



RESEARCH ARTICLE - ANTS

Ants (Hymenoptera: Formicidae) and Spiders (Araneae) Co-occurring in the Ground of Vineyards from Douro Demarcated Region

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Abstract

This study, held in vineyards from Douro Demarcated Region, aimed to: a) identify the communities and main functional groups of spiders and ants; b) check patterns of co-occurrence between the two communities; and c) evaluate the impact of ground cover and non-crop habitats adjacent to vineyards, on the two communities. Samplings were done using pitfall trapping. Twenty species of ants and 44 species of spiders were identified. The most abundant were: *Aphaenogaster gibbosa* (Latreille 1798), *Aphaenogaster iberica* Emery 1908, *Cataglyphis hispanica* (Emery 1906), *Cataglyphis iberica* (Emery 1906), *Messor barbarus* (L. 1767) and *Tapinoma nigerrimum* (Nylander 1856) which totalized 71.21% of ants; and *Alopecosa albofasciata* (Brullé 1832), *Callilepis concolor* Simon 1914, *Eratigena feminea* Simon 1870, *Zodarion alacre* (Simon 1870) and *Zodarion styliferum* (Simon 1870) which accounted for 38% of spiders. Three Iberian endemic ants and nine Iberian endemic spiders were also identified. Abundance of both ant-mimicking and ant-eating spiders were positively correlated with abundance of Formicinae, while only abundance of ant-eating spiders showed positive correlation with abundance of Myrmicinae ants. All genera/ species of ant-associated spider were associated with one or more genera/specie of ants. Both spiders and ants have not benefited from the adjacent non-crop habitat. Sheet web weaver spiders were found to be positively correlated with the percentage of ground cover. These results show that a) vineyard agroecosystem support a rich assemblage of ants and spiders evincing that wine production and species conservation is possible and b) non-random co-occurrence between ants and ant-associated spiders exist in the field.

Introduction

Ants (Hymenoptera, Formicidae) and spiders (Arachnida, Aranea) are two ubiquitous arthropods and keystone taxa in terrestrial communities, where they can interact directly or indirectly, resulting in strong effects on the abundance and distribution of each other (Marín et al., 2015).

Ants are one of the most abundant organisms in terrestrial surface being found in most ecosystems (Huang et al., 2011), where they impose a strong ecological footprint

through their diverse ecological functions, mainly as biological regulators and ecosystem engineers (Ward, 2006). Most species are omnivorous and generalists (Cerdá & Dejean, 2011). Others are important predators (Karhu, 1998), herbivorous (Albert et al., 2005; Rodriguez et al., 2008) and scavengers (feeding on decaying organic matter) (Perez & Dupo, 2013). While others feed on honeydew (Detrain et al., 2010), pollen (Urbani & de Andrade, 1997) and extrafloral nectar and glandular corpuscles (Kost & Heil, 2005; Stefani et al., 2015; Del-Claro et al., 2016). Ants are involved in mutualistic relationships with



hemipterans, protecting them from their enemies, in exchange for honeydew (Styrsky & Eubanks, 2007). Moreover, they are important for pollination (Hickman, 1974), and dispersal of numerous plants (Beattie & Culver, 1981). In addition, they are ecosystem engineers, because of their effects on soil structure and processes, which directly and indirectly affect the flow of energy and material in ecosystems, as well as the habitats of other species (Folgarait, 1998). Through their activity, ants modify the physical, chemical and microbiological properties of soil (Dauber & Wolters, 2000; Dostál et al., 2005; Jouquet et al., 2006).

Through evolution, ants developed both structural (stings, spines, strong mandibles, chemical secretions) and behavioral (aggressiveness, deployment of polymorphic workers) defense mechanisms that allow them to escape from most predators (Hunt, 1983). This evolutionary advantage makes them ideal models for mimics (Mciver & Stonedahl, 1993) and also available food for specialist predators. In fact, hunters that evolves strategies for overcoming ant's defenses and aggression faces relatively little competition for a nearly unlimited food resource (Cushing, 2012), since that they are rare and typically use special hunting tactics (Mciver & Stonedahl, 1993).

Three types of associations between ants and other species can be find: myrmecomorphy (species that mimic ants acquiring morphological, behavioural, chemical or textural similarity to the model, currently known as ant-mimics), myrmecophagy (species that feed on ants, currently known as ant-eaters), myrmecophily (species that live in symbiosis with ants in or near of their nests) (Cushing, 1997; 2012; Pekár et al., 2012a).

Spiders are ubiquitous predators in terrestrial ecosystems that feed primarily on insects but also on other arthropods including other spiders (Wise, 1993). Although it is assumed that in general, they are euryphagous or generalists, being able to subsist on a wide variety of prey types (Cardoso et al., 2011), the fact is that some species specialize in hunting in a singular prey group. From this point of view, Pekár et al. (2012a) report six categories of stenophagy among spiders, namely: araneophagy, lepidopterophagy, termitophagy, dipterophagy, crustaceophagy and myrmecophagy. Indeed, although most of spiders are averse to ant predation most of the specialized species are myrmecophagous, perhaps as a consequence of ants being numerous in their habitats (Pekár, 2004). Examples of myrmecophagy are found in a variety of families, including Gnaphosidae, Oecobiidae, Salticidae, Theridiidae, Thomisidae, and Zodariidae (reviewed by Pekár, 2009). Moreover, some species of spiders also mimic ants; spiders disguise as ants to deceive primarily their predators (Ceccarelli, 2013) being considered as a case of Batesian mimicry (Nelson & Jackson, 2012), where a palatable mimic spider escapes from predators that have experienced unpalatable ants (Hölldobler & Wilson, 1990). The spiders corresponding mimicking mechanisms includes morphological, chemical and/or behavioral resemblance to ants (McIver & Stonedahl, 1993). Constrictions on the abdomen

giving the illusion of three body regions (Cushing, 2012), shiny opisthosoma (Ceccarelli, 2008), and long and thin legs (Oliveira, 1988; Durkee et al., 2011) are some of these mechanisms. Also, their movement frequently becomes ant-like, including wave their forelegs to mimic the antennal movement of ants (in a phenomenon referred as “antennal illusion”) (Ceccarelli, 2008; Cushing, 2012). Examples of myrmecomorphy spiders are mainly found in Salticidae and Clubionidae. However, Theridiidae, Araneidae, Eresidae, Thomisidae, Gnaphosidae, Zodariidae and Aphantochilidae also have ant-like members (review by Oliveira, 1988).

In vineyards, ants are one of the most abundant arthropod group (Addison et al., 2013; Thomson et al., 2004), while spiders are one of the most abundant predator group (Gaigher & Samways, 2010; 2014; Pérez-Bote & Romero, 2012).

