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Understanding the trophic relationships amongst arthropods in olive grove by δN^{15} and δC^{13} stable isotope analysis

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Abstract

So far the limited knowledge about the diet of omnivores and generalist predators in olive groves has not allowed the clarification of their role as natural enemies. Stable isotope (δN^{15} and δC^{13}) analysis is a useful tool for predicting the trophic position of a high number of species, the variety of basal resources and the flux of energy in the food web. We have explored the possible consumers of two important pests in the olive grove: adults of *Prays oleae* Bern (Lepidoptera: Praydidae) during its anthophagous generation and the pupae of *Bactrocera oleae* (Rossi) (Diptera: Tephritidae). In addition, we have included in the study the adult instar of the secondary pest *Euphyllura olivina* (Costa) (Hemiptera: Psyllidae). These arthropods were clustered in isotopic groups according to their similarities in δN^{15} and δC^{13} content assuming that, in this case, they shared similar feeding habits. Using this criterion, we obtained eight isotopically different groups of predators and eleven groups of phytophagous insects. We have used Bayesian mixing models in order to identify the potential predators of the different pests included in our study and the proportion that each pest occupied in the diet of the identified predators. Different taxa of spiders and *Anthocoris nemoralis* (Fabricius) (Hemiptera: Anthocoridae) have emerged as potential predators of *B. oleae*. Moreover, Gnaphosidae (Araneae) showed suitable isotopic characteristics to be identified as potential predator of *P. oleae* and *A. nemoralis* has been confirmed as a predator of *E. olivina*. The presence of *E. olivina* as an abundant resource encourages the settlement of natural enemies in olive orchards which feed on this secondary pest, but are also ready to feed on any insect outbreak, for example *P. oleae*.

KEYWORDS
Bactrocera oleae, *Euphyllura olivina*, food web, *Prays oleae*, predators

1 | INTRODUCTION

Biodiversity is known to promote resilience to outbreaks of pests and diseases in agroecosystems (Andow, 1991; García et al., 2018; Isbell et al., 2017; Kremen & Merenlender, 2018; Tschumi et al., 2016).

Particularly, the importance of entomophagous arthropods and parasitoids in pest population control has been widely demonstrated in cereal crops, stone and citrus fruits and vegetable crops (Dib et al., 2010; Nelson et al., 2012; Pérez-Rodríguez et al., 2019; Schmidt et al., 2003). Many factors such as environmental conditions,

agricultural practices and the behaviour of arthropods (i.e. intraguild predation or lack of migration of natural enemies from the natural vegetation to the crop) may affect the efficiency of natural pest control (Felipe-Lucia et al., 2020; Gliessman et al., 2007; Tscharntke et al., 2016). Therefore, the study of the ecology of potential natural enemies and their linkage with other organisms in the community is essential to achieve a safer and more highly effective biological pest control.

Olives are one of the most important crops in many Mediterranean countries (European Commission, 2021) and areas beyond Europe such as Africa, Australia and the Americas (Daane & Johnson, 2010). Olive groves cover 4.6 million hectares in the Mediterranean basin (EUROSTAT, 2020) promoting the loss and isolation of the natural habitats in the Mediterranean landscape (de Graaff & Eppink, 1999; Milgroom et al., 2007; Parra-López & Calatrava-Requena, 2006). These changes, along with an intensification of the production methods, have resulted in huge environmental and ecological disturbances leading to a simplification of the agroecosystem (Beaufoy & Pienkowski, 2000; Biaggini et al., 2007; Gómez Calero, 2009; Metzidakis et al., 2008). Specifically, the simplification of the communities of arthropods leads to agroecosystems dominated by a few common species and the appearance of empty niches, which together contribute to outbreaks of pests (Hillebrand et al., 2008; Matson et al., 1997; Swift & Anderson, 1994).

Arthropods are an important part of the biodiversity of olive groves (Santos et al., 2007) and form a complex structure of different functional groups including phytophagous, predators, parasitoids and detritivore species (Gonçalves & Pereira, 2012; Rodríguez et al., 2003; Ruano et al., 2004). Diptera, Hymenoptera, Coleoptera and Neuroptera have been identified as the main orders of predators in the olive tree canopy with Acari, Araneae, Ichneumonidae (Hymenoptera) and Chrysopidae (Neuroptera) being the most abundant bio-control agents (Gkisakis et al., 2020; Iannotta et al., 2007). *Bactrocera oleae* (Rossi) (Diptera, Tephritidae) and *Prays oleae* (Bern) (Lepidoptera: Praydidae) are the two most harmful pests in olive groves. The most important damage caused by these two species is related to the larva feeding on the inside of the fruit, damaging it and causing its premature fall (Molina de la Rosa et al., 2017; Ramos et al., 1998). Furthermore, *Euphyllura olivina* (Costa) (Hemiptera, Psyllidae) is a secondary pest that feeds on the flower buds impeding their development. Currently, this pest is not causing significant yield loses (Molina de la Rosa et al., 2017). Nevertheless, climate change may benefit its population growth in a future scenario, thus increasing the potential damage to olive groves (Malumphy, 2011).

