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ORIGINAL ARTICLE

Stones on the ground in olive groves promote the presence of spiders (Araneae)

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Key words. Araneae, biological control, ground hunter, predator, abundance, diversity, shelter

Abstract. Spiders are generalist predators that contribute to the control of pests in agroecosystems. Land use management determines habitats including refuges for hibernation and aestivation. The availability of shelters on the ground can be crucial for maintaining populations of spider within crops. We studied the effect of the number of stones on the surface of the soil on the spider community in selected olive groves in Trás-os-Montes (northeastern Portugal). The number of stones significantly influenced the overall diversity of spiders, abundance of immature individuals and abundance of ground hunters. Agricultural management practices aimed at the conservation of soil microhabitats such as hedgerows, stonewalls and stones on the ground should be promoted in order to maintain or increase the number of shelters for potential natural enemies of pests.

INTRODUCTION

The cultivation of olive trees (*Olea europaea* L., 1753) is a common agricultural activity in the Mediterranean region, where it is of high economic and cultural importance (Breton et al., 2009; Benhadi-Marín et al., 2016). Olive trees are susceptible to attack by different species of pests such as the olive fruit fly *Bactrocera oleae* (Rossi) (Diptera: Tephritidae) and olive moth *Prays oleae* Bernard (Lepidoptera: Praydidae), which cause important quantitative and qualitative losses in the main olive crop areas every year (Ramos et al., 1998; González-Núñez et al., 2008).

Olive groves can be managed in one of three main ways: the conventional system (based on chemical pest control), the integrated production system (based on a narrow spectrum tools), and the organic farming system, which avoids the use of synthetic chemicals (Cárdenas et al., 2015).

Among the arthropods inhabiting olive groves, spiders are one of the dominant groups (Cárdenas et al., 2015). Since spiders are euryphagous predators (i.e., they are non-selective and can consume a great variety of species of prey) they can contribute to the reduction of important pests. There are several examples of biological control provided by spiders in different crops such as wheat (Chiverton, 1986; Kuusk et al., 2008; Oelbermann & Scheu, 2009), cotton (Ghavami, 2008), apple (Laszló et al., 2015) and citrus (Monzó et al., 2010). Also, within the olive agroecosystem spiders can control the olive fruit fly (Picchi et al., 2016).

However, different management practices within integrated production and organic farming systems, such as superficial tillage and plowing, could affect the community of spiders in different ways, for instance, by reducing the habitat complexity and destroying shelters. Several habitats (e.g. pounds, dry stone walls and hedges) are often used as ecological infrastructures by animals including small mammals, birds, reptiles, amphibians, molluscs, grasshoppers, ground beetles, dragonflies, butterflies and bees (see Boller et al., 2004). Nonetheless, the influence of potential ground shelters, such as stones on the surface of the ground, on animal biodiversity in agroecosystems has been poorly investigated. The objective of this work was to study the effect of the number of stones occurring on soil, on the abundance, richness and guilds of the ground spider community in selected olive groves in Trás-os-Montes (Portugal).

MATERIALS AND METHODS

Field sampling sites were located in eight olive groves near Mirandela (northeastern Portugal), Avantos Bio (41°33´34.39˝N, –7°05´37.17˝W), Avantos Prodi (41°32´17.31˝N, –7°05´43.89˝W), Cedães (41°29´16.86˝N, –7°07´34.02˝W), Guribanes (41°34´12.25˝N, –7°09´59.01˝W), São Pedro Bio (41°25´44.91˝N, –7°12´20.71˝W), São Pedro Prodi (41°26´38.09˝N, –7°13´28.69˝W), Suçães (41°29´30.02˝N, –7°15´28.72˝W) and Valbom-dos-Figos (41°33´00.58˝N, –7°08´39.92˝W). Organic farming was carried out at Avantos Bio, Guribanes, São Pedro Bio and Valbom-dos-Figos and integrated pest management at Avantos Prodi, Cedães, São Pedro Prodi and Suçães.

