

ORIGINAL ARTICLE

Functional diversity of epigeal spiders in the olive grove agroecosystem in northeastern Portugal: a comparison between crop and surrounding semi-natural habitats

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Abstract

The olive grove agroecosystem (*Olea europaea* L., Oleaceae) is very important in terms of economy and culture throughout the Mediterranean region. In Trás-os-Montes (Portugal), olive groves are commonly surrounded by semi-natural areas consisting of Mediterranean shrublands. Understanding the role of potential predators of olive pests is crucial to enhancing biological control in sustainable agriculture. This study aimed to investigate the community structure of ground-inhabiting spiders (Arachnida: Araneae) in the olive grove and their surrounding shrublands in Trás-os-Montes. We found that the community of spiders was dominated by ground hunters such as Lycosidae and Gnaphosidae. Lycosidae were more abundant in olive groves than in surrounding shrublands in 2015 only, whereas Gnaphosidae were more abundant in olive groves in both years of the study (2015 and 2016). Hence, the two habitats displayed a low complementarity of spider families. The Mediterranean shrubland areas could act as a reservoir and refuge for potential pest biocontrol agents. Conservation of surrounding semi-natural areas may contribute to the natural limitation of pests exerted by spiders in the olive grove agroecosystem. Nevertheless, further long-time and species-level studies are needed to provide insights into the role of spiders as natural enemies.

KEYWORDS

diversity, Arachnida, Araneae, guilds, semi-natural area, olive grove, agroecosystem, biological control, *Olea europaea*, Oleaceae, community structure, ground-inhabiting spiders

INTRODUCTION

The olive grove agroecosystem (*Olea europaea* L., Oleaceae) encompasses a series of relevant economic and cultural activities throughout the Mediterranean basin. Olive trees and groves are considered important repositories of biodiversity (Rouini, 2008), housing many arthropods (Coutinho, 2007). The community of terrestrial arthropods in olive groves is highly diverse and positively influences the maintenance of fundamental ecosystem services, such as pest limitation (Torres, 2007; Santorufo et al., 2012). The larvae and pupae of an important olive pest, the olive fruit fly,

Bactrocera oleae (Rossi) (Diptera: Tephritidae), develop in the soil. The larvae drop from the canopy, then bury themselves in the soil, and after development, the teneral adults emerge. During this time in the soil, *B. oleae* is exposed to predation by ground-dwelling organisms (Picchi et al., 2017). This pool of organisms includes Acari, Chilopoda, Collembola, Dermaptera, Diplopoda, Hemiptera, Isopoda, Malacostraca, Orthoptera, spiders (Arachnida: Araneae) (e.g., Lycosidae and Gnaphosidae), and various families of Coleoptera (e.g., Carabidae, Staphylinidae, and Elateridae), encompassing polyphagous species that are considered potential natural enemies of key olive pests (Santos et al.,

2007; Gonçalves & Pereira, 2012; Eyre et al., 2013; Paredes et al., 2013; Gonçalves, 2014; Dinis et al., 2016a,b; Castro et al., 2017; Benhadi-Marín et al., 2018; Carpio et al., 2018; Morente et al., 2018; Chafaa et al., 2019; Lantero et al., 2019).

As larvae and pupae of *B. oleae* are accessible to soil predators, the community of spiders has received considerable attention regarding biological control. For example, gnaphosids, such as *Haplodrassus rufipes* (Lucas), inhabiting olive groves have been observed preying on adults and pupae of *B. oleae* in the laboratory (J Benhadi-Marín, pers. comm.). Also, the effect of genetically engineered olive flies on the survival of *Pardosa* spp. has been tested (Marubbi et al., 2017). The gut content of species of the stalker genus *Oxyopes* was found to test positive for *Philaenus spumarius* (L.), a vector of the phytopathogenic bacterium *Xylella fastidiosa* Wells et al. (I Rodrigues, pers. comm.). However, research on the actual effects of specific species of spiders on olive pests is still scarce.