Carabidae, *Tapinoma nigerrimum s.l.* (Nylander) (Hymenoptera: Formicidae), several Araneae or parasitoids such as *Psytallia concolor* (Szepligeti) (Hymenoptera: Braconidae) contribute to the population decrease in *B. oleae* (Albertini et al., 2017; Dinis et al., 2016) whilst Formicidae, *Chrysoperla carnea s.l.* (Stephens) (Neuroptera: Chrysopidae), *Xanthandrus comtus* (Harris) (Diptera: Syrphidae) and *Trichogramma cacoeciae* (Marchal) (Hymenoptera:

Trichogrammatidae) have been identified as potential natural enemies of *P. oleae* (Morris, Campos, Kidd, & Symondson, 1999; Sacchetti, 1990).

Conventionally, studies about biological control in olive groves have mainly focused on a very specific group of taxa of predators and parasitoids, addressing the temporal matching with the pests and changes in abundance (Albertini et al., 2017; Álvarez et al., 2021; Dinis et al., 2016; Morris, Campos, Kidd, Jervis, & Symondson, 1999; Sacchetti, 1990; Paredes et al., 2019). Nevertheless, the study of the trophic linkages of generalist predators with potential preys including pests may clarify their ecological role in the agroecosystem and their importance as beneficial arthropods. This approach has scarcely been addressed in olive groves with serological techniques (Morris, Campos, Kidd, Jervis, & Symondson, 1999) or DNA analysis of gut content (Albertini et al., 2018; Panni & Pizzolotto, 2018; Rejili et al., 2018) that are useful techniques to identify the feeding preferences of an individual or group of individuals over specific conditions and a specific period of time.

Alternatively, the analysis of C and N stable isotopes permit the determination of the relative dietary contributions of different food sources in multi-species communities (Ikeda et al., 2010; Mcnabb et al., 2001). In contrast to other systems, the use of stable isotopes in terrestrial insects is not widespread (Boecklen et al., 2011; Quinby et al., 2020), and, specifically, there is a limited application of the technique in agroecosystems. In recent years, C^{13} and N^{15} analyses have been used in the study of trophic linkages and the ecological role of several arthropods in crops such as ants (Mollot et al., 2014; Ottonetti et al., 2008) spiders and carabids (Mcnabb et al., 2001; Mestre et al., 2013) and ladybirds (Ostrom et al., 1997). Organisms metabolize the molecules from their diet and incorporate them into their body tissues (DeNiro & Epstein, 1976). The proportion in which these molecules are assimilated depends on the ratio of the molecules in the food web baseline and the metabolic pathways that are exposed in their assimilation (Post, 2002). Regarding carbon and nitrogen isotopes, the heavy isotopes C^{13} and N^{15} tend to be stored. N^{14} is excreted (Gannes et al., 1998) whilst the mechanism of accumulation of C^{13} is still unclear (Potapov et al., 2019). Thus, stable isotope analysis takes advantage of the differences in the ratio of heavy to light stable isotopes (C^{13}/C^{12} and N^{15}/N^{14}) such as those accumulated in the tissues. Therefore, an isotopic enrichment exists in the tissues of the consumer in relation to its diet (Ponsard & Arditi, 2000). Due to N^{15} being accumulated more quickly in every trophic change than C^{13}, it is used to establish the trophic position of the organism whilst C^{13} indicates the main basal food resource of different organisms when it changes its isotopic content (e.g. the primary consumers of C3 and C4 plants) (Post, 2002).

The isotopic content is proportional to the isotopic composition of the diet (Bearhop et al., 2004; Fernandes et al., 2014; Phillips & Gregg, 2003). The currently available Bayesian mixing models also allow the conversion of the isotopic data into estimates of food source contributions from the different resources of an animal diet (Parnell et al., 2010, 2013; Phillips, 2012; Phillips et al., 2014).

Nevertheless, a good understanding of the study system is essential before using stable isotope mixing models to determine the diet of consumers (Phillips et al., 2014).

In this study, we have used stable isotope analyses and Bayesian mixing models to: (1) identify the most probable trophic groups and the role of the most abundant arthropods that make up the food web in olive groves, (2) compare our results on feeding habits to other observational studies in literature, (3) identify from all taxa collected, the most plausible predators of the three most common and abundant olive pests (i.e. *P. oleae*, *B. oleae* and *E. olivina* (Alvarado, 2004; MAPAMA, 2014)) and (4) assess the predation pressure exerted by the identified predators on the olive pests from the percentage of the predator diet which is made up of the prey.

2 | MATERIAL AND METHODS

2.1 | Study site, collection of arthropods and taxonomic identification

The study was carried out in Granada (south-eastern Spain), one of the main provinces producing olive oil. Two commercial olive groves with centenary trees of the Lucio variety were sampled in the study. The groves were under the same environmental conditions and managed under organic practices. The ground cover was established one year before the samplings. Neither *Bacillus thuringiensis* (Berliner) nor permitted insecticides were applied during our study. The olive groves were in the peri-urban park Dehesa del Generalife. The first olive grove (37°10'36.45''N, 3°34'35.02''W, 900 m a.s.l.) had an area of 11,098 ha and was 619 m away from the second grove (37°10'17.83''N, 3°34'27.52''W, 870 m a.s.l.) with an area of 9,032 ha. Each grove was divided into two plots obtaining a total of four plots with a separation of more than 50 m between each plot (Appendix S4).