Sampling took place in the spring of 2011 using pitfall traps. A total of 16 pitfall traps distributed in the form of a regular 4 × 4 square grid, spaced between 45–50 m from one another and located in the center of each of the olive groves studied. Each trap consisted of a plastic cup (115 mm in diameter at the top and 130 mm in height) dug into the ground and filled with 250 ml of ethylene glycol as a preservative. Traps were operated over a period of seven nights. In the laboratory, all the spiders were preserved in 70% ethanol, sorted and identified to species (when possible) using a binocular stereomicroscope and following Nentwig et al. (2018).

Since stones are located on the ground in a non-random way 12 areas of 1 m^2 were randomly selected in each olive grove independently to the position of the pitfall traps. In each area, the number of stones was counted and scaled to the mean number of stones/m^2 in each grove. Considering the importance of herbaceous vegetation and moisture on the arthropod communities within agroecosystems (Stamps & Linit, 1998), the percentage of vegetation cover and relative humidity at the location of each pitfall trap were included as explanatory variables. Also, the factor "management type" (organic vs. integrated) and the random effect of grove were included in the models.

The dependent variables considered were: (1) total abundance of spiders, (2) total species richness, (3) abundance of adults, (4) abundance of immatures and (5) abundance of functional groups (i.e., six guilds) according to Cardoso et al. (2011). The guild corresponding to orb-weavers was excluded from the analysis because it was represented by a singleton. The effect of the number of stones on each dependent variable was evaluated using generalized mixed linear models following Zuur et al. (2009). Since all the dependent variables were count data, they were modelled using a random intercept and slope model with negative binomial distribution (to deal with over dispersion) and logarithmic link. For each dependent variable, a full model was firstly fitted of the generic form:

$$Yi \sim NB(\mu_i, k)$$
$$E(Y_i) = \mu_i \text{ and } \mathrm{var}(Y_i) = \mu_i + \mu^2/k$$
$$\log(\mu_i) = \eta(X_{i1}, \dots, X_{iq}) = \alpha + \beta_1 \times X_{i1} + \dots + \beta_q \times X_{iq} + Z_i \times b_i \quad \text{[Eq. 1]}$$

were α denotes the intercept, β the parameters to be estimated, X each explanatory variable, and the term $Z_i \times b_i$ the random effect of the grove. Then we used backward model selection based on the Akaike information criterion (AIC) to obtain the optimal model for each response variable (Zuur et al., 2009). In the cases where the effect of management was statistically significant, an independent model was built for each management and the model selection performed as described above. The random effect term was systematically kept in all models. All statistical analyses and modelling were performed in R (R Core Team, 2017).

RESULTS AND DISCUSSION

A total of 1621 spiders, 1105 adults (9.13 ± 0.44) (mean number per trap ± SE) and 516 immatures (4.26 ± 1.19) (mean number per trap ± SE) were captured. Among the collected material there were 19 families, 60 species (Table S1) and seven functional groups. The guild of ground hunters (8.32 ± 0.76) (mean number per trap ± SE) was the most abundant functional group, followed by specialists (2.12 ± 0.19) (mean number per trap ± SE), sheet web builders (1.12 ± 0.10), ambushers (0.87 ± 0.08), other hunters (0.69 ± 0.06), space web builders (0.22 ± 0.02) and orb weavers (one individual).

Among the dependent variables considered, the number of stones had a statistically significant effect on total spider abundance, species richness, abundance of immatures (Fig. 1), abundance of sheet web builders under integrated pest management, and abundance of ground hunters (Fig. 2, Table S2). Also, the percentage of vegetation cover significantly affected the abundance of space web builders, whereas a significant effect of management was found only for the abundance of sheet web builders (Table S2). In all cases, the effect of the number of stones was found to be positive when statistically significant whereas the effect of the percentage of vegetation cover negatively influenced the abundance of space web builders (Table S3).