In Douro Demarcated Region (DDR) vineyards, little is known about the composition of ant and spider communities, and how they interact each other. The aims of this study were to: a) assess the richness and functional diversity of ant and spider communities in vineyards of DDR; b) evaluate the co-occurrence pattern between ants and ant-associated spiders and c) evaluate the impact of ground cover and of non-crop habitats adjacent to vineyards on ant and spider communities.

Material and Methods

Study area

The study was carried out during the growing season of 2013, in five commercial vineyard farms (Aciprestes (41°12'30"N, 7°25'58"W), Arnozelo (41°8'1"N, 7°18'25"W), Carvalhas (41°10'36"N, 7°32'26"W), Cidrô (41°8'30"N, 7°22'51"W) and Granja (41°15'4"N, 7°28'50"W)) from DDR.

In each farm, one vineyard with ground cover in the inter-row and an adjacent non-crop habitat, was selected as study site. Adjacent non-crop habitats were shelterbelts (mainly composed by *Cistus albidus* L., *Cistus ladanifer* subsp. *ladanifer* L., *Cistus salvifolius* L., *Cytisus multiflorus* (L'Hér.) Sweet, *Erica arborea* L., *Erica umbellata* Loeffl. ex L., *Genista anglica* L., *Genista triacanthos* Brot., *Halimium lasianthum* (Lam.) Spach, *Juniperus oxycedrus* L., *Lavandula pedunculata* (Mill.) Cav., *Pistacia terebinthus* L., *Rubus ulmifolius* Schott, *Ulex minor* Roth, *Xolantha guttata* (L.) Rafin.), woodlands (mainly composed by *Arbutus unedo* L., *Pinus pinaster* Aiton, *Quercus x coutinhoi* Samp., *Quercus faginea* Lam., *Quercus pyrenaica* Willd., *Quercus rotundifolia* Lam.) and groves (*Olea europaea* L., *Prunus dulcis* (Mill.) D. A. Webb). The ground cover of each vineyard consisted in a complex of resident vegetation (predominantly *Andryala integrifolia* L., *Bromus madritensis* L., *Coleostephus myconis* (L.) Rchb. f., *Cynodon dactylon* (L.) Pers., *Echium plantagineum* L., *Ornithopus compressus* L., *Silene gallica* L., *Sonchus oleraceus* L., *Trifolium* sp.). In all farms, the vegetation in the inter-row was mowed in the beginning of spring, then allowed to regrow, mature and set seed, and again mowed. Moreover,

while in two vineyards (Arnozelo and Carvalhas), the same procedure was performed to control the vegetation in the vine row, in the other three farms, herbicide was applied in the vine row (Cidrô, Aciprestes and Granja). The mowed residues remained in the soil, acting as mulching.

Sampling data

Spiders and ants collection

Spiders and ants were sampled between April and September 2013, with a periodicity of 35 to 45 days, totalizing four sampling dates in each farm (two samplings per each of the season's spring and summer). The first period was between April 20th and June 6th and the second was between July 1st and September 23rd. Nine pitfall traps were placed in the inter-row of each vineyard, at the rate of three traps per each of the following distances, 5, 50 and 100 m, from the adjacent non-crop habitat inward the vineyard. The pitfall traps consisted on plastic cups measuring 16 cm in height and 9 cm in diameter. The cups were filled to half its volume with a 3:1 mixture of water and polypropylene-glycol solution and were left in the field for 72 hours. Ant specimen's identification was based on Collingwood and Prince (1998) and Gómez and Espadaler (2007). Spider specimen's identification was based on World Spider Catalog (2017) and Nentwig et al. (2016). Individuals were identified to the species level whenever possible and in a minority of cases, fragmented specimen's identification was considered reliable only to the genus level.

Ground cover vegetation

For each plot, in each trap location, the richness (number of plant species) and the percentage of ground cover were assessed in 1 m² area. Observations were done between the end of May and the beginning of June.

Data analysis

Classification of ants and spiders

Using Roig and Espadaler (2010) classification, Formicidae was separated in four functional groups: (1) generalists and/or opportunistic (G/O), (2) cold-climate specialists and/or shade habitats (CCS/SH), (3) hot climate specialists and/or open habitats (HCS/OH), (4) and cryptic (Cr). Following the same authors, these groups can be classified as to their relative importance in three global indicators: global indicator of disturbance (G/O), global indicator of stability (HCS/OH and CCS/SH) and a silent group of cryptic ants (C). Moreover, trophic guild was also assessed by using the literature (see Table S1 in Supplementary Materials).

Araneae were classified following Cardoso et al. (2011), based on their foraging strategy (type of web and hunting method), prey range (stenophagous or euryphagous), vertical stratification (ground or foliage) and circadian activity (diurnal or nocturnal). Eight guilds were assessed: (1) sensing web

weavers (SeW), (2) sheet web weavers (ShW), (3) space web weavers (SpW), (4) orb web weavers (OrW), (5) specialists (Sp), (6) ambush hunters (AH), (7) ground hunters (GH), and (8) other hunters (OH).

Ant associated spiders were divided into two groups: ant-eating "myrmecophages" and ant-mimicking "myrmecomorphs" (Cushing, 1997, 2012; McIver & Stonedahl, 1993; Nentwig et al., 2016; Pekár et al., 2012a; Pekár & Cárdenas, 2015; Pekár & Jarab, 2011).

Statistical analysis

Non-metric multidimensional scaling (NMDS) was performed to visualize and to examine the similarities of functional groups of ant and spider communities among the studied sites and seasons. Prior to analysis, observations with no individuals were removed. NMDS were obtained fixing a 2-dimensional solution and using all the available dissimilarities indices in "vegdist" function, choosing the convergent solution with lowest stress value under 0.2. Analysis were performed by using the *vegan* package facilities R (Oksanen et al., 2016) and NMDS plots were produced by using the R package *ggplot2* (Wickham, 2009).

For the co-occurrence studies, Spearman correlations were used to explore correlations between abundance of ant-associated spiders and ants. Moreover, null models were performed to detect possible non-random of co-occurrence. The co-occurrence analyses allowed to test for non-random patterns of species co-occurrence in a presence-absence matrix. The null-model matrices are Monte-Carlo randomizations of the real matrix in order to create null expectations for the C-score. The C-score was used as an index which measure the degree to which pairs co-occur. A "fixed rows-equiprobable columns" model for 5,000 randomizations was performed. The model randomizes the occurrence of each species among the sites, assuming that sites are equiprobable. When used in fixed-equiprobable' model, C-score has good statistical properties and are invulnerable to type I errors (false positives) (Gotelli, 2000). For a better understanding of the results, standardized effect size (S.E.S) are presented in the results. S.E.S is calculated as (observed C-score – mean of simulated C-scores)/standard deviation of simulated C-scores; values of S.E.S greater than 1.96 and less than -1.96 indicate a negative and positive non-random co-occurrence pattern, respectively. These analyses included only species/genera with more than five individuals collected during the study.

