

Article

Trees Increase Ant Species Richness and Change Community Composition in Iberian Oak Savannahs

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Abstract: Iberian man-made oak savannahs (so called *dehesas*) are traditional silvopastoral systems with a high natural value. Scattered trees provide shelter and additional food to livestock (cattle in our study sites), which also makes possible for animals depending on trees in a grass-dominated landscape to be present. We compared *dehesas* with nearby treeless grasslands to assess the effects of oaks on ant communities. *Formica subrufa*, a species associated with decayed wood, was by far the most abundant species, especially in savannahs. Taxa specialized in warm habitats were the most common both in *dehesas* and grasslands, as expected in areas with a Mediterranean climate. Within *dehesas*, the number of species was higher below oak canopies than outside tree cover. Compared to treeless grasslands, the presence of oaks resulted in a higher species richness of aphid-herding and predator ants, probably because trees offer shelter and resources to predators. The presence of oaks changed also the species composition, which differed between grasslands and *dehesas*. In self-standing scattered oaks, ant communities did not differ between the trunks and soil below canopies. These results stress the conservation value of trees in *dehesas*; within grasslands, they offer an additional microhabitat for species that would otherwise be scarce or absent.

Keywords: ants; biodiversity; bioindicators; functional groups; *dehesas*; resource specialization



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1. Introduction

Both farmers and conservationists acknowledge the value of traditional silvopastoral systems for sustainable food production and biodiversity [1,2]. In Europe, the largest extensions of silvopastoral systems are usually in areas in which environmental restrictions (e.g., poor soils and harsh climatic conditions) impede intensive farming, as in many Mediterranean and Boreal regions [3]. In the Iberian Peninsula, one of these systems spreads over thousands of hectares, namely man-made oak (*Quercus* spp.) savannahs (so called “*dehesas*” in Spain and “*montados*” in Portugal) in which livestock rearing is the main land-use form [4]. The presence of trees interspersed within grasslands provides additional food for livestock at the same time that promotes biodiversity [1]. Nonetheless, intensive livestock management is threatening natural tree recruitment and conservation [4–6].

The ecological value of *dehesas* largely relies on the presence of trees [7–9]. Isolated trees increase the environmental heterogeneity of these ecosystems, allowing the presence of organisms (specially, small ones) that depend on trees in a grassland-dominated landscape [1,10,11]. Accordingly, arboreal cover has shown to have a positive impact on arthropods, amongst others [11,12], and house-specific guilds and functional groups [13,14].

The origin of *dehesas* is semi-natural, with a strong impact of human management [15]. For centuries, humans have cleared evergreen Mediterranean forests and turned them into *dehesas* designed and managed for livestock farming [4]. Extensive livestock management can be aligned with conservation of *dehesas*, however, increased livestock density

jeopardizes the sustainability of these systems [16]. When the number of domestic animals increases too much, acorn predation, lack of seed dispersal by rodents because of their lower density due to the elimination of their shelters (shrubs), and seedling trampling/predation may dramatically reduce natural tree regeneration [16,17]. In the long term, if regeneration of trees completely fails, *dehesas* could turn into pastures/grasslands with a consequent negative impact on biodiversity (e.g., ants in this study) [18–20].

Previous studies have used ants as indicators of forest disturbances [21–23] by considering their distribution, abundance and diversity [24]. Ants can be also classified according to their food resource utilization or their functional groups. For example, scavenger ants decompose organic matter or living in symbiosis with other animals or plants and perform beneficial functions as soil aeration, organic matter transport, or water retention [21]. Ants have a high functional importance in ecosystems; are sensitive to environmental changes; and are relatively easy to sample, identify, and classify [24]. Thus, interpreting changes on ant community composition is possible to disentangle symptoms of habitat disturbances [24]. Habitat degradation by humans usually entails the partial or total extinction of many organisms. Nevertheless, disturbances rarely provoke disappearance in ants but change their local relative abundance [21].

