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ORIGINAL ARTICLE

Structure of canopy and ground-dwelling arthropod communities in olive orchards is determined by the type of soil cover

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Abstract. The intensification of agriculture in olive groves, especially the modification or elimination of spontaneous vegetation, alters the relationships in arthropod communities and reduces their interactions and ecosystem services. This study was carried out in nine olive groves in which there was either a planted cover crop, spontaneous cover crop or bare ground. The interactions of ground-dwelling, canopy and flying arthropods in trophic webs were calculated for each olive grove soil management regime at the family level taking into consideration their different functional traits: feeding guilds, specific agricultural traits and trophic level. Olive groves with spontaneous cover had trophic webs with a higher number of plausible links between arthropod families and a more balanced distribution of specimens among trophic levels compared to those with planted cover and bare ground. There was a similar number of arthropod families consisting of both pests and their natural enemies in the planted cover regime, while olive groves with bare ground had simpler trophic webs. The complexity of plausible trophic links was greater in olive groves with spontaneous plant cover despite the similar values for family richness in the three-olive grove soil management regimes. Qualitative values (such as functional traits) were more diverse in agroecosystems with spontaneous plant cover in which there were more sources of food.

INTRODUCTION

Agricultural intensification includes practices, such as, the use of synthetic fertilisers and pesticides, increases in the size of fields, removal of hedgerows and woodlands and the intensification of tillage, which has led to a decline in biodiversity in cropping system and surrounding areas (McLaughlin & Mineau, 1995; Médiène et al., 2011). Perhaps of more concern is the consequences of the loss of biodiversity for ecosystem functioning and services (Naeem et al., 1994; Loreau et al., 2001). The loss of biodiversity in agroecosystems is, directly or indirectly, related to the reduction of ecosystem services in terms of pollination (Kremen et al., 2002), carbon sequestration (Kazemi et al., 2018), increases in soil erosion (Bender et al., 2016) and appearance and prevalence of pests (Karamaouna et al., 2019).

One example of agricultural intensification concerns olive groves, which led to the removal of ground vegetation (Weissteiner et al., 2011). The negative effects of olive growing detected in the Mediterranean basin include soil erosion, loss of biodiversity, overexploitation of water resources and water pollution (Gómez-Limón et al., 2012; Romero-Gámez et al., 2017). However, the use of environmentally friendly systems (zero chemical weeding, less use of synthetic pesticides and fertilizers and application of environmentally-friendly ground vegetation management) are also spreading in Mediterranean Europe resulting in considerable benefits in terms biodiversity and soil loss (Berg et al., 2018; Camarsa et al., 2018; De Luca et al., 2018).

Over the last decade an increasing number of farmers have avoided using herbicides in order to maintain a cover crop and prevent soil erosion in woody crops, such as olive groves (Gómez et al., 2009) and vineyards (Irvin et al., 2016). Also, the common farming policy regulations in Europe have included mandatory requirements to increase the ground cover in olive groves when the slopes are steeper than 15% (MAPAMA 2017). Nonetheless, olive groves are commonly treated continuously with herbicides (Pleguezuelo et al., 2018).

Despite continuous applications of herbicides, recent studies have shown that herbaceous cover crops in olive groves actually has a positive effect on the abundance and species richness of birds (Castro-Caro et al., 2015), lizards (Carpio et al., 2017) and arthropods (Paredes et al., 2013; Cárdenas et al., 2015; Gómez et al., 2018; Carpio et al., 2019; Benhadi-Marín et al., 2020). Also, plant cover in olive groves is known to increase interactions between flora and fauna due to the improvement in structural complexity (Rosas-Ramos et al., 2019). In this sense, the preservation of ecological infrastructures is important for maintaining ecosystem functions and delivering ecosystem services, such as pollination and biological control, which largely determine food security (including food availability, access, utilization and stability) and agricultural productivity (Rosas-Ramos et al., 2018). Arthropod communities provide essential and related ecosystem services, such as nutrient cycling, pollination, biological control and seed dispersal (Kremen & Chaplin-Kramer, 2007). The differences in arthropod communities depending on the presence/absence of cover in olive groves are not only limited to the numbers of some taxa. Carpio et al. (2019) found differences in species composition of arthropod communities related to the presence/absence of spontaneous vegetation, in the most diverse communities in agroecosystems with cover of vegetation. Álvarez et al. (2021) show how ground cover in organic olive orchards affects the interaction of natural enemies of *Prays oleae*, promoting an effective predation of their eggs.

Species' functional roles in ecosystems involve interactions among species. These interactions are usually governed by trait matching between partner species in food webs (Dehling et al., 2016). However, the conservation and promotion of diversity does not usually take into account the importance of the interactions among various groups of organisms (Moonen & Bàrberi, 2008; Bàrberi et al., 2010). Therefore, it is of great interest to quantify the structure of ecological networks (Dáttilo et al., 2019); since this can help us better understand the role of ecological interactions in maintaining biodiversity (Dáttilo & Rico-Gray, 2018). The success of the implementation and maintenance of ground cover (planted or spontaneous) in olive groves, in order to establish more complex and diverse habitats, requires a better understanding of food webs (Pywell et al., 2005; Karamaouna et al., 2019). However, little is known about the effect of ground cover on the trophic networks of arthropods and their subsequent ecosystem services in agroecosystems (but see Morente et al., 2018).

Several quantitative descriptors are used for comparing and analysing community structure, such as: the number of taxa (S), the number of trophic connections (trophic links); the ratio of the total number of links to the total number of species (link density, Bersier et al., 2002; Jiang et al., 2015), the number of actual links over the number of possible links (connectance; Martinez, 1992), the mean number of consumers per prey (vulnerability, Schoener, 1989) and the mean number of prey per consumer (generality, Schoener, 1989).