Generalized linear mixed models (GLMM) (with Poisson error distribution or negative binomial distribution to account with over dispersion when necessary, and a log link function) were developed to fit both the abundance and richness of spiders and ants as a function of the season (spring vs summer), the distance to the adjacent non-crop habitat (5, 50, 100 m), and the richness and percentage of ground cover. The farm was included into the model as random factor, as it was intended to generalize the results of this experiment

to all field. When a random effect for farm is added, this characterizes idiosyncratic variation that is due to individual differences. The procedure was done for the most significant functional groups of spiders and ants. For each season, data from each trap were pooled resulting in a single sample per trap.

Co-occurrence analyses were carried out using EcoSim program version 7.0 (Acquired Intelligence, Inc., & Pinyon Publishing, 2016). GLMM and Spearman correlations were performed by using IBM SPSS v20 (SPSS Inc. IBM Company, 2010). Significance was reported at the level of $p < 0.05$.

Results

Ant community

A total of 6,322 ant individuals from three subfamilies and 12 genera were found, which corresponded to 20 species (Table S1). The most abundant subfamily was Myrmicinae (45.7%), followed by Formicinae (42.3%) and Dolichoderinae (12.0%). However, the one represented by higher number of taxa was Formicinae (with six genera and 13 species), followed by Myrmicinae (five genera and six species) and lastly by Dolichoderinae (one genus and one species). The most abundant ant species, which together amounted 32.8% of the catches, were *Messor barbarus* (Myrmicinae), which was captured in all farms, and *Cataglyphis hispanica* (Formicinae), which was captured in four farms. Other abundant species were *Aphaenogaster gibbosa*, *Aphaenogaster iberica*, *Cataglyphis iberica* and *Tapinoma nigerrimum* that totalized 38.5% of the catches.

Nine ant species were present in all farms (i.e. *A. gibbosa*, *Crematogaster auberti*, *Camponotus cruentatus*, *Iberoformica subrufa*, *M. barbarus*, *Pheidole pallidula*, *Cataglyphis* sp., *Plagiolepis schmitzii* and *T. nigerrimum*), while two species, (i.e. *Camponotus foreli* and *Camponotus piceus*) were collected in a single farm. Three species, i.e. *C. hispanica*, *C. iberica* and *A. iberica* are endemic from Iberian Peninsula.

According to the trophic group, 1.4% of the collected ants were classified as nectar feeders (*C. foreli*, *C. piceus* and *Camponotus pilicornis*), 2.5% as honeydew feeders (*Camponotus sylvaticus*, *Lasius grandis* and *P. schmitzii*), 44.4% as omnivorous (*A. gibbosa*, *A. iberica*, *C. auberti*, *C. cruentatus*, *Formica fusca*, *I. subrufa*, *P. pallidula*, *P. pygmaea*, *Solenopsis* sp. and *T. nigerrimum*), 17.4% as herbivorous (*M. barbarus*) and 27.3% as scavengers (all *Cataglyphis*), in spite of some of them could complement their diet with other diets (Table S1).

Ant community was grouped in four functional groups: hot climate specialists and/or open habitats (HCS/OH) (46.2% of captures), generalists and/ or opportunistic (G/O) (32.4%), cryptic (Cr) (11.2%) and cold climate specialists and/or shade habitats (CCS/SH) (2.1%) (Fig 1, Table S1). About 30.0% of the species were G/O, 45.0% HCS/OH, 15.0% CCS/SH and 10.0% Cr (Fig 2).

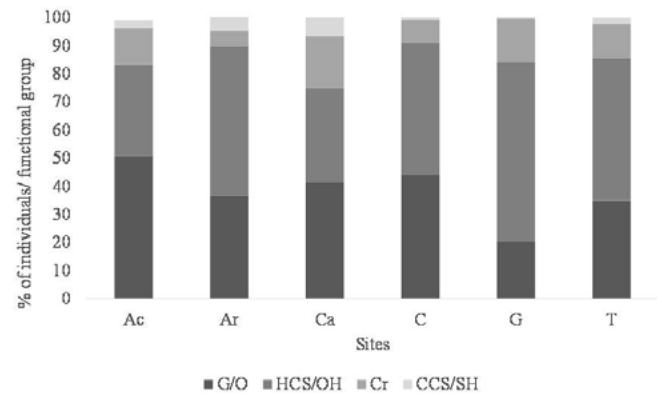


Fig 1. Percentage of ants per functional group. Ac – Aciprestes; Ar – Arnozelo; Ca – Carvalhas; C – Cidrô; G – Granja; T – all sites combined; G/O - generalists and/ or opportunistic; HCS/OH - hot climate specialists and/or open habitats; Cr - cryptics; CCS/SH - cold climate specialists and/or shade habitats.

The NMDS analysis, showed a high degree of overlap between different sites for functional groups of ants without a formation of clear groups concerning season and farms (having in mind that farms have different soil management, namely the use of herbicide in the row in three of them) (Fig 3).

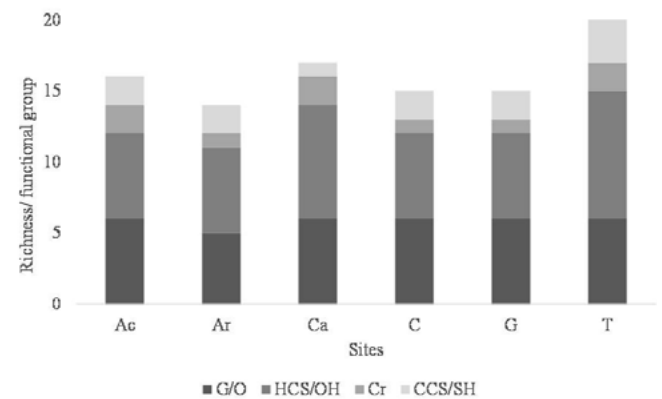


Fig 2. Richness of ants per functional group. Ac – Aciprestes; Ar – Arnozelo; Ca – Carvalhas; C – Cidrô; G – Granja; T – all sites combined; G/O - generalists and/ or opportunistic; HCS/OH - hot climate specialists and/or open habitats; Cr - cryptics; CCS/SH - cold climate specialists and/or shade habitats.