Intensive management of crops may lower the diversity and abundance of natural enemies in the crop, thus affecting the balance of the agroecosystem (Zilli et al., 2003). The loss of natural areas and increase in monocrops results in a decrease in the complexity of the landscape. This influences the biodiversity of the invertebrate community in these environments (Barros et al., 2008; Concepción et al., 2008; Schmidt et al., 2008). Moreover, the agroecosystems maintain close connections with the surrounding areas. For example, Madeira et al. (2016) found a consistent spillover of carabids and spiders from surrounding areas to areas of wheat cultivation, suggesting that these areas with high natural value could contribute to the conservation of beneficial arthropods in the crop. Also, Schneider et al. (2013) concluded that the movement patterns of terrestrial arthropods depend on the type of surrounding habitats. Their management and conservation are crucial for enhancing ecosystem functions (e.g., biological pest control).

The semi-natural areas surrounding the olive groves are considered biodiversity repositories where ecological interactions are established and shelter is provided for taxa that serve as prey for predatory arthropods (Picchi et al., 2016). Semi-natural areas such as the Mediterranean shrublands, with a higher vertical complexity of plant structure, could act as a temporary shelter for spiders during disturbances caused by agronomic practices and act as a source of diversity providing alternative food resources when they are scarce in the olive grove (e.g., during the overwintering period). Therefore, the entire area surrounding the olive grove can be crucial for increasing functional diversity and enhancing main ecosystem services such as biological control (Santos et al., 2007). Picchi et al. (2016) and Pascual et al. (2017) highlighted the importance of diversity and structure of the surrounding landscape for the arthropod assemblages in the olive grove. However, the structure and ecology of the arthropod community associated with olive cultivation are not yet fully understood; many aspects remain to be clarified, in terms of its value and role in natural limitation of pests. For this, an approach based on specific traits (e.g., diet or hunting strategy) related to pest

control could help to establish diversity patterns in a broad geographical context, regardless of the identity of individuals at the species level (Benhadi-Marín et al., 2020).

In descriptive studies, the use of guilds, or functional groups of organisms, instead of species facilitates identifying functional counterparts (i.e., different species contributing similarly to an ecosystem function) between regions sharing similar climatic conditions (e.g., various regions in the Mediterranean climate). A guild is defined as an assemblage of organisms with similar functional trait attributes or different species using the same class of resources in a behaviorally similar way (Simberloff & Dayan, 1991; Harrington et al., 2010). This reductionist approach is useful to understand how spiders play a role as predators considering groups of species with similar characteristics, thus helping to generalize about the role of spiders in the whole community (Wise, 1993). Among the various ways to categorize the families of spiders (e.g., diurnal/nocturnal), the hunting strategy has been widely used to cluster them into functional groups (e.g., Uetz et al., 1999; Cardoso et al., 2011).

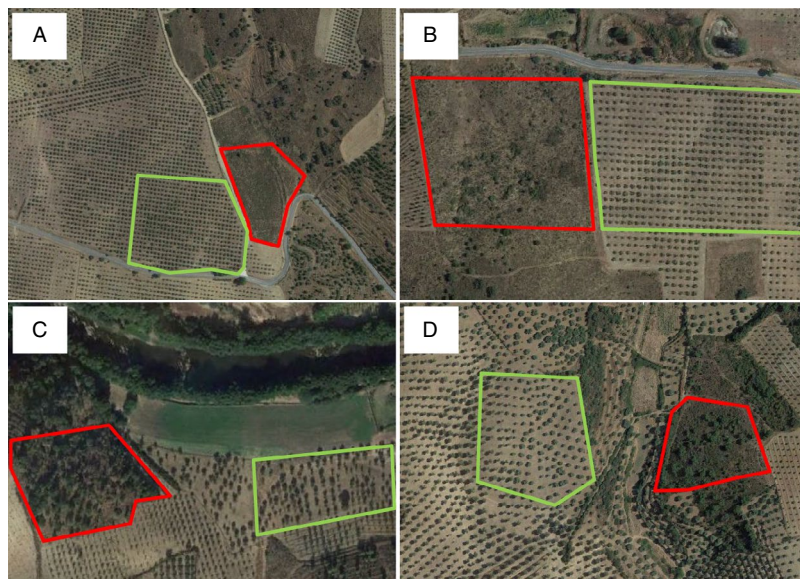
In this context, this study aimed to assess the community structure of the spring and early summer ground-inhabiting Araneae in olive groves and surrounding shrublands in Trás-os-Montes (Portugal) from a functional point of view.