The main aim of this study is to analyse the effect of the type of soil management used in olive groves on ground-dwelling, canopy and flying arthropod communities. In this study we compare the effect of three different types of soil cover in non-organic olive groves (bare ground, planted cover and spontaneous cover) using two different approaches: (a) determining the community structure associated with each soil management regime and comparing their unweighted quantitative descriptors, and (b) identifying the type of ecosystem service provided by the arthropods recorded in each soil management system. We hypothesised that the complexity of the structure of the arthropod community (reflected in possible link density, connectance, family richness, vulnerability and generality) will be higher in the olive groves with a ground cover of spontaneously developing plants.

MATERIAL AND METHODS

Study sites and soil management regimes

Nine sites with three different soil cover management regimes were selected in Southern Spain in the province of Cordoba: three with bare ground, three with planted cover (*Bromus rubens* L. and *Anthemis arvensis*) and three with naturally developed ground cover (see Table S1 for more details). The floral composition and the differences in weed diversity in different soil covers are described in a previous study carried out at the same sites (Carpio et al., 2019, 2020). The sites are located at 37°30´– 37°58´N, 4°17´–4°56´W; between 159–369 m a.s.l., in a representative geographical range of olive groves in the Guadalquivir valley (Fig. 1). The cultivated olives trees were of medium size (3–4 m tall) and their density was between 100 and 200 trees ha^{-1}. The planting distances varies between 7 × 7 and 10 × 10 m with traditional globular shaped trees. We selected olive groves surrounded by other olive groves to prevent a border effect. The area surrounding the study sites is an olive-dominated landscape in which most of the spontaneous vegetation has been eliminated by agricultural intensification (Rey, 2011).

The greatest differences in arthropod activity and abundance occurs during the middle of May (Ruano et al., 2004; Cotes et al., 2010), the period during which the sampling was carried out in 2014. The values of mean humidity, mean temperature and

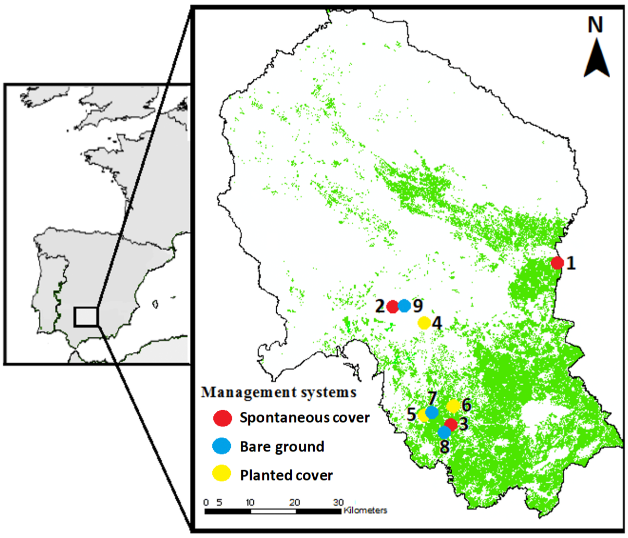

Fig. 1. Map showing the locations of the olive groves with different soil managements in the province of Cordoba (Spain). Sites studied (coloured dots) and the distribution of olive groves with spontaneous cover (red dots), bare ground (blue) and planted cover (yellow).

mean rainfall were obtained from three meteorological stations located close to the olive groves. The nine sites studied experienced the same weather conditions during the sampling period: 54.37% ± 0.95% (mean humidity ± SE), 20.56 ± 0.27°C (mean temperature ± SE) and 12.67 ± 4.31 mm (rainfall ± SE). Similar farming methods (tillage, mineral fertilization and planting using a traditional crop) were used at each site. All the olive groves received the same treatment against the olive fruit fly (comprising bait applications, with 40% dimethoate plus hydrolysed protein). Additional information about agricultural practices is presented in Table S1.

Arthropod sampling

We used three methods to sample the arthropods: pan traps, sweep netting and bait traps, which are appropriate methods for sampling ground-dwelling, canopy and flying arthropods, but not soil arthropods which were not included in this study. Each method was deployed in two transects at each site on three consecutive days. The arthropods collected on different days along the same transect were pooled in order to equate the arthropods captured in the pan and bait traps with those captured sweep netting (6 samples for each sampling method (3); 18 samples per ground management regime).

Ten pan traps were placed (spaced every 10 m) in two transects (each 90 m in length). These traps were placed above the ground and between olive trees and easily visible to ground-dwelling arthropods. The traps were made from bowls (400 ml, 110 mm in diameter, 70 mm high) made of polyethylene and painted a UV fluorescent yellow (Popic et al., 2013). To break the surface tension soapy water was added to each pan. The pans were checked and cleared of captures daily and the arthropods were transferred to plastic bottles containing 70% ethanol for transport to the laboratory. As mentioned above, the arthropods collected on different days along the same transect were pooled in order to compare the three methods.

Canopy and flower-visiting arthropods were sampled along two sweep-netting transects at each site. This was always done by the same collector (A. J. C.) for three consecutive days at each site. The sweep netting transects were 90 m in length and 5 m in width (Popic et al., 2013) and the collector sampled arthropods from all the species of plants along both transects for 1 h (each transect was sampled for 30 min). A total of 39 h was spent sweep netting. The captured arthropods were transferred to 5 ml vials for transport. As in case of the pan traps transects, the arthropods captured along the same transect on three different days were pooled for comparison with the pan trap and bait trap catches.

Bait traps were set in the same way as pan traps (two transects at each site with 10 bait traps spaced every 10 m for three consecutive days). The traps were made from 1.5 L plastic bottles (Allemand & Aberlenc, 1991), the tops of which were cut off to increase the size of the entrance (98 mm in diameter approximately) and replaced with funnels to prevent arthropods escaping. The plastic bottles were each filled with flowers from the surrounding area (mainly species belonging to the families Asteraceae, Brassicaceae and Fabaceae) and 100 ml of soapy water. The traps were collected each day and the flowers replaced daily. The arthropods caught on the different days along the same transect were pooled to allow comparison with arthropods captured by sweep netting.