The significantly negative effect of a higher percentage of vegetation recorded for space web builders could be due to a numerical artifact because of zero-inflation. However, the positive effect of the abundance of stones on the abundance of ground hunters was consistent and can be explained in terms of spider growth and their need to hide from predators. Birds and other spiders are common predators of spiders. While large spiders ($\geq$2.5 mm) seem to be more vulnerable to bird predation, intraguild predation may have a greater effect on small individuals ($\leq$2.5 mm), especially during winter (Gunnarsson, 1983). However, there is still a lack of knowledge on the effect of predators on spider richness (Gunnarsson, 2007). In fact, intraguild predation is an important community driver for predator population regulation. Within structurally-simple habitats such as most agricultural landscapes, intraguild predation between predators can reduce the pressure of predators on the herbivore community (Finke & Denno, 2006). Hence, sites with a high availability of stones for refuge may help both immature and adult spiders to cope with different selective forces by providing a spatial refuge from predators and reducing intraguild predation (i.e. allowing coexistence) that could enhance pest suppression.

Finally, environmental factors such as light and temperature affect the embryogenesis and post-embryogenesis of spiders (Napiórkowska et al., 2018). Thus, the survival of spiders, especially nocturnal species (e.g. Agelenidae and Gnaphosidae) may depend on the existence of dark and warm (in winter) or fresh (in summer) breeding sites (i.e. under stones) in which immature development is accelerated and mortality reduced.

To our knowledge, this study focuses for the first time on the effect of the number of stones on the surface of the soil