Arthropods were sampled in 2013 once a month from May to July and again in September in two strata: the olive tree canopy and the natural ground cover. According to Ruano et al., 2004, May to July cover the months where arthropods are more abundant in the olive grove. After hot summer, when the temperatures go down, the arthropod abundance gradually increases or is maintained. This should be the best moment to detect *B. oleae* predators and others as can be seen in Ruano et al., 2001. The samples were randomly collected from 20 olive trees from the above described plots. We sampled four branches per tree (one per orientation) by beating five times into a plastic bag (55 × 60 cm) (Ruano et al., 2004). The arthropods on the natural vegetation cover (in the drive rows of the grove) were sampled by a sweeping net collecting five samples per plot passing the net three times per sample. Each sweeping was ten metres from the preceding one.

The olive fruit fly (*B. oleae*) was collected as recent pupae from olives in the studied groves, as the maggot abandons the fruit to pupate in the soil in the autumn (Cavalloro & Delrio, 1975).

The samples were chilled in the field and stored at −20°C in the laboratory until analysis. Individual arthropods were separated out and identified to the lowest taxonomic level possible in collaboration with different taxonomists (Appendix S1).

2.2 | Isotopic analysis

Isotopic analyses were performed in SIRFER (Stable Isotope Analysis Service) at the University of Utah using a mass spectrometer IRMSs Delta Plus XL and Delta Plus Advantage coupled with Conflo III connected to Carlo Erba EA. The samples were kept in a laboratory oven at 60°C for 48 hr and, later, were freeze-dried and ground, thus obtaining a fine powder. 0.4 mg of freeze-dried tissue per sample was used for analysis with at least four replicates per taxon. The number of arthropods used per replicate in the analysis was dependent on the body size and the abundance of each taxon. The C^{13} signature changes faster in body fat or reproductive organs than in the metabolically inert tissues such as the exoskeleton (Gratton & Forbes, 2006). Given the impossibility of removing the abdomens in all taxa, we used whole bodies in all cases to ensure that the error produced by the faster change of C^{13} in metabolically active tissues is the same in all cases. The results were expressed in relation to a referenced standard value of the ratio of heavy to light isotope of a particular element. VPDB (Vienna Pee Dee Belemnite) for C^{13} and atmospheric nitrogen for N^{15} were used as standard values. Results were transformed to the standard notation multiplying by 1,000 to facilitate management (DeNiro & Epstein, 1976, 1981).

The synthesis and accumulation of lipids, which are depleted in the C^{13} isotope, affects the C^{13} isotopic signature of the individual generating more negative values than those from proteins or carbohydrates (DeNiro & Epstein, 1976; McConnaughey & McRoy, 1979). Thus, for animals, the C:N ratio is an indicator of the proportion of lipids in the sample. In this way, a C:N ratio lower than 4 for terrestrial animals indicates that the lipid content is low and does not affect the C^{13} signature of the individuals (Post et al., 2007).

2.3 | Statistical analysis

2.3.1 | Clustering of trophic groups

Based on the mean δC^{13} and δN^{15} values, we identified the trophic groups, that is arthropods that shared similar basal resources and trophic position (Dassou et al., 2016; Mestre et al., 2013). We performed a hierarchical agglomerative cluster analysis by Euclidean distances (Murtagh & Legendre, 2011) calculated by the dist function in R. The hclust function in R with the complete linkage as method of agglomeration was used to create the hierarchical trees (Scrucca et al., 2016). Then, trees were produced by the fviz_dend function in the factoextra R package (Kassambara & Mundt, 2017).

Cluster trees were verified by computing the correlation between the cophenetic distances and the original distance data generated by the dist() function. Correlations greater than 0.75 were regarded as valid (Alboukadel Kassambara, 2017). The analyses were performed with R version 3.5.1. (R Core Team, 2018).

## 2.3.2 | Estimation of the proportion of pest consumption

To assess the most possible contribution of the different pests to the diet of each predator, Bayesian mixing model analyses were performed with the R package MixSIAR 3.1 (Stock & Semmens, 2016). δN^{15} and δC^{13} were used as tracers, and consumer taxa were included as the fixed factor in the model. In order to fit the most complete model as possible with our data, apart from the pests (*P. oleae*, *E. olivina* and *B. oleae*), we also considered other potential prey from the groups of primary consumers (Stock & Semmens, 2016). The candidate preys were selected according to their isotopic content and their congruent position in the isotopic space. Thus, the analysed primary consumers form a convex mixing polygon that fits a minimum bounding rectangle containing the analysed predators. No prey that formed a concave angle in the polygon was considered (Phillips et al., 2014).

Considering that the stable isotope analysis was carried out for more than one individual per sample and replicated at least four times, and that the samples were collected in more than one location, the residual error variance was considered to account for other factors affecting the consumer variability, such as individual metabolism, process error or the variation in the consumer isotopic signature due to the sampling process in the analysis (Stock et al., 2018; Stock & Semmens, 2016). The Bayesian mixing model was run for three chains over 300,000 iterations, removing 200,000 for burn-in and thinning by a factor of 100. The Gelman–Rubin and Geweke diagnostic tests were used to assess the convergence of the model.

The use of discrimination trophic factors from empirical studies remains limited (Kadye et al., 2020), and most cases show some uncertainty and variability associated with the discrimination trophic factors (Phillips et al., 2014; Potapov et al., 2019). Nevertheless, MixSIAR allows the specification of a standard deviation around the discrimination trophic factor estimate to account for this uncertainty in the mixing analysis (Phillips et al., 2014). Due to the large number of taxa included in this study, the determination of every discrimination trophic factor was unapproachable. Instead, we used the general average fractionation values (i.e. ΔN^{15}: 3.4 ± 1.1‰ and ΔC^{13}: 0.3 ± 1.4‰) calculated from published stable isotope ratios by various authors (McCutchan et al., 2003; Vanderklift & Ponsard, 2003).

