1 Title:

2 Ground cover presence in organic olive orchards affects the interaction of natural
3 enemies against *Prays oleae*, promoting an effective egg predation

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18 Abstract

19 The olive moth, *Prays oleae*, is one of the most common insects that damages olives in
20 the Mediterranean region. The establishment of ground cover within olive orchards has
21 been promoted in this region in recent years to avoid erosion and soil degradation.
22 Nevertheless, its role as a shelter for natural enemies of pests has been controversial. In
23 this study, we have investigated the effectiveness of the biological control of *P. oleae* in
24 organic olive orchards with ground cover (mowed) and without ground cover (tilled).
25 For this, (1) we assessed the relationship between predated eggs and the abundance of
26 natural enemies in both types of orchards; (2) we compared both the potential damage
27 of the pest and the egg hatching in the two types of orchards; and (3) we examined the
28 interaction amongst families of natural enemies and *P. oleae* (as adults and as predated
29 eggs). The results showed that there is a high rate of predation in the studied olive
30 orchards, 81% of the eggs were predated, 12.2% hatched, and 6.9% were live eggs.
31 However, mowed orchards were more effective for controlling *P. oleae* by means of
32 egg predation rather than tilled orchards, i.e., in mowed orchards, whilst the potential
33 damage of the pest was higher, egg hatching was rather low. The structure of the adult
34 arthropod community, i.e., the composition and abundance of families of natural
35 enemies did not differ between the orchards, but the abundance of the families
36 Anthocoridae, Miridae and Scelionidae was significantly higher in the mowed orchards.
37 Finally, the interaction amongst natural enemies and *P. oleae* showed that the families
38 that better explained the effects on egg predation were Aeolothripidae, Anthocoridae,
39 Miridae, Chrysopidae (predators), and Formicidae (omnivore). We discuss the results in
40 terms of ecological interactions of trophic guilds and we conclude that the establishment
41 and maintenance of ground cover in organic olive orchards, at least in June and July, is
42 of great significance because it positively affects the egg predation of *P. oleae*. This

effect is especially significant when there is a low abundance of natural enemies in the olive orchards.

Keywords:

Biological control

Ecological infrastructures

Inter-row management

Trophic guilds

Trophic interactions

1. Introduction

The organic management in olive orchards has been increasing in the Mediterranean region in recent years (Alonso-Mielgo et al., 2001; Torres-Millares et al., 2017). This type of management frequently involves the establishment of ground cover within the orchard, and when possible, the conservation of adjacent semi-natural habitats (Boller et al., 2004; Landis et al., 2005; Malavolta and Perdakis, 2018). In this region, one of the most common insects that damages olives is the olive moth, *Prays oleae* Bern (Lepidoptera: Praydidae) (Tzanakakis, 2006; RAIF, 2018). *Prays oleae*, produces three generations per year: (1) the phyllophagous generation (feeds on olive leaves from November to April, and overwinters in the canopy); (2) the anthophagous generation (feeds on floral buttons from April to June and is the one that lays eggs mainly on the calice of the olive fruits); and (3) the carpophagous generation (larvae penetrate the fruit and feed on the stone from June to October). All three generations can cause damage to olive orchards and each generation plays an important role in configuring the size of the next generation. However, the carpophagous larvae can generate significant

68 damage to olives, which potentially reduces the yield production. Thus, much of the
69 efforts of pest control are focused on the anthophagous and carpophagous generations
70 (Ramos et al., 1998; Bento et al., 2001).