Accumulation curves were plotted using the number of families recorded (Fobs) in each soil management regime in order to determine the sampling efficacy per family (Fig. S1). To avoid the edge effect (the greater vegetal complexity or simultaneous availability of one or more elements, Yahner, 1988), all the transects were > 30 m from the nearest edge, with a distance of 100 m between transects to ensure their independence and avoid pseudoreplication. See Castro et al. (2017) for more details of each of these sampling methods.

Arthropod identification

The specimens captured were identified to family using a binocular microscope (Nikon SMZ-U) and several taxonomic keys (Dindal, 1990; Goulet & Huber, 1993; Barrientos, 2004; Chinery, 2005). In addition, the families of the arthropods captured were classified based on their functional traits: feeding guilds (phytophagous, predator, omnivorous, detritivores, fungivores, necrophagous, parasitoids and microbivores); specific agricultural traits (pest, natural enemies of pests (which includes predators and parasitoids), decomposer, pollinator and "no data") and trophic level (basal, intermediate and top predator/parasitoid). These classifications were based on the available literature (Table S2). However, in some cases the information was not sufficient or reliable and the families were classified as "no data" for their specific agricultural traits. Mean and total abundance were calculated for all of these categories for each functional trait and management regime.

Data analysis

PERMANOVA

In order to test for dissimilarity in the arthropod functional traits (feeding guilds, specific agricultural trait and trophic level) at the community level in the different soil management regimes (bare ground, spontaneous and planted cover) a permutational multivariate analysis of variance (PERMANOVA) was used. Type III Sum of Squares was used since it is appropriate in the case of an unbalanced design. In order to increase the power and precision of the analysis (Anderson et al., 2008) all tests were based on 9999 permutations. When the main test showed significant differences, a posteriori pair-wise test was performed with 9999 permutations. The permutation approach has the advantage that it is "distribution free" and not constrained by the typical assumptions of parametric statistics (Walters & Coen, 2006). PERMANOVA was done using the PRIMER v6 computer programme (Clarke & Gorley, 2006), including the PERMANOVA+ add-on package (Anderson et al., 2008).

Generalized linear mixed models

In order to determine the relationships between each type of olive grove regime (bare ground, spontaneous cover crop or planted cover) and sampling method (bait traps, pan traps and sweep netting), and the abundance and richness of the different specific functional traits, 8 generalized linear mixed models were developed (four for abundance and four for family richness). The soil management regimes (three levels) and sampling methods (three levels) were added as fixed factors, whereas the site (nine levels) was considered as a random factor. Poisson distribution and the log-link function were used in these models. Fisher's least significant difference test (LSD test) for comparisons of the estimated means within a mixed analysis was used to check for differences between the three levels of treatment and sampling methods. Statistical analyses were done using InfoStats software (Balzarini et al., 2002).

Community structure and quantitative descriptors

Community structure for each olive grove soil management regime was determined using the trophic level functional trait (Table S2). An s-by-s predation matrix (Bersier et al., 2002) was used to calculate six quantitative descriptors (Bersier et al., 2002; Morente et al., 2018): the number of taxa in a community or family richness (S), possible link density (LDq´), connectance (Cq´), vulnerability (Vq´), generality (Gq´) and number of plausible trophic links (L). Since we did not determine the trophic relationships in the field, the trophic links are classified as "plausible" or "possible" since they are described in other studies (see Table S2). The family richness (S) describes the number of different families of arthropods or richness of taxa. Eight classes were described for feeding guilds' functional traits: phytophagous, predators, omnivorous, detritivore, fungivores, necrophagous, parasitoid and microbivores. The link-density is defined as being equal to the ratio of the total number of links to the total number of species (Bersier et al., 2002; Jiang et al., 2015). The connectance is defined as the number of actual links over the number of possible links, including cannibalistic loops (Martinez, 1992). Vulnerability and generality are defined as the mean number of consumers per prey, and the mean number of different prey**s** per consumer, respectively (Schoener, 1989). Vulnerability and generality are usually positively correlated (Schoener, 1989) and there is a strong numerical response of predator guilds to prey density (Dominik et al., 2018). Finally, the number of trophic links is the number of connections present in a trophic network. This is considered to be an indicator of the complexity of trophic webs (Torres-Campos et al., 2020).

To establish trophic relations between families we used an s-by-s predation matrix (Bersier et al., 2002; Morente et al., 2018). In this matrix, the trophic relation between two taxonomic groups (taxon *j* and taxon *i*, for example) was scored as 1 if taxa *j* preyed or parasitized taxa *i* ($a_{ij} = 1$), and as 0 ($a_{ij} = 0$) if the relationship was different (Morente et al., 2018). These trophic relationships were based on the literature (see Table S2). The rare families, which are those with fewer than 5 individuals, were not included in the s-by-s matrix unlike Magurran (2004) in which rare is 10 or fewer individuals. The rare families are presented in Tables S3, S4 and S5 for spontaneous cover, planted cover and bare ground, respectively.