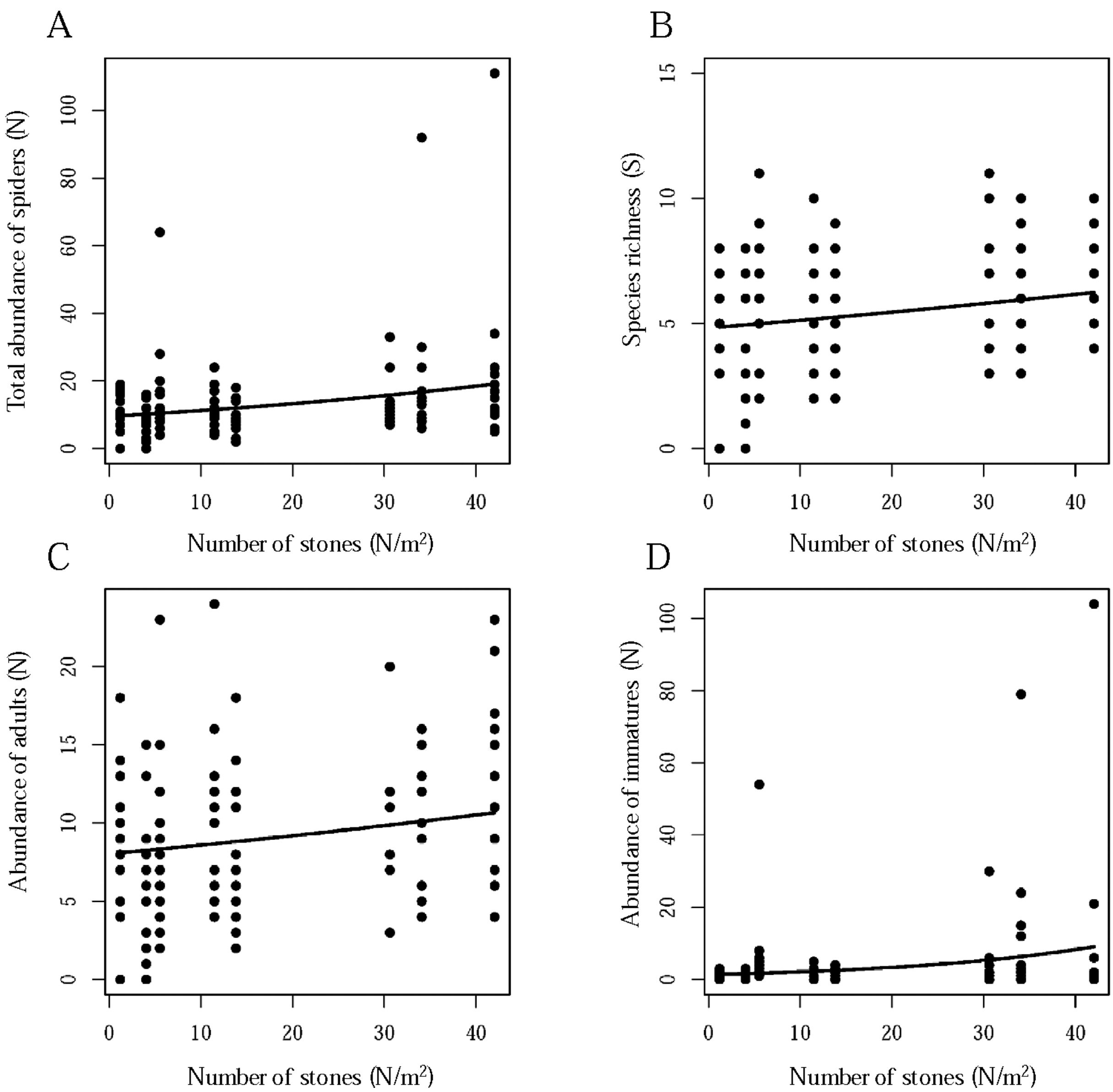

Fig. 1. Total abundance of spiders (A), species richness (B), abundance of adult spiders (C) and immatures (D) relative to the number of stones. Each line indicates the relationship between spider abundance and the number of stones per square meter.

on the spider community. In this context, roots, logs and stones can provide refuges for many species and provide a complex structure of microhabitats (Lecq et al., 2017). In this study, the diversity of spiders, both in terms of abundance and species diversity are positively associated with the number of stones on the surface of the soil, most likely due to their need for shelter in the early stages of development in the case of immature spiders, and as places where food and shelter can be found as well as places for reproduction in the case of adult ground hunters. The results are similar to those reported by Lecq et al. (2017) on the availability of shelter in agricultural hedgerows. For example, they report that the trend in the relative abundance of the morph species, *Tegenaria* sp. (Agelenidae), a species of spider that depends on ground refuges for shelter, was opposite to that of species inhabiting open habitats such as *Microtus* sp. (Cricetidae). As da Silva et al. (2017) suggest, conservation and management strategies within agricultural landscapes need to consider small-scale changes in landscape architecture.

The 'habitat heterogeneity hypothesis' assumes that complex habitats provide a greater diversity of niches and ways of exploiting environmental resources, which results in an increase in species diversity (Bazzaz, 1975; Tews et al., 2004). Moreover, species can be closely linked to "keystone structures" (i.e. distinct spatial structures that provide resources, shelter or "goods and services" that may determine biological diversity) whose detection is important for conservation and biodiversity management (Tews et al., 2004). Land management determines the number of habitats, abundance of food and refuges, and hibernation, and estivation shelters (Duru et al., 2015) and an understanding the resources needed by natural enemies can help to identify the key factors determining their diversity. In terms of shelter, providing habitats for overwintering and reducing the use of pesticides (Landis et al., 2000) may enhance the