71

72 Recently, it has been observed that olive orchards have great potential to boost
73 populations of natural enemies within the orchard, especially when ground cover is
74 present rather than orchards with bare ground (Herz et al., 2005; Lousão et al., 2007;
75 Cárdenas et al., 2012; Rodríguez et al., 2012; Paredes et al., 2013a). From a
76 “biodiversity-ecosystem function” point of view, semi-natural vegetation interspersed
77 within the growing area or located at their margins can reinforce microclimate
78 conditions in crops and orchards, and thus provide food and shelter to natural enemies
79 of insect pests (Tscharntke et al., 2012; Wan et al., 2018). Accordingly, in olive
80 orchards ground cover plays a major role in modulating such a tendency. For example,
81 it has been suggested the existence of synergistic effects between ground cover and
82 natural adjacent vegetation, which jointly promote a high abundance of some (but not
83 all) predator arthropods of *P. oleae* and *Euphyllura olivina* Costa (Hemiptera: Psyllidae)
84 within the olive-tree canopy (Paredes et al., 2013a). Recently, Álvarez et al. (2019a)
85 demonstrated such a synergistic relationship by describing the abundance and
86 movement of the natural enemies which are boosted by the ground cover. Moreover,
87 Villa et al. (2016a) observed that ground cover favoured the parasitism of *P. oleae*
88 larvae by *Ageniaspis fuscicollis* (Dalman) (Hymenoptera: Encyrtidae), whereas
89 herbicide applications had negative effects.

90

91 Nonetheless, a higher abundance of natural enemies does not always suppress pest
92 abundance and pest damage, which is a problem that has arisen in conservational

93 biological control (Rusch et al., 2010; Karp et al., 2018). In addition, and unfortunately,
 94 it has been recognized that the positive effects generated by a higher biodiversity on
 95 ecosystem function, i.e., the control of pests, are conditioned by a myriad of factors
 96 (Bianchi et al., 2006; Rusch et al., 2010; Tschamtker et al., 2016; Karp et al., 2018).
 97
 98 Significant efforts have been made by various authors to describe the effects of semi-
 99 natural habitats on the abundance of natural enemies and olive pests (Ruano et al., 2004;
 100 Paredes et al., 2013a; 2013b; Gkisakis et al., 2016; Villa et al., 2016a; 2016b; Porcel et
 101 al., 2017; Álvarez et al., 2019a). However, to the best of our knowledge, there is no
 102 study that has focussed on jointly assessing the effects of ground cover on both the
 103 abundance of natural enemies and the egg predation of *P. oleae*. The aim of this study
 104 was to assess the effectiveness of predation in organic olive orchards with both tilled
 105 and mowed management of the ground cover. Specific goals of the study were: (1) to
 106 assess the relationship between the abundance of natural enemies and egg predation in
 107 both managements, (2) to compare the effectiveness of egg predation between both
 108 managements, and (3) to explore the interaction amongst families of natural enemies
 109 and *P. oleae* adults and predated eggs using unconstrained ordination. We have
 110 hypothesised that when a ground cover is mowed (1) key taxa of natural enemies would
 111 be positively affected; therefore (2) the biological control of *P. oleae*, by means of egg
 112 predation, would increase.

113

114 2. Material and methods

115 2.1. Study area and sampling design

116 The study was conducted in three consecutive years from 2011 to 2013 in southern
 117 Spain, in the province of Granada. We selected eight organic olive orchards based on

118 (1) the absence of ground cover (tillage in late spring; tilled) and (2) the use of mowing
 119 techniques during late spring to maintain the ground cover (mowed) (see Table A.1 in
 120 supplementary data). All the orchards were located in areas surrounded by extended
 121 semi-natural habitats interspersed in an olive-orchard matrix including different
 122 management systems (Fig. 1). Agricultural management in these organic orchards was
 123 based on a system of natural regulation (*sensu* Pajarón Sotomayor, 2006), and thus, pest
 124 management did not differ amongst the orchards in the years of study. The distance of
 125 planting was 10×10 m, and two varieties of olive trees were grown: Picual (location
 126 Deifontes) and Lucio (location Granada). The climatic and topographic conditions were
 127 typical of the olive orchards in the study area (see Paredes et al., 2013a; Álvarez et al.,
 128 2019a).

129
 130 June and July are the months when the anthophagous generation of *P. oleae* laid their
 131 eggs on newly growing olives. We carried out three different types of sampling in both
 132 months per year. Firstly, adult arthropods were collected twice a month by batting four
 133 branches per tree over an entomological net (a sample per tree). Olive trees were
 134 sampled in randomly selected plots formed by four parallel transects with a separation
 135 of 100 m between the transects. Each transect consisted of ten trees of which only five
 136 trees were sampled, following a discontinuous sequence, i.e., 20 samples per plot. After
 137 being collected, the samples were transported to the Department of Zoology, University
 138 of Granada and the Zaidin Experimental Station. The samples were stored individually
 139 and maintained at -20°C until the specimens were identified. The arthropods were
 140 identified to family level, otherwise specified, and the natural enemies were separated
 141 and used for this study. Identification of the natural enemies was based on literature data
 142 (see Table A.4 in supplementary data). Secondly, 200 olives were collected from four