MATERIALS AND METHODS

Study area

The study was conducted in the 'Terra Quente Transmontana' region near Mirandela (northeast Portugal). According to the Köppen and Geiger classification, the climate of the region is Csa type (Peel et al., 2007), characterized as temperate, with hot and dry summers and mild and humid winters, and with typically Mediterranean vegetation and agriculture. The average annual precipitation is 776 mm, with an average annual temperature of 13.8 °C (Fick & Hijmans, 2017) and predominantly shallow soils classified as leptosols (Anjos et al., 2015). Four olive grove habitats and the closest four surrounding Mediterranean shrubland habitats were selected (Figure 1). The four olive groves are maintained under integrated pest management (IPM), not tilled, and the soil is mainly covered with unknown spontaneous vegetation and stones. No chemicals were applied during the study period (further characteristics of the olive crops in Table S1). The surrounding shrubland habitat represents an important type of land cover in the study area, corresponding to a typical Mediterranean habitat. The sampled areas are homogeneous and mainly characterized by an herbaceous stratum dominated by plants belonging to the families Asteraceae, Poaceae, and Fabaceae, a stratum of shrubs dominated by species such as *Cistus ladanifer* L., *Cytisus* spp., *Lavandula* spp., *Rosmarinus officinalis* L., *Rubus ulmifolius* Schott, and *Crataegus monogyna* Jacq., and an upper layer dominated by trees such

FIGURE 1 Selected olive groves (green outlines) and adjacent Mediterranean shrublands (red outlines) in Trás-os-Montes (Portugal), where the occurrence of ground-dwelling spiders was sampled. (A) Cedães 1, (B) Cedães 2, (C) Guribanês, and (D) Valbom dos Figos. The olive grove areas were 8.90, 4.01, 2.10, and 4.00 ha, respectively; the shrubland areas were 5.22, 3.18, 2.63, and 2.23 ha, respectively (see Table S1)



as *Quercus rotundifolia* Lam., *Quercus pyrenaica* Willd., and *Arbutus unedo* L. (Benhadi-Marín et al., 2020).

Sampling of arthropods

Sampling was conducted for 7 weeks in spring, in 2015 and 2016 (between 1 May to 20 June). Four sites were sampled, each containing one olive grove and the nearest surrounding shrubland habitat. Nine pitfall traps were placed in each habitat at each site (Figure 2A). In each grove and shrubland habitat, the pitfall traps were regularly distributed in the form of a 3 × 3 grid, each spaced approximately 50 m apart within the grid to minimize interference, resulting in a total of 1008 samples (i.e., nine traps at two areas in four groves, replaced weekly during 7 weeks, in 2 years). At each sampling point, a hole was dug in the soil with width and depth sufficient to place a 200 ml plastic cup (7 cm diameter at the top, 9 cm high) with its edge leveled to the soil surface (Figure 2B). Each trap was filled with 100 ml of a mixture of ethylene glycol, water, and detergent (2:2:1) as a preservative solution. Plastic covers fixed to the ground with wire (5 cm above the soil surface) were used to prevent flooding due to rainwater and falling of animals of medium/large size (e.g., rodents and small lizards) from making the preservative solution impracticable and compromising the quality of the samples.

In each year, during the sampling period, the traps were changed every 7 days, during seven consecutive weeks. The traps were transported to the Agrobiotechnology Laboratory of the Centro de Investigação de Montanha (CIMO, Polytechnic Institute, Bragança, Portugal). The content of the traps was removed and the Araneae were sorted and preserved in 70% ethanol for subsequent identification using a stereomicroscope and specific identification keys (Nentwig et al., 2020). Finally, the identified families were assigned to guilds following Uetz et al. (1999) and Cardoso et al. (2011).

