



Microhabitat heterogeneity promotes soil fertility and ground-dwelling arthropod diversity in Mediterranean wood-pastures

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ABSTRACT

Mediterranean wood-pastures are extensive agroforestry systems that hold great ecological, social and cultural values, which consist of mixtures of grassland, scattered trees and shrubs, primarily used for livestock grazing. For centuries, low-intensity management in these landscapes has resulted in multiple microhabitats that favour biodiversity and are considered key elements for the long-term persistence of wood-pastures. However, the relative contribution of each microhabitat type to wood-pasture biodiversity and functioning remains poorly studied. We investigated the impact that different wood-pasture microhabitats have on soil chemical fertility and the decomposition food web. We analysed the two main microhabitats that make wood-pastures up – open grasslands and isolated Trees – and three additional “litter-trapping” microhabitats – shrubs scattered in the grassland matrix, canopied shrubs and piles of pruning debris—in terms of soil chemical properties (organic matter content, total N, C:N ratio, available P, and exchangeable base cations), collembolan and dipteran (mostly detritivores) abundance, and carabid (seed-eaters and predators) and staphylinid (mostly predators) beetle abundance, body size, biomass, species richness and composition. Grasslands were the most different microhabitats, with the lowest soil nutrient content and particular carabid and staphylinid species composition. Trees had the highest soil fertility levels and abundance of Diptera and staphylinids, and held unique staphylinid assemblages. “Litter-trapping” microhabitats had medium to high soil nutrient values and shared a distinct staphylinid assemblage compared to grasslands and trees. Besides, scattered shrubs provided shelter for large-sized carabid and staphylinid predators, while canopied shrubs held the highest carabid abundance and biomass. “Litter-trapping” microhabitats retained tree leaves that would otherwise be lost to the wood-pasture, recovering nutrients to the system, and provided new habitat, shelter and food for detritivores and unique predator assemblages. “Litter-trapping” microhabitats thus enhanced soil fertility and the decomposition process, at the same time as increased the abundance and diversity of the communities of ground-dwelling detritivores and predators inhabiting wood-pastures. These findings confirmed that microhabitat heterogeneity resulting from low-intensity management is essential to maintain both the primary production and the biodiversity conservation value of wood-pastures.

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1. Introduction

Mediterranean wood-pastures are multipurpose agroforestry systems that hold great ecological, social and cultural values, where extensive livestock grazing co-occurs with multiple land uses like cereal cropping and firewood harvesting, and high levels of biodiversity (Plieninger et al., 2015; Torralba et al., 2016). Wood-pastures provide high-quality food products and important ecosystem services such as fodder, watershed maintenance, carbon sequestration and wildlife conservation (Bugalho et al., 2011; Campos et al., 2013; Torralba et al., 2016), and are therefore encouraged as a sustainable land use system in different regions of the world (see Mosquera-Losada et al., 2005). In Europe, wood-pastures have persisted for centuries owing to traditional low-intensity management practices, being particularly common in Spain and Portugal (called *dehesas* and *montados*; Plieninger et al., 2015).

However, wood-pastures are currently threatened by both land use intensification and abandonment (Moreno and Pulido, 2009; Plieninger et al., 2015), the latter leading to shrub encroachment that reduces heterogeneity and negatively affects biodiversity and ecosystem functioning (García-Tejero et al., 2013; Moreno et al., 2013; Peco et al., 2012).

Traditional management of wood-pastures results in a wide variety of coexisting microhabitats, like open grasslands, isolated trees, scattered shrubs, agricultural crops, hedges and water bodies (see e.g., Moreno et al., 2016). Such microhabitat heterogeneity enhances biological diversity by providing different niches, environmental conditions and resources for species that require many of these elements to live, like numerous bird and arthropod species do (DeMars et al., 2010; Diacon-Bolli et al., 2012; Hartel et al., 2014; Moreno et al., 2016). In wood-pastures, grasslands constitute the dominant microhabitat type, play the major economic role providing food for livestock and are crucial to biodiversity conservation (Diacon-Bolli et al., 2012; Taboada et al., 2011). Direct sunlight and the absence of shrub

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or tree cover in grasslands leads to sharp temperature and moisture contrasts that influence nutrient mineralisation (Köchy and Wilson, 1997) and the ground-dwelling arthropod fauna (e.g., Thiele, 1977). Isolated trees in wood-pastures act as keystone structures (Fischer et al., 2010; Manning et al., 2006; Tews et al., 2004), since they (1) create a distinct and mild microclimate through their shade, affecting arthropod species composition and abundance (Lindsay and Cunningham, 2009; Rossetti et al., 2015; Taboada et al., 2006), (2) provide shelter for livestock, (3) are essential for nutrient cycling (Escudero et al., 1985; Gea-Izquierdo et al., 2010; Vetaas, 1992), and (4) constitute suitable habitats for specialized taxa like epiphytic flora, saproxylic fauna, birds and bats (Fischer et al., 2010; Manning et al., 2006). Scattered shrubs often constitute the third main microhabitat type in wood-pastures and savanna-like landscapes (Bergmeier et al., 2010; Bugalho et al., 2011; Plieninger et al., 2015; Vetaas, 1992); however, their importance to ecosystem functioning and wildlife conservation has rarely been studied (but see Moreno et al., 2016). Shrubs can provide roosting, nesting, resting and signing places for birds (Hartel et al., 2014), and shelter for reptiles (Godinho et al., 2011; Martín and Lopez, 2002) and butterflies (Dover et al., 1997). Moreover, in open ventilated landscapes such as many wood-pastures, shrubs retain tree leaves that would otherwise be blown away by the wind (Facelli and Pickett, 1991; see also Rossetti et al., 2015), most likely altering the nutrient cycle and providing new habitat for litter-dwelling fauna (Sayer, 2005).