143 trees (total of 50 olives per tree) randomly selected in each orchard per month (June and
144 July) and the same tree was never re-sampled. The olives were collected to examine the
145 eggs laid by *P. oleae*. Thirdly, *P. oleae* adults were collected using pheromone traps (2
146 traps per orchard), which were randomly distributed in each orchard and changed every
147 10 days in June and July. Adults and eggs of *P. oleae* were stored and identified at the
148 Zaidin Experimental Station (CSIC).

149

150 2.2. Identification of egg damage

151 The olives were observed with the help of a microscope-stereoscope to record the
152 number of olives with laid eggs of *P. oleae*, and to characterize the appearance of the
153 eggs (Fig. 1). Then, the number of (1) eggs that had hatched and give place to a larva
154 inside the olive was recorded (hatched eggs); (2) eggs that had not hatched and were
155 still alive (live eggs) and showed a white to yellowish colour; and (3) eggs that had been
156 damaged by predators (predated eggs) and of which only the translucent chorion
157 adhering to the fruit remained.

158

159 2.3. Data analysis

160 For comparison purposes the site (orchard) was used as our experimental unit. Thus, we
161 pooled together samples by (1) orchard and (2) months for the three years to avoid
162 pseudo-replication. The orchards were not always the same throughout years, of the
163 eight orchards, four were sampled in 2011 (2 tilled and 2 mowed), five in 2012 (3 tilled
164 and 2 mowed, of which 2 were new), and seven in 2013 (2 tilled and 5 mowed, of which
165 2 were new) (see Table A.1 in supplementary data). Monthly samples were considered
166 independently. Therefore, for each site we obtained a representative measure of
167 arthropod abundance and *P. oleae* egg counts.

168

169 Raw data of the abundance of natural enemies and *P. oleae* adults was subjected to a
170 logistic regression approach in order to detect differences between managements. We
171 used this method instead of mean or median comparison because it is a more suitable
172 method to detect statistical differences due to the nature of our experimental unit (see
173 Peng et al., 2002).

174

175 We used two approaches to assess the differences in egg predation between the tilled
176 and mowed managements. Firstly, we fitted a generalized linear mixed model (GLMM)
177 using a Poisson tendency to test whether or not the relationship between the abundance
178 of natural enemies and the amount of the predation changed in the two types of
179 managements. We used a GLMM approach because our experimental unit (orchard)
180 changed throughout the years of study, in some of the re-sampled orchards farmers
181 passed from a tilled to a mowed management. Then, to control for such inter-annual
182 variation and site-management variation we included in the model year and site as
183 nested random effects. The number of predated eggs was included as the dependent
184 variable and the type of management and the total abundance of natural enemies were
185 included as fixed effects (see Table A.2 in supplementary data). Secondly, we assessed
186 the effectiveness of predation by analysing the potential damage of the pest (number of
187 olives with any kind of eggs laid $\times 100$ / total of observed olives) and the rate of egg
188 hatching (number of hatched eggs $\times 100$ / all observed eggs minus the predated ones)
189 (for more detail on these parameters see Ramos et al., 1987; Ramos and Ramos, 1990).
190 Then, we subjected the data after this transformation to a logistic regression approach in
191 order to compare both parameters and detect differences between managements.

192

193 Finally, non-metric multidimensional scaling (NMDS) was used to assess the overall
 194 pattern of species composition of the natural enemies. Data used for the NMDS were
 195 square-root transformed and subjected to Wisconsin double standardization (Legendre
 196 and Gallagher, 2001). The Bray-Curtis dissimilarity distance was used to compute the
 197 resemblance matrix amongst sites. Species scores, representing the different natural
 198 enemy taxa were added to the final NMDS plot as weighted averages. Based on the
 199 NMDS, smooth surfaces were generated with the data of *P. oleae* adult abundance and
 200 predated eggs to explore associations between families of natural enemies and *P. oleae*.
 201 Smooth surfaces result from fitting thin plate splines in two dimensions using
 202 generalized additive models. The function selects the degree of smoothing by
 203 generalized cross-validation and interpolates the fitted values on the NMDS plot
 204 represented by lines ranking in a gradient (Oksanen et al., 2018) (see Table A.3 in
 205 supplementary data). This method allowed us to indirectly relate different levels of the
 206 abundance of predated eggs and adults of *P. oleae* with the abundance and
 207 correspondence of different families of natural enemies.