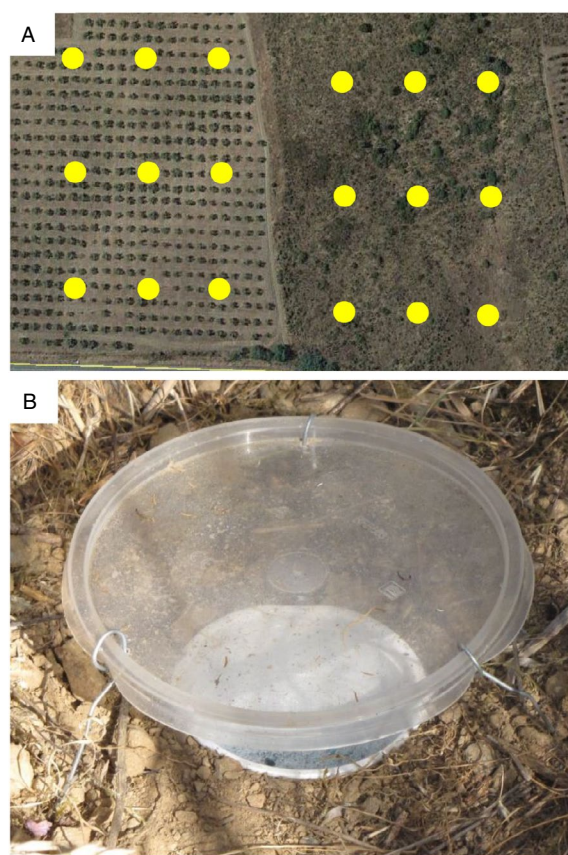


FIGURE 2 (A) Example of the sampling design in one of the study areas (Cedães 2, Trás-os-Montes, Portugal). The dots indicate the positions of the pitfall traps used to capture ground-dwelling spiders. (B) Pitfall trap with a plastic roof

Data analysis

The community structure of Araneae was assessed in terms of abundance, richness, and diversity. Data for each year of

study (2015 and 2016) were treated independently to avoid bias due to interannual variability. All statistical analyzes were performed in R v.5.3.1. (R Core Team, 2018). The total abundance was calculated as the number of individuals present in each sample (n), whereas richness (S) was calculated as the number of families or guilds present in each sample.

A complementarity analysis (Colwell & Coddington, 1994) was used to compare the list of families in both habitats (olive grove and surrounding shrublands) as:

$$S_{jk} = S_j + S_k - V_{jk}, \quad (1)$$

where S_{jk} is the total combined richness, S_j indicates the total family richness of the first area, S_k indicates the total richness of the second area, and V_{jk} corresponds to the number of families in common between the two areas. The number of unique species U_{jk} to either inventory is:

$$U_{jk} = S_j + S_k - 2V_{jk}, \quad (2)$$

and the complementarity is measured by C_{jk} as:

$$C_{jk} = U_{jk} / S_{jk}, \quad (3)$$

so that C_{jk} ranges from 0 (when the lists of organisms are identical) to 1 (when the lists of organisms are completely different). The complementarity of families between habitats was calculated for the total richness recorded across all four groves and the seven sample dates throughout each year of study.

The community composition in terms of families was assessed through canonical correspondence analysis (CCA), and accumulation curves for families were developed based on the number of individuals captured using the functions provided by the 'vegan' package (Oksanen et al., 2019).

Due to the low number of replicates (i.e., four sites), the effects of habitat type (olive grove or shrubland) on the total abundance of spiders, the abundance of the two dominant families of ground-dweller spiders, and the richness (S) and diversity (D) of families and guilds were investigated using generalized estimating equations (GEE) ($\alpha = 0.001$), an extension of the generalized linear models (GLM). An interchangeable correlation structure between samples (a single correlation parameter ρ) was assumed, and the Poisson distribution with logarithmic link function was used due to count data (Zuur et al., 2009; Pekár & Brabec, 2018). Although the phenology of spiders is out of the scope of this work, sampling week was used as explanatory variable to cope with temporal variation within each year of sampling, whereas location was used as random term.

Finally, the Simpson index (Simpson, 1949) was calculated as a measure of diversity per sample. This index reflects the probability that two individuals randomly captured in the community belong to the same family in this

case study. The index varies from 0 to 1, and the closer to 1, the greater the probability that individuals belong to the same species, that is, the greater the dominance and the less the diversity. The index was calculated for each year as:

$$D = 1 - \sum n_i [(n_i - 1) / N(N - 1)] c, \quad (4)$$

where D is the Simpson index (i.e., sample diversity), n_i indicates the abundance of each family, and N represents the total number of individuals in the sample. The diversity (D) of families and guilds was modeled using GEEs as explained before.

RESULTS

In total, 6984 spiders were captured, encompassing 26 families. In both years and in both habitats, the ground runners Lycosidae (51% in the olive grove, 32% in the shrubland area in 2015; 43% in the olive grove, 41% in the shrubland area in 2016) and Gnaphosidae (25% in both the olive grove and the shrubland area in 2015; 25% in the olive grove and 17% in the shrubland area in 2016) were the dominant ones (Table 1). The CCA models were significant, although the habitat only explained 7.2 and 6.1% of the variation in 2015 ($\chi^2 = 0.35$) and 2016 ($\chi^2 = 0.31$, both d.f. = 7, $P = 0.001$), respectively (Figure 3). The accumulation curves indicated that the richness of families in the olive grove is likely to reach an asymptote at a lower abundance than in the shrubland, especially in 2015 (Figure 4).