RESULTS

Abundance and diversity

A total of 2863, 2503 and 1636 arthropods were caught in the olive groves with planted, spontaneous and bare ground cover, respectively (excluding rare families and soil fauna). Of these arthropods 3802 were caught by pan traps, 2478 by sweep netting and 722 by baited traps. The specimens were classified into 233 families and 21 orders: Araneae, Coleoptera, Collembola, Dermaptera, Diptera, Embioptera, Hemiptera (Homoptera and Heteroptera suborders separately), Hymenoptera, Isopoda, Ixodida, Prostigmata, Lepidoptera, Gamasida, Neuroptera, Orthoptera, Pseudoscorpionida, Psocoptera, Raphidioptera, Thysanoptera, Trombidiformes and Thysanura. Typical orders of soil fauna (Collembola, Gamasida, Isopoda, Prostigmata and

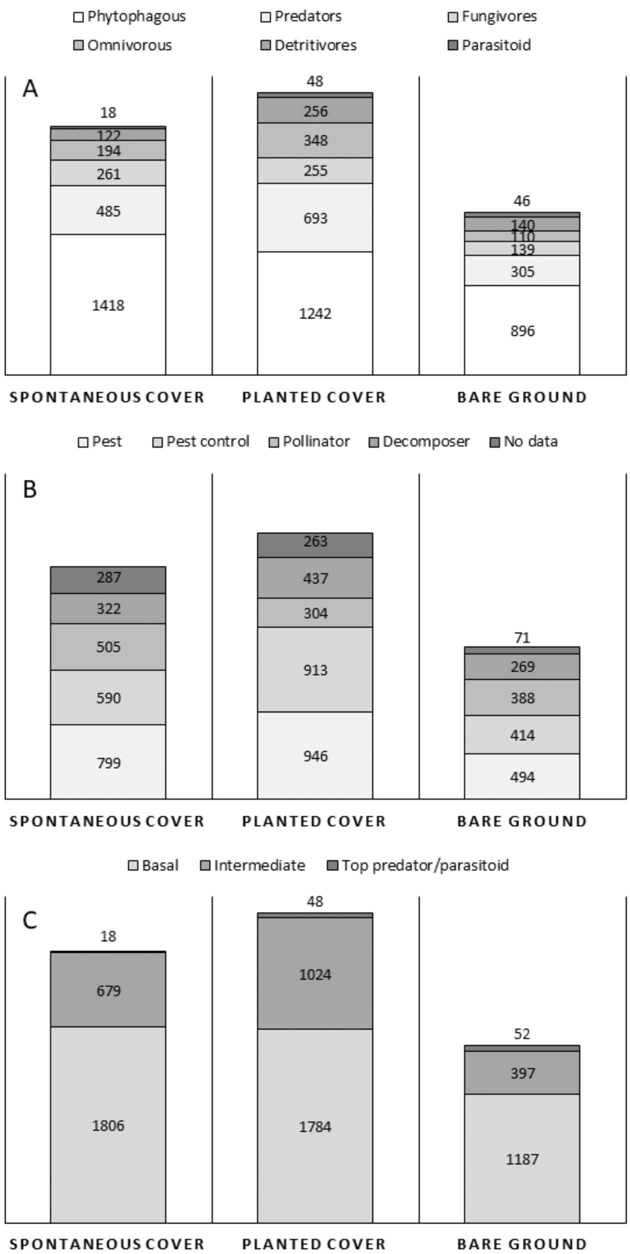

Fig. 2. Total abundance of different functional traits of feeding guilds (A), specific agricultural trait (B) and trophic level (C) in spontaneous cover, planted cover and bare ground managements regimes. Microbivores, necrophagous and parasitoids are not shown due to the low numbers caught.

Table 1. Arthropods caught, mean, abundance, family richness and number of rare and soil fauna families caught in each olive grove soil management regime using different sampling methods.

Soil management regime	Sampling method	Total arthropods caught	Mean abundance ± SE	Family richness	Rare families (fewer than 5 individuals)	Soil fauna families
Spontaneous cover	Pan traps	1435	26.57 ± 3.64	44	36	5
	Sweep netting	850	15.74 ± 2.17	40	27	1
	Baited traps	218	4.03 ± 0.56	20	11	3
Planted cover	Pan traps	1570	26.16 ± 6.09	47	27	4
	Sweep netting	988	16.46 ± 4.69	44	36	0
	Baited traps	305	5.05 ± 1.63	31	7	0
Bare ground	Pan traps	797	14.23 ± 2.81	47	24	2
	Sweep netting	640	11.49 ± 3.43	42	24	0
	Baited traps	199	3.55 ± 1.10	24	8	2

Table 2. Results of PERMANOVA and pair-wise tests of each functional trait studied in each soil cover management regime.

Differences in family composition – Main results	d.f.	MS	Pseudo-F	P
Soil management regime	2	4960	1.854	0.016
Residual	51	2675.4		
Total	53			
Families – Pair-wise tests	t		P	
Planted cover, Bare ground	1.092		0.271	
Planted cover, Spontaneous cover	1.473		0.025	
Bare ground, Spontaneous cover	1.498		0.018	
Differences in the compositions of the feeding guilds – Main results	d.f.	MS	Pseudo-F	P
Soil management disturbance regime	2	503.04	0.93843	0.4629
Residual	51	536.05		
Total	53			
Differences in the composition of specific agricultural traits – Main results	d.f.	MS	Pseudo-F	P
Soil management regime	2	877.33	2.363	0.042
Residual	51	371.35		
Total	53			
Differences in the composition of specific agricultural traits – Pair-wise tests	t		P	
Planted cover, Bare ground	1.734		0.038	
Planted cover, Spontaneous cover	0.544		0.795	
Bare ground, Spontaneous cover	2.000		0.010	
Differences in composition in terms of trophic level – Main results	d.f.	MS	Pseudo-F	P
Soil management regime	2	329.51	1.785	0.150
Residual	51	184.57		
Total	53			

Pseudoscorpionida) were not included in the analyses. We considered those taxa for which fewer than 5 individuals were caught as rare, as mentioned above. In olive groves with spontaneous cover, 126 families (54 excluding rare families and soil fauna) were recorded, 125 in those with planted cover (60 excluding rare species and soil fauna) and 103 in olive groves with bare ground (56 excluding rare species and soil fauna). The number of rare families and typical orders of soil fauna caught by each sampling method in the three different soil cover regimes are shown in Table 1.