208

209 Analyses were computed in the R software v.3.6.2 (R Developmental Core Team,
 210 2019). Accordingly, the “lme4” package (Bates et al., 2020) was used to fit GLMM and
 211 the “vegan” package (Oksanen et al., 2018) was used to compute NMDS and smooth
 212 surfaces. Package lme4 was used because whilst other packages are more mature and
 213 better documented, lme4 is fastest, offers built-in facilities for likelihood profiling and
 214 parametric bootstrapping and especially it offers tools for crossed designs (Bates, 2010;
 215 Bates et al., 2018).

216

217 3. Results

Overall, 6,400 olives were observed with a total of 15,412 laid eggs of *P. oleae*. 81% of the eggs were predated, 12.2% hatched, and 6.9% were live eggs. We collected a total of 62,008 adults of *P. oleae* and a total of 4,001 natural enemy arthropods, of which 36 families were identified (Table 1). 70.7% of the natural enemy specimens were predators, 26.8% were omnivores, and 2.5% were parasitoids. The most abundant families of predators were: Anthocoridae, Miridae (order Hemiptera); Chrysopidae (order Neuroptera); and Thomisidae (order Araneae). Amongst hymenopterans the most abundant family of parasitoids was the Scelionidae, and Formicidae was the most abundant family of omnivores and of all the natural enemies.

The structure of the arthropod community, i.e., the composition and abundance of arthropod families, is mostly the same between tilled and mowed orchards (Fig. 2). However, six families of natural enemies were present only in one of the two managements, i.e., mowed: Liocranidae, Uloboridae (order Araneae), Nabidae (order Hemiptera), Aeolothripidae (order Thysanoptera); and tilled: Malachiidae (order Coleoptera), Ichneumonidae (order Hymenoptera). Moreover, the abundance of three families of natural enemies was significantly higher in the mowed orchards, Anthocoridae (Wald $\chi^2 = 3.928$, df = 1, $p = 0.047$), Miridae (order Hemiptera) (Wald $\chi^2 = 5.247$, df = 1, $p = 0.021$), and Scelionidae (order Hymenoptera) (Wald $\chi^2 = 5.071$, df = 1, $p = 0.024$) (Fig. 2), as well as the abundance of *P. oleae* adults (Wald $\chi^2 = 4.624$, df = 1, $p = 0.031$).

GLMM analysis showed that there is a positive relationship between the abundance of natural enemies and the amount of predated eggs in both managements (Fig. 3). Both effects, natural enemy abundance and management, were statistically significant (Table

243 2). The relationship tended to be high in the mowed orchards and this pattern appeared
 244 at the lowest abundance of natural enemies (Fig. 3). Furthermore, there are differences
 245 in the effectiveness of predation of *P. oleae* eggs between managements, i.e., in mowed
 246 orchards the potential damage of the pest was significantly higher (Wald $\chi^2 = 8.996$, df
 247 = 1, $p = 0.002$) but egg hatching was significantly lower (Wald $\chi^2 = 5.295$, df = 1, $p =$
 248 0.021) than tilled orchards.