In general, the accumulation of litter buffers soil temperatures and increases soil moisture, benefiting decomposers and detritivores (Facelli and Pickett, 1991; Sayer, 2005). Since up to 90% of the energy obtained in primary production goes to the decomposition pathway (Chen and Wise, 1999), this food web is an essential part of the ecosystem that contributes to the provision of multiple services like water supply, nutrient cycling and soil formation (Lavelle et al., 2006). Among detritivores, Collembola and Diptera are key arthropod functional groups, which feed directly on decaying matter (including faeces in case of Diptera) and on decomposers such as fungi (Frouz, 1999; Hövemeyer, 1992; Rusek, 1998), while at the same time serve as food to many invertebrate predators (e.g., Thiele, 1977). Among predators, carabids (Coleoptera: Carabidae) and staphylinids (Coleoptera: Staphylinidae) are predominant, highly diverse, ground-dwelling beetles that respond to changes in habitat structure, microclimate, nutrient input, and prey abundance and composition (Bohac, 1999; Kotze et al., 2011), and are essential food items for higher trophic levels (Kotze et al., 2011; Vickery et al., 2001).

In this study we investigate how differences in environmental conditions and resource provisioning among wood-pasture microhabitats influence soil fertility and the functioning of the decomposition food web. We surveyed soil chemical properties, collembolan and dipteran (mostly detritivores) abundance, and carabid beetle (seed-eaters and predators) and staphylinid beetle (mostly predators) abundance, body size, biomass, species richness and composition, in five types of microhabitats: open grasslands, isolated trees, shrubs scattered in the grassland matrix, canopied shrubs, and piles of pruning debris. Opposite to open grasslands and isolated trees, tree leaves accumulate in scattered and canopied shrubs and pruning piles (hereafter referred as “litter-trapping microhabitats”), very likely providing food and favourable microclimate for detritivores and their predators, which in turn may influence nutrient return to the soil layer (Sayer, 2005). We predict that: (i) soil nutrient content will be highest in litter-trapping microhabitats and lowest in grasslands, where nutrients are rapidly removed by growing grasses (Otieno et al., 2011); (ii) suitable microclimate conditions and enhanced nutrient supply in litter-trapping microhabitats and trees will foster high detritivore and predator abundances (Koivula et al., 1999; Rossetti et al., 2015); (iii) litter-trapping

microhabitats will provide shelter for large-sized predators in agreement with the “enemy-free space hypothesis”, which states that complex habitat structures allow large species to escape from natural enemies (Brose, 2003); and (iv) grasslands will hold particular seed-eater and predator assemblages due to their unique plant species composition and more severe microclimate conditions (García-Tejero et al., 2013; Taboada et al., 2011). This study sheds light on the role that litter-trapping microhabitats play in the functioning of wood-pasture ecosystems by enhancing soil fertility and nutrient recycling, and providing new habitat and shelter for detritivores and predators. The study also gives practical advice to develop management guidelines aimed at maximizing wood-pasture microhabitat heterogeneity and biodiversity conservation, while not compromising productivity.

2. Material and methods

2.1. Study area

The study was conducted in three traditionally managed *Quercus pyrenaica* Willd. wood-pastures (public renting *dehesa* systems used as communal pasturelands, typically shared by the livestock holders of neighbouring locations) at the lower slopes of the Cantabrian mountain range in north-west Spain (Mediterranean region; 42°33'–42°46'N, 4°55'–5°08'W; 975–1130 m a.s.l.; 0–10% slope). Mean annual temperature is 10.9 °C, mean annual precipitation 927 mm, with a dry period in July and August, and the type of soil is humic cambisol (soil pH = 5.84 ± 0.43; soil texture (%): sand = 66.23 ± 5.81, silt = 28.50 ± 4.27, and clay = 5.27 ± 1.65). The uniqueness of these wood-pastures is reinforced by their cultural and historical values as being part of the traditional transhumance routes used for centuries to shepherd livestock (mainly sheep) between summer highland and winter lowland pasturelands (‘Cañada Leonesa Oriental’, ca. 60,000 units in 1940–60; Rodríguez Pascual, 2001). Over the last decades, traditional transhumant shepherding has become uneconomical in the study area as in the rest of Europe leading to a decline in the number of transhumant sheep stock, and to an increase of sedentary livestock farming (Rodríguez Pascual, 2001). The three wood-pasture sites are embedded in a matrix of agricultural land, dense mature oak forests and pine plantations, and are currently tree pruned (tree density ca. 50 trees/ha) and extensively grazed by moderate-size sheep flocks with similar grazing intensity (2–3 LU/ha, ca. 600–900 LU/landscape). Five different microhabitats typically found in these agroforestry systems were studied in each wood-pasture (Fig. 1, Table 1): (i) Grasslands constitute the most extensive microhabitat and are dominated by annual and perennial herb species such as *Agrostis capillaris*, *Aira caryophyllea*, *Hieracium* gr. *pilosella*, *Trifolium campestre*, *Tuberaria guttata*, and *Vulpia bromoides* (Tárrega et al., 2009). (ii) Isolated trees are about 10–12 m high and 1–1.5 m in perimeter at breast height, and were pruned occasionally to favour horizontal branches and provide shade, browsing and acorn production. (iii) Scattered shrubs are formed by one or several small bushes clustered together (mainly *Crataegus monogyna* and *Calluna vulgaris*), extending on average 1.8 m², separated a minimum of 10 m from the closest tree. (iv) Canopied shrubs consist of a cluster of bushes and/or oak root sprouts, which occupied on average 16.1 m², located around the trunk of one or two mature trees growing together. (v) Pruning piles consist of small branches, which are no longer used for firewood exploitation, piled up in the last two years after the pruning of nearby trees, and extended 15.1 m². Further details on microhabitat characteristics are found in Table 1. In each wood-pasture, four replicates of each microhabitat type were selected as sampling points. Sampling points were at least 25 m apart from site edges and