As ecological indicators, the presence of specific species of ants may indicate a good ecological integrity, but absence is not indicating the opposite. Only the presence of some specific ant species related with human activities can indicate disturbances [21]. The predictive power of individual ant species is low [25], and it is necessary to study ant communities or their behavior [26]. Comparisons among ant communities with low similarity in species composition may inform us about differences in climate, type of soil, and/or vegetation disturbances [25]. The aim of this work is to assess the potential effect of tree loss (by studying the lack of trees) on ant community composition and functional diversity. Comparisons will be performed at different scales to disentangle the effect of trees on these variables. We hypothesized that the presence of oaks offers microhabitats that can be scarce or absent in grasslands. Thus, we expected that functional groups, trophic habits, and community composition of ants nesting in the soil differ between *dehesas* and grasslands. Within *dehesas*, we expect to find differences in functional groups and trophic habits of ants nesting in the soil below and outside the tree canopies. Additionally, we expect that ant community composition differs among ants nesting in the soil outside canopy cover, below the canopy, and those inhabiting tree trunk/branches.

2. Materials and Methods

2.1. Study Area

We carried out the sampling in 8 study sites (Coordinates included in Table S1) of 100 ha each (800 ha in total) from the locality of Trujillo (province of Caceres, Extremadura, southwest of Spain) (Figure 1). Four of these sites were *dehesas*, with holm oaks (*Quercus rotundifolia* Lam. = *Quercus ilex* L. subsp. *rotundifolia* (Lam.) O.Schwarz) interspersed within a grassland matrix (henceforth “*dehesas*”). The other four study sites were grasslands/pastures in which trees had been lost due to the lack of regeneration (henceforth “grasslands”). The soil in all study sites is acid, with both low nutrient and organic matter content [27]. The climate is Mediterranean with hot summers; yearly mean temperature of 16 °C, reaching 33 °C during July and August, and an annual precipitation of 623.1 mm [28].

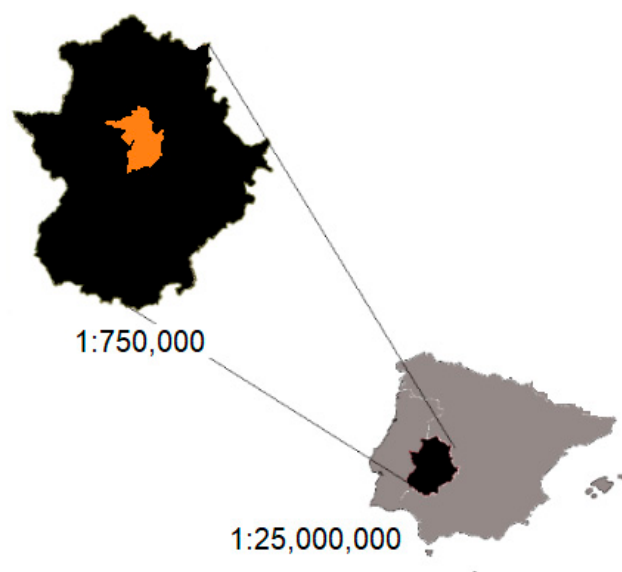


Figure 1. The geographical location of the study area in the Iberian Peninsula (orange).

2.2. Field Sampling and Material Identification

To sample ants nesting in the soil, we placed 8 pitfall traps (capacity 175 cc) per study site. All of them were filled with a mix of 30 cc of alcohol (70%) and glycerin in a proportion of 10 mL of glycerin per 1 L of alcohol. The minimum distance between traps was 150 m. We set pitfall traps on 15 May 2015 and collected them 5 days later. In total, we placed 32 traps in *dehesas* and other 32 in grasslands. In *dehesas*, we placed one trap per site below tree canopy and the other 7 traps were placed in grasslands surrounding the trees (i.e., >2 m outside the canopy cover).

To sample arboreal ants, we placed a piece of tuna on the trunk (c. 2 m above the ground, one per tree) and collected all ants attracted after 1 min and brushing for an additional 1 min to a pot with alcohol 70%. We sampled arboreal ants with the attractor in the same 4 oaks in which we placed pitfall traps below canopy. In the laboratory, we sieved samples extracting soil and plant material, and then, we carefully inspected the content and removed all other arthropods except ants. We identified all ants to species level by using the morphological taxonomic keys developed by Gomez and Espadaler [29] and García-García [30]. We identified our material at species level when this was possible (in some specimens, the characters important for species level determination were ripped, smashed, or absent).