249

250 The results of the NMDS, which represents the relationship and structure of the
 251 communities of natural enemies and their association with egg predation and the
 252 abundance of adults of *P. oleae*, are shown in Figure 4. Accordingly, the families
 253 Araneidae, Linyphiidae, Liocranidae, Oxiopidae, Salticidae, Therididae, Thomisidae,
 254 Uloboridae (order Araneae); Coccinellidae, Malachiidae, Staphylinidae (order
 255 Coleoptera); Anthocoridae, Lygaeidae, Miridae, Nabidae, Reduviidae (order
 256 Hemiptera); Braconidae, Elasmidae, Formicidae, Pteromalidae, Scelionidae (order
 257 Hymenoptera); Chrysopidae (order Neuroptera); Mantidae (order Mantodea);
 258 Raphidiidae (order Raphidioptera); and Aeolothripidae (order Thysanoptera) were
 259 associated with elevated egg predation (Fig. 4a). However, the families Corinidae,
 260 Oxiopidae, Salticidae (order Araneae); Cantharidae, Coccinellidae (order Coleoptera);
 261 Lygaeidae (order Hemiptera); Encyrtidae, Eulophidae, Ichneumonidae (order
 262 Hymenoptera); and Coniopterygidae (order Neuroptera) were associated with a low
 263 abundance of *P. oleae* adults (Fig. 4b). In this type of analysis, an association of a
 264 family of natural enemies with a high number of predated eggs implies that these taxa
 265 could be involved in egg predation (or egg damage), increasing predation rates.
 266 Conversely, an association with a low or intermediate abundance of adults of *P. oleae*

267 means that such taxa could be feeding on adults, decreasing their abundance to a lower
268 rate.

269

270 Based on the NMDS, trophic status, size, and the morphological features of each family,
271 the families that are more likely to damage the eggs of *P. oleae* are: Coccinellidae,
272 Staphylinidae (order Coleoptera); Anthocoridae, Miridae, Nabidae, Reduviidae (order
273 Hemiptera); Braconidae, Formicidae (order Hymenoptera); Chrysopidae (order
274 Neuroptera) and Aeolothripidae (order Thysanoptera). However, we have ruled out the
275 families that had (1) a low abundance in both managements (Coccinellidae,
276 Staphylinidae, Nabidae, Reduviidae), and (2) no predatory form of feeding (parasitoids:
277 Braconidae). Hence, only Aeolothripidae, Anthocoridae, Chrysopidae, Formicidae, and
278 Miridae are the families that could explain the differences in egg predation between the
279 tilled and mowed orchards.

280

281 4. Discussion

282 In this study, we have assessed the effectiveness of the biological control of *P. oleae* in
283 organic olive orchards in terms of egg predation by natural enemies. As expected, the
284 presence of ground cover within the orchards positively affected the predation of eggs
285 laid by the antophagous generation of *P. oleae*, and thus, egg predation was more
286 effective in mowed orchards than in tilled orchards.

287

288 Organic orchards are very balanced and stable systems (Vossen, 2007). The orchards
289 that we measured were very similar in their agricultural practices and in their landscape
290 structure (with the exception of the ground cover management). This was reflected in
291 the composition and abundance of families of natural enemies. Both local and large-

scale factors can affect the abundance of natural enemies and pests in olive orchards, such as less pesticide application or microclimate conditions and landscape diversity or patch size, respectively (Boccaccio and Petacchi, 2009; Rodríguez et al., 2009; Ortega and Pascual, 2014; Villa et al., 2016a; 2020; Morente et al., 2018; Álvarez et al., 2019a; 2019b; 2021). This may explain why the structure of the arthropod community tended not to differ in our study. Nonetheless, it has been shown that the abundance of natural enemies is positively affected by ground cover (Lousão et al., 2007; Cárdenas et al., 2012; Rodríguez et al., 2012; Álvarez et al., 2019a; 2019b). When analysing the relationship between egg predation and natural enemy abundance in both managements, mowed orchards tended to have higher predation as the abundance of natural enemies increased. Interestingly, the highest differences in predated eggs between mowed and tilled orchards appeared especially when the levels of natural enemies were low. This implies that the differences in predation were caused by a subtle, but still higher abundance of natural enemies.