Phytophagous arthropods were the most abundant guild followed by predators, fungivores, omnivores and detritivores in all three soil management regimes (Fig. 2A). When aggregated in terms of specific agricultural traits, the two most abundant groups were pests and their natural enemies in all three soil management regimes, followed by decomposers in the planted cover management regime and

Table 3. Results for abundance of Specific agricultural traits (Model 1–4). Coefficients for the level of fixed factors were calculated using the reference values of the "Planted cover" in soil cover management regimes and "Baited traps" in sampling methods.

Specific agricultural traits – Model 1: Pests				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Soil management regime	61.7	<0.0001	2	Bare ground: –0.59 ± 0.05 Spontaneous cover: –0.11 ± 0.05
Sampling methods	247.3	<0.0001	2	Sweep netting: 1.61 ± 0.08 Pan traps: 1.61 ± 0.08
Specific agricultural trait – Model 2: Decomposers				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Soil management regime	20.4	<0.0001	2	Bare ground: –0.48 ± 0.08 Spontaneous cover: –0.28 ± 0.07
Sampling methods	369.1	<0.0001	2	Sweep netting: 0.15 ± 0.14 Pan traps: 2.22 ± 0.11
Specific agricultural trait – Model 3: Natural enemies of pests				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Soil management regime	88.1	<0.0001	2	Bare ground –0.73 ± 0.06 Spontaneous cover –0.39 ± 0.05
Sampling methods	378.4	<0.0001	2	Sweep netting: 0.35 ± 0.07 Pan traps: 1.45 ± 0.06
Specific agricultural trait – Model 4: Pollinators				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Soil management regime	20.6	0.0064	2	Bare ground: 0.20 ± 0.07 Spontaneous cover: 0.45 ± 0.07
Sampling methods	252.1	<0.0001	2	Sweep netting: 3.62 ± 0.21 Pan traps: 2.62 ± 0.2

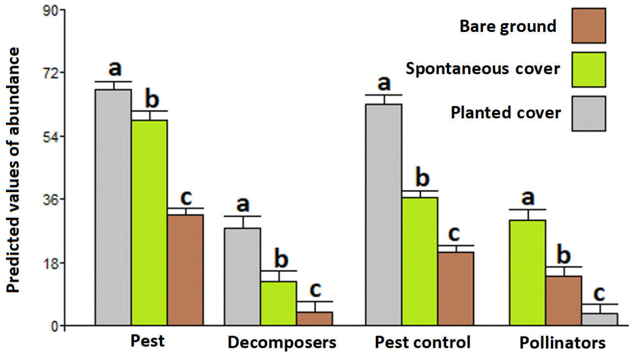

Fig. 3. Abundances of specific agricultural traits. Predicted mean values (± S.E.) of abundance for the different categories of specific agricultural traits: pest, decomposer, pest control agents and pollinator families in olive groves with different soil management regimes. Lower case letters indicate significant differences ($p < 0.05$) among regimes based on Fisher LSD tests.

pollinators in the spontaneous and bare ground soil cover management regimes (Fig. 2B). Finally, the relative abundances of the different trophic level categories were the same in all three soil cover managements: 'basal' arthropods were the most abundant followed by 'intermediate' and 'top predators/parasitoids' (Fig. 2C).

Community composition

The main results of the PERMANOVA were the statistically significant differences in the compositions of the communities in different soil management regimes in terms of families and specific agricultural traits (Table 2). However, the composition of communities according to feeding guilds and trophic level did not differ in the three soil management regimes (Table 2).

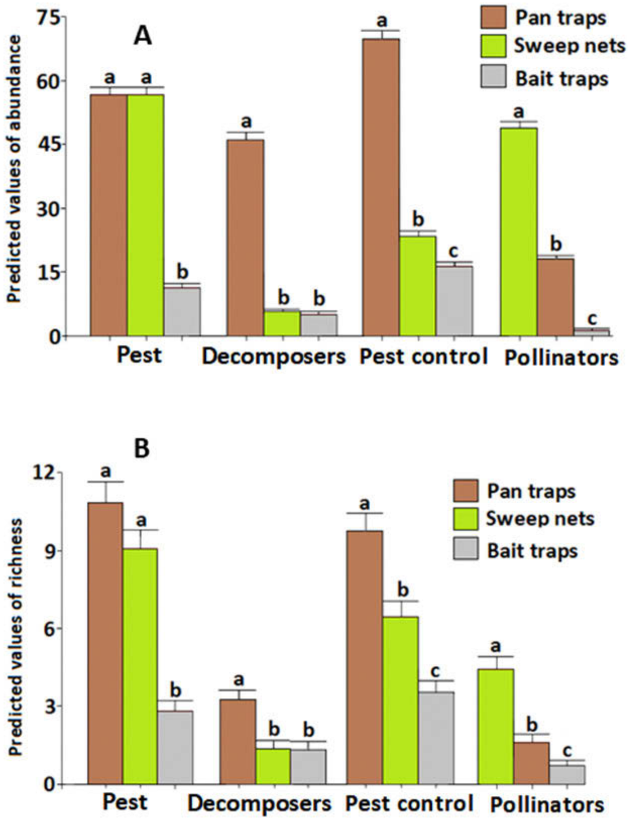

Fig. 4. Abundances of specific agricultural traits. Predicted mean values (± S.E.) of abundance (A) and family richness (B) according to sampling method for the different categories of specific agricultural traits: pest, decomposer, natural enemies of pests and pollinator families in olive groves with different soil management regimes. Lower case letters indicate significant differences ($p < 0.05$) among regimes based on Fisher LSD tests.