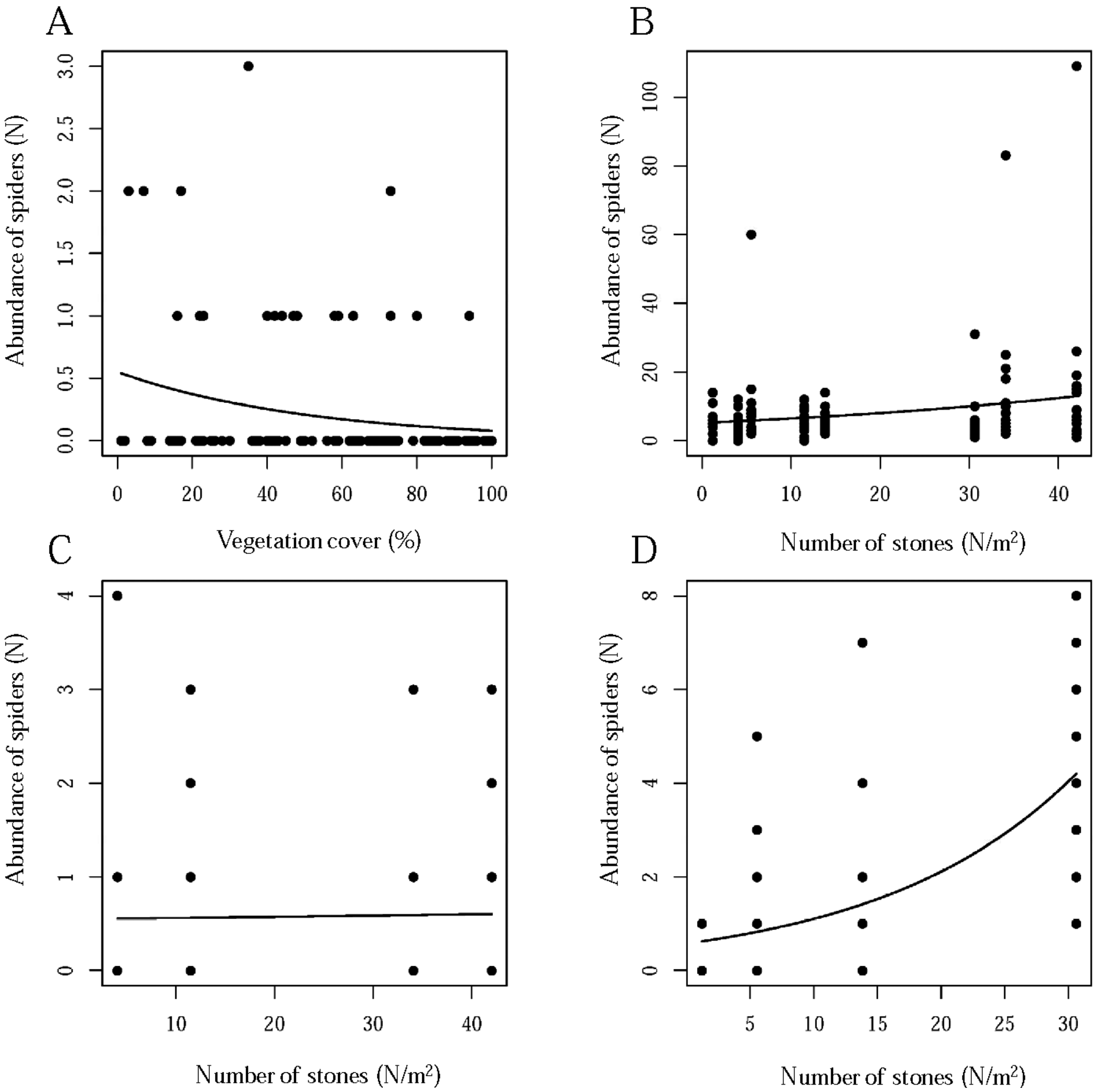

Fig. 2. Total abundance of different guilds of spiders: space web weavers (A), ground hunters (B) and sheet web weavers under organic (C), and integrated management (D) relative to the number of stones. Each line indicates the relationship between spider abundance and the number of stones per square meter.

overall action of natural enemies. This conforms with our results, especially in the case of the sheet web builders' guild, which was clearly favoured by a higher number of stones in groves under integrated production management, which indicates that maintaining keystone structures such as shelter is especially important in non-organic farming.

Regarding spiders in general, increasing the number of stones within crops could be a promising area in biological control. In this context, further research on how small-scale shelters (e.g. stones, ground holes, roots, and logs) and other potentially collinear local variables such as ground density, soil pliability and vegetation structure influence the community of natural enemies is needed.

In conclusion, low-cost activities for the farmer such as building dry stone walls, and maintaining hedgerows can provide abundant ground refuges (Le Viol et al., 2008; Lecq et al., 2017). The manipulation of habitat structure with the objective of increasing its complexity can improve the biocontrol service provided by spiders (Michalko et al., 2017). In addition, we also recommend reducing aggressive agrarian practices that affect the structure of the soil (e.g. deep plowing) which alters its physical characteristics. Instead, soil scarification is a method traditionally used for natural regeneration (Jäärats et al., 2012) that can also help in controlling weeds in agricultural landscapes and is more respectful of the ground refuges of potential natural enemies, such as spiders.