On the other hand, previous studies on olive orchards showed that the presence of ground cover had no effect on the abundance of *P. oleae* adults when tilled and mowed orchards were compared (Paredes et al., 2013b; Paredes et al., 2015a). Nonetheless, it has been found that certain plant species in the ground cover could promote an increase in the abundance of *P. oleae* (Villa et al., 2016c). Our results follow such a tendency, ground cover may increase the abundance of adults of *P. oleae*. Based on the former results one could assume that ground cover does not promote biological control by itself. However, we showed that egg hatching of *P. oleae* is lower in orchards with a ground cover, and thus, less hatching implies that there are potentially less larvae of *P. oleae* that could damage olives. Therefore, we can assume that the effects of the ground

317 cover to control *P. oleae* lead towards the predation of eggs rather than attacking the
318 adults.
319
320 Regarding the predators, our results are in agreement with previous studies that have
321 recorded the role of predator heteropterans, such as Anthocoridae and several species of
322 Miridae as major predators of olive pests (Mazomenos et al., 1994; Cantero, 1997;
323 López-Villalta, 1999; Morris et al., 1999; Alvarado et al., 2004; Paredes et al., 2013a;
324 2015b). The fact that these groups are positively affected by the presence of ground
325 cover suggests their sensitivity to perturbation. However, it has been shown that
326 predator heteropterans are more sensitive to the presence of native adjacent vegetation
327 rather than ground cover, although some species such as *Deraeocoris punctum*
328 (Rambur), have shown the opposite (Paredes et al., 2013a) implying that differences at
329 species level are important. These inconsistencies may be the result of the movement of
330 the natural enemies across habitats within and outside olive orchards. For example,
331 Álvarez et al. (2019a) showed that predators and parasitoids move from ground cover to
332 adjacent vegetation and olive trees, respectively, but omnivores move from adjacent
333 vegetation to ground cover and olive trees, specifically when the ground cover withers.
334 In addition, there is evidence that *Anthocoris nemoralis* (Fabricius), (Plata et al., 2017)
335 and some lacewings (Chrysopidae) (Porcel et al., 2017) move from ground cover to
336 adjacent vegetation.
337
338 Lacewing larvae, for example, have been described as one of the main natural enemies
339 that attack *P. oleae* (Bento et al., 1999; Torres, 2006; Villa et al., 2016b). Lacewing
340 larvae are positively affected by ground cover (Villa et al., 2016b). Interestingly, in our
341 study this group did not differ between the tilled and mowed orchards, although we

342 mainly sampled adults which are very stable geographically (Alcalá-Herrera et al.,
343 2019). This could be explained by the fact that winged adults have high ranges of
344 movement (Rusch et al., 2010) and it is possible that they move across the region from
345 one orchard to another to lay their eggs. Nevertheless, in our study, lacewings were
346 related with high levels of egg predation, which supports the hypothesis that this group
347 is of great importance in the biological control of *P. oleae*.

348

349 Another family that showed interesting patterns was Aeolothripidae. In our study, it
350 showed an important interaction with egg predation, but this family was present only in
351 the mowed orchards. The role of Aeolothripidae as a natural enemy of olive pests has
352 been poorly documented (reviewed by Torres, 2006). It is known that Aeolothripidae
353 attack other Thysanoptera, however, it also has been suggested that some genera of
354 Aeolothripidae can feed on the eggs of lepidopterans (Lewis, 1973). Moreover, some
355 species of European *Aeolothrips* sp. can feed on mites, larvae, and eggs of psyllids and
356 whiteflies, as well as on aphids (Trdan et al., 2005). Thus, the role of Aeolothripidae in
357 the predation of the eggs of *P. oleae* should be investigated more thoroughly.

358

359 In the case of the omnivores, it is known that ants are important predators of *P. oleae*
360 (Morris et al., 1999; 2002). Our results showed that ants had the highest abundance
361 within olive orchards, however, we did not find differences in the abundance of ants
362 between mowed and tilled orchards. This is of great importance, because a predator that
363 is not affected by management and has high abundances could be used to enhance local
364 biological control strategies. Several studies have shown *Tapinoma* ants as the most
365 abundant type of ant within olive orchards, sometimes representing more than 50 % of
366 the relative abundance amongst omnivores within olive orchards (Morris et al., 1998a;

1998b;1999; 2002; Morris and Campos, 1999; Redolfi et al., 1999; Pereira et al., 2004; Rodriguez et al., 2005; Santos et al., 2007; Campos et al., 2011), which makes it one of the strongest candidates for controlling *P. oleae*. Indeed, some species of the *T. nigerrimum* complex are beneficial in olive orchards in the southern area of the Iberian Peninsula (Seifert et al., 2017). Furthermore, it has been found that it is possible to boost the abundance and trophic interactions of *Tapinoma* ants within the canopy of olive trees with mature ground cover (Álvarez et al., 2019b) and less pesticide use (Morente et al., 2018).