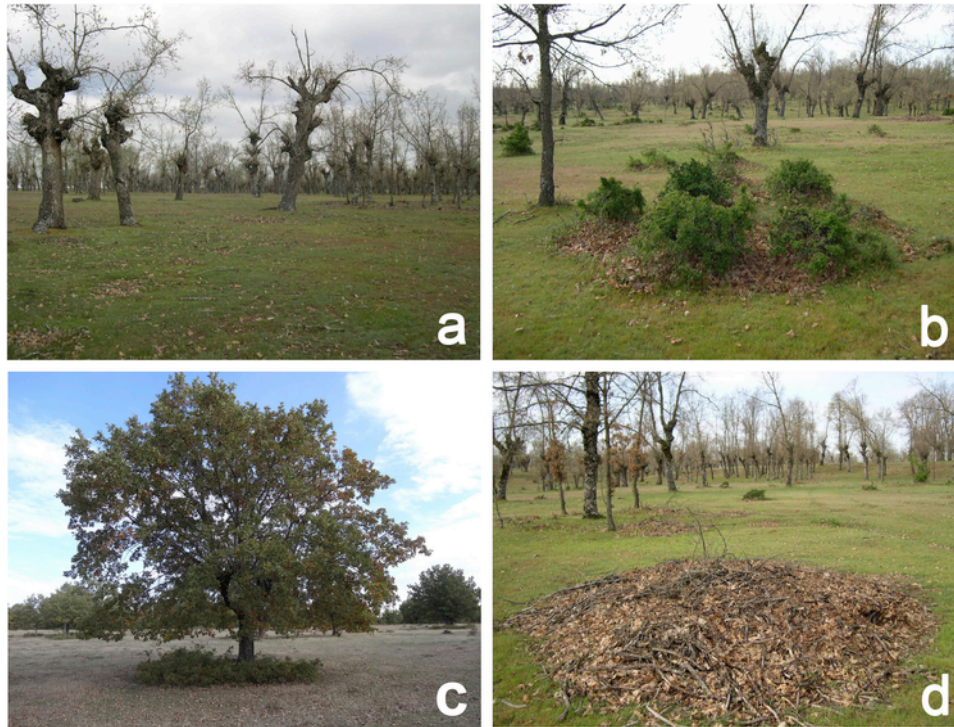


Fig. 1. The five types of microhabitats studied: (a) tree and grassland, (b) scattered shrub, (c) canopied shrub, (d) pruning pile.

Table 1

Environmental characteristics (mean \pm SE) of each microhabitat type. $N = 12$. Vegetation layer: lower (0–50 cm), medium (50–200 cm), upper (>200 cm).

	Microhabitat				
	Grassland	Tree	Scattered shrub	Canopied shrub	Pruning pile
Bare soil cover (%)	4.44 \pm 1.73	2.25 \pm 1.10	4.13 \pm 1.44	3.10 \pm 1.12	5.19 \pm 1.74
Litter cover (%)	1.54 \pm 0.67	16.50 \pm 5.52	10.81 \pm 1.83	65.69 \pm 4.49	59.54 \pm 6.23
Litter depth (cm)	0.98 \pm 0.28	2.33 \pm 0.48	7.23 \pm 0.80	6.51 \pm 0.57	11.31 \pm 1.21
Coarse woody debris (%)	1.42 \pm 0.61	10.04 \pm 1.56	1.08 \pm 0.16	8.08 \pm 1.57	28.85 \pm 3.67
Lower vegetation layer cover (%)	96.27 \pm 1.50	94.81 \pm 1.57	94.69 \pm 1.34	75.81 \pm 5.92	44.79 \pm 6.19
Medium vegetation layer cover (%)	0.00 \pm 0.00	0.40 \pm 0.27	0.98 \pm 0.31	25.09 \pm 3.68	0.85 \pm 0.54
Upper vegetation layer cover (%)	0.00 \pm 0.00	85.83 \pm 3.56	0.83 \pm 0.56	78.61 \pm 5.92	16.10 \pm 7.82
Distance to nearest tree (m)	16.08 \pm 2.13	0.63 \pm 0.05	12.81 \pm 1.50	1.10 \pm 0.11	6.15 \pm 0.69
Height of nearest tree (m)	11.42 \pm 0.93	13.33 \pm 0.47	12.25 \pm 0.58	10.08 \pm 0.69	11.75 \pm 0.82
Area of shrub/pile (m ²)	0.00 \pm 0.00	0.00 \pm 0.00	1.76 \pm 0.27	16.08 \pm 1.01	15.07 \pm 1.79
Height of shrub/pile (cm)	0.00 \pm 0.00	0.00 \pm 0.00	67.58 \pm 7.72	49.51 \pm 7.00	40.42 \pm 6.99

from each other so they constitute independent replicates for arthropod captures (Digweed et al., 1995).

2.2. Soil sampling

We analysed organic matter content (O.M.), total nitrogen (N), C/N ratio, available phosphorus (P), and exchangeable calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) from the first five centimetres of the soil layer. Five samples (0.5–2 m apart from microhabitat centre) of approximately one litre in volume were manually collected at each sampling point in June 2007, homogenised, air-dried and passed through a 2 mm mesh sieve before chemical analyses, following the official methods of soil analysis (M.A.P.A., 1994). Organic matter was determined by oxidation with acid-dichromate potassium and titration of dichromate excess with ferrous sulfate; total N by a semimicro-Kjeldahl procedure; available P by the

Bray–Kurtz method (Kalra and Maynard, 1991); and exchangeable Ca^{2+} , K^+ , Mg^{2+} and Na^+ were extracted with ammonium acetate 1 N pH = 7 (5 g soil to 50 ml AcNH_4) and determined by atomic absorption spectrophotometry.