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Table S1. Total number of Araneae and spider guilds identified in all the samples collected on the ground in the olive groves at the eight sites studied in 2011. (1) ambush hunters, (2) ground hunters, (3) orb web weavers, (4) other hunters, (5) sheet web weavers, (6) space web weavers, (7) specialists.

Family (guild) / Species	Total
Agelenidae (5)	
Eratigena picta (Simon, 1870)	1
Eratigena feminea (Simon, 1870)	13
Agelenidae unid. immatures	1
Subtotal Agelenidae	15
Araneidae (3)	
Hypsosinga albovittata (Westring, 1851)	1
Subtotal Araneidae	1
Dictynidae (6)	
Dictynidae sp. 1	1
Subtotal Dictynidae	1
Dysderidae (7)	
Dysdera fuscipes Simon, 1882	1
Subtotal Dysderidae	1
Gnaphosidae (2)	
Drassodes lapidosus (Walckenaer, 1802)	13
Drassodes sp. 1	2
Haplodrassus dalmatensis (L. Koch, 1866)	71
Haplodrassus invalidus (O. P.-Cambridge, 1872)	3
Haplodrassus severus (C.L. Koch, 1839)	15
Haplodrassus signifer (C.L. Koch, 1839)	11
Micaria pallipes (Lucas, 1846)	1
Nomisia exornata (C.L. Koch, 1839)	258
Setaphis carmeli (O. P.-Cambridge, 1872)	19
Zelotes thorelli Simon, 1914	18
Zelotes sp. 1	13
Gnaphosidae unid. immatures	64
Subtotal Gnaphosidae	488
Linyphiidae (4)	
Erigone promiscua (O. P.-Cambridge, 1873)	16
Agyneta fuscipalpa (C.L. Koch, 1836)	32
Agyneta pseudorurestris Wunderlich, 1980	1
Agyneta rurestris (C.L. Koch, 1836)	10
Oedothorax fuscus (Blackwall, 1834)	2
Ostearius melanopygius (O. P.-Cambridge, 1879)	1
Ouedia rufithorax (Simon, 1881)	1
Pelecopsis bicornuta Hillyard, 1980	3
Pelecopsis inedita (O. P.-Cambridge, 1875)	5
Pelecopsis sp.	1
Prinerigone vagans (Audouin, 1826)	11
Trichopterna cucurbitina (Simon, 1881)	2
Typhochrestus bogarti Bosmans, 1990	7
Walckenaeria dalmasi (Simon, 1914)	1
Linyphiidae immatures	19
Subtotal Linyphiidae	112
Liocranidae (2)	
Mesiotelus mauritanicus Simon, 1909	7
Subtotal Liocranidae	7
Lycosidae (2)	
Alopecosa albofasciata (Brullé, 1832)	79
Arctosa perita (Latreille, 1799)	3
Arctosa villica (Lucas, 1846)	8
Hogna radiata (Latreille, 1817)	11
Pardosa proxima (C. L. Koch, 1847)	41
Lycosidae unid. immatures	367
Subtotal Lycosidae	509
Miturgidae (2)	
Zora spinimana (Sundevall, 1833)	1
Subtotal Miturgidae	1
Oxyopidae (4)	
Oxyopes heterophthalmus (Latreille, 1804)	2
Subtotal Oxyopidae	2
Philodromidae (4)	
Philodromus sp.	17
Subtotal Philodromidae	17
Phrurolithidae (2)	
Phrurolithus nigrinus (Simon, 1878)	1
Phrurolithus sp.	1
Subtotal Phrurolithidae	2
Pisauridae (5)	
Pisaura mirabilis (Clerck, 1757)	8
Subtotal Pisauridae	8
Salticidae (4)	
Aelurillus luctuosus (Lucas, 1846)	3
Chalcoscirtus infimus (Simon, 1868)	4
Euophrys gambosa (Simon, 1868)	2
Euophrys herbigrada (Simon, 1871)	3
Evarcha jucunda (Lucas, 1846)	2
Neaetha membrosa (Simon, 1868)	9
Pellenes brevis (Simon, 1868)	21
Pellenes geniculatus (Simon, 1868)	4
Phlegra bresnieri (Lucas, 1846)	13
Salticidae unid. immatures	2
Subtotal Salticidae	63
Sparassidae (4)	
Micrommata ligurina (C.L. Koch, 1845)	1
Subtotal Sparassidae	1
Theridiidae (6)	
Asagena phalerata (Panzer, 1801)	12
Euryopis episinoides (Walckenaer, 1847)	1
Steatoda albomaculata (De Geer, 1778)	12
Subtotal Theridiidae	25
Thomisidae (1)	
Ozyptila pauxilla (Simon, 1870)	15
Xysticus bliteus (Simon, 1875)	2
Xysticus ferrugineus Menge, 1876	3
Xysticus kochi Thorell, 1872	72
Xysticus sp.	1
Thomisidae unid. immatures	12
Subtotal Thomisidae	105
Titanoecidae (6)	
Titanoeca monticola (Simon, 1870)	1
Subtotal Titanoecidae	1
Zodariidae (7)	
Selamia reticulata (Simon, 1870)	1
Zodarion alacre (Simon, 1870)	168
Zodarion duriense Cardoso, 2003	25
Zodarion styliferum (Simon, 1870)	51
Zodarion sp.	10
Subtotal Zodariidae	255
Araneae unid. immatures	7
Total	1621