Table 4. Results for family richness of Specific agricultural (Model 5–8) traits. Coefficients for the level of fixed factors were calculated using the reference values of the "Planted cover" in soil cover management regimes and "Baited traps" in sampling methods.

Specific agricultural trait – Model 5: Pests				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Management regime	10.09	<0.001	2	Bare ground: 0.08 ± 0.13 Spontaneous cover: 0.48 ± 0.12
Sampling method	37.92	<0.0001	2	Sweep netting: 1.17± 0.16 Pan traps: 1.35±0.16
Specific agricultural trait – Model 6: Decomposers				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Management regime	0.40	n.s.	2	Bare ground: –0.03 ± 0.24 Spontaneous cover: 0.16 ± 0.23
Sampling method	9.87	<0.001	2	Sweep netting: 0.04± 0.29 Pan traps: 0.88±0.24
Specific agricultural trait – Model 7: Natural enemies of pests				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Management regime	2.27	n.s.	2	Bare ground –0.24 ± 0.13 Spontaneous cover –0.23 ± 0.13
Sampling method	24.77	<0.001	2	Sweep netting: 0.6± 0.16 Pan traps: 1.01±0.15
Specific agricultural trait – Model 8: Pollinators				
Variable	Z-Value	p-value	DF	Estimate ± S.E.
Management regime	2.44	n.s.	2	Bare ground: –0.39 ± 0.22 Spontaneous cover: 0.41 ± 0.22
Sampling method	24.98	<0.001	2	Sweep netting: 1.83± 0.30 Pan traps: 0.84±0.33

Table 5. Quantitative descriptors of community structure for each olive grove soil management regime.

	Spontaneous cover	Planted cover	Bare ground
Family richness (S)	54	57	55
Plausible trophic links (L)	358	337	189
Plausible link density (LDq´)	6.63	5.91	3.44
Connectance (Cq´)	0.12	0.10	0.06
Vulnerability (Vq´)	6.88	6.02	3.50
Generality (Gq´)	18.50	14.65	9.95
Top families (T)	2	1	1
Intermediate families (I)	18	22	18
Basal families (B)	34	34	36

Based on the compositions in terms of arthropod families, planted cover and bare ground did not differ significantly (Table 2). However, spontaneous cover differed significantly in terms of arthropod composition from that recorded for the sites with planted cover and bare ground (Table 2). Different results were obtained using PERMANOVA and specific agricultural traits. Spontaneous and planted cover sites had a similar composition of specific agricultural traits, while those with bare ground differed significantly from those with planted and spontaneous cover (Table 2).

DIFFERENCES IN THE NUMBERS OF FUNCTIONAL TRAITS

The four generalized linear mixed models revealed significant differences in the abundance of each category of functional trait studied (Table 3). For specific agricultural traits, the same results were obtained for the numbers of pests, decomposers and number of natural enemies of pests (Fig. 3). The numbers of these three functional traits were significantly different in the three ground management regimes, they were greater under planted cover followed by spontaneous cover and bare ground (Fig. 3). However, in the case of number of pollinators, the greatest number was recorded for spontaneous cover, followed by bare ground and planted cover, respectively (Fig. 3).

In the case of the sampling method, there were significant differences between the three sampling methods in terms of the number of specific agricultural traits (Table 3). For decomposers and natural enemies of pests, pan traps caught significantly more individuals, while in terms of pollinators, sweep netting caught a greater number (Fig. 4A). For pests, both sweep netting and pan traps caught more individuals than bait traps (Fig. 4A).

In the four models of family richness, only pests differed significantly (Table 4). In the case of the sampling method, the three methods differed significantly in terms of the richness of specific agricultural traits (Table 4). As in the previous case, pan traps caught more families of decomposers and natural enemies of pests, while sweep netting caught more families of pollinators. For pests, both sweep netting and pan traps caught more families than bait traps (Fig. 4B).

COMMUNITY STRUCTURE AND QUANTITATIVE DESCRIPTORS

The comparison of the structures of the communities indicated that the sites with spontaneous cover had the highest values for most of the quantitative descriptors (Table 5). Specifically, the values of the number of possible links, connectance, vulnerability, generality and number of plausible trophic links were higher than in the planted cover and bare ground regimes (Table 5). In addition, a higher number of families in the top predator level was recorded for sites with spontaneous cover, whereas sites with planted cover had the highest number of taxa and arthropods in families at the intermediate level (Table 5). Sites with bare ground had the highest number of families at the basal level (Table 5).

Community structure associated with spontaneous cover

The community structure recorded in olive groves with spontaneous ground cover had two top taxa belonging to the order Hymenoptera (Sphecidae and Ichneumonidae), 18 intermediate taxa and 34 basal taxa (Table 5). Among the top taxa, there were two different feeding guilds of wasps: parasitic wasps (Ichneumonidae) and predatory wasps specialized in hunting spiders (Sphecidae). The intermediate level in spontaneous cover is dominated by predators, as 13 of the 18 taxa are predators while the remaining families belong to omnivorous and parasitic feeding guilds. In terms of numbers caught, this level was dominated by Aeolothripidae (Thysanoptera) followed by Formicidae (Hymenoptera) and Staphylinidae (Coleoptera) (Table S3). The main feeding guild at the basal level was phytophagous (but bear in mind this feeding group is composed of xylem and phloem feeders, pollinators and leaf feeders), with a minimal representation of fungivores and detritivores. In terms of numbers the most important orders were Hymenoptera (Apidae and Halictidae) and Homoptera (Adelgidae, Aphididae and Cicadellidae) (Table S3).