2.3. Arthropod sampling

We collected Collembola, Diptera, carabids and staphylinids using plastic pitfall traps (depth 86 mm, diameter 60 mm), covered by 10×10 cm roofs, partly filled with 25% propylene glycol, and flush to the soil surface. In litter-trapping microhabitats, pitfall traps were covered with a 2 cm wire mesh to prevent them from getting clogged with litter. Two pitfall traps, 50–200 cm apart, were placed at each sampling point (i.e., 40 traps per site, 120 traps in total). Arthropods were collected continuously from 1 June to 20 October 2007, emptying the traps every three weeks. Trap loss was low, accounting for

4.3% of the total number of trapping days. Pitfall catches reflect arthropod activity-density (Thiele, 1977), which will be referred hereafter as abundance or number of individuals. We counted the number of Collembola and adults of Diptera, carabids and staphylinids. Carabid and staphylinid beetles were identified to the species level using standard keys, and named according to current species catalogues (Supplementary Table S1). Staphylinid individuals that could not be assigned to a particular species (63 individuals, 2.1%) were only included in the analysis of overall abundance. Data on average body length, carabid diet (predator, omnivore, and seed-eater) and staphylinid resource preference (litter-dweller, mycophilous, and coprophilous) were obtained for each species from the literature (see Supplementary Table S1). Mean biomass for each carabid and staphylinid species was estimated using family-specific length versus weight regression equations (Hóðar, 1996). Biomass data were included in this study because they can provide a more detailed picture of the arthropod contribution to ecosystem functioning, especially in relation to resource use and energy flow (Saint-Germain et al., 2007).

2.4. Data analysis

We used linear mixed models (LMMs) to look for differences between microhabitats in soil chemical properties and beetle community weighted mean (CWM) body length (calculated as the weighted arithmetic mean of the body length of all individuals in each sampling point), and generalised linear mixed models (GLMMs) with a negative binomial error distribution to compare arthropod abundances among microhabitats. Site was included as a random factor in the models to account for the randomized block sampling design. Prior to the analyses, arthropod catches were pooled for the whole trapping period, and organic matter and N content were logit-transformed (Warton and Hui, 2011).

For each carabid diet and staphylinid resource preference group in the five microhabitat types, total beetle biomass was calculated as the sum of the mean biomass values of all species multiplied by the total number of individuals collected for each species. Results were compared among microhabitats using LMMs.

Arthropod abundance and biomass models included the number of days the traps were active as an offset term in order to account for differences in trapping effort. In all cases, LMMs and GLMMs tested the null hypothesis that the mean values of the analysed variables did not differ among microhabitats. When the null hypothesis was rejected ($P < 0.05$), pair-wise comparisons between microhabitats were carried out, and P values were corrected for multiple testing using the Holm method.

We calculated sample-based rarefaction curves to compare beetle species richness between microhabitats taking into account differences in catch size. We used the 95% confidence intervals of the randomization curves to assess the significance of differences.

We used multivariate regression trees (MRT) (De'Ath, 2002) to explore similarities and differences in beetle species composition between microhabitats. Beetle species abundance was recursively partitioned according to microhabitat types, resulting in dichotomous trees that split the data in clusters that maximize between-group and minimize within-group differences in species composition. We retained the largest trees where all splits were significant ($P < 0.05$, 9999 permutations) according to permutational multivariate analyses of variance (Anderson, 2001). Prior to multivariate analyses, species abundance data were pooled for each microhabitat type and wood-pasture, and then Hellinger-transformed so the model preserved Hellinger distances, which are meaningful to assess ecological patterns (see Borcard et al., 2011).

Analyses were carried out with widely available free statistical programs: R (R Core Team, 2015) – packages *MASS* (Venables and Ripley, 2002), *multcomp* (Hothorn et al., 2008) *nlme* (Pinheiro et al., 2015), *mvpart* (De'Ath, 2014) and *rpart* (Therneau et al., 2015) –, EstimateS (Colwell, 2006) and DISTLM (Anderson, 2001).

3. Results

3.1. Soil chemical fertility

Most soil chemical properties significantly differed between microhabitats and were highest in canopied shrubs and trees and lowest in grasslands (Fig. 2): organic matter content ($F = 5.71$, $P < 0.001$), total N ($F = 11.07$, $P < 0.001$), and exchangeable Ca^{2+} ($F = 22.88$, $P < 0.001$), Mg^{2+} ($F = 23.34$, $P < 0.001$), K^+ ($F = 10.53$, $P < 0.001$) and Na^+ ($F = 3.77$, $P = 0.009$). No significant differences were found in C:N ratio and available P between microhabitats.

3.2. Arthropod abundance

We collected 162,850 collembolan and 10,315 dipteran individuals, and their abundances significantly differed between microhabitats (respectively, $F = 20.75$, $P < 0.001$; $F = 21.99$, $P < 0.001$). Collembola were very abundant in grasslands and scarce in litter-trapping microhabitats (Fig. 3a). Dipteran abundance was highest under trees and lowest in scattered shrubs and pruning piles (Fig. 3b).

We collected 5128 carabid and 2981 staphylinid individuals, whose numbers differed between microhabitats (respectively, $F = 7.28$, $P = 0.009$; $F = 4.19$, $P = 0.040$). Carabids were more abundant in canopied shrubs and staphylinids in trees and canopied shrubs than in the other microhabitats (Figs. 3c, d).

3.3. Beetle length and biomass

Carabid CWM body length was highest in scattered shrubs ($F = 5.73$, $P < 0.001$; Fig. 4a). Staphylinid CWM body length also differed between microhabitats ($F = 23.88$, $P < 0.001$) and species were on average bigger in scattered shrubs and smaller in grasslands and trees (Fig. 4b). Total carabid biomass was highest in canopied shrubs and mainly composed of predators and omnivores (Fig. 4c). Carabid biomass significantly differed between microhabitats for all diet groups (predators: $F = 3.09$, $P = 0.023$; omnivores: $F = 12.13$, $P < 0.001$; seed-eaters: $F = 18.75$, $P < 0.001$). Biomass of predators and omnivores was highest in canopied shrubs and that of seed-eaters in grasslands. Total staphylinid biomass was lowest in grasslands and similar in all other microhabitat types, where it was mainly composed of litter dwellers (Fig. 4d). Staphylinid biomass significantly differed between microhabitats for all resource preference groups (litter dwellers: $F = 6.43$, $P < 0.001$; coprophilous: $F = 3.86$, $P = 0.008$; mycophilous: $F = 3.93$, $P = 0.007$). Biomass of litter dwellers and mycophilous species was highest in canopied shrubs and that of coprophilous species in grasslands, followed by trees.