Spider community

A total of 511 spiders were captured. About 10.4% of those individuals were damaged and could not be classified into families; the remaining were grouped in 19 families and 40 genera. Only adults (about 67.3%) were identified, totalizing 44 species (Table S2 in Supplementary Materials). The most abundant family was Zodariidae (29.2%), followed by Gnaphosidae (23.5%), Lycosidae (13.5%), Thomisidae (8.9%) and Agelenidae (8.7%). Nine other families accounted, each one, for less than 1% of the total catches. Gnaphosidae had the highest number of species (13), followed by Salticidae (10), Lycosidae and Thomisidae (both with 6), and Agelenidae (5).

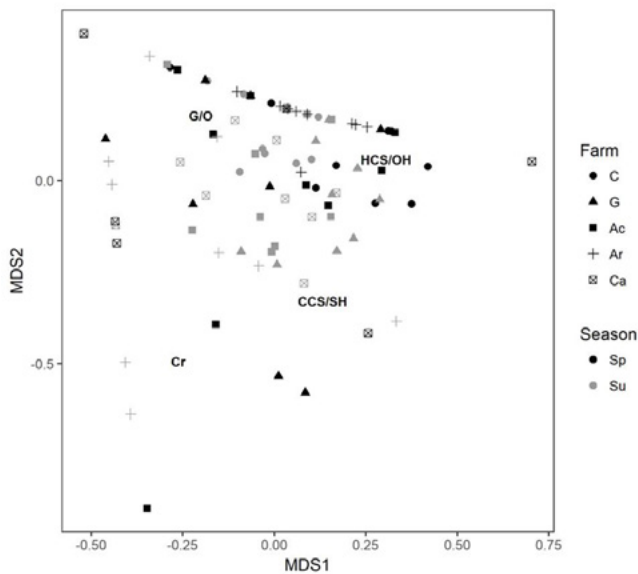


Fig 3. NMDS ordination plots of functional groups of ants associated with the study vineyards. The ultimate 2-dimensional NMDS solution was found with Euclidean dissimilarity and had an associated stress of 0.108. Ac – Aciprestes; Ar – Arnozelo; Ca – Carvalhas; C – Cidrô; G – Granja; Sp – spring; Su – summer; G/O - generalists and/ or opportunistic; HCS/OH - hot climate specialists and/ or open habitats; Cr - cryptics; CCS/SH - cold climate specialists and/ or shade habitats. In Ac, C and G the row was treated with herbicide while in Ar and Ca no herbicide was applied.

The most abundant species was *Zodarion styliferum* (Zodariidae) (20.3%), followed by *Alopecosa albofasciata* (Lycosidae) (5.9%) and *Eratigena feminea* (Agelenidae) (5.2%). *Z. styliferum* and *E. feminea* were present in all farms. Nine species (representing together about 12.2% of the catches) (i.e. *Eratigena bucculenta*, *E. feminea*, *Eratigena montigena* and *Tegenaria ramblae* from Agelenidae; *Zodarion alacre* and *Zodarion duriense* from Zodariidae; *Castianeira badia* from Corinnidae; *Nemesia athiasi* from Nemesiidae and *Oecobius machadoi* from Oecobiidae) are endemic species from Iberian Peninsula (Table S2).

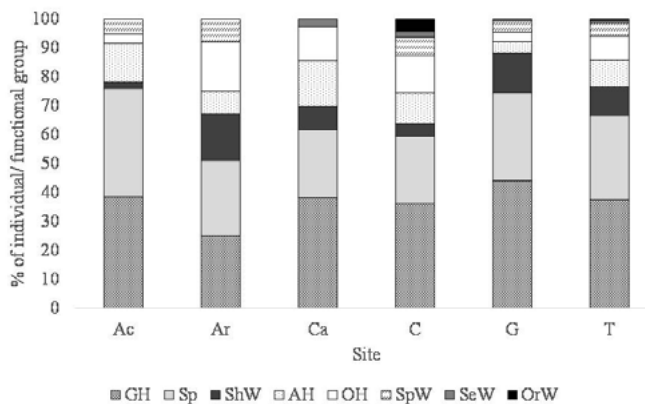


Fig 4. Percentage of spiders per functional group. Ac – Aciprestes; Ar – Arnozelo; Ca – Carvalhas; C – Cidrô; G – Granja; T – all sites combined; GH – ground hunters; Sp – specialists; ShW – sheet web weavers; AH – ambush hunters; OH – other hunters; SpW - space web weavers; SeW - sensing web weavers; OrW - orb web weavers.

Spiders were grouped into eight guilds: ground hunters (GH) (Corinnidae, Gnaphosidae, Lycosidae and Oonopidae) (37.5% of the identified individuals), specialist (Sp) (Zodariidae) (29.2%), sheet web weavers (ShW) (Agelenidae and *Agyneta fuscipalpa* from Linyphiidae) (9.8%), ambush hunters (AH) (Sicariidae and Thomisidae) (9.4%), other hunters (OH) (other Linyphiidae, Oxyopidae, Philodromidae, Salticidae and Scytodidae) (8.3%), space web weavers (SpW) (Dictynidae, Theridiidae and Titanocidae) (4.6%), sensing web weavers (SeW) (Nemesiidae and Oecobiidae) (0.9%) and orb web weavers (Araneidae) (0.4%) (Fig 4; Table S2).

The NMDS analysis, evidenced a high degree of overlap between different sites; even though, a trend could be observed for the establishment of distinct groups (Fig 5). Arnozelo and Carvalhas (both farms without herbicide in the row) showed a tendency to be separated from Granja and Aciprestes (both with herbicide in the row). While SeW, OH and AH spiders were more associated with the first two farms, GH and Sp spiders were more associated with the last two.