In 2015, the shrubland habitat contained more exclusive families than the olive groves. In the shrubland habitat, the families Liocranidae and Zoridae were registered as exclusive, whereas Dictynidae was exclusive to the olive grove. The complementarity between the pool of families in the olive grove and the surrounding habitat was low (0.10). In 2016, fewer exclusive families were registered in the shrubland habitat (three), and the same number of exclusive families was registered in the olive groves (two) compared with 2015. In the shrubland habitat, Liocranidae was again an exclusive family, whereas in the olive groves, there was a change to Oxyopidae and Pholcidae as exclusive to the area. Again, the complementarity between the pool of families was low (0.11) (Table 1).

The total abundance of spiders was significantly higher in the olive grove than in the shrubland area in 2015 (Table 2). Among the two dominant families, the abundance of Lycosidae and Gnaphosidae in 2015 was significantly higher in the olive grove compared to the shrubland area, whereas in 2016, only the gnaphosids were significantly more abundant in the grove. The richness of families was significantly higher in the olive grove in both years of study compared to the shrubland area; the sampling week had a significant effect only in 2016. The Simpson index (D) for the assemblage of families was not significantly different between the olive groves and the shrubland habitat. The richness of guilds was significantly higher in the olive

TABLE 1 Abundance of families and corresponding guilds of Araneae captured in olive groves and surrounding shrublands in 2015 and 2016 in Trás-os-Montes (Portugal)

No. in Figure 3	Family	Guild	2015		2016	
			Olive groves (n = 252)	Surrounding shrublands (n = 252)	Olive groves (n = 252)	Surrounding shrublands (n = 252)
11	Lycosidae	Ground runners	1591	451	679	374
7	Gnaphosidae	Ground runners	788	351	398	153
25	Zodariidae	Specialists	137	257	88	167
9	Linyphiidae	WSTW ¹	105	66	166	44
16	Philodromidae	Ambushers	239	35	49	8
23	Thomisidae	Ambushers	107	24	95	20
20	Salticidae	Stalkers	43	50	32	40
1	Agelenidae	Sheet web-builders	11	53	9	47
22	Theridiidae	Space web-builders	37	22	43	1
6	Dysderidae	Ground runners	1	11	0	26
15	Oxyopidae	Stalkers	22	5	2	0
4	Clubionidae	Foliage runners	2	25	0	0
21	Scytodidae	Stalkers	5	14	1	4
26	Zoridae	Ground runners	0	2	4	9
3	Araneidae	Orb-weavers	8	2	2	1
19	Pisauridae	Ambushers	1	5	3	4
10	Liocranidae	Ground runners	0	7	0	4
24	Titanoecidae	Space web-builders	1	5	0	0
8	Hahniidae	Sheet web-builders	1	4	0	0
5	Dictynidae	Space web-builders	3	0	0	0
12	Miturgidae	Ground runners	1	1	0	0
2	Anyphaenidae	Foliage runners	0	1	0	0
13	Mygalomorphae ²	Sheet web-builders	0	0	0	1
14	Oecobiidae	Sheet web-builders	0	1	0	0
17	Pholcidae	Space web-builders	0	0	1	0
18	Phrurolithidae	Ground runners	1	0	0	0
	Immatures	–	8	5	0	0
Mean ± SE	Abundance		12.34 ± 1.38a	5.54 ± 0.43b	6.23 ± 0.70A	3.58 ± 0.46A
	Richness of families		3.11 ± 0.11a	2.47 ± 0.11b	2.70 ± 0.10A	1.73 ± 0.08B
	Simpson index (families)		0.54 ± 0.02a	0.49 ± 0.02a	0.49 ± 0.02A	0.48 ± 0.02A
	Richness of guilds		2.42 ± 0.08a	2.13 ± 0.09a	2.21 ± 0.08A	1.52 ± 0.07B
	Simpson index (guilds)		0.30 ± 0.02a	0.30 ± 0.03a	0.19 ± 0.02A	0.39 ± 0.03A

Means within a year followed by different letters are significantly different between areas (GEE: $P < 0.001$).