3.4. Beetle diversity and composition

We collected 51 carabid and 116 staphylinid species (Supplementary Tables S2 and S3). Rarefied carabid species richness was significantly higher in scattered shrubs and grasslands compared to canopied shrubs and pruning piles (Fig. 5a). Rarefied staphylinid species richness did not differ between microhabitats (Fig. 5b).

The multivariate regression tree on carabid species composition first separated grasslands from the other microhabitats, this split accounting for 24.2% of the total variation of the data. The remaining

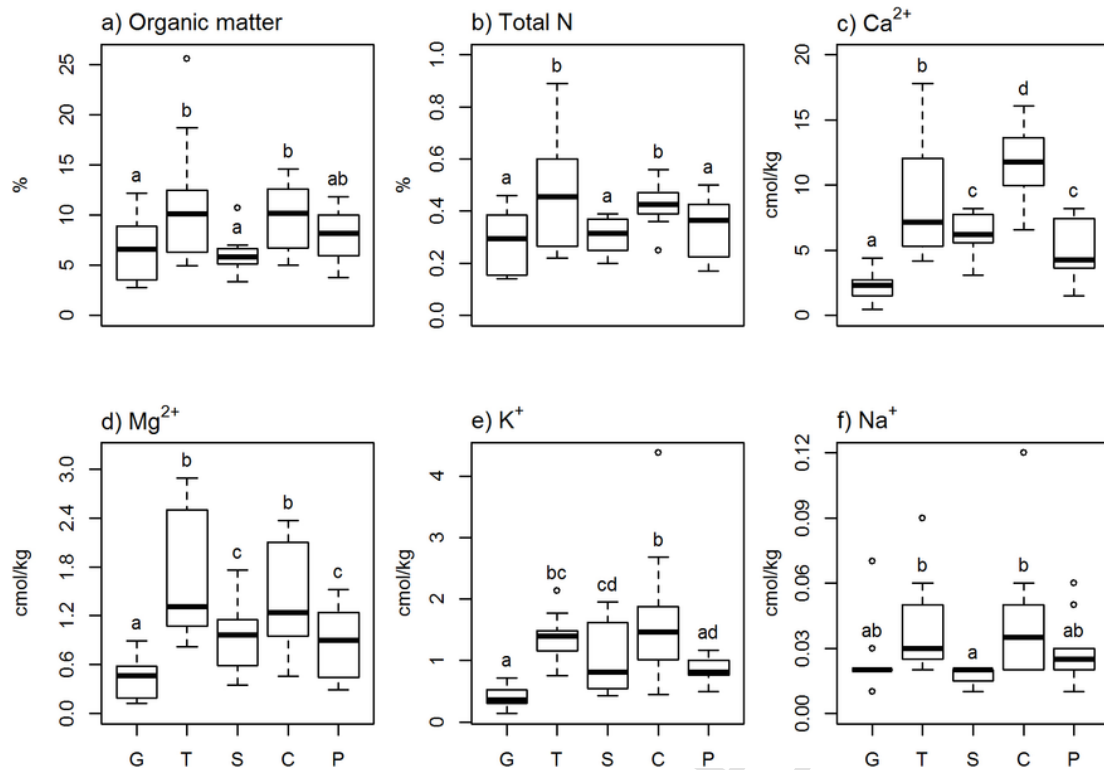


Fig. 2. Boxplots of the soil variables measured at the five microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box), 1.5 times the interquartile range from the box (ends of the whiskers) and values out of these limits (individual dots). Different letters indicate significant differences ($P < 0.05$) between microhabitats after Holm correction.

microhabitats were then split in two groups according to canopy presence, which explained 12.3% of the total variation: trees and canopied shrubs versus scattered shrubs and pruning piles (Fig. 6a). Staphylinid assemblages were first separated into those of litter-trapping microhabitats and the rest, this split accounting for 32.9% of the total variation. Grasslands and trees further split, explaining 8.7% of the total variation in the data (Fig. 6b).

4. Discussion

Differences in resources and environmental conditions provided by each microhabitat type influenced soil chemical properties and the ground-dwelling arthropod fauna of wood-pastures. Grasslands had low soil organic matter and nutrient content, very abundant Collembola, high carabid species richness, and particular carabid and staphylinid beetle assemblages. Trees had high soil organic matter and nutrient content, abundant Diptera and staphylinids, and a distinct assemblage of small-sized staphylinids. Litter-trapping microhabitats shared intermediate to high soil nutrient content and a common assemblage of medium to large staphylinids. However, scattered shrubs held high carabid species richness (as high as in grasslands) and large-sized carabid and staphylinid beetles; while canopied shrubs held the highest carabid abundance and carabid and staphylinid biomass.

4.1. Differences between microhabitats

Soil nutrient content was lowest in grasslands, in agreement with our prediction (i) and the results of previous studies (Gallardo, 2003; Gea-Izquierdo et al., 2010). Grasslands receive nutrients from livestock faeces and grass litter (Escudero et al., 1985; Otieno et al.,

2011), which mineralise faster than tree leaves, especially when exposed to the sharp changes in moisture that characterise this microhabitat type (Köchy and Wilson, 1997; Vetaas, 1992). Fast mineralisation and direct sunlight promote primary production in grasslands, accelerating the nutrient cycle (Otieno et al., 2011) and resulting in low soil nutrient accumulation (Wardle et al., 2004). Despite nutrient recycling may also be rapid under trees as primary production is usually as high as in grasslands (Rivest et al., 2013), soil nutrient content here was elevated due to the numerous sources of nutrient input (e.g., livestock faeces, bird droppings, stemflow, through-fall, leaf and grass litter) (Escudero et al., 1985; Gallardo, 2003; Gea-Izquierdo et al., 2010; Vetaas, 1992). Furthermore, tree roots bring up nutrients from deep soil layers where they are inaccessible to grasses, and subsequently return them as leaf litter (Moreno and Pulido, 2009; Vetaas, 1992), thus enhancing nutrient recycling (see also Moreno et al., 2007). In the studied wood-pastures, most tree leaves were blown away by the wind and only retained under scattered and canopied shrubs and pruning piles, where the accumulation of litter is expected to increase decomposition rates (Chen et al., 2014) at the same time as augments the generally low soil fertility of Mediterranean wood-pastures (Moreno and Pulido, 2009; Moreno et al., 2007). Indeed, soil organic matter and nutrient content were highest in canopied shrubs, probably because these microhabitats persist longer in the wood-pasture than pruning piles, and are of greater size and less exposed to litter renewal by wind and to nutrient uptake by grasses than scattered shrubs. Altogether, these results showed that two rather distinct nutrient cycles occur in wood pastures: a faster one in grasslands and trees, where easily decomposable grass litter and livestock faeces return nutrients to the soil that are rapidly used in primary production; and a slower one in litter-trapping microhabi-