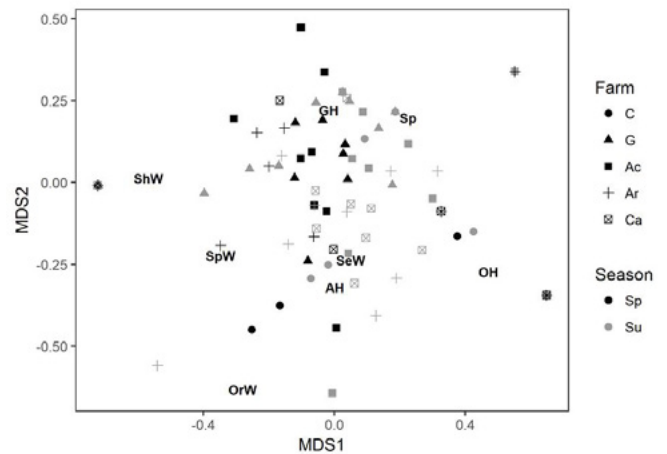


Fig 5. NMDS ordination plots of functional groups of spiders associated with the study vineyards. The ultimate 2-dimensional NMDS solution was found with Euclidean dissimilarity and had an associated stress of 0.194. Ac – Aciprestes; Ar – Arnozelo; Ca – Carvalhas; C – Cidrô; G – Granja; Sp – spring; Su – summer; GH – ground hunters; Sp – specialists; ShW – sheet web weavers; AH – ambush hunters; OH – other hunters; SpW – space web weavers; SeW – sensing web weavers; OrW – orb web weavers. Ac, C and G were treated with herbicide in the inter-row while Ar and Ca were not treated with herbicide.

Co-occurrence between ants and ant-associated spiders

Six genera of spiders were found to include ant-eater individuals, namely *Callilepsis*, *Euryopsis*, *Nomisia*, *Oecobius*, *Oxyopes* and *Zodarion*. Individuals of these genera accounted for 37% of the total catches. On the other hand, 2% of spiders belonged to three genera included ant-mimic spiders: *Castianeira* and *Micaria* (both known as ant-mimicking sac spiders) and *Myrmarachne* (known as ant-mimicking jumping spiders). *Euryopsis episinoides* and *Zodarion* spp. are also mimic ants; however, they were included in the ant-eaters group as their mimic behavior, viewed as inaccurate mimics, has as adjacent objective the predation of ants.

A strong and positive correlation was found between the abundance of ant-associated spiders and abundance of total ants; moreover, a strong and positive correlation was also found between the abundance of ant-associated spiders and that of both Formicinae and Myrmicinae, but no correlation could be found the abundance of Dolichoderinae. On the other hand, the abundance of ant-eating spiders was significant and positively correlated with that of both Formicinae and Myrmicinae, while ant-mimics spider numbers only correlated positively with those of Formicinae (Table 1).

The abundance of *Callilepis* spiders was significant and positively correlated with that of *Cataglyphis* ants, more precisely with the species *C. pilicornis* and *C. auberti* (Table 2). Null model tests of co-occurrence detected significant association between *Callilepis* and both *C. auberti* and *M. barbarus* ants, while the association was near of significance between *C. pilicornis* and *Cataglyphis* genus (Table 3).

The abundance of *Nomisia* spiders correlated significant and positively with the abundance of ants from *Plagiolepis* and *Aphaenogaster* genera and *A. iberica* and *A. gibbosa* species (Table 2). Null model tests only found significant association with *Plagiolepis* genus (Table 3).

Table 1. Spearman correlation coefficients (Rho) between abundance of ants (total and subfamily groups) and abundance of ant-associated spiders (total, ant-eaters and ant-mimics).

Ant-associated spiders	Ants			
	Total	Dolichoderinae	Formicinae	Myrmicinae
Total	0.494 ***	0.152 n.s	0.517 ***	0.331 **
Ant-eaters	0.476 ***	0.010 n.s	0.495 ***	0.338 **
Ant-mimics	0.205 n.s	0.136 n.s	0.257 *	-0.131 n.s

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s $p \geq 0.05$

The abundance of *Zodarion* spiders correlated significant and positively with that of *Cataglyphis* and *Aphaenogaster* genera, as well as the species *I. subrufa*, *A. iberica*, *A. gibbosa* and *M. barbarus* (Table 2); null model tests detected significant association between spiders from *Zodarion* genus and ants from *Aphaenogaster* genus, and *I. subrufa*, *A. iberica* and *A. gibbosa* species (Table 3).

Z. styliferum abundance, the most abundant spider in this study, was significant and positively correlated with that of ants from *Camponotus*, *Cataglyphis* and *Aphaenogaster*

Table 2. Spearman correlation coefficients (Rho) between abundance of ant-associated spiders and abundance of ants (genera and species). Only genera/species with at least five occurrences were included in the analysis.

Ant subfamily/genus/species	Spiders					
	Ant-eaters					Ant-mimics
	<i>Callilepis</i> spp.	<i>Nomisia</i> spp.	<i>Zodarion</i> spp.	<i>Z. styliferum</i>	<i>Z. alacre</i>	<i>Micaria</i> spp.
Dolichoderinae						
<i>Tapinoma nigerrimum</i>	0.098 n.s	-0.150 n.s	0.099 n.s	0.167 n.s	-0.125 n.s	-0.006 n.s
Formicinae						
<i>Camponotus</i> spp.	0.096 n.s	0.163 n.s	0.116 n.s	0.228 *	-0.114 n.s	0.332 **
<i>C. cruentatus</i>	0.104 n.s	0.127 n.s	0.115 n.s	0.210 *	-0.083 n.s	0.341 **
<i>C. pilicornis</i>	0.212 *	0.161 n.s	0.189 n.s	0.289 *	-0.125 n.s	0.476 ***
<i>Cataglyphis</i> spp.	0.286 **	-0.123 n.s	0.228 *	0.235 *	-0.082 n.s	0.276 **
<i>C. hispanica</i>	0.104 n.s	-0.193 n.s	0.141 n.s	0.131 n.s	0.004 n.s	0.083 n.s
<i>C. iberica</i>	0.108 n.s	-0.139 n.s	0.029 n.s	0.099 n.s	-0.096 n.s	-0.023 n.s
<i>Iberoformica subrufa</i>	0.084 n.s	0.140 n.s	0.408 ***	0.307 **	-0.107 n.s	0.467 ***
<i>Plagiolepis</i> spp.	0.186 n.s	0.252 *	0.067 n.s	0.085 n.s	-0.094 n.s	-0.017 n.s
<i>P. pygmaea</i>	0.177 n.s	0.131 n.s	0.053 n.s	0.027 n.s	-0.016 n.s	0.057 n.s
<i>P. schmitzii</i>	0.177 n.s	0.169 n.s	0.056 n.s	0.051 n.s	-0.125 n.s	-0.094 n.s
Myrmicinae						
<i>Aphaenogaster</i> spp.	0.046 n.s	0.225 *	0.401 ***	0.488 ***	-0.046 n.s	0.195 n.s
<i>A. iberica</i>	-0.072 n.s	0.265 *	0.236 *	0.331 **	-0.230 *	0.288 **
<i>A. gibbosa</i>	0.073 n.s	0.219 *	0.448 ***	0.433 ***	0.018 n.s	0.033 n.s
<i>Crematogaster auberti</i>	0.288 **	0.090 n.s	0.176 n.s	0.254 *	-0.159 n.s	-0.046 n.s
<i>Messor barbarus</i>	0.190 n.s	0.117 n.s	0.274 **	0.252 *	-0.066 n.s	-0.004 n.s
<i>Pheidole pallidula</i>	-0.070 n.s	0.022 n.s	0.046 n.s	0.047 n.s	-0.011 n.s	-0.144 n.s

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s $p \geq 0.05$

genera, and the species *C. cruentatus*, *C. pilicornis*, *I. subrufa*, *A. iberica*, *A. gibbosa*, *C. auberti* and *M. barbarous* (Table 2). Null model tests of co-occurrence detected a significant association between *Z. styliferum* and the former taxa, except for *Cataglyphis* genus and *M. barbarous* (Table 3).