We categorized resource specialization as: (i) ants that feed on aphid secretions, (ii) nectivorous, (iii) predators, (iv) scavengers, and (v) granivorous. We categorized functional groups according with the classification proposed by Roig and Espadaler [24] as: (i) cryptic (C), (ii) cold and/or shadow habitat specialists (CCS/SH), (iii) generalist and/or opportunist (GO), and (iv) hot and/or open habitat specialists (HCS/OH). In total, we sampled 8253 individuals from 31 ant species (Table 1) and stored them in the entomological collection of University of Extremadura, Spain (Campus of Plasencia).

Table 1. Studied material with records of abundance, frequency (number of pitfall traps in which each species was recorded), their functional group (following Roig and Espadaler [24]: HCS/OH = hot and/or open habitat specialists, CCS/SH = cold and/or shadow habitat specialists, GO = Generalist and/or opportunist, C = cryptic), and their main food resource (A = aphid secretions, N = nectar, P = predator, S = seeds, SC = scavenger and ?—Unknown).

Species	Abundance	Frequency	Guild	Resource
Subfamily Myrmicinae	1402	227		
<i>Messor barbarus</i>	441	53	HCS/OH	S
<i>Messor capitatus</i>	258	39	HCS/OH	S
<i>Messor bouvieri</i>	1	1	HCS/OH	S
<i>Messor lusitanicus</i>	2	1	HCS/OH	S
<i>Messor hispanicus</i>	1	1	HCS/OH	S
<i>Messor</i> sp.	2	2	HCS/OH	S
<i>Aphaenogaster gibbosa</i>	2	1	C	P, S, SC
<i>Aphaenogaster iberica</i>	334	53	GO	P, S, SC
<i>Aphaenogaster senilis</i>	9	1	GO	P, S, SC
<i>Aphaenogaster dulciniae</i>	2	1	C	P, S, SC
<i>Tetramorium forte</i>	162	34	GO	S
<i>Temnothorax</i> sp.	22	11	C	?
<i>Leptothorax</i> sp.	12	4	C	?
<i>Crematogaster scutellaris</i>	108	14	GO	A, N
<i>Crematogaster auberti</i>	3	2	GO	A, N
<i>Gonionmma</i> sp.	7	5	HCS/OH	S
<i>Oxyopomyrmex</i> sp.	10	3	HCS/OH	S
<i>Phelloide pallidula</i>	26	1	GO	N, P, SC
Subfamily Formicinae	6603	152		
<i>Cataglyphis hispanica</i>	95	39	HCS/OH	SC
<i>Cataglyphis iberica</i>	6	4	HCS/OH	SC
<i>Cataglyphis</i> sp.	42	16	HCS/OH	SC
<i>Formica sanguinea</i>	9	4	HCS/OH	A, P
<i>Formica subrufa</i>	6337	64	HCS/OH	A, P
<i>Camponotus cruentatus</i>	83	11	HCS/OH	A, N, P
<i>Camponotus pilicornis</i>	1	1	HCS/OH	A, N, P
<i>Camponotus</i> sp.	2	1	HCS/OH	A, N, P
<i>Lasius brunneus</i>	16	5	CCS/OH	A, N
<i>Proformica</i> sp.	12	7	HCS/OH	?
Subfamily Dolichoderinae	239	51		
<i>Tapinoma nigerrinum</i>	200	40	GO	A, N, P, SC
<i>Tapinoma erraticum</i>	25	9	GO	A, N, P, SC
<i>Tapinoma madeirense</i>	14	2	GO	A, N, P, SC
TOTAL	8157			

2.3. Statistical Analyses

We used a set of Linear Mixed Models (LMMs) to analyze the effect of the type of habitat (*dehesa* vs. grassland) and microhabitat (below vs. outside canopy) on the number of species of each functional group (i) cryptic, (ii) generalistic and/or opportunistic, and (iii) HCS/OH= hot and/or open habitat specialists) in separated models. We did the same to analyze the differences between habitats (*dehesa* vs. grassland) and microhabitats (below vs. outside canopy) in the number of species of ants that feed on: (i) aphid secretions, (ii) nectar, (iii) other animals (predators), (iv) scavengers, and (v) seeds). In all analyses, the dependent variable was the average number of species per pitfall trap and the site was included as a random factor. To account for different numbers of traps in each site, we divided the average number of species per trap by the number of traps per site (i.e., the total number of species in traps outside canopy was divided by 7 traps outside canopy).