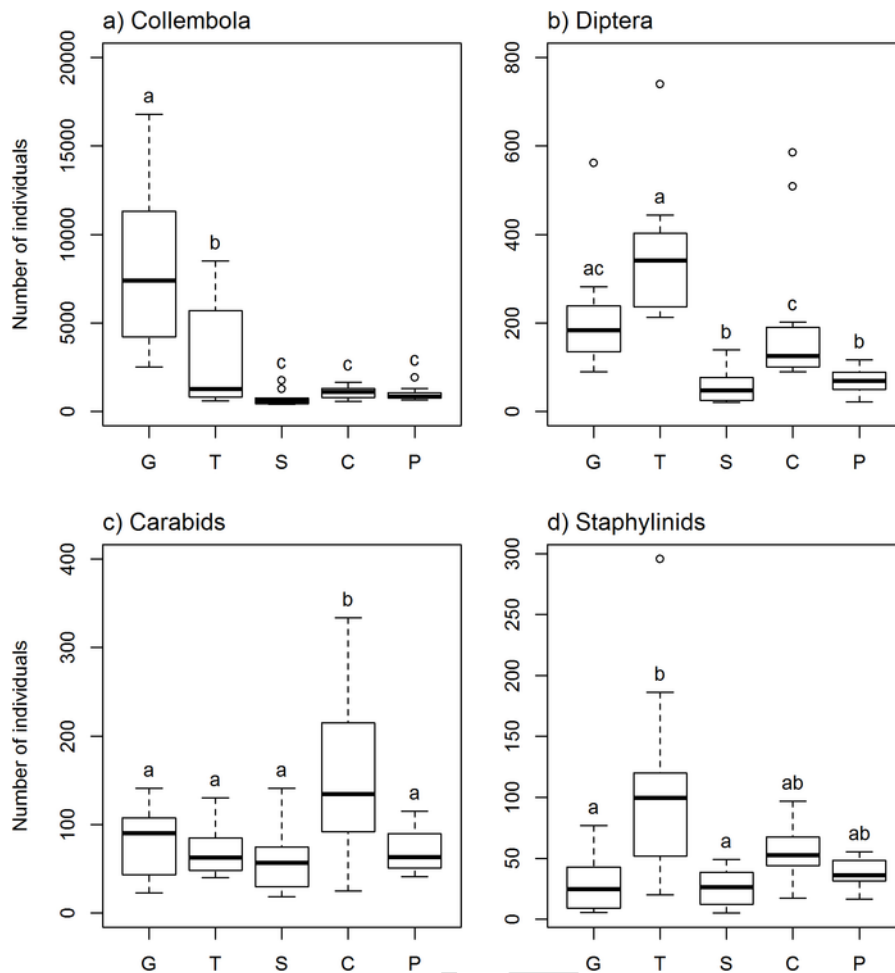


Fig. 3. Boxplots of the number of individuals of (a) Collembola, (b) Diptera, (c) carabids and (d) staphylinids captured at the five microhabitat types. The number of captured individuals was standardised to the median number of days the traps were active at each sampling point (282 days) prior to plotting. Different letters indicate significant differences ($P < 0.05$) between microhabitats after Holm correction. See Fig. 2 for further details.

tats, where recalcitrant tree leaf litter is slowly decomposed and soil organic matter and nutrients are stored (Wardle et al., 2004).

Contrary to our expectations, Collembola were much more abundant in grasslands than in litter-trapping microhabitats. Collembola may have preferred grasslands to the other microhabitat types (see Rusek, 1998), but our results may have as well been greatly influenced by differences in collembolan activity among microhabitat types. Collembola thriving in grasslands where sharp changes in moisture conditions occur may have been attracted by the humid environment inside the traps, thus overestimating abundance (Joosse and Groen, 1970; see also Rossetti et al., 2015). But it may as well be that Collembola did not particularly favour litter accumulation (Ponge et al., 1993), or that the great structural complexity of the litter layer may have hindered their capture in litter-trapping microhabitats (Melbourne, 1999). However, it must be noted that pitfall traps may not be the most appropriate method to assess collembolan abundance since they may mainly reflect the density of the most active species and underestimate the abundance of the less mobile ones, particularly in structurally complex microhabitats. The abundance of Diptera, carabids and staphylinids was highest under treed microhabitats (i.e., isolated trees and/or canopied shrubs), which partly agrees with our prediction (ii) and previous studies (Lindsay and Cunningham, 2009; Taboada et al., 2006). Treed microhabitats provide food, shelter, leaf litter (particularly canopied shrubs), logs and shade for invertebrates (Lindsay and Cunningham, 2009). For Diptera, large amounts of fresh

livestock faeces under trees may have attracted abundant coprophilous species, while the moister conditions beneath the thick litter layer of canopied shrubs may have favoured hemi-edaphic species (Frouz, 1999; Hövemeyer, 1992). The combination of tree shade and leaf litter accumulation especially benefited carabids, which were twice as abundant under canopied shrubs as in the other microhabitat types (see Koivula et al., 1999). Finally, tree presence also favoured staphylinids, which dominated under trees and canopied shrubs, where they could benefit from a favourable environment and feed on abundant Diptera, one of their preferred preys (Thayer, 2005).