The abundance of *Z. alacre* spiders was correlated negatively with that of *A. iberica* ants and negative non-random co-occurrence ($P(O \geq E) = 0.018$ and $SES = 2.535$) was also found between them.

Both Spearman correlations and null model tests revealed significantly positive associations between *Micaria* spiders and ants from the *Camponotus* and *Cataglyphis* genera, and *C. cruentatus*, *C. pilicornis*, *I. subrufa* and *A. iberica* species. (Tables 2 and 3).

Impact of adjacent non-crop habitats and ground cover on the spider and ant communities

The abundance and richness of generalists/ opportunists (G/O), specialist of warm climates and/ or open habitats (HCS/OH) as well as of cryptic (Cr) ants was significantly higher in summer than in spring (Table 4). Moreover, the

abundance of G/O and Cr ants was higher in the distance of 100 m from adjacent non-crop habitat than in the distance of 5 m, and the abundance of HCS/OH ants was higher in 100 m than in both 5 m and 50 m. Also, the abundance of HCS/OH ants was positively related to the richness of ground cover.

Concerning spiders, the abundance and richness of Sp spiders and the richness of OH spiders was significantly higher in summer than in spring, while no differences between seasons occurred in the abundance and richness of GH, ShW and AH spiders.

Both the abundance and richness of GH spiders, as well as the abundance of Sp spiders, were higher in the distance of 100 m of the adjacent non-crop habitat than in the distances of 5 and 50 m (Table 4). On the other hand, the richness of OH spiders was higher in the distance of 5 m from the adjacent non-crop habitat than in the distances of 50 or 100 m.

Both abundance and richness of GH spiders were positively related to the richness of ground cover (Table 4), while the abundance and richness of ShW spiders were positively related to the percentage of ground cover (Table 4). The relationship between abundance of Sp spiders and the percentage of ground cover was positive, although only near of significance.

Table 3. Standard effect size (SES) for the co-occurrence of ant associated spiders and ants (genera and species) in null model tests. Significant values are reported in bold. The significance level of $p < 0.05$ is reported for the number of samples for which the observed value of the index was significantly less than the expected by chance ($O < E$). Only genera/species with at least five occurrences were included in the analysis.

Ant subfamily/genus/species	Ant-eaters					Ant-mimics
	<i>Callilepis</i> spp.	<i>Nomisia</i> spp.	<i>Zodarion</i> spp.	<i>Z. styliferum</i>	<i>Z. alacre</i>	<i>Micaria</i> spp.
Dolichoderinae						
<i>Tapinoma nigerrimum</i>	-0.603 ^{n.s.}	1.235 ^{n.s.}	-1.209 ^{n.s.}	-1.085 ^{n.s.}	0.714 ^{n.s.}	0.035 ^{n.s.}
Formicinae						
<i>Camponotus</i> spp.	-0.273 ^{n.s.}	-1.894 ^{n.s.}	-1.391 ^{n.s.}	-2.286 **	1.184 ^{n.s.}	-2.303 *
<i>C. cruentatus</i>	-0.598 ^{n.s.}	-1.413 ^{n.s.}	-1.547 ^{n.s.}	-2.192 *	0.872 ^{n.s.}	-2.518 *
<i>C. pilicornis</i>	-1.892 ^{n.s.}	-1.513 ^{n.s.}	-1.556 ^{n.s.}	-2.457 *	1.243 ^{n.s.}	-3.715 **
<i>Cataglyphis</i> spp.	-1.794 ^{n.s.}	1.111 ^{n.s.}	-0.605 ^{n.s.}	-0.299 ^{n.s.}	0.1295 ^{n.s.}	-1.926 *
<i>C. hispanica</i>	-0.094 ^{n.s.}	1.964 ^{n.s.}	-0.076 ^{n.s.}	0.185 ^{n.s.}	-0.097 ^{n.s.}	-0.892 ^{n.s.}
<i>C. iberica</i>	-0.968 ^{n.s.}	1.374 ^{n.s.}	0.306 ^{n.s.}	-0.682 ^{n.s.}	0.764 ^{n.s.}	0.106 ^{n.s.}
<i>Iberoformica subrufa</i>	-0.7650 ^{n.s.}	-1.407 ^{n.s.}	-3.235 ***	-2.490 **	0.924 ^{n.s.}	-3.314 ***
<i>Plagiolepis</i> spp.	-1.331 ^{n.s.}	-2.243 *	-0.109 ^{n.s.}	-0.845 ^{n.s.}	0.813 ^{n.s.}	-0.146 ^{n.s.}
<i>P. pygmaea</i>	-1.508 ^{n.s.}	-1.452 ^{n.s.}	0.450 ^{n.s.}	-0.764 ^{n.s.}	0.039 ^{n.s.}	-1.682 ^{n.s.}
<i>P. schmitzii</i>	-0.987 ^{n.s.}	-1.526 ^{n.s.}	0.450 ^{n.s.}	-0.047 ^{n.s.}	1.250 ^{n.s.}	-0.480 ^{n.s.}
Myrmicinae						
<i>Aphaenogaster</i> spp	0.097 ^{n.s.}	-0.322 ^{n.s.}	-2.648 **	-2.420 **	0.079 ^{n.s.}	-1.228 ^{n.s.}
<i>A. iberica</i>	0.313 ^{n.s.}	-1.644 ^{n.s.}	-1.831 *	-2.307 **	2.535 ^{n.s.}	-2.178 *
<i>A. gibbosa</i>	-0.096 ^{n.s.}	-0.968 ^{n.s.}	-2.975 ***	-2.579 **	-0.109 ^{n.s.}	-0.787 ^{n.s.}
<i>Crematogaster auberti</i>	-1.993 *	-1.053 ^{n.s.}	-1.697 ^{n.s.}	-2.327 **	1.307 ^{n.s.}	0.254 ^{n.s.}
<i>Messor barbarus</i>	-3.834 ***	0.713 ^{n.s.}	-0.942 ^{n.s.}	-1.071 ^{n.s.}	1.158 ^{n.s.}	-0.526 ^{n.s.}
<i>Pheidole pallidula</i>	0.576 ^{n.s.}	-0.2533 ^{n.s.}	0.325 ^{n.s.}	0.369 ^{n.s.}	0.591 ^{n.s.}	1.176 ^{n.s.}