Table S2. Results of the generalized linear mixed model selection of the different components of spiders diversity considered (Response) against different crop variables in olive groves at Trás-os-Montes. The full and the optimal model (in bold) after model selection is presented for each diversity component. Stones – number of stones/m^2; Vegetation – percentage of vegetation cover; Management – integrated vs. organic; Moisture – percentage of relative humidity; Stones|Grove – random effect component for the olive grove. Df – degrees of freedom; AIC – Akaike information criterion; Organic – organic management; IPM – integrated pest management. An asterisk indicates statistical significance at α < 0.05.

Response	Model	IV	Df	χ^2	P	**AIC**
Total spider abundance (TSA)	TSA ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	128.267	**<0.001***	850.044
		Vegetation	1	0.1242	0.725	
		Management	1	15.684	0.210	
		Moisture	1	27.519	0.097	
	TSA ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	83.038	**0.004***	845.658
Species richness (S)	S ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	60.074	**0.014***	547.030
		Vegetation	1	0.4818	0.488	
		Management	1	11.675	0.280	
		Moisture	1	0.0374	0.847	
	S ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	53.364	**0.021***	542.516
Abundance of adults (A)	A ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	38.414	0.050	722.114
		Vegetation	1	0.9124	0.340	
		Management	1	11.883	0.276	
		Moisture	1	22.204	0.136	
	AA ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	35.851	0.058	719.050
Abundance of immatures (I)	I ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	77.087	**0.005***	559.320
		Vegetation	1	0.4032	0.525	
		Management	1	0.2724	0.602	
		Moisture	1	0.0021	0.964	
	AI ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	73.745	**0.007***	554.088
Abundance of ambush hunters (AH)	AH ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 + Moisture + β_5 × (Stones|Grove)	Stones	1	0.7482	0.387	307.356
		Vegetation	1	0.2613	0.609	
		Management	1	0.7961	0.372	
		Moisture	1	17.323	0.188	
	AAH ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	0.5829	0.445	303.812
Abundance of space web builders (SpW)	SpW ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	11.217	0.290	147.544
		Vegetation	1	50.529	**0.025***	
		Management	1	0.6079	0.436	
		Moisture	1	12.245	0.268	
	ASpW ~ $\alpha + \beta_1$ × Vegetation + β_2 × (Stones|Grove)	Vegetation	1	6.2141	**0.012***	143.885
Abundance of specialists (AS)	AS ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	0.6900	0.406	469.514
		Vegetation	1	0.0104	0.919	
		Management	1	10.993	0.294	
		Moisture	1	0.6553	0.418	
	AS ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	0.4697	0.493	463.648
Abundance of sheet web builders (ShW)	ShW ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	106.402	**0.001***	334.392
		Vegetation	1	0.0036	0.952	
		Management	1	104.531	**0.001***	
		Moisture	1	57.999	**0.016***	
	Organic: AShW ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 ×Moisture + β_4 × (Stones|Grove)	Stones	1	0.004	0.948	145.258
		Management	1	1.281	0.258	
		Moisture	1	0.000	0.984	
	$AShW_{Organic}$ ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	0.045	0.832	142.651
	Integrated: AShW ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Moisture + β_4 × (Stones|Grove)	Stones	1	23.647	**<0.001***	198.699
		Management	1	0.122	0.727	
		Moisture	1	0.903	0.342	
	$AShW_{IPM}$ ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	53.952	**<0.001***	194.590
Abundance of ground hunters (GH)	GH ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	84.232	**0.004***	764.188
		Vegetation	1	0.0032	0.955	
		Management	1	0.0827	0.774	
		Moisture	1	0.4589	0.498	
	AGH ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	86.355	**0.003***	758.596
Abundance of other hunters (OH)	OH ~ $\alpha + \beta_1$ × Stones + β_2 × Vegetation + β_3 × Management + β_4 × Moisture + β_5 × (Stones|Grove)	Stones	1	0.7915	0.374	287.642
		Vegetation	1	24.038	0.121	
		Management	1	0.0007	0.978	
		Moisture	1	0.0092	0.923	
	AOH ~ $\alpha + \beta_1$ × Stones + β_2 × (Stones|Grove)	Stones	1	0.6255	0.429	284.140