In addition, we found that the family Braconidae shows an important association with predators upon egg predation. Only one species of Braconidae is known to parasitize the eggs of *P. oleae*: *Chelonus eleaphilus* Silv (Arambourg, 1986). This species is a poliembryonic parasite, i.e., females oviposit inside the eggs of their prey (Grbic et al., 1998; Segoli et al., 2010). This species is one of the most important and specific parasitoids of *P. oleae* in the Mediterranean region. The fact that Braconidae populations respond to ground cover management may be due to their need for flowers to feed on (Nave et al., 2016). On the other hand, in our analysis Elasmidae and Scelionidae showed a similar pattern to Braconidae, but Scelionidae had higher abundances in mowed orchards. Some species of the family Scelionidae may attack other natural enemies causing intra-guild predation, such as *Telenomus acrobater* Giard, which has been described as parasitizing the eggs of lacewings (Alrouedchi, 1981; Campos, 1986; Rodríguez et al., 2012).

Finally, it is important to point out that the species composition of natural enemies showed interesting patterns (Fig. 4). The fact that the tendency of the variable predated

eggs depends on the tendency of *P. oleae* adult abundance should be taken into account, i.e., the more *P. oleae* adults there are, the more the eggs they can lay, and thus, be predated. This is why the panels in Figure 4, are very similar. However, the families that are related with the predation on adults are well defined. The spiders are the arthropods that are most likely to predate adults, which is in agreement with previous studies (Paredes et al., 2015b). Interestingly, and according to what we have mentioned, in the NMDS natural enemies assembled in different groups that correspond to their trophic status. Consequently, several assemblages might fulfil complementary functional roles determined by the way they catch prey (Uetz et al., 1999; Straub et al., 2008). For example, it has been found that a single assemblage of natural enemies, such as *A. nemoralis*, *Brachynotocoris* sp., and *Pseudoloxops coccineus* (Meyer Dur), is better correlated with the control of *P. oleae* (Paredes et al., 2015b). The assemblage of these species has been explained as the result of the (complex) life cycle of *P. oleae* (Wilby et al., 2005) and their preference for eggs (Paredes et al., 2015b). In addition, the arachnid families Araneidae and Linyphiidae, which are orb-weaving and sheet-weaving spiders respectively, are most likely to play a role in reducing the adults of *P. oleae* (Paredes et al., 2015b).

409

410 5. Conclusions

411 A mowing management of the ground cover within olive orchards positively affected
412 the key natural enemies that play an important role predating *P. oleae*, even though
413 arthropod communities were similar between tilled and mowed orchards. Hence, the
414 establishment and maintenance of ground cover in organic olive orchards is of great
415 significance due to its potential to promote the biological control of *P. oleae* by means
416 of egg predation, especially when there is a low abundance of natural enemies. The

hypothesis is that an olive orchard with ground cover produces more active and voracious natural enemies, and it may allow the establishment of more and efficient key predators. To the best of our knowledge this is the first time that this type of empirical data has been recorded for olive orchards. The fact that in our study the differences in the biological control of pests were shown by eggs rather than the abundance of adults suggests that the studies on biological control should focus on specific instars of the development of pests where the biological control is more likely to occur, which is a concern that has already been pointed out for conservation biological control (Karp et al., 2018). Thus, the effect of landscape structure on egg predation of *P. oleae* specifically in olive orchards needs to be investigated more thoroughly.

Authors contributions

H.A.A. and F.R. conceived the ideas. F.R. and M.C. designed fieldwork and R.J.M. and M.M. conducted fieldwork. H.A.A. performed data analysis and write the manuscript. All authors revised the final version and gave their approval for submission.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors want to thank the owners of the orchards, especially Norberto Recio and Manuel Recio; Carlos Martínez for his help in the laboratory (UGR collaboration grant); and all the taxonomist who helped us identifying arthropods. Thanks to Angela Tate for editing the English language of the manuscript. H. A. Álvarez is grateful to

442 Gemma Clemente Orta for her help conceptualizing graphic representations and
443 CONACyT for providing him with an international PhD student grant (registry
444 332659). This study was financed by The Alhambra and Generalife Governing Board
445 (contract: 3548-00 and 3548-01) and the Spanish Ministry of Science, Innovation, and
446 Universities, General Sub-direction of Projects (project AGL2009-09878).