2.3.3 | Other potential trophic interactions

N^{15} and C^{13} distances between predators and phytophagous insects were used to infer other potential trophic links including taxa that,
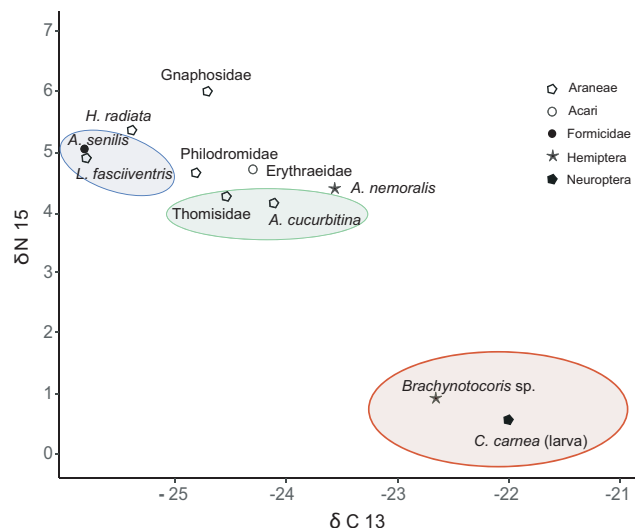
FIGURE 1 Isotopic signature of the predator and omnivorous arthropods in the olive grove food web. Standard error bars have been removed in order to clarify the graph. Taxa belonging to the same trophic groups are clustered in ellipses. The numbers correspond to the number of the trophic group

because of their position in the isotopic space, were not possible to use in the Bayesian mixing model. Then, a potential trophic interaction was considered when the trophic distance between the basal resource and the predator fitted with the general average fractionation values used in the Bayesian mixing model.

3 | RESULTS

The isotopic analysis included 26 taxa from the most abundant arthropods belonging to three different feeding guilds (according to the literature 9 species of predators, 15 of phytophagous insects, 3 of omnivores) (Appendix S2). The results obtained from the hierarchical clustering (by Euclidean distances and the complete linkage method) by δN^{15} and δC^{13} led to the definition of eight trophic groups of predators and 11 trophic groups of phytophagous (Appendix S3). The cophenetic distances were highly correlated to Euclidean distances in predators (0.95) and phytophagous taxa (0.78) verified the cluster trees.

3.1 | Trophic groups of predators

Predators showed a range of δN^{15} values from 0.63‰ for the predator larval *C. carnea s.l.* to 6.04‰ of spiders Gnaphosidae (Figure 1, Appendix S2). Furthermore, the δC^{13} values covered values from an isotopic ratio of −22.02‰ of the larval *C. carnea s.l.* to −25.80‰ of *Aphaenogaster senilis* (Mayr) (Hymenoptera: Formicidae) and *Lycosa fasciiventris* (Dufour) (Araneae: Lycosidae) (Figure 1, Appendix S2). Predators were clustered in five groups that contained single taxa and three groups formed by more than single taxa (Figure 1,

Appendix S3). The trophic group formed by the larval *C. carnea s.l.* and *Brachynotocoris* sp. (Hemiptera: Miridae) showed isotopic signatures very far from the other groups containing the lowest δN^{15} (0.74 ± 0.28) and the highest δC^{13} (−22.26 ± 0.52) signatures (Figure 1, Appendix S2, S3). Moreover, *Araniella cucurbitina* (Clerck) (Araneae: Araneidae) and the spiders Thomisidae formed a second group that showed mean δN^{15} levels of 4.26 ± 0.28 and δC^{13} of −24.32 ± 0.14. The omnivorous ant species *A. senilis* showed a very similar isotopic content to the spider *L. fasciiventris* (Figure 1, Appendix S2, S3) shaping the third trophic group (mean δN^{15} =5 ± 0.42 and mean δC^{13}=−25.8 ± 0.43). Finally, *Hogna radiata* (Latreille) (Araneae: Lycosidae) (δN^{15}=5.4 ± 0.18 and δC^{13}=−24.4 ± 0.36), Gnaphosidae (δN^{15}=6.04 ± 0.84 and δC^{13}=−24.71 ± 0.52), Erythraeidae (δN^{15}=4.69 ± 0.20 and δC^{13}=24.29 ± 0.13), Philodromidae (δN^{15}=4.73 ± 0.06 and δC^{13}=24.83 ± 0.14) and *Anthocoris nemoralis* (Fabricius) (Hemiptera: Anthocoridae) (δN^{15}=4.36 ± 0.18 and δC^{13}=−23.56 ± 0.17) showed isotopic values different from the other taxa (Figure 1, Appendix S2, S3).