Community structure associated with planted cover

The community structure in olive groves with planted cover had just one taxon at the top level (Hymenoptera: Ichneumonidae), 22 families at the intermediate level and 34 families at the basal level (Table 5). Most of the taxa recorded at the intermediate level belonged to the predator-feeding guild (17 families, Table 5). However, in terms of numbers, the dominant feeding guild was omnivorous due to the high abundance of Formicidae (Hymenoptera) and Muscidae (Diptera) belonging to this feeding group (Table S4). At the basal level there were 34 phytophagous families and taxa with mainly detritivore and fungivore diets. The high number of nymphs of Homoptera makes them the dominant group in this soil management regime (Table S4).

Community structure associated with bare ground

The top level in the bare ground regime consisted of Ichneumonidae (Hymenoptera), which are parasitic. At the intermediate level there were 18 families (Table 5), belonging to a wide variety of feeding guilds (predators, parasitoids and omnivores). The family Aeolothripidae (Thysanoptera) has a relevant role at this level in terms of abundance. At the basal level there were 36 families (Table 5). Phytophagous families dominated at this level, but other feeding guilds are more important than in the other soil management regimes, such as fungivores (Sciaridae, Mycetophilidae and Phlaeothripidae).

DISCUSSION

Our results show that soil management in olive groves that results in a highly complex and structured diversity of herbaceous plants support the most diverse and interconnected arthropod communities. As previous studies describe (Landis, 2016; Gómez et al., 2018; Rosas-Ramos et al., 2018; Gonçalves et al., 2020), spontaneous cover provided the most diverse ecological niches and food resources for arthropods. Our study shows that the different soil cover managements favour arthropods with different functional traits.

In relation to the composition of the communities, PERMANOVA indicates differences between spontaneous cover and the other two soil management regimes. The main difference is the high abundance of Apidae recorded in spontaneous cover compared with planted and bare ground regimes, which is due to the strong relationship of this family with flowering plants (Goulet & Huber, 1993). The results for pollinator abundances agree with those recorded by Nicholls & Altieri (2012), who report that the removal of the cover crop (by tillage or herbicides) severely affects pollinator populations. One of the advantages of spontaneous cover is the presence of a great diversity of species of weeds (for more details on the floristic composition, see Carpio et al., 2020) with different phenologies that provide food for a greater variety of pollinators in different seasons (Willmer, 2011). On the contrary, in olive groves with bare ground weeds are scarce and, consequently, there are few or no food resources for pollinators (Nicholls & Altieri, 2012). Pott et al. (2006) have shown that the habitat characteristics associated with structuring of pollinator communities are floral diversity, floral abundance, nectar availability and the variety of sources of nectar. These environmental characteristics are very scarce in olive groves with bare ground and, to a lesser extent, in those with planted cover (Carpio et al., 2019) and could be the reason why the abundance of pollinators was less in these soil cover regimes. Pollinator abundances were higher in spontaneous soil cover regimes because of their dependence on floral resources. A previous study carried out at some of the same sites (Carpio et al., 2019) reports a high plant biodiversity in the spontaneous soil cover regime, which could result in a greater diversity of pollinators.

However, not all arthropod taxa and functional groups respond in the same way to plant heterogeneity (Dominik et al., 2018). Contrary to what might be expected, the abundance of insects that control pests was greater in planted cover than spontaneous cover regimes. The planted cover benefited parasitoids and predators, which depend also on the presence/abundance of their host and prey (Álvarez et al., 2021). However, this is a general observation based on identification of arthropods at family level and different species in the same family could respond differently to the same soil cover management.

Previous studies report a large positive effect of adjacent ground cover on parasitic Hymenoptera (Boccaccio & Petacchi, 2009; Rodríguez et al., 2012; Paredes et al., 2013), since it provides food resources, shelter and breeding sites (Landis et al., 2000). However, in our study we found no evidence of the beneficial effects of spontaneous cover on the percentages and total numbers of parasitoids. Menalled et al. (1999) also do not report differences in parasitoid populations according to landscape complexity. In our case, the absence of differences in parasitoid numbers in the three soil cover management regimes is possibly due to the homogenised surrounding landscape, since the sites were located in an olive-dominated landscape, where agricultural intensification has eliminated spontaneous vegetation.

It is remarkable that a high percentage of the predators recorded in spontaneous and planted cover regimes (see Tables S3 and S4) belonged to the Aeolothripidae (Thysanoptera). This family includes both phytophagous and predatory species (Mound et al., 1976), which indicates the problem posed by the level of taxonomic resolution. Among the predators collected in planted cover regimes those belonging to the Empididae (Diptera) were the most numerous. This could be due to a high abundance of aphids (Bortolotto et al., 2016; Pfister et al., 2017), which were numerous in this soil cover regime. The Coleoptera were well represented among the predators in the spontaneous cover regime, which supports the bioindicator role of this order in the evaluation of olive-orchard management regimes (Ruano et al., 2004). The ecological infrastructures present in Mediterranean groves with vegetation, such as hedges or strips of vegetation enhance the populations of important predator groups such as spiders (Rosas-Ramos et al., 2018). Spiders were the second most numerous group of predators recorded in planted cover regimes and they are described as the dominant predator group on the ground and in the canopies of olive groves (Morris et al., 1999; Picchi et al., 2016, 2020) and the increase in ecological infrastructures, depends on the number of species, spider guilds and body size (Rosas-Ramos et al., 2018). However, the low number of spiders in the total number of predators in the three soil cover regimes contrasts with the results of these authors.

The high abundance of arthropod considered to be pests in olive groves with planted cover consists mainly of Hemiptera (Miridae, Aphididae and nymphs of unidentified Homoptera). Gratton & Denno (2003) describe the effect of plant resources in terms of bottom-up (host plants can affect herbivores directly by determining their performance and survival) or top-down (predatory effects of natural enemies) effects. In our case, *Bromus rubens* does not appear be the host plant of any of the families mentioned above, so that a monospecific plant cover and phytophagous families could be indirectly related to seasonal shifts in bottom-up and top-down effects (Gratton & Denno, 2003). The high abundance of aphids recorded in the planted cover regime (but also in the spontaneous and bare ground regimes) could be related to the biological characteristics of this taxon, such as high reproductive rates and passive windborne dispersal (Sorensen, 2009). On the other hand, the low numbers of pest arthropods recorded in the bare ground regime might be due to its reduced food and shelter availability (Nicholls & Altieri, 2012). This result is in accordance with observations of Shi et al. (2013) who suggest that the relationship between two adjacent trophic levels is stronger than that of two nonadjacent trophic levels.