To assess the degree of species' overlap among ant communities from different habitats and microhabitats, we ran two Principal Component Analyses (PCAs). The first compared grasslands and *dehesas*, the second compared the ant communities in the open (outside tree canopy), below tree canopy, and on trunks/branches.

All analyses were performed using the statistical software R [31]. To run the GLMMs, we used the function “*glmer*” implemented in the R-package “*lme4*” [32]. In the case of PCAs, we used the function “*prcomp*” implemented in the default R-package “*stats*.”

3. Results

3.1. Differences between Functional Groups

Overall, we captured a similar number of species in *dehesas* and grasslands, none of the separate analyses for each functional group showed any difference between these habitats (Figure 2a and Table 2). In both, the most abundant group was that of the ants specialized in warm or open habitats. At scale of microhabitat, within *dehesas*, we captured a significantly higher number of species below tree canopies than outside them in all functional groups (Figure 2b and Table 2).

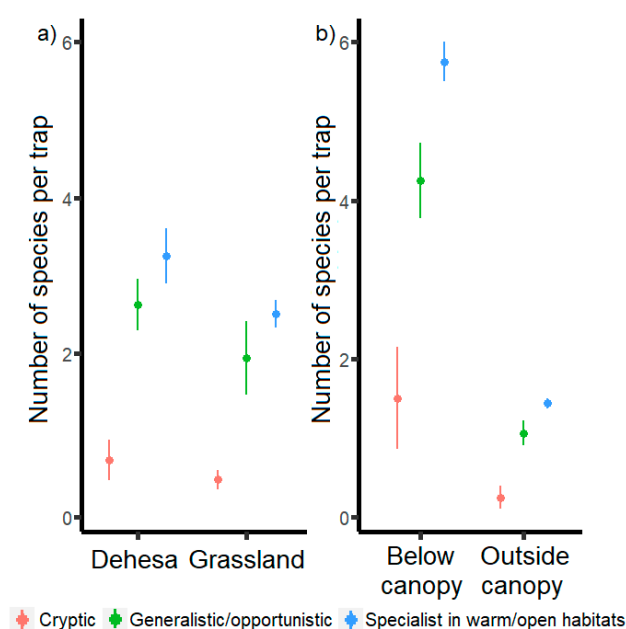


Figure 2. Graph depicting the number of species of soil nesting ants collected per pitfall trap (*mean* \pm *SE*) in: (a) grasslands and *dehesas* and (b) below and outside tree canopies within *dehesas*. Different colors represent the different functional groups (C = cryptic species, GO = generalists and/or opportunists and HCS/OH = specialists in warm and/or open habitats).

Table 2. Differences between habitats (grasslands vs. *dehesas*) and between microhabitats (below and outside oak canopies within *dehesas*) in the number of species of the different functional groups (C = cryptic species, GO = generalists and/or opportunists and HCS/OH = specialists in warm and/or open habitats). Significant *p*-values are shown in bold.

Response Variable	Predictors	χ^2	df	<i>p</i>
C	Grasslands vs. <i>Dehesas</i>	0.979	1	0.615
	Below canopy vs. Outside canopy	4.41	1	0.036
GO	Grasslands vs. <i>Dehesas</i>	0.42	1	0.519
	Below canopy vs. Outside canopy	22.82	1	<0.001
HCS/OH	Grasslands vs. <i>Dehesas</i>	0.39	1	0.531
	Below canopy vs. Outside Canopy	280.06	1	<0.001

3.2. Differences between Trophic Groups

The number of aphid-herding and predator species in *dehesas* was significantly higher than in grasslands (Figure 3a, Table 3). At the microhabitat scale, within *dehesas*, we trapped more species of all functional groups below the tree canopy than outside oak cover (Figure 3b, Table 3).