Mean carabid and staphylinid body length was highest under scattered shrubs; a result that partly agrees with our prediction (iii) and complies with the “enemy-free space” hypothesis (Brose, 2003). Scattered shrubs embedded in the grassland matrix can be crucial as refuges for large predators that hunt in open grasslands and take shelter in dense vegetation or under stones (Bohac, 1999; Morris, 2000). Oppositely, small-sized predators, particularly staphylinids, are able to escape natural enemies by hiding into crevices, thanks to their slender and flexible body form (Bohac, 1999). The great abundance of medium- and large-sized individuals collected in canopied shrubs resulted in high beetle biomass, particularly of omnivorous and predatory carabids and litter-dwelling staphylinids, which very likely reflect high decomposer and detritivore biomass at lower trophic levels (Chen and Wise, 1999; Ponsard et al., 2000). A few mycophilous

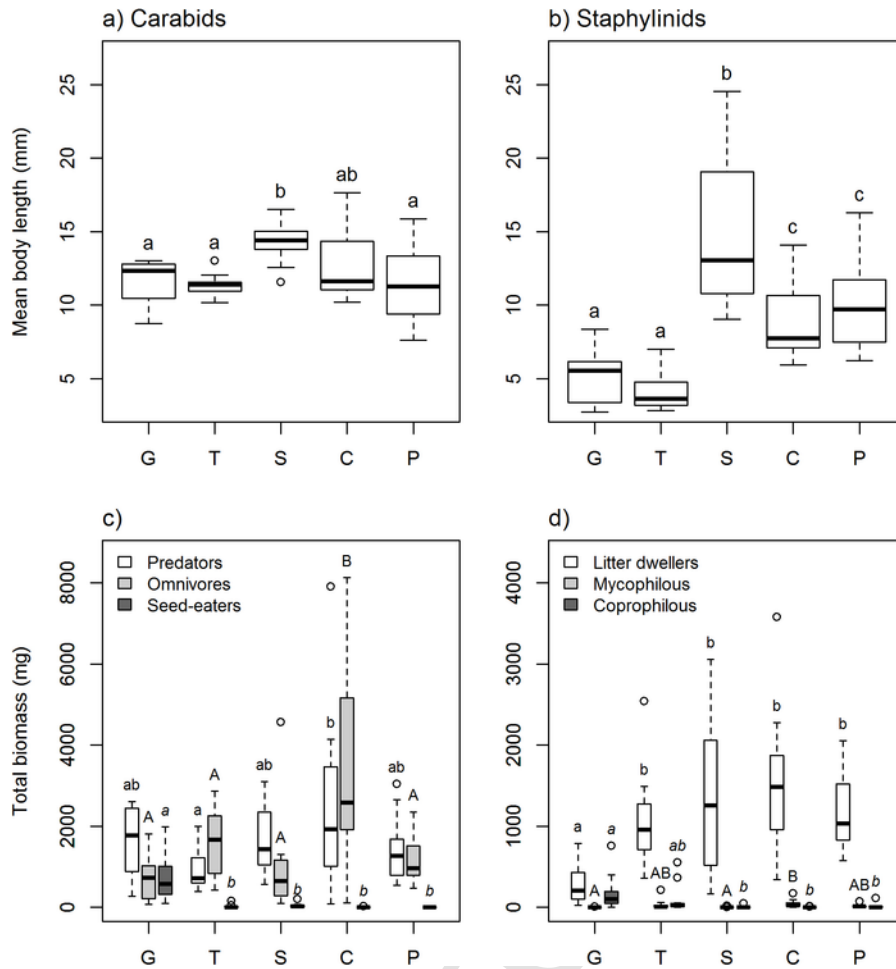


Fig. 4. Boxplots of the mean body length and total biomass of (a, c) carabids and (b, d) staphylinids at the five microhabitat types. Total biomass was calculated separately for each carabid diet group (predators, omnivores, and seed-eaters) and staphylinid resource preference group (litter dwellers, mycophilous, and coprophilous). Different letters of the same typography indicate significant differences ($P < 0.05$) between microhabitats after Holm correction for each carabid diet group and staphylinid resource preference group. See Fig. 2 for further details.

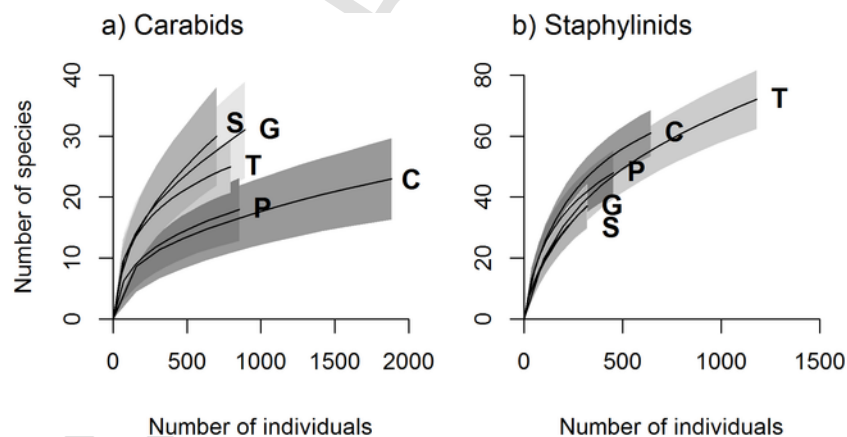


Fig. 5. Rarefaction curves for (a) carabids and (b) staphylinids. Rarefaction curves represent the number of species relative to the number of individuals for each microhabitat type. 95% confidence intervals for each curve are indicated in grey shading. See Fig. 2 for abbreviations.

staphylinids were also present in canopied shrubs and trees, where moist conditions, mild temperatures and copious decomposing matter (including woody debris from fallen branches) may favour fungi development and fructification (Nordén et al., 2004; Pinna et al., 2010).