Regarding decomposers, there were differences between the three management regimes and were particularly numerous in olive groves with planted ground cover. Gonçalves et al. (2020) show that ground cover significantly enhance**s** the activity density of detritivores in vineyards. The higher abundance of detritivores in planted cover treatments might be related to the possibility of these specimens feeding on organic residues of the plants planted. The leaf litter they produce could provide food for detritivores, thus also enhancing their abundance (Roger-Estrade et al., 2010).

In relation to the effectiveness of the sampling methods, the results indicate that pan traps are the most effective in terms of high representativeness of abundance and family richness of pests, decomposers and natural enemies of pests. These results complement the statements of Nielsen et al. (2011) and Spafford & Lortie (2013) who indicate that pan traps are highly effective for determining arthropod species richness. However, sweep netting has proven to be the most effective method for obtaining representative data on the abundance and family richness of pollinator insects despite the fact that this method has a high level of bias (Westphal et al., 2008).

The descriptors studied other than number of taxa (S) show similar trends: higher values in spontaneous cover compared with bare ground, with the values recorded in planted cover in between. Despite the similar incidence of S in the three-olive grove soil management regimes, we recorded more complex, diverse and connected trophic webs in spontaneous cover regimes. The beneficial effects of spontaneous cover are especially marked when comparing the quantitative descriptor values in the bare ground regime. These results indicate an inverse relationship between the intensity of the cover management and the number of plausible trophic links as is also reported by Torres-Campos et al. (2020), who report that the complexity of trophic webs decreased from olive groves with spontaneous cover to those with bare ground.

The plausible trophic links in a community occur between species that are assembled in pairs (Torres-Campos et al., 2020) and consequently an increase in the number of species does not always enhances connectance. Our results indicate that the variation in connectance and number of plausible links respond more to qualitative (who's there?) than quantitative characters (how many are there?).

In addition, the olive groves with spontaneous cover crops had a higher value of connectance in their trophic webs and diversity and complexity when they are compared with those with planted cover and bare ground. Previous studies indicate that connectance is inversely related with the richness of species (Schoenly et al., 1991; Banašek-Richter et al., 2009). However, our results do not support this statement and are more in accordance with those of Morente et al. (2018) who report that connectivity values are independent of the S values. Our results also agree with those of Torres-Campos et al. (2020) who maintain that adding species to ecosystems increases the number of potential trophic interactions, but not necessary their occurrence. Other authors report a positive relation between connectance of trophic webs and structural complexity of ecosystems (Beckerman, 2006; van Altena et al., 2016) confirming the notion of 'complexity begets stability'. As mentioned above, vulnerability and generality are usually positively correlated (Schoener, 1989) as recorded in this research. As for other community structure quantifiers, the lowest values were recorded in olive groves with bare ground. Both quantifiers are closely related to the diversity of shelters, ecological niches and food availability (Gómez et al., 2018; Rosas-Ramos et al., 2018). The higher structural complexity of spontaneous cover provides a greater availability of these environmental resources compared with bare ground, which has a direct effect on vulnerability and generality.

In conclusion, arthropod families differing in functional traits respond differently to the different olive grove soil cover regimes. As expected, the diversity of food resources in spontaneous cover enhances the abundances and diversity of pollinators. The low diversity of plants in planted cover favoured the arthropods capable of exploiting this resource. The complexity of trophic webs (in terms of the values of quantitative descriptors) decreased with increase in plant diversity. This is in accordance with our hypothesis predicting a greater complexity in olive groves with spontaneous cover than in those with bare ground. On the other hand, the values recorded for the quantitative descriptor, S, were similar in the different soil management regimes, which indicates that the complexity of trophic webs is more dependent on the qualitative characteristics of the members of the community than their quantitative values.

However, these conclusions have to be treated with caution because we only identified the insects to family level. In some cases, species may differ from the majority of the family members in terms of their trophic group or preference for a particular type of food, especially in the case of spiders for which the family level does not best explain their trophic interaction. Furthermore, trophic interactions vary seasonally, so the arthropod communities and the trophic webs may be affected by environmental conditions throughout the year. Also, in any future study, the strength of the links should be considered.

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STATEMENT OF AUTHORS' CONTRIBUTIONS. AJC, FST and JC conceived and designed the experiment. AJC performed the data collections. JC identified the specimens. AJC and JC analysed the data, and both wrote the first draft of the manuscript. All authors read and approved the final manuscript.

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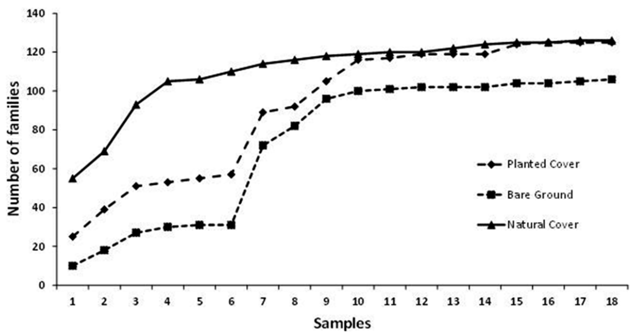

Fig. S1. Families-accumulation curves for the arthropods identified in three olive grove management regimes.

Online supplementary file:
Table S1–S5 (http://www.eje.cz/2021/017/S01.xlsx).