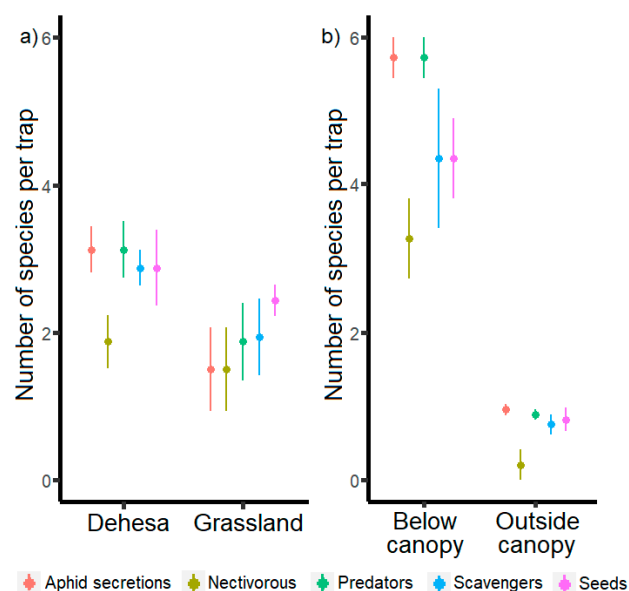


Figure 3. Graph depicting the number of species of soil nesting ants collected per pitfall trap (*mean* \pm *SE*) in: (a) grasslands and *dehesas* and (b) below and outside tree canopies within *dehesas*. Different colors represent the different trophic groups (ants feeding on aphid secretions, nectivorous, predators, granivorous, and scavengers).

Table 3. Differences between habitats (grasslands vs. *dehesas*) and between microhabitats (below and outside oak canopies within *dehesas*) in the number of species of the different trophic groups (ants feeding on aphid secretions, nectivorous, predators, granivorous and scavengers). Significant *p*-values are shown in bold.

Response Variable	Predictors	χ^2	df	<i>p</i>
Aphid secretions	Grasslands vs. <i>Dehesas</i>	5.28	1	0.046
	Below canopy vs. Outside canopy	408.33	1	<0.001
Nectivorous	Grasslands vs <i>Dehesas</i>	0.28	1	0.598
	Below canopy vs. Outside canopy	27.74	1	<0.001
Predators	Grasslands vs. <i>Dehesas</i>	4.74	1	0.029
	Below canopy vs. Outside canopy	351.70	1	<0.001
Granivorous	Grasslands vs. <i>Dehesas</i>	0.38	1	0.463
	Below canopy vs. Outside canopy	56.1	1	<0.001
Scavengers	Grasslands vs. <i>Dehesas</i>	2.88	1	0.089
	Below canopy vs. Outside Canopy	15.63	1	<0.001

3.3. Assessing Overlap of Ant Communities

In the two Principal Component Analyses (PCAs), the first component (x-axis) explained 27% of the variance. In the first PCA, this component segregated grasslands and *dehesas*, showing differences between habitats (Figure 4a). In the second PCA (analysis at microhabitat level within *dehesas*), it segregated ant communities outside and below tree canopies (Figure 4b). At level of individual trees, the differences on species composition below the canopies and on the trunk/branches are small (Figure 4b).