Table S3. Statistics of the optimal generalized linear mixed models of the different components of spiders diversity considered (Response) against different crop variables in olive groves at Trás-os-Montes. Estimate – coefficients derived from the regression; SE – standard error of the estimates; Stones – number of stones / m^2; Vegetation – percentage of vegetation cover; Stones|Grove – random effect component for olive grove. Organic – Organic management; IPM – Integrated Pest Management. An asterisk indicates statistical significance at α < 0.05 for the target within-grove explanatory variables.

Response	Final model	IV	Estimate	SE	Z-value	P
Total spider abundance (TSA)	TSA ~ Stones + (Stones|Grove)	Intercept	225.643	0.134	16.810	<0.001
		Stones	0.0165	0.006	2.880	**0.004***
Species richness (S)	S ~ Stones + (Stones|Grove)	Intercept	157.343	0.064	24.460	<0.001
		Stones	0.00613	0.003	2.310	**0.021***
Abundance of adults (A)	A ~ Stones + (Stones|Grove)	Intercept	208.509	0.084	24.960	<0.001
		Stones	0.00667	0.004	1.890	0.058
Abundance of immatures (I)	I ~ Stones + (Stones|Grove)	Intercept	0.3109	0.393	0.790	0.429
		Stones	0.0451	0.017	2.720	**0.007***
Abundance of ambush hunters (AH)	AH ~ Stones + (Stones|Grove)	Intercept	–0.4861	0.366	–1.330	0.180
		Stones	0.0117	0.015	0.760	0.450
Abundance of space web builders (SpW)	SpW ~ Vegetation + (Stones|Grove)	Intercept	–0.59737	0.394	–1.520	0.129
		Vegetation	–0.01937	0.008	–2.490	**0.013***
Abundance of specialists (AS)	AS ~ Stones + (Stones|Grove)	Intercept	0.7411	0.384	1.930	0.054
		Stones	–0.0201	0.029	–0.690	0.493
Abundance of sheet web builders (ShW)	$ShW_{Organic}$ ~ Stones + (Stones|Grove)	Intercept	–0.59726	0.305	–1.960	0.051
		Stones	0.00226	0.011	0.210	0.832
	ShW_{IPM} ~ Stones + (Stones|Grove)	Intercept	–0.5445	0.209	–2.600	0.009
		Stones	0.0647	0.009	7.350	**<0.001***
Abundance of ground hunters (GH)	GH ~ Stones + (Stones|Grove)	Intercept	165.194	0.174	9.510	<0.001
		Stones	0.02169	0.007	2.940	**0.003***
Abundance of other hunters (OH)	OH ~ Stones + (Stones|Grove)	Intercept	–0.50547	0.211	–2.400	0.016
		Stones	0.00688	0.009	0.790	0.429