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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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Abstract

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

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

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

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

Introduction

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

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

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

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

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

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

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

Materials and methods

Study area and sampling design

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

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

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

Species data

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

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

Environmental variables across scales

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

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

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

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

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

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

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

Spatial modelling

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

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

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

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

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

Community similarity within and among LWs

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

Variance partitioning along the land-use gradient

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

Non-spatial model

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

Space versus Environment

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

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

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

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

Results

Overview on species richness and composition across LUs

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

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

Variance partitioning: non-spatial model

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

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

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

Spatial versus environmental effects across spatial scales

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

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

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

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

Discussion

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

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

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

Effect of space across groups of soil fauna

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

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

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

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

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

Effect of environmental factors at different spatial scales

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

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

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

Implications for fundamental and applied ecology

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

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

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

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

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Table 1. Characterization of the land-use windows (LW1, LW2, LW3 and LW4) selected for this study. At the regional scale, the landscape structure reflected by the 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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Table 2. R and P-values derived from ANOSIM pairwise comparisons of collembolan 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

Table 3. Selected environmental variables (at plot-patch-landscape levels) obtained from the RDA forward selection procedure performed for each taxonomic group. Detailed descriptions of each variable are provided in Supplementary material Table A1 (“Herb” - percentage coverage of herbaceous vegetation; “Density” – “cattle density”, “Area Cork” - area with cork production, “Time Cork” - time since last cork removal, “Area Cut” – forest area harvested; “G_NP” –number of grassland patches, “F_Contig” - spatial connectedness, or contiguity, of forest patches, “F_Shape” and “G_Shape” - shape index of cork-oak patches in forest and grassland habitats, respectively, “G_Prox” - 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
	Man	1 Density	5	0.051	0.035	3.128	0.001
		2 TimeCork	3	0.085	0.053	2.089	0.006
	Lan	1 G_NP	10	0.051	0.035	3.106	0.001
		2 F_Contig	7	0.089	0.057	2.400	0.006
Carabidae	Hab	1 Herb	5	0.088	0.072	5.586	0.001
	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

Figures captions:

Figure 1. Sampling points (spatial coordinates) of the selected landscape windows

(LWs1-4) along the consolidated alluvial plain of the river Tagus (Alcochete). LW1 – unmanaged cork-oak woodland, LW2 – managed closed woodlands, LW3 – managed agro-forest dominated by open woodlands, LW4 - managed agro-forest dominated by open woodlands and pastures (see Table A1 for details on landscape structure among the different LWs).

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

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

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

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