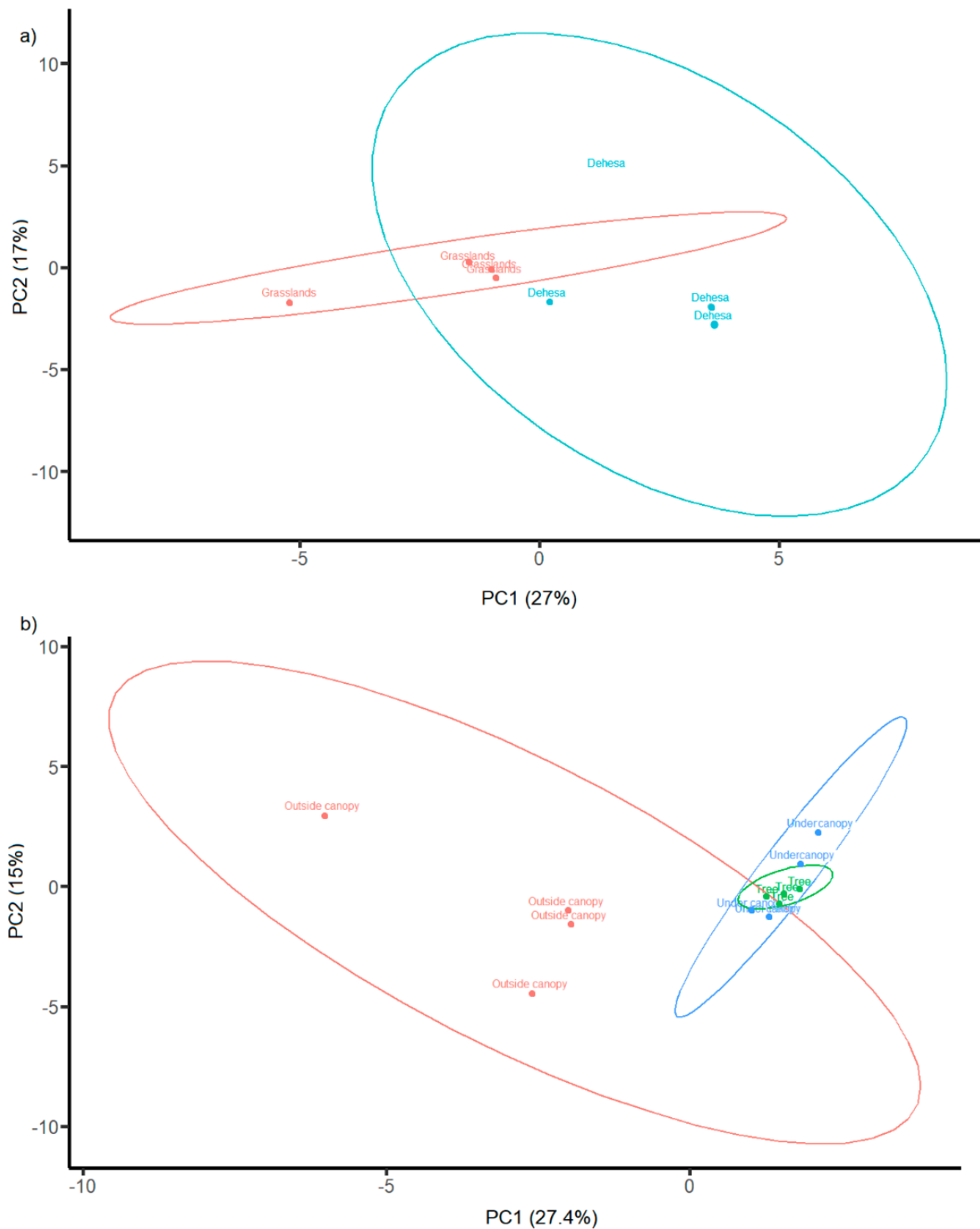


Figure 4. Principal Component Analyses comparing the ant communities from (a) grasslands and *dehesas* and (b) within *dehesas*: outside canopy, under canopy, and in the trunk.

Some ant species contributed more to the segregation between habitats than others (those with higher and lower scores in PC1). In the first PCA (showing the differences between grasslands and *dehesas*), some examples are *Crematogaster scutellaris* and *Formica sanguinea* (very positive scores) or *Messor barbarous* and *Messor capitatus* (negative scores) (Table S2). In the second PCA (differences between microhabitats within *dehesas*), those with a stronger effect in the separation along the PC1 axis were *Crematogaster scutellaris*,

Cataglyphis hispanica (positive scores), *Messor capitatus*, and *Gonomma* sp. (scores below zero) (Table S3).

4. Discussion

Our results show that the presence of oaks increases the number of ant species within *dehesas*. Irrespective of the functional group or trophic specialization, the number of soil-nesting species collected per pitfall trap was higher below the tree canopies than outside oak cover. When the *dehesas* were compared against treeless grasslands, there were significant differences in the number of species of aphid-herding and predator ants.

We collected 31 morphospecies out of the 57 species reported by Gomez and Espadaler [29] for the province of Caceres (the same province in which our study was carried out). Moreover, our sampling added a new record (*Aphaenogaster dulciniae*) not only for Caceres, but for the Region of Extremadura. We captured a high number of species linked to *dehesas*, however, the province of Caceres has a significant environmental variability (including not only oak savannahs/forests but also high mountain ecosystems or wetlands) that can house other species that are not present in *dehesas*. The dominance of *Formica subrufa* could be explained by its gregarious habits and its high level of activity [29]. At the subfamily level, Myrmicinae had the highest number of species followed by Formicinae and Dolichoderinae. Since we did not use baits or attractors for ants nesting in the soil, the presence of species with specific food preference may be under-estimated [21]. In addition, predatory species might not be fully represented either, because, usually, they stay hidden while stalking preys [21]. Nonetheless, as the trapping methodology was the same for habitats and microhabitats, such potential deviations cannot account for the differences found. However, we prudently interpreted our contrasts on microhabitats due the low number of traps below canopies.