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ^{n.s.} $p \geq 0.05$

Discussion

Ant community

A total of 20 ant species were identified. More than half of the collected individuals belonged to five species (*M. barbarus*, *C. hispanica*, *A. gibbosa*, *A. iberica* and *C. iberica*). *Messor barbarus* is widely distributed in the Mediterranean

region, being an herbivorous species, commonly known as “harvest ant”, which collect and feed on seeds and fruits from grassland and scrubland plants (Azcárate et al., 2005). *Cataglyphis hispanica* and *A. iberica*, two Iberian endemic species, are scavengers that feed mainly on dead arthropods (Lenoir et al., 2009; Boulay et al., 2005); *Cataglyphis iberica* is also scavenger (Martínez et al., 2002) while *A. gibbosa* is an omnivorous species (Lázaro-González et al., 2013).

Table 4. Generalized linear mixed model (GLMM) analysis for main functional groups of spiders and ants captured in pitfall traps evaluating the impact of season (spring and summer), distance from adjacent vegetation (5, 50 and 100 m), and richness and percentage of ground cover in their abundance (N) and richness (S). GH - ground hunters; Sp - specialists; ShW - sheet web weavers; OH - other hunters; AH - ambush hunters; HCS/OH - hot climate specialists and/or open habitats; G/O - generalists/ opportunists; Cr - cryptic.

		Season		Distance to non-crop habitat		% ground cover		Ground cover richness	
		F	p	F	p	F	p	F	p
HCS/OH	N	387.524	<0.001	53.675	<0.001	2.479	0.119	23.992	<0.001
	S	12.665	0.001	0.963	0.386	0.255	0.615	0.571	0.452
GO	N	488.977	<0.001	11.460	<0.001	0.377	0.541	0.375	0.542
	S	14.559	<0.001	0.227	0.797	1.379	0.244	0.026	0.871
Cr	N	271.880	<0.001	8.783	<0.001	3.787	0.055	0.075	0.785
	S	2.073	0.154	0.129	0.879	0.035	0.852	0.565	0.452
GH	N	0.023	0.879	4.893	0.010	1.638	0.204	5.493	0.021
	S	3.471	0.066	3.787	0.027	0.247	0.620	3.956	0.050
Sp	N	37.620	<0.001	5.452	0.006	3.763	0.056	0.369	0.545
	S	7.458	0.008	1.126	0.329	1.525	0.220	0.546	0.462
ShW	N	0.062	0.804	2.140	0.124	13.760	<0.001	0.178	0.674
	S	0.229	0.634	0.351	0.705	4.872	0.030	0.350	0.556
OH	N	2.462	0.120	1.823	0.168	1.382	0.243	1.751	0.189
	S	8.188	0.005	3.378	0.039	2.442	0.122	3.667	0.059
AH	N	2.643	0.108	0.265	0.768	0.011	0.917	0.161	0.690
	S	1.084	0.301	0.478	0.622	0.001	0.976	0.002	0.969

In the present study, the number of ant species belonging to G/O, the group associated with disturbance was, in general, lower than the number of species belonging to HCS/OH and CCS/SH groups, that together constitute an indicator of stability (Roig & Espadaler, 2010). Although the percentage of disturbance was expected to be higher in study sites with herbicide in the row, it was only slightly higher in these plots (between 35.3 and 37.5%) compared to the study sites without herbicide (33.3%). On the other hand, NMDS analysis also did not show clear differences between farms, with respect to the functional groups of ants.

Spider community

A total of 44 species of spiders were collected, from which nine are Iberian endemic species, which represent about 11% of the endemic species known in the Iberian Peninsula (Cardoso & Morano, 2010).

Ground hunters and specialist spiders accounted, respectively, for 37.5% and 29.2% of the total individuals, and included the three most representative families (Gnaphosidae

and Lycosidae, in the first case and Zodariidae, in the second). Ground hunters were reported as the most abundant spider guild in the ground of vineyards from Italia (Caprio et al., 2015), South Africa (Gaigher & Samways, 2014), California (Hogg & Daane, 2010), North America (Bolduc et al., 2005) and Australia (D’Alberto et al., 2012). From the most abundant species collected, two i.e. *Z. styliferum* and *E. feminea* were present in all farms indicating that they are widely distributed and clearly adapted to DDR region.

Although the NMDS have shown two distinct groups of farms (the first one consisting of two farms where no herbicide was applied, and a second one consisting of two farms where herbicide was applied on the row) we believe that this difference was mainly due to the percentage of ground cover of the inter-row, which was higher in the last two farms (data not shown).

Co-occurrence between ants and ant-associated spiders

Results suggest that the specificity of the association between ants and spiders was relatively extensive, with ant-

associated spiders correlating with more than one ant genera or species. It was found that both ant-mimicking and ant-eating spiders were positively correlated with Formicinae ants while only ant-eating spiders were positively correlated with Myrmicinae. Rákóczi and Samu (2014) also only found positive association between ant-mimicking spiders and Formicinae, indicating that this could be related to the numerical dominance of Formicinae, which makes them a better model for Batesian-mimicry.

The correlation between ant-eating spiders and Formicinae ants was higher than the correlation between ant-eating spiders and Myrmicinae ants, and this was also reported by Rákóczi and Samu (2014), who explained that this difference could be related with the different types of defenses that these ant groups exhibit; thus, while Myrmicinae have thick cuticle, cuticle structures, a distinct postpetiole and a functional sting, Formicinae are deprived of postpetiole and functional stings and their defense is based on the use of their strong mandibles and toxin exudation (formic acid or anal gland secretions).