¹WSTW = wandering sheet/tangle weavers.

²The singleton could not be identified to family level.

grove only in 2016. Sampling week had a significant effect on the richness of guilds only in 2016 (Table 2).

DISCUSSION

In this study, 26 spider families were identified from the 56 families recorded on the Iberian Peninsula, i.e., 46% of known spider families in the area (Branco et al., 2019). These

families are typically found in Mediterranean habitats, coinciding with olive-growing areas. These results agree with those obtained in previous studies (Cárdenas et al., 2012; Dinis et al., 2016a; Picchi et al., 2016; Benhadi-Marin et al., 2018, 2020).

The composition of the Araneae community in the two sampling years was dominated by the ground runners Lycosidae and Gnaphosidae in both olive groves and the surrounding shrubland habitats. Their abundance was

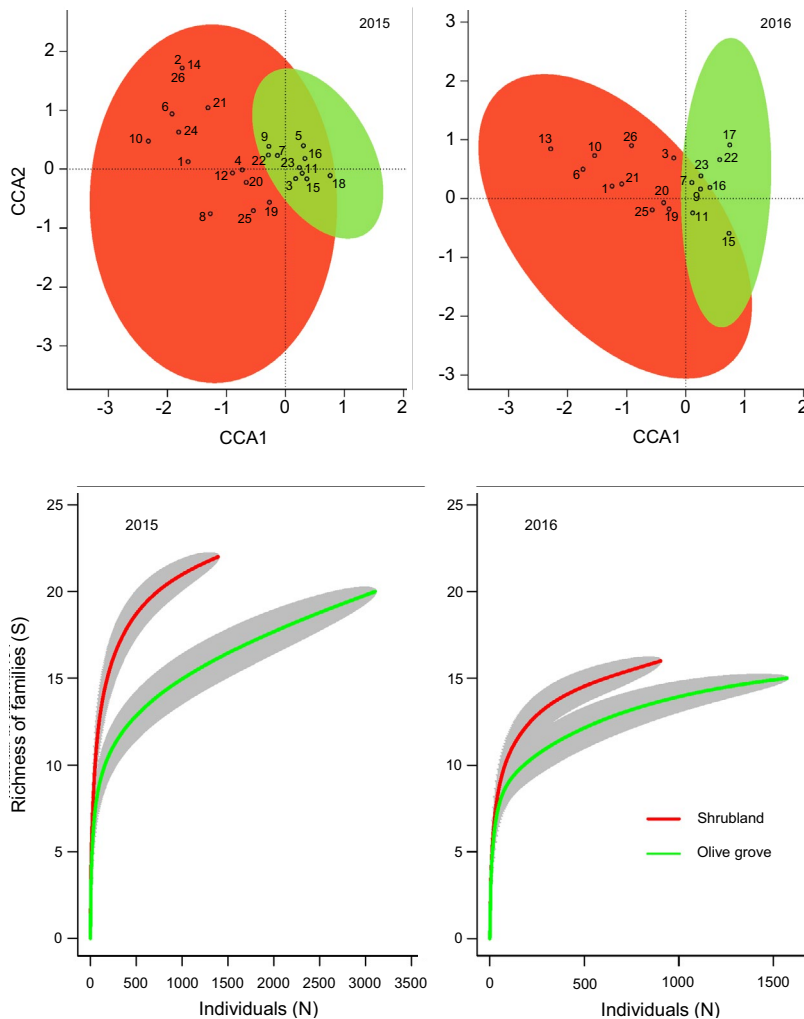


FIGURE 3 Ordination plot (canonical correspondence analysis, CCA) for the complete pool of spider families found in olive groves (green) and shrubland (red) in Trás-os-Montes (Portugal) in 2015 and 2016. The first and second axes explained 16.7 and 8.1% of variation in 2015, and 14.4 and 7.4% in 2016, respectively. Ellipses represent standard deviation. The numbers within the panels correspond with the names of the families in Table 1