3.2 | Trophic groups of phytophagous insects

The phytophagous insects analysed were clustered in 11 trophic groups, four of them containing more than single taxa (Figure 2, Appendix S3). The δN^{15} values ranged from −0.85‰ of Cicadomorpha plus Fulgoromorpha to 5.4‰ of *Conostethus roseus* (Fallen) (Hemiptera: Miridae), and the δC^{13} signatures ranged from −28.3‰ of *Calocoris* sp. (Hemiptera: Miridae) to −23.02‰ of *E. olivina*. From the 16 taxa, Blattodea, *B. oleae* and Cicadomorpha plus Fulgoromorpha shared similar isotopic signatures shaping a trophic group with a mean δN^{15} of −0.19 ± 0.92 and δC^{13} of −24.96 ± 1.14 (Figure 2, Appendix S2, S3). Moreover, the group formed by Orthoptera and *Emblethis duplicatus* (Seidenstücker) (Hemiptera: Lygaeidae) showed δN^{15} values of 1.8 ± 0.89 and δC^{13} of −26.73 ± 0.34. Chrysomelidae (Coleoptera) and *Hycleus scutellatus*,
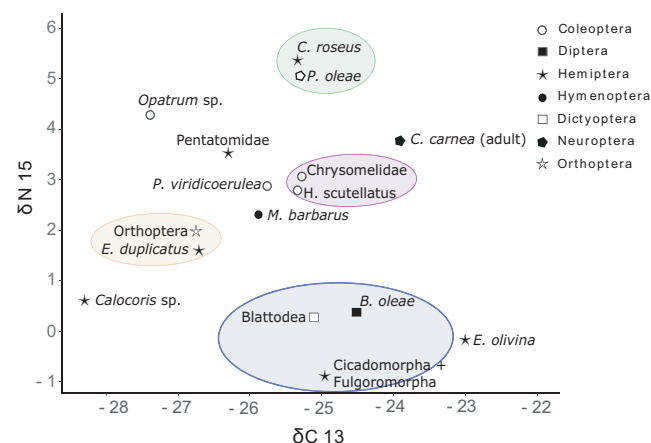
FIGURE 2 Isotopic signature of the phytophagous arthropods in the olive grove food web. Standard error bars have been removed in order to clarify the graph. Taxa belonging to the same trophic groups are clustered in ellipses

Rosenhauer (Coleoptera: Meloidae) were clustered in a group with mean values of δN^{15}=3 ± 0.82 and δC^{13}=−25.73 ± 0.46 (Figure 2, Appendix S2, S3). The fourth group, shaped by *Conostethus roseus* (Fallén) (Hemiptera: Miridae) and *P. oleae*, showed the highest δN^{15} signature 5.21 ± 0.23 and δC^{13} values of −25.32 ± 0.5 (Figure 2, Appendices S2 and S3). *Euphyllura olivina, Calocoris* sp. (Hemiptera: Miridae), *Messor barbarus* L. (Hymenoptera: Formicidae), Pentatomidae (Hemiptera), *C carnea s.l.* adult, *Psilothrix viridicoerulea* (Geoffroy) (Coleoptera: Dasytidae) and *Opatrum* sp. (Coleoptera: Tenebrionidae) did not share a group with any other taxa (see isotopic signatures in Appendix S2) (Figure 2, Appendix S3). Despite the two olive pests *E. olivina* and *B. oleae* pupae being similar in the δN^{15} content, they showed significant differences in their δC^{13} levels and belonged to two different trophic groups (Figure 2, Appendices S2 and S3). Moreover, the adult olive moth, *P. oleae*, showed isotopic values very distant from the other two pests (Figure 2, Appendix S2).

3.3 | Estimation of the proportion of pest consumption

The Bayesian mixing model included four predators (*A. nemoralis, A. cucurbitina*, Philodromidae and Thomisidae) and six primary consumers (the adult of *P. oleae*, the pupae of *B. oleae*, the adult of *E. olivina*, Pentatomidae, *M. barbarus* and the adult of *C. carnea*) that form a convex mixing polygon that fits a minimum bounding rectangle containing the analysed predators (Figure 3). Feeding reconstructions showed that from the six sources proposed, the pupae of *B. oleae, E. olivina* and *M. barbarus* were the prey that were consumed in a higher proportion (Table 1). Thus, Thomisidae, *A. cucurbitina* and Philodromidae showed an appreciable preference by *B. oleae* resulting in 52.6% of the sources of Thomisidae and roughly 30% in the *A. cucurbitina* and Philodromidae diet (Table 1). Moreover, *A. nemoralis* analysis showed that from the diet proposed, 20% was based on *B. oleae*. Furthermore, *E. olivina* occupied a high proportion of the diet of *A. nemoralis* with 32.8% and, to a lesser extent, 27.3% in *A. cucurbitina*. Moreover, from the 6 primary sources in the analysis, 30% of the diet of Philodromidae was based on *M. barbarous*, whilst Thomisidae and *A. cucurbitina* showed a percentage of 18.1% and 16.5% respectively. Finally, the predators showed a low proportion of feeding on Pentatomidae and the adult of *C. carnea s.l.*, except for *A. nemoralis* with 17.5% of the diet made up of the adult lacewing.

3.4 | Other potential trophic interactions

According to the general average fractionation values (i.e. ΔN^{15}: 3.4 ± 1.1‰ and ΔC^{13}: 0.3 ± 1.4‰) used in our study, other predators of *E. olivina*, Pentatomidae and *M. barbarus* were identified (see trophic enrichments in Table 2). *Brachynotocoris* sp. and the larval *C. carnea s.l.* showed a C^{13} trophic enrichment in relation to *E. olivina* of 0.39 and 1‰ respectively which identify these taxa as potential predators of the olive psylla. Furthermore, *A. senilis, L.*

fasciiventris and *H. radiata* were identified as potential predators of Pentatomidae and *M. barbarus.* Moreover, Gnaphosidae showed a trophic enrichment (N[15] 0.96 and C[13] 0.58‰) which may indicate a potential predation on the adult of *P. oleae* and *C. roseus* (N[15] 0.64 and C[13] 0.63‰).