Zodarion, the most abundant ant-eating spider genus collected, is considered to be adapted to hunt ants (Pekár, 2004; Pekár et al., 2005; 2012a; Pekár & Toft, 2009), presenting nutritional limitations if non-ant prey is used as food (Cushing, 2012 and references therein). Moreover, it seems to be behaviorally and physiologically constrained to feed only on certain ant species (Pekár, 2004; Pekár & Toft 2009). Some *Zodarion* species are Batesian mimics, with various colour patterns and morphological resemblance to ants (Korenko et al., 2013). In the present study, the abundance of *Zodarion* was correlated with that of both Formicinae and Myrmicinae ants. Despite Pekár (2005) and Pekár et al. (2005) stated that Formicinae are paralyzed more quickly by the venom of *Zodarion* than Myrmicinae, some *Zodarion* species have demonstrated the preference for Myrmicinae (e.g. *Zodarion cyrenaicum* which mimics and feed on *Messor* spp. ants). However, the generalization to the subfamily level should be viewed with caution since it was found that some species (such as *Z. rubidum*) are specialists at an even lower taxonomic rank (Cárdenas et al., 2012). In this case, for instance, spiders are able to recognize intraspecific chemical signals produced by the ants. In fact, a study conducted by Pekár et al. (2012b), suggests that the speciation of ant-eating *Zodarion* spiders is induced by prey-shifting. Moreover, Pekár et al. (2012b) found that while individuals of *Z. styliferum* from mainland Portugal hunted predominantly *Messor* ants (Myrmicinae), those from Madeira island hunted *Lasius* ants (Formicinae). On the other hand, Pekár (2009), showed that in some spider species (e.g. *Zodarion asiaticum*), the feeding habits change over the lifespan; thus, initially they are adapted to feed primarily on species of small Dolichoderinae and Myrmicinae ants, while the large juvenile and the adults are adapted to feed on large Formicinae ants.

Spiders from *Micaria* genus, that were found to be associated with *Camponotus* (the genus as a whole, as well as the species *C. cruentatus* and *C. pilicornis*), *Cataglyphis* spp., *I. subrufa*, and *A. iberica*, are thin-legged ant-mimic spiders whose bodies are often banded and peppered with iridescent scales, and their anterior lateral spinnerets are comparatively small (Adams, 2014).

Other ant-associated spiders found in the present study in very low numbers, were not included in statistical analysis. This is the case of the ant-eaters from *Euryopis*, *Oecobius* and *Oxyopes* genera, as well as of the ant-mimics from *Castianeira* and *Myrmarachne* genera. *Euryopis episinoides*, is a tiny, 3-mm-long spider that catches ants, particularly from *Messor* spp. (Pekár & Cárdenas, 2015) but also attacks *Crematogaster* spp. (Cushing, 2012). Conveniently, females lay her egg sacks close to the nests of these ant genera and once hatched, the young spiders experience their first meal acquiring information about preferred prey and how successfully locate them (Pekár & Cárdenas, 2015). The spiders of the *Castianeira* genus are mimics of large ants. Though these spiders do not really resemble ants in shape and appearance, they behave like them. Some species raise their first pair of legs and wave them like antennae, and walk on six legs (Deeleman-Reinhold, 2001). Also, the members of *Myrmarachne* are regarded as perfect ant mimics and are very similar to ants both morphologically and behaviorally (Huang et al., 2011). The males of some species of *Myrmarachne* have greatly enlarged chelicerae that extend anteriorly apparently to mimic encumbered ants (worker ants carrying items in their mandibles) (see Cushing, 2012). Species of this genera resemble ants, to avoid predation, through the first pair of legs movement to look like the ant antennal movement (Ceccarelli, 2008).

Impact of adjacent non-crop habitats and ground cover on the spider and ant communities

Abundance of both G/O, HCS/OH and Cr ants was high at the highest distance (100 m) from adjacent non-crop habitat, suggesting that their populations are established in the vineyards and apparently do not recolonize vineyards from these natural habitats.

Concerning to spiders, the impact of the season, the distance to the adjacent non-crop habitat, and the ground cover differed between guilds. While abundance and richness of Sp spiders and richness of OH spiders were higher in summer than in spring, abundance and richness of GH, ShW and AH spiders did not differ between seasons. Results showed that, in general, spiders did not benefit from the proximity of adjacent non-crop habitats. Abundance and richness of GH spiders was higher at the distances of 5 and 100 m from non-crop habitat than in 50 m. In a study conducted in Californian vineyards, Hogg and Danne (2010) also found that dispersal activity of ground spiders did not change over the time; they also stated that ground spiders were unaffected by transect distance, from the adjacent non-crop habitat to the inside of

vineyard, speculating that or transects may not have been long enough to observe an effect on ground spiders or, ground spiders may be unaffected by seasonal changes in vineyards, and may not recolonize vineyards from natural habitats. Other studies have suggested that spiders did not move from these non-crop habitats to adjacent crop fields (Wu et al., 2009; D'Alberto et al., 2012).

The abundance of Sp spiders was also higher in the distance of 100 m from adjacent non-crop habitat than in 5 or 50 m. Being Sp spiders specialist ant-eating spiders, it is admissible that their presence could have been related to the presence of ants, whose abundance was also higher at 100 m from the adjacent non-crop habitat than in the other studied distances. A strong influence of ants on the abundance and spatial distribution of the Linyphiidae spiders, *Pocobletus* sp. was also documented by Marín et al. (2015).

The positive effect of the percentage of ground cover on abundance and richness of ShW spiders found in the present study, is in line with Balfour and Rypstra (1998) who observed high densities of ShW spiders in areas with high densities of weeds. As reviewed by these authors web-building spiders are particularly sensitive to structural features of their environment because of the specific spatial requirements of web placement.

No significant impact of ground cover on abundance and richness of the remaining spider guilds was found, although a positive effect of the percentage of ground cover in abundance of Sp group was found to be near of significance. In olive groves, Cárdenas et al. (2012), found that the cover crop removal affected positively the abundance of ground spider's populations, namely *Z. styliferum* (specialist) and other running spiders belonging to the families Gnaphosidae and Lycosidae (ground hunters), but not their diversity. Still, according to the same authors, the preference of *Z. styliferum* to uncovered soils could apparently be related with an easier facility to found shelter under stones; assuming this, the surface of soils in DDR vineyards is rich in stones even when ground cover is present.

In short, results indicate that the DDR vineyard agroecosystem support a rich assemblage of ants and spiders, as evidenced by the occurrence in the studied vineyards, of 20 species of ants and 44 species of spiders, of which three and nine respectively are Iberian endemics. The abundance of spiders seems to be mostly related with ground cover as well as the occurrence of prey. Thus, the abundance of ShW spiders seems to be particularly dependent on the ground cover, where they can build their webs, while that of Sp spiders seems to be mostly related with the abundance of ants, since that it was higher in the areas where ant density was also higher. Results still support the hypothesis that non-random co-occurrence between ants and ant-associated spiders exist in the field. Notwithstanding further studies should be done in order to confirm the ability of these spiders to mimic and/or feed on ants.

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Supplementary Material

<http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/1934/0>

Supplementary Table S1

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Supplementary Table S2

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