Open grasslands were richest in carabid species and, as predicted (iv), held particular carabid and staphylinid beetle assemblages different from the other microhabitat types. Grassland beetle assemblages included guilds of species that were rare elsewhere, like seed-eating

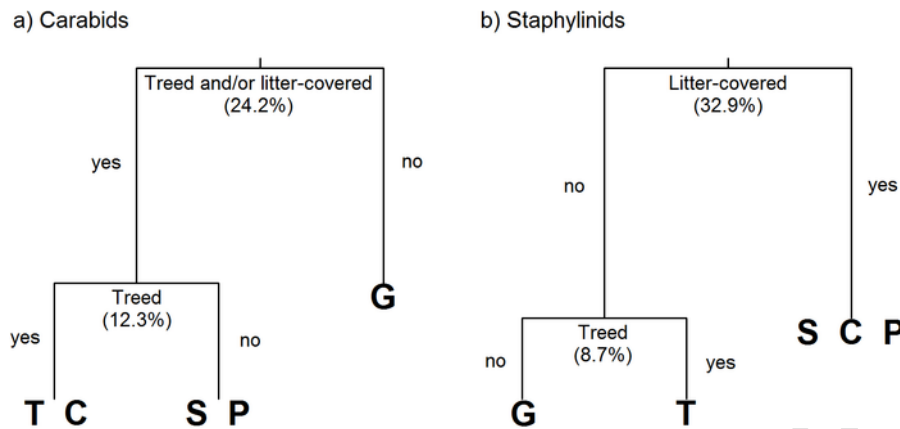


Fig. 6. Multivariate regression trees on species composition data of (a) carabids (Error = 0.545; CV Error = 0.951; SE = 0.100) and (b) staphylinids (Error = 0.501; CV Error = 0.817; SE = 0.059). The criteria for partitioning and the percentages of explained variance (R^2_{adj}) are indicated below each split. Only significant splits, according to a permutational multivariate analysis of variance ($P < 0.05$; 9999 permutations), were retained. See Fig. 2 for abbreviations.

carabids that usually thrive in warm and sun exposed habitats (Thiele, 1977), and coprophilous staphylinids that depend closely on livestock faeces. Also, great carabid species richness was found for scattered shrubs, a fact that suggests that this microhabitat type may be a keystone structure for these beetles as occurs in drier biotopes (Mazía et al., 2006). Differences in carabid beetle assemblages among the remaining microhabitats were determined by the presence of trees, stressing the influence that shade has on carabid species distribution (Taboada et al., 2006). On the other hand, staphylinid beetle assemblages responded strongly to litter accumulation, to which many species are particularly adapted (Mckenna et al., 2015), causing all litter-trapping microhabitats to share a common staphylinid assemblage. Although grasslands and trees offered similar resources to staphylinids, such as coprophilous Diptera, they held distinct staphylinid assemblages, maybe due to the different environmental conditions provided by tree shade.

4.2. Conservation and management implications

The differences found in soil fertility and in the abundance and distribution of detritivores and predators among the five microhabitat types most likely affect the functioning and service provisioning of wood-pastures (Bugalho et al., 2011; Howlett et al., 2011; Torralba et al., 2016). Overall, our results confirmed the idea that the high biodiversity of Mediterranean wood-pastures depends on the coexistence of a wide mosaic of microhabitats, in accordance with prior studies (Moreno et al., 2016). Litter-trapping microhabitats in particular proved to be essential for promoting nutrient recycling and for the arthropod fauna, offering new habitat and shelter for large-sized beetles, and enhancing the biodiversity sustained by grasslands and isolated trees, like other equivalent complex vegetation structures in different agroforestry systems across Europe (Rossetti et al., 2015; Vickery et al., 2001; Woodcock et al., 2009). Scattered and canopied shrubs may additionally function as keystone structures for species requiring multiple habitats to live (DeMars et al., 2010; Fischer et al., 2010), and as safe sites (*sensu* Rolo et al., 2013) for effective tree recruitment by protecting oak seedlings against herbivory and desiccation, hence benefiting the long-term persistence of Mediterranean wood-pastures. Moreover, great arthropod biomass under canopied shrubs implies enhanced prey availability for higher trophic levels including lizards, rodents, shrews and birds (Thiele, 1977), thus contributing to wildlife conservation (Kotze et al., 2011; Vickery et al., 2001; Woodcock et al., 2009).

From a management point of view, our results evidenced that a moderate density of scattered and/or canopied shrubs should be preserved in wood-pastures to augment heterogeneity, provided that shrub encroachment is prevented due to its negative effects on soil fertility, plant and arthropod diversity, and community composition (García-Tejero et al., 2013; Peco et al., 2012; Tárrega et al., 2009). Even though shrub encroachment frequently promotes oak tree regeneration (Canteiro et al., 2011; Plieninger et al., 2003), it does not maintain the functioning and provision of services of wood-pastures in the long-term (Moreno and Pulido, 2009; Moreno et al., 2013; Ramírez and Díaz, 2008). Since low-intensity grazing limits the expansion of shrubs without suppressing them (Álvarez-Martínez et al., 2016), the cost of preserving scattered and canopied shrubs in wood-pastures is expected to be low compared to other microhabitats that require supplementary management measures such as fencing (see Woodcock et al., 2009). However, the maintenance of shrubs to enhance microhabitat heterogeneity and overall biodiversity must be accomplished without detriment to open grasslands and isolated trees, which play the main productive roles in wood-pastures (Hartel et al., 2014; Moreno et al., 2013) and are crucial for the conservation of specialized taxa (García-Tejero et al., 2013; Manning et al., 2006; Robles et al., 2007, 2011; Sebek et al., 2013). Grasslands should continue to be preserved by extensive livestock grazing and trees should be regularly pruned or pollarded (i.e., pruned removing the upper branches) to promote horizontal canopy growth (Moreno and Pulido, 2009); while the resulting small-sized fragments from pruning should be temporally piled up and disseminated in the grassland matrix at a minor extra cost. Low-intensity management practices, such as extensive livestock grazing and tree pruning or pollarding, are, therefore, necessary to preserve the microhabitat mosaic that characterises Mediterranean wood-pastures and sustains their high biodiversity value (Moreno et al., 2016); but these practices need to be supported by adequate agricultural and conservation policies to assure long-term sustainability (Bergmeier et al., 2010; Bugalho et al., 2011; Díaz et al., 2013; Plieninger et al., 2015; Torralba et al., 2016).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.09.004>.

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