Apart from the resources used in the Bayesian mixing model, *A. senilis* and *L. fasciiventris* may predate on Orthoptera and *E. duplicatus.* Thomisidae and Philodromidae may feed on *H. scutellatus* and Chrysomelidae. Moreover, Philodromidae may prey on *P. viridicoerulea* together with *H. radiata* and Gnaphosidae (Table 2).

4 | DISCUSSION

In this study, we have explored the trophic roles of the most abundant arthropods in olive groves. We have clustered the most abundant arthropods in the olive groves by their isotopic signature (δN^{15}
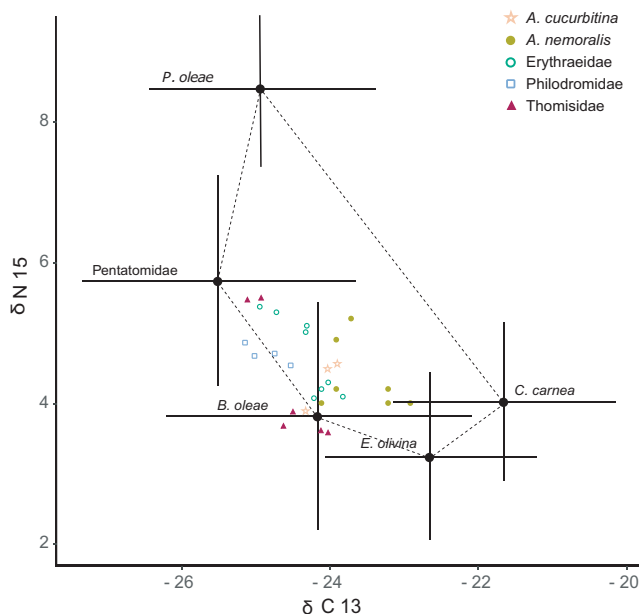
FIGURE 3 δN^{15} and δC^{13} ratios (means ± *SD*) of candidate food taxa of four predators in the olive grove. Raw values of $\delta^{15}N$ and $\delta^{13}C$ of the different replicates of predator samples are plotted. The concave polygon formed by the candidate resources used in the Bayesian mixing model is indicated with dashed lines. The larval *Chrysoperla carnea* and *Brachynotocoris* sp. were excluded from the analysis because they were out of the polygon

and δC^{13}) to identify groups with similar feeding behaviour (trophic groups). The generalist character of predators and the presence of semi-natural vegetation in olive grove results in a wide number of trophic groups, some of them with more than a single taxa.

Bayesian mixing models showed several predation events on the olive pest *E. olivina, B. oleae* and *M. barbarus* involving the four predators included in the analysis (*A. nemoralis, A. cucurbitina,* Philodromidae and Thomisidae). Moreover, the isotopic distance between Gnaphosidae and the adult of *P. oleae* identified this family of spider as a potential predator of the olive moth.

4.1 | Trophic groups of predators

The wide range of 3.78‰ between the lowest and the highest isotope signature of δC^{13} in the eight groups of predators showed a high variety of dietary resources that is congruent with the generalist character of most of the predators in olive groves (Cárdenas et al., 2006; Gonçalves & Pereira, 2012). For instance, *A. nemoralis* has been described as a polyphagous predator which preys mostly on thrips, aphids and psyllids (Herard, 1986; Mejdalani, 1998; Meyling et al., 2003; Solomon et al., 2000). Moreover, two of the trophic groups (Groups 5 and 8 in Appendix S3) clustered several spider taxa together with *A. senilis,* all of them generalists or showing other feeding habits such as intraguild predation and/or cannibalism (Riechert & Lockley, 1984; Riechert & Luczak, 1982; Wagner & Wise, 1996; Wise, 2006). *Aphaenogaster senilis,* sharing trophic group with *L. fasciiventris,* is an omnivorous ant that feeds on a large variety of food resources, including animals amongst others (Cerdá et al., 1988). This species presents a high plasticity in its foraging rate during the year including a predatory behaviour mainly on caterpillars, coleopterans and aphids (Caut et al., 2013).

The trophic group formed by the larval *C. carnea s.l.* and the mirid *Brachynotocoris* sp. showed δN^{15} values far below the other predators (Table 1, Figure 1), which may indicate that in our study, these two species were preying on a different trophic chain in the food web of the olive groves. The larvae of *C. carnea s.l.* are able to prey on a wide range of pest species, such as aphids, scale insects, leafhoppers, whiteflies and psyllids (Principi & Canard, 1984). Moreover, they feed on pollen and nectar when animal prey are less abundant (Canard, 2001; Patt et al., 2003; Villa et al., 2016), whilst *Brachynotocoris* sp., with omnivorous feeding behaviour, has been signalled as an important predator of olive grove pests (Morris,

TABLE 1 Estimated percentage obtained by Bayesian mixing modelling of prey consumed by each predator included in this study (the predators are listed in the first column and the sources above)

	Bactrocera oleae	Euphyllura olivina	Prays oleae	Messor barbarus	Pentatomidae	Chrysoperla carnea s.l. adult
Araniella cucurbitina	30.06	23.7	3.3	18.1	8.1	11.3
Anthocoris nemoralis	19.6	32.8	2.6	10.6	5.7	17.5
Philodromidae	28.7	12.7	2.5	29.7	11.9	5.7
Thomisidae	52.6	10.9	1.7	16.5	4.3	4.7