FIGURE 4 Accumulation curves of families of Araneae found in olive groves (green) and shrubland (red) in Trás-os-Montes (Portugal) in 2015 and 2016. Grey areas represent the standard error of the estimates

consistent between years. The fact that we found a large amount of ground-dwelling spiders can be explained by the sampling method: the pitfall traps mostly catch active individuals (Foelix, 2011). In fact, spiders belonging to other guilds, such as orbicular or three-dimensional web-builders, generally make their webs in higher places, taking advantage of the spatial structure of vegetation (Foelix, 2011). It is less likely that these types of spiders are captured in pitfall traps. Another factor to consider is the sampling period. Sampling took place during spring, coinciding with the flowering season of the olive trees (Cohen et al., 2010), a time of high activity and abundance of the arthropodofauna throughout the region, which in turn represents an increase in the number of potential prey for spiders, with a positive impact on their abundance (Cárdenas, 2008; Rallo & Cuevas, 2017). The week of sampling had a significant effect on the abundance and richness in a non-consistent way (i.e., only in 2016); thus, this effect could only be due to natural (e.g., interannual) variability.

The family Lycosidae includes active day and night foragers, which may eventually use a sit-and-wait strategy to hunt (Ford, 1978; Suter & Benson, 2014). However, they rely on vibratory and visual stimuli to locate and detect prey (Uetz et al., 2016). Their diet is not monotypic, with low

species-specific prey preference (Persons & Rypstra, 2000). They have a preference for medium-sized vegetation (Major et al., 2006) and low-disturbed soils, where populations develop in suitable habitats for reproduction, shelter, and ambush points (Mashavakure et al., 2019). In 2015, abundance was higher in olive groves than in surrounding shrublands, whereas in 2016, there were no significant differences in abundance. This may be due to the dispersal capacity of this group; individuals may wander freely between olive groves and adjacent shrubland.

The family Gnaphosidae is typical in Mediterranean habitats (Cardoso et al., 2007). This family is mainly represented by night hunters that move quickly on the ground and are commonly found sheltered under rocks or debris. Indeed, there were high number of stones on the soil surface of the studied olive groves (see Benhadi-Marín et al., 2018), which function as physical structures for refuge and reproduction. In both years of the study, the abundance of gnaphosids was higher in the olive grove. As these spiders largely depend on the presence of accessible and suitable stones to develop their life cycle, the soil management of the selected groves may favor their presence, leading to spatial stability of populations over time (Benhadi-Marín et al., 2018).

TABLE 2 Summary statistics for the models developed to assess the effect of the area (olive groves vs. surrounding shrublands) and week of sampling on the diversity of Araneae in Trás-os-Montes (Portugal) in 2015 and 2016

Year	Dependent variable	Independent variable	d.f.	Total (all families)		Guilds		
				χ^2	P	χ^2	P	
2015	Total abundance	Area	1	20.8	<0.001*			
		Date	6	20.6	<0.001*			
	Abundance of Lycosidae	Area	1	11.3	<0.001*			
		Date	6	147.0	<0.001*			
	Abundance of Gnaphosidae	Area	1	24.1	<0.001*			
		Date	6	5.6	0.47			
	Richness	Area	1	12	<0.001*	4.42	0.04	
		Date	6	15.5	0.02	12.6	0.50	
	Simpson index (D)	Area	1	3.19	0.07	0.00	0.98	
		Date	6	1.91	0.93	7.70	0.26	
	2016	Total abundance	Area	1	8.09	0.005		
			Date	6	11.1	0.09		
Abundance of Lycosidae		Area	1	2.3	0.13			
		Date	6	6.59	0.36			
Abundance of Gnaphosidae		Area	1	37.3	<0.001*			
		Date	6	59.5	<0.001*			
Richness		Area	1	21.7	<0.001*	21.7	<0.001*	
		Date	6	78.1	<0.001*	78.1	<0.001*	
Simpson index (D)		Area	1	0.20	0.66	7.46	0.006	
		Date	6	9.32	0.16	6.38	0.38	

An asterisk indicates a significant difference between areas (olive grove vs. surrounding shrublands) or sampling dates (GEE: $P < 0.001$).

The family Zodariidae was also relatively abundant. This family encompasses specialist myrmecophilous spiders (Pekár, 2005). As spiders specialized in ants, the abundance of this group is related to the presence of Formicidae. Most zodariids occur in the Mediterranean region (73% of species worldwide), especially in the western region of Europe (e.g., the Iberian Peninsula) (Pekár et al., 2003). The higher abundance of Zodariidae in shrublands compared to the olive groves may be related to a higher diversity of ants in less disturbed areas, or less exposure to predators due to higher vegetation complexity. On the other hand, the community of soil arthropods is numerically dominated by Formicidae in the olive grove (Santos et al., 2007), which represents food for specialist spiders and provides great part of the diet of other species such as *Nomisia* spp., *Haplodrassus* spp., *Xysticus* spp., *Ozyptila* spp., and *Eratigena* spp. (J Benhadi-Marín, pers. comm.).

