) *Biology of the Springtails*. Oxford University Press, Oxford

704

705 Ingimarsdóttir M, Caruso T, Ripa J, Magnúsdóttir OB, Migliorini M, Hedlund K (2012)  
706 Primary assembly of soil communities - Disentangling the effect of dispersal and local  
707 environment. *Oecologia* 170:745-54

708

709 Kneitel JM, Chase JM (2004) Trade-offs in community ecology: linking spatial scales  
710 and species coexistence. *Ecol Lett* 7:69–80

711

712 Kotze DJ, Brandmayr P, Casale A, Dauffy-Richard E, Dekoninck W, Koivula MJ,  
713 Lövei GL, Mossakowski D, Noordijk J, Paarmann W, Pizzolotto R, Saska P, Schwerk

714 A, Serrano J, Szyszko J, Taboada A, Turin H, Venn S, Vermeulen R, Zetto T (2011)  
715 Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and  
716 population studies to bioindication, habitat assessment and conservation. *ZooKeys*  
717 100:55–148  
718  
719 Kotze DJ, O’Hara RB (2003) Species decline – but why? Explanations of carabid beetle  
720 (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135:138–148  
721  
722 Jonason D, Smith HG, Bengtsson J, Birkhofer K (2013) Landscape simplification  
723 promotes weed seed predation by carabid beetles. *Landscape Ecol* 28:478-494  
724  
725 Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for  
726 ordination of species data. *Oecologia* 129:271-280  
727  
728 Legendre P, Legendre L (2012) Numerical ecology, 3rd English edition. Developments  
729 in Environmental Modelling, Vol. 24. Elsevier Science BV, Amsterdam  
730  
731 Legendre P, Borcard D, Roberts DW (2012) Variation partitioning involving orthogonal  
732 spatial eigenfunction submodels. *Ecology* 93:1234-1240  
733  
734 Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt  
735 RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity  
736 concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613  
737

738 Lemessa D, Hambäck PA, Hylander K (2014) The effect of local and landscape level  
739 land-use composition on predatory arthropods in a tropical agricultural landscape.  
740 *Landscape Ecol* (in press: DOI 10.1007/s10980-014-0115-y)  
741

742 Lindberg N, Bengtsson J (2005) Population responses of oribatid mites and  
743 collembolans after drought. *Appl Soil Ecol* 28:163-174  
744

745 Lindo Z, Winchester NN (2009) Spatial and environmental factors contributing to  
746 patterns in arboreal and terrestrial oribatid mite diversity across spatial  
747 scales. *Oecologia* 160:817-825  
748

749 Lövei GL, Sunderland KD (1996) Ecology and behavior of ground beetles (Coleoptera,  
750 Carabidae). *Annu Rev Entomol* 41:231-256  
751

752 Martins da Silva P, Aguiar CAS, Niemelä J, Sousa JP, Serrano ARM (2008) Diversity  
753 patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use  
754 disturbance. *Agric Ecosyst Environ* 124:270–274  
755

756 Martins da Silva P, Berg MP, Serrano ARM, Dubs F, Sousa JP (2012) Environmental  
757 factors at different spatial scales governing soil fauna community patterns in fragmented  
758 forests. *Landsc Ecol* 27:1337–1349  
759

760 McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial pattern  
761 analysis program for categorical maps. Computer software program produced by the



762 authors at the University of Massachusetts, Amherst. Available from  
763 [www.umass.edu/landeco/research/fragstats/fragstats.html](http://www.umass.edu/landeco/research/fragstats/fragstats.html)  
764  
765 Moran P (1948) The interpretation of statistical maps. *J R Stat Soc Series B Stat*  
766 *Methodol* 10:243-251  
767  
768 Myers JA, Chase JM, Jiménez I, Jørgensen PM, Araujo-Murakami A, Paniagua-  
769 Zambrana N, Seidel R (2013) Beta-diversity in temperate and tropical forests reflects  
770 dissimilar mechanisms of community assembly. *Ecol Lett* 16:151–157  
771  
772 Nabe-Nielsen J, Sibly RM, Forchhammer MC, Forbes VE, Topping CJ (2010) The  
773 effects of landscape modifications on the long-term persistence of animal populations.  
774 *PLOS One* 5:1-7  
775  
776 Niemelä J, Kotze DJ (2009) Carabid beetle assemblages along urban to rural gradients:  
777 A review. *Landsc Urban Plan* 92:65–71  
778  
779 Niemelä J, Haila Y, Halme E, Pajunen T, Punttila P (1992) Heterogeneity in the Spatial  
780 Distribution of Carabid Beetles in the Southern Finnish Taiga. *J Biogeogr* 19:173-181  
781  
782 Ojala R, Huhta V (2001) Dispersal of microarthropods in forest soil. *Pedobiologia*  
783 45:443–450  
784

785 Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL,  
786 Solymos P, Stevens HH, Wagner H (2013) Vegan: community ecology package. R  
787 package version 2.0–3 (<http://cran.r-project.org>)  
788

789 Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species  
790 data matrices: Estimation and comparison of fractions. *Ecology* 87:2614–2625  
791

792 Ponge JF, Dubs F, Gillet S, Sousa JP, Lavelle P (2006) Decreased biodiversity in soil  
793 springtail communities: the importance of dispersal and landuse history in  
794 heterogeneous landscapes. *Soil Biol Biochem* 38:1158-1161  
795