TABLE 2 N^{15} and C^{13} trophic enrichment between predators (first column) and their potential resources (first row) in the olive grove of the study

	Prays oleae N^{15}	Prays oleae C^{13}	Euphyllura olivina N^{15}	Euphyllura olivina C^{13}	Messor barbarus N^{15}	Messor barbarus C^{13}	Pentatomidae N^{15}	Pentatomidae C^{13}	Orthoptera N^{15}	Orthoptera C^{13}	Emblethis duplicatus N^{15}	Emblethis duplicatus C^{13}	Hycleus scutellatus N^{15}	Hycleus scutellatus C^{13}	Chrysomelidae N^{15}	Chrysomelidae C^{13}	Psilothrix viridicoerulea N^{15}	Psilothrix viridicoerulea C^{13}	Conostethus roseus N^{15}	Conostethus roseus C^{13}
Brachynotocoris sp.			0.75	0.39																
Larval C. carnea			0.48	1																
Aphaenogaster senilis					2.68	0.08	1.43	0.53	3.05	0.95	3.4	0.93								
Lycosa fasciiventris					2.63	0.48	1.38	0.93	3	0.95	3.35	0.93								
Hogna radiata					3.05	0.08	1.80	0.53									2.47	0.33		
Gnaphosidae	0.96	0.58															3.11	1.01		
Thomisidae													1.42	0.82	1.26	0.76				
Philodromidae													1.85	0.52	1.69	0.46	1.80	0.90	0.64	0.63

Campos, Kidd, Jervis, & Symondson, 1999; Paredes et al., 2013; Rodríguez et al., 2012).

4.2 | Trophic groups of phytophagous insects

The wide δC^{13} range in the phytophagous insect guild is an indicator of a high variety of basal resources, as the studied olive groves were surrounded by different semi-natural habitats. Thus, this result may be related to the different taxa that form primer consumer groups in this study and are from two different strata of the grove, the ground vegetation cover and the olive tree canopy.

The olive psyllid *E. olivina* appeared as a main phytophagous insect, which has a specific diet limited to the flower and the vegetative buds of olive trees. Therefore, this pest does not share its trophic group with other phytophagous insects included in this study. Moreover, *E. olivina* has an isotopic content quite different to other important pests of olive groves, *B. oleae*, with the δC^{13} content being 1.5‰ higher in the former and showing similar δN^{15} content (Figure 2). This result is consistent as the *B. oleae* pupae feed on the mesocarp of the olive fruit during maturation, whilst *E. olivina* feed on the olive tree sap (Molina de la Rosa et al., 2017) and these tissues have different levels of C^{13} content (Ruano, personal communication). Therefore, olive fruit mesocarp contains a high content of lipids, probably with a lower content in C^{13} than carbohydrates which explains this notable difference in the δC^{13} between the two olive pests, although always under the required C:N ratio of four (DeNiro & Epstein, 1976; Post et al., 2007).

Conversely, adults of the olive moth, *P. oleae* and the mirid *C. roseus*, showed an extremely high δN^{15} value for phytophagous insects. The *P. oleae* adult has been described as a consumer of nectar and honeydew (Pascual et al., 2010; Villa et al., 2017) whilst *C. roseus* is a phytophagous insect feeding on several species of *Trifolium* spp (Woodroffe, 1959) and grasses (Aukema, 1988). Nevertheless, the similar isotopic content of *C. roseus* and *P. oleae* indicates that these two species may share some resources. Probably *C. roseus*, such as other mirids, presents some level of omnivory.

Although the adults of *C. carnea s.l.* and *P. oleae* share a diet based on nectar and/or honeydew (Villa et al., 2016, 2017), unlike *P. oleae*, the lacewing feeds on pollen as well (Villa et al., 2016). This difference in feeding resources could be related to the differences in the isotopic levels between the two species. Moreover, particularities in the metamorphosis process may increase the differences in the N^{15} signature (Patt et al., 2003; Tibbets et al., 2008).

4.3 | Estimation of the proportion of pest consumption

4.3.1 | Bactrocera oleae

The main result of our mixed model is that *A. nemoralis* showed a predator activity on *B. oleae* where the pest may make up to 20% of

its diet. Until now this species has been considered as a widely known natural enemy of the olive pest species *P. oleae* and *E. olivina* (Morris, Campos, Kidd, Jervis, & Symondson, 1999; Paredes et al., 2013, 2019). Our results reconfirm the role of *A. nemoralis* in the predation of *E. olivina* and quantify its impact in the effective control of olive pests. Recently, it has been proposed that *A. nemoralis* is attracted by the presence of *E. olivina* on the olive tree, promoting the migration of the anthocorid from the natural vegetation to the olive tree branches and its settlement in spring (Álvarez et al., 2019; Batuecas et al., 2013). Moreover, Paredes et al., 2019 described a direct dependence of the abundance of *A. nemoralis* with the abundance of *E. olivina* in olive groves.