The overall dominance of ants specialized in warm or open habitats did not differ from that expected for an area of Mediterranean climate with dry summers. The most abundant species, *Formica subrufa*, belongs to this functional group. In the second place, we recorded generalist/opportunistic species (e.g., *Aphaenogaster* spp., *Crematogaster* spp., and *Tapinoma* spp.), which are generally indicators of disturbance [24]. This could be due to the centuries-long human use of *dehesas* and grasslands, as high livestock densities reduce vegetation cover and erode the soil [4].

Trophic specialization differed between habitats, predator, and aphid-herding species being significantly more abundant in *dehesas*. Within *dehesas*, these species were mainly trapped on the trunks or beneath the oak canopies. Previous samplings in Mediterranean orange orchards have also found this link between aphid-herding ants and trees [33]. Some of the species recorded in those studies, like *Crematogaster* spp., were also common in oaks. They nest beneath the bark, in wood hollows or in nests abandoned by other arthropods [34]. Other aphid herders as *Camponotus* spp. were more abundant in *dehesas* and, more specifically, below oak canopies (positive scores in the first axis of the two PCAs). This species is commonly collected on trunks too, as their nests may be placed either under the litter or within tree hollows/crevices [34]. The same is valid for *Formica subrufa*, a species superabundant in *dehesas* [35]. This species, endemic of Iberian Peninsula and southern France, nests beneath stones and is linked to oak forests (more or less degraded) or other woody habitats (e.g., heathlands *Erica* spp.) [36]. They prey on arthropods [37], but also feed on aphid secretions.

Differences in species composition could indicate that, in our study sites, aphids are restricted to areas with trees and also sampling dates might affect the presence of some aphid species. In mid-May, temperatures are usually high already, and grass has started to dry up. Aphids feed on phloem sap, which is lacking in dry herbs. Hence, from then on, that food resource would only be available for aphids in new oak shoots. Accordingly, multi-spectral images have shown that, during the drought period, the photosynthetic activity is restricted to the trees in *dehesas* [38]. Thus, we cannot know whether aphid-herding species could be more spread outside the tree canopies in other periods of the year,

although this seems unlikely. Suay-Cano et al. [33] showed that aphid–ant relationship is very specific, so that ants would not be expected to move too much from trees unless their target aphid species does so.

Granivorous *Messor* spp. were more prevalent in treeless grasslands. This could be due to the effect of canopy shade or livestock activity, which reduces the availability of grass seeds [9,11]. Within *dehesas*, *Messor* spp. were more abundant in the open than below the tree canopies. These ants are common in grasslands, savannahs, semi-deserts/deserts [39] and also in arable fields, where they may provoke major seed losses [40]. However, further studies have shown that the negative impact is not so high and they have a beneficial role as weed controllers and granivorous ants [41,42].

To conclude, our study supports the role of trees as keystone structures in agroecosystems [1]. Trees offer a new microhabitat (food resources/refuges) for species that would otherwise be absent in treeless grasslands. In Iberia, further comparisons of ant communities between self-standing oaks in wood pastures versus nearby oak forests are needed (see [43] for a similar study in Central Europe). Such studies could show whether some species are only present or more abundant in oak savannahs because they do not tolerate well closed canopy conditions. Previous studies have addressed the role of trees for arthropod conservation in temperate wood pastures in other European areas [18–20,43]. However, to the best of our knowledge, this study has addressed, for the first time, the reasons underlying ant species segregation in Iberian *dehesas*. So far, differences in ant communities below and outside tree canopies had been attributed to the degree of shade tolerance [44], but not analyzed according to functional groups or trophic habits. Our results stress the importance of the heterogeneous vegetation structure of Iberian oak savannahs not only for livestock productivity [4,45] but also for biodiversity conservation.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/3/115/s1>, Table S1: Coordinates (in decimal degrees) from sampled areas, Table S2: PC1 and PC2 output values for each species corresponding with the PCA analysis from Figure 4a, Table S3: PC1 and PC2 output values for each species corresponding with the PCA analysis from Figure 4b.

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