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Table 1. Relative abundance (RA), acronyms, presence in orchards: tilled (T) and mowed (M), and trophic guilds of the families of natural enemies ($n = 36$) identified in organic olive orchards. Numbers represent presence (1) and absence (0).

Guild	Order	Family	Acronym	T	M	RA (%)
Omnivores	Dermaptera	Forficulidae	Fo	1	1	1,51
	Hymenoptera	Formicidae	For	1	1	98,49
Parasitoids	Hymenoptera	Braconidae	Bra	1	1	8,49
		Elasmidae	El	1	1	12,26
		Encirtidae	En	1	1	5,66
		Eulophidae	Eu	1	1	3,77
		Ichneumonidae	Ich	1	0	0,94
		Pteromalidae	Pt	1	1	26,42
		Scelionidae	Sc	1	1	42,45
Predators	Araneae	Araneidae	Ar	1	1	1,48
		Corinidae	Co	1	1	0,74
		Linyphiidae	Li	1	1	0,60
		Liochranidae	Lio	0	1	0,07
		Oxyopidae	Ox	1	1	2,41
		Philodromidae	Ph	1	1	2,35
		Salticidae	Sa	1	1	6,61
		Theridiidae	The	1	1	1,17
		Thomisidae	Tho	1	1	19,95
		Uloboridae	Ul	0	1	0,03
	Coleoptera	Cantharidae	Ca	1	1	0,74
		Carabidae	Car	1	1	0,07
		Coccinelidae	Coc	1	1	6,17
		Malachiidae	Ma	1	0	0,07
		Staphylinidae	St	1	1	0,10
	Diptera	Asilidae	As	1	1	0,13
		Empididae	Em	1	1	0,64
	Hemiptera	Anthocoridae	An	1	1	11,64
		Lygaeidae	Ly	1	1	0,37
		Miridae	Mi	1	1	31,05
		Nabidae	Na	0	1	0,07
		Reduviidae	Re	1	1	1,11
	Mantodea	Mantidae	Man	1	1	0,47
	Neuroptera	Chrysopidae	Chr	1	1	10,43
		Coniopterygidae	Con	1	1	0,54

	Raphidioptera	Raphidiidae	Ra	1	1	0,13
	Thysanoptera	Aeolothripidae	Ae	0	1	0,87

669

670

671 Table 2. Fixed effects of the fitted model (GLMM) explaining egg predation: type of

672 management and natural enemy abundance.

Variable	df	Wald χ^2	<i>p</i>
Management (tilled or mowed)	1	4.524	0.033
Natural enemy abundance	1	5.841	0.015

673

674 Figure 1

675

676 Fig. 1. Panoramic view of tilled (left) and mowed (right) organic olive orchards (a).

677 Oviposition site of *Prays oleae* on an olive (b). Appearance of laid eggs of *P. oleae* on

678 an olive: live egg (c), hatched egg (d), and predated egg (e). Site and eggs are indicated

679 by triangles.

680 Figure 2

703 Fig. 2. Natural enemy abundance classified by management: tilled (white bars) and
704 mowed (grey bars). Families are grouped by orders and trophic information. An asterisk
705 indicates that a family of natural enemy showed significantly differences between
706 managements. Black points indicate the families that were present in only one of the
707 managements.

708 Figure 3

709

710 Fig. 3. Relation amongst variables according to GLMM analysis: egg predation, the
 711 natural enemy (NE) abundance, and management.

712 Figure 4

713

714 Figure 4: Non metric multi-dimensional scaling (NMDS) of the total abundance of
715 natural enemies. Proximity amongst families of natural enemies within the ordination
716 plot indicates that their abundances are positively related. Lines (smooth surfaces)

717 represent different levels, in the form of a gradient, of predated egg counts (A) and adult
718 abundance (B) of *P. oleae*, according to generalised additive models. See family
719 acronyms in Table 1.