More results from the Bayesian mixing model in this study, point to the spiders Thomisidae and Philodromidae showing preferences in consuming *B. oleae* and *M. barbarus* whilst *Araniella cucurbitina* (Clerk), a common orb-spider in olive groves (Benhadi-Marín et al., 2020), showed preferences in feeding on *B. oleae* pupae, *E. olivina* and *M. barbarus*. *Araniella cucurbitina* is an orb-builder species that builds silky flat webs between leaves and flowers whilst Philodromidae and Thomisidae are active hunters with an ambush strategy (Cardoso et al., 2011; Uetz et al., 1999). The *B. oleae* pupae might be captured in orbs when they leave the fruit and drop to the ground to pupate in the soil (Dimou et al., 2003). The interest in the natural enemies of *B. oleae* has been focused on the identification of several parasitoids (Arambourg, 1986; Boccaccio & Petacchi, 2009) and the study of the community of edaphic predators of the most vulnerable instars, pupae and maggots that move to the soil in the autumn (Dinis et al., 2016; Neuenschwander et al., 1983; Orsini et al., 2007; Picchi et al., 2017). Nevertheless, knowledge about the role of spiders in the *B. oleae* predation is scarce. The family Araneidae has been related to the predation on *B. oleae* (Lantero et al., 2019). Moreover, *A. cucurbitina* has been proposed as an important natural enemy in the olive tree canopy (Benhadi-Marín et al., 2020). Nevertheless, to the best of our knowledge, neither *A. cucurbitina* nor Philodromidae have been directly described as potential predators of *B. oleae* before. Regarding Thomisidae, our results support the correlation made by Dinis et al. (2016) that relate the abundance of epigeal Araneae, including Thomisidae amongst others, to the increase in the predation rate of *B. oleae* pupae in the soil. Despite the fact that hunting spiders are considered better natural enemies in pest control than web-builders (Marc et al., 1999; Nyffeler, 1999), the presence of *A. cucurbitina* in olive trees and ground cover may increase the predation pressure exerted on *B. oleae* in the crop. Furthermore, in our study, *A. cucurbitina* showed a predatory activity on *E. olivina*, which may increase the importance of this species in the population control of olive grove pests.

4.3.2 | Euphyllura olivina

Other results from our Bayesian mixing model show that despite *Brachynotocoris* sp. and larval *C. carnea s.l.* being out of the convex polygon of primary consumers, they were placed very close to

E. olivina, which may indicate that they exert a predation pressure on the latter (Figure 3). Nevertheless, it would be necessary to add other candidate resources fitting a convex mixing polygon suitable to the position of this trophic group in the isotopic space. There are examples where the pest density needs to be high to attract natural enemies and this seems to justify the over-consumption of *E. olivina* as an alternative prey (Bohan et al., 2000; Bryan & Wratten, 1984). The presence of *E. olivina* in olive groves is essential for maintaining generalist predator populations near the olive trees throughout the season, thus maintaining the balance in the community and avoiding uncontrolled pest outbreaks (Coll & Guershon, 2001; Matson et al., 1997; Swift & Anderson, 1994). Thus, the consumption of *E. olivina* by *Brachynotocoris* sp. and the larva of *C. carnea s.l.* might be very important in the case of an olive pest outbreak (i.e. *P. oleae* or *B. oleae*), which can frequently reduce olive production by 50%–60% (Ramos et al., 1998).

4.3.3 | Prays oleae

Despite Bayesian mixing models not providing any remarkable result about the predation on the adult *P. oleae*, Gnaphosidae did show a trophic enrichment congruent with a predator of the adult olive moth (Table 2).

Most studies have focused on the biological control of *P. oleae* concerning the predation on the larva instar and the eggs. Nevertheless, during the carpophagous generation, the larva instar of *P. oleae* is inaccessible to predators which only prey on the exposed eggs (Morris, Campos, Kidd, & Symondson, 1999). As there is a strong correlation between the number of adults of the flower generation and the degree of olive fruit infestation (Ramos et al., 1998), it is important to consider the natural control of adults apart from the most vulnerable instars.

Paredes et al. (2015) asserted that an assemblage of predators could be better at controlling pest species with a complex life cycle. In our study, the stable isotope results show a system based on spiders with different hunting strategies together with *A. nemoralis* that, potentially, could exert a predator pressure on *B. oleae* and *E. olivina*. Regarding previous results and those revealed in this study, the composition of this group of natural enemies could control these pests in their different life cycle instars resulting in a very efficient biological control.

Finally, stable isotope analyses together with Bayesian mixing models have proved to be powerful tools for managing the study of complex trophic webs in field studies. The opportunity to analyse the composition of the diet of generalist predators may help to clarify their trophic links in agroecosystems. This technique may clarify the role in the biological control of controversial generalists such as spiders whose laboratory testing provides a limited perception of their natural diet (Mezőfi et al., 2020). In this study, several predator groups, all of them generalists, have been identified as potentially effective control agents. Thus, we describe for the first time *A. cucurbitina*, Thomisidae, Philodromidae and

A. nemoralis as potential predators of the *B. oleae* pupae and *A. cucurbitina* as predator of *E. olivina*. Furthermore, we support the role of *A. nemoralis* as predator of *E. olivina*, which emphasizes the importance of this secondary pest in the attraction and settlement of predators close to olive trees.

To sum up, our results have generated knowledge that has launched the first clues to developing new studies on the biological control of *B. oleae* and the adults of *P. oleae* in olive groves.

AUTHOR CONTRIBUTIONS
MM is a co-author, collected the data and analysed the study. FR is a co-author secured funding, project design and data collection.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in https://doi.org/10.5281/zenodo.5652779

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