796 Puech C, Poggi S, Baudry J, Aviron S (2014) Do farming practices affect natural  
797 enemies at the landscape scale? *Landscape Ecol* (in press: DOI 10.1007/s10980-014-  
798 0103-2)  
799

800 Querner P, Bruckner A, Drapela T, Moser D, Zaller JG, Frank T (2013) Landscape and  
801 site effects on Collembola diversity and abundance in winter oilseed rape fields in  
802 eastern Austria. *Agric Ecosyst Environ* 164:145-154  
803

804 R Core Team (2013) R: A language and environment for statistical computing. R  
805 Foundation for Statistical Computing, Vienna.  
806

807 Rantalainen M-L, Fritze H, Haimi J, Pennanen T, Setälä H (2005) Colonisation of  
808 newly established habitats by soil decomposer organisms: the effect of habitat corridors  
809 in relation to colonisation distance and habitat size. *Appl Soil Ecol* 28:67-77

810

811 Ribera I, Dolédec S, Downie IS, Foster GN (2001) Effect of land disturbance and stress  
812 on species traits of ground beetle assemblages. *Ecology* 82:1112–1129

813

814 Ricklefs RE (1987) Community diversity: relative roles of local and regional processes.  
815 *Science* 235:167–171

816

817 Sarthou J-P, Badoz A, Vaissière B, Chevallier A, Rusch A (2014) Local more than  
818 landscape parameters structure natural enemy communities during their overwintering  
819 in semi-natural habitats. *Agric Ecosyst Environ* 194:17–28

820

821 Sattler T, Duelli P, Obrist MK, Arlettaz R, Moretti M (2010) Response of arthropod  
822 species richness and functional groups to urban habitat structure and management.  
823 *Landscape Ecol* 25:941-954

824

825 Schuldt A, Assmann T, Schaefer M (2013) Scale-dependent diversity patterns affect  
826 spider assemblages of two contrasting forest ecosystems. *Acta Oecol* 49:17-22

827

828 Siqueira T, Bin LM, Roque FO, Pepinelli M, Ramos RC, Marques Couceiro SR,  
829 Trivinho-Strixino S, Cottenie K (2012) Common and rare species respond to similar  
830 niche processes in macroinvertebrate metacommunities. *Ecography* 35:183-192

831

832 Smith TW, Lundholm JT (2010) Variation partitioning as a tool to distinguish between  
833 niche and neutral processes. *Ecography* 33:648-655

834

835 Sousa JP, Gama MM, Pinto C, Keating A, Calh a F, Lemos M, Castro C, Luz T, Leit o  
836 P, Dias S (2004) Effects of land-use on Collembola diversity patterns in a  
837 Mediterranean landscape. *Pedobiologia* 48:609-622  
838  
839 Tanner J (2003) Patch shape and orientation influences on seagrass epifauna are  
840 mediated by dispersal abilities. *Oikos* 100:517–524  
841  
842 Thompson R, Townsend C (2006) A truce with neutral theory: local deterministic  
843 factors, species traits and dispersal limitation together determine patterns of diversity in  
844 stream invertebrates. *J Anim Ecol* 75:476-484  
845  
846 Turner MG, Gardner RH, O’Neill RV (2001) Pattern and process: landscape ecology in  
847 theory and practice. Springer, New York  
848  
849 van de Meutter F, de Meester L, Stoks R (2007) Metacommunity structure of pond  
850 macroinvertebrates: effects of dispersal mode and generation time. *Ecology* 88:1687–  
851 1695  
852  
853 Vandewalle M, de Bello F, Berg MP, Bolger T, Dol dec S, Dubs F, Feld CK,  
854 Harrington R, Harrison PA, Lavorel S, Martins da Silva P, Moretti M, Niemel  J,  
855 Santos P, Sattler T, Sousa JP, Sykes MT, Vanbergen AJ, Woodcock BA (2010)  
856 Functional traits as indicators of biodiversity response to land use changes across  
857 ecosystems and organisms. *Biodivers Conserv* 19:2921–2947  
858

859 Woltz JM, Isaacs R, Landis DA (2012) Landscape structure and habitat management  
860 differentially influence insect natural enemies in an agricultural landscape. *Agric*  
861 *Ecosyst Environ* 152:40-49  
862

863 Woodcock BA, Redhead J, Vanbergen AJ, Hulmes L, Hulmes S, Peyton J,  
864 Nowakowski M, Pywell RF, Heard MS (2010) Impact of habitat type and landscape  
865 structure on biomass, species richness and functional diversity of ground beetles. *Agric*  
866 *Ecosyst Environ* 139:181–186  
867

868 Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations  
869 *Landscape Ecol* 19:125–138  
870

871 Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: An  
872 idiosyncratic synthesis *Landscape Ecology* 17:355-365  
873

874 Wu J, Loucks OL (1995) From balance-of-nature to hierarchical patch dynamics: a  
875 paradigm shift in ecology. *Q Rev Biol* 70:439–466  
876

877 Yaacobi G, Ziv Y, Rosenzweig ML (2007) Effects of interactive scale-dependent  
878 variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape*  
879 *Ecol* 22:687–703