Although the sampling method focused on ground dwellers, the web-builders Linyphiidae were well represented in both years of study. Interestingly, Picchi et al. (2016) found a decrease in the density of Linyphiidae with the proportion of Mediterranean garigue in Italy.

The Simpson index did not reflect differences in diversity between the olive grove and the surrounding shrublands for families, and only reflected a non-significant higher diversity in shrublands than in olive groves for guilds in 2016.

The low sensitivity of D for the diversity could reflect a weakness of this measure derived by the sampling method and taxonomic rank. For example, removing or adding singletons from a dataset with a low number of guilds may result in significant differences regardless of interannual variability. Maximized inventories using complementary sampling methods (see Cardoso, 2009) could help to shed light on this phenomenon in this sense. On the other hand, the accumulation curves suggest that the richness of families could be greater in the surrounding shrubland habitat at low population densities. This fact may be related to the complexity of the vegetation structure in the shrubs. With a higher density of vegetation and large rock structures on the soil, these areas could increase the richness of guilds hosting different groups at ground level (Caprio et al., 2015; Benhadi-Marín et al., 2018). Besides, surrounding semi-natural areas could act as a refuge for the spiders in the face of disturbances derived from agricultural practices in the crop areas, providing alternative food resources when they are scarce in the olive grove (Landis et al., 2000; Picchi et al., 2017). Indeed, surrounding vegetation to the grove represents an alternative habitat for natural enemies when the ground cover withers in summer (Álvarez et al., 2019).

There was a higher abundance of spiders (in 2015) and richness of families (in both years) in the olive groves compared to the surrounding semi-natural areas. This suggests

that olive groves are not a particularly hostile environment for ground spiders, whereas a temporary reduction of the superficial grass cover in the shrublands could result in diminished habitat suitability due to shelter unavailability. Moreover, the differences shown by the accumulation curves of families are most likely due to an overrepresentation of dominant families at a low abundance of individuals. In fact, regarding the slopes, the asymptote of the shrubland curves could be reached earlier compared with olive groves as the number of captured individuals increases, especially in 2015. In addition, the low complementarity may suggest a movement of spiders between both habitats. Although this is still unclear, it may support the movement patterns suggested by Álvarez et al. (2019), who found a flow of predators from the ground cover to the adjacent vegetation and the olive grove from May to July in organic olive orchards, coinciding with our sampling period.

Our results support the management of olive groves aimed to avoid the decrease in biodiversity associated with intensification or abandonment. Indeed, the olive groves could encompass suitable habitats for spiders at a level equivalent to semi-wild Mediterranean surrounding areas, supporting a balanced diversity at the family and guild level. The management of the crop and the diversity of food sources and shelters may contribute to the establishment of species with the potential to exert natural regulation of *B. oleae* and other olive pests, such as lycosids and gnaphosids. The shrubland habitat could contribute to the conservation of ground-dwelling species and, consequently, to the natural limitation of pests in neighboring agroecosystems, e.g., the olive grove in Trás-os-Montes. However, this study focused on the active community of spiders during spring and early summer and further research during other key periods (i.e., autumn and winter), coinciding with the susceptibility of preimaginal forms of *B. oleae* to predators, is mandatory.

Although the functional approach is useful, studies at the taxonomic level of species and the integration of environmental variables are still necessary to deepen the knowledge of the temporal and spatial population dynamics of predators (e.g., the extent to which the potential predators and pests overlap in time and space), as well as to better establish their contribution to the natural limitation of various olive pests. For example, mark-recapture experiments would help to provide insights to the migration patterns of spiders between the grove and surrounding areas, whereas functional response assays can help to assess the potential natural limitation exerted by selected species on key olive pests.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Ketrin Lorhayne Kubiak: Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – original draft

(equal); Writing – review & editing (equal). José Alberto Pereira: Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review & editing (equal). Dinéia Tessaro: Supervision (equal); Validation (equal). Sónia Santos: Conceptualization (equal); Funding acquisition (equal); Methodology (equal). Jacinto Benhadi-Marín: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, JB-M, upon reasonable request.

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