Tittle:

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

Authors:

Hugo Alejandro Álvarez[a]*, Raquel Jiménez-Muñoz[a], Marina Morente[a], Mercedes Campos[b], Francisca Ruano[a]

Affiliations:

[a] Department of Zoology, University of Granada, Granada, Spain

[b] Department of Environmental Protection, Zaidin Experimental Station (CSIC), Granada, Spain

* Corresponding author at: Department of Zoology, Faculty of Sciences, University of Granada, Av. Fuente Nueva s/n 18071, Granada, Spain.

E-mail addresses: hugoalvarez01@gmail.com, hugoalvarez01@correo.ugr.es (H.A. Álvarez)

Abstract

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

1. Introduction

The organic management in olive orchards has been increasing in the circum-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 Perdikis, 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 chalice 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, but the carpophagous larvae can generate

68 significant damage to olives which potentially reduces the yield production, and thus
69 much of the efforts of pest control are focused on the anthophagous and carpophagous
70 generations (Ramos et al., 1998; Bento et al., 2001).
71
72 Recently, it has been shown that olive orchards have great potential to boost populations
73 of natural enemies within the orchard, especially when ground cover is present rather
74 than orchards with bare ground (Herz et al., 2005; Lousão et al., 2007; Cárdenas et al.,
75 2012; Rodríguez et al., 2012; Paredes et al., 2013a). From a "biodiversity-ecosystem
76 function" point of view, semi-natural vegetation interspersed within the growing area or
77 located at their margins can reinforce microclimate conditions in crops and orchards,
78 and thus provide food and shelter to natural enemies of insect pests (Tscharntke et al.,
79 2012; Wan et al., 2018). Accordingly, in olive orchards ground cover plays a major role
80 in modulating such a tendency. For example, it has been suggested the existence of
81 synergistic effects between ground cover and natural adjacent vegetation, which jointly
82 promote a high abundance of some (but not all) predator arthropods of *P. oleae* and
83 *Euphyllura olivina* Costa (Hemiptera: Psyllidae) within the olive-tree canopy (Paredes
84 et al., 2013a). Recently, Álvarez et al. (2019a) demonstrated such a synergistic
85 relationship by describing the abundance and movement of the natural enemies which
86 are boosted by the ground cover. Moreover, Villa et al. (2016a) showed that overall
87 parasitism of *P. oleae* larvae by *Ageniaspis fuscicollis* (Dalman) (Hymenoptera:
88 Encyrtidae), was favoured by ground cover and negatively affected by herbicide
89 applications.
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

biological control (Rusch et al. 2010; Karp et al. 2018). In addition, and unfortunately, it has been recognized that the positive effects generated by a higher biodiversity on ecosystem function, i.e., the control of pests, are conditioned by a myriad of factors (Bianchi et al. 2006; Rusch et al. 2010; Tscharntke et al., 2016; Karp et al., 2018).

Significant efforts have been made by various authors to describe the effects of semi-natural habitats on the abundance of natural enemies and olive pests (Ruano et al., 2004; Paredes et al., 2013a; 2013b; Gkisakis et al., 2016; Villa et al., 2016a; 2016b; Porcel et al., 2017; Álvarez et al., 2019), but to the best of our knowledge, there is no study that has focussed on jointly assessing the effects of ground cover on both the abundance of natural enemies and the egg predation of *P. oleae*. The aim of this study was to assess the effectiveness of predation in organic olive orchards with both tilled and mowed management of the ground cover. Specific goals of the study were: (1) to assess the relationship between the abundance of natural enemies and egg predation in both managements, (2) to compare the effectiveness of egg predation between both managements, and (3) to explore the interaction amongst families of natural enemies and *P. oleae* adults and predated eggs using unconstrained ordination. We hypothesised that when a ground cover is mowed (1) key taxa of natural enemies would be positively affected; therefore (2) the biological control of *P. oleae*, by means of egg predation, would increase.

2. Material and methods

2.1. Study zone and sampling design

The study was conducted in three consecutive years from 2011 to 2013 in southern 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) and the herbaceous
134 plants below. Olive trees were sampled in randomly selected plots formed by four
135 parallel transects with a separation of 100 m between the transects. Each transect
136 consisted of ten trees of which only five trees were sampled, following a discontinuous
137 sequence, i.e., 20 samples per plot. After being collected, the samples were transported
138 to the Department of Zoology, University of Granada and the Zaidin Experimental
139 Station. The samples were stored individually and maintained at −20°C until the
140 specimens were identified. The arthropods were identified to family level, otherwise
141 specified, and the natural enemies were separated and used for this study. Identification
142 of the natural enemies was based on literature data (see Table A.4 in supplementary

143 data). Secondly, 200 olives were collected from four trees (total of 50 olives per tree)
144 randomly selected in each orchard per month (June and July) and the same tree was
145 never re-sampled. The olives were collected to examine the eggs laid by *P. oleae*.
146 Thirdly, *P. oleae* adults were collected using pheromone traps (2 traps per orchard),
147 which were randomly distributed in each orchard and changed every 10 days in June
148 and July. Adults and eggs of *P. oleae* were stored and identified at the Zaidin
149 Experimental Station (CSIC).
150
151 *2.2. Identification of egg damage*
152 The olives were observed with the help of a microscope-stereoscope to record the
153 number of olives with laid eggs of *P. oleae*, and to characterize the appearance of the
154 eggs (Fig. 1). Then, the number of (1) eggs that had hatched and give place to a larva
155 inside the olive was recorded (hatched eggs); (2) eggs that had not hatched and were
156 still alive (live eggs) and showed a white to yellowish colour; and (3) eggs that had been
157 damaged by predators (predated eggs) and of which only the translucent chorion
158 adhering to the fruit remained.
159
160 *2.3. Data analysis*
161 For comparison purposes the site (orchard) was used as our experimental unit. Thus, we
162 pooled together samples by (1) orchard and (2) months for the three years to avoid
163 pseudo-replication. The orchards were not always the same throughout years, of the
164 eight orchards, four were sampled in 2011 (2 tilled and 2 mowed), five in 2012 (3 tilled
165 and 2 mowed, of which 2 were new), and seven in 2013 (2 tilled and 5 mowed, of which
166 2 were new) (see Table A.1 in supplementary data). Monthly samples were considered

167 independently. Therefore, for each site we obtained a representative measure of
168 arthropod abundance and *P. oleae* egg counts.
169
170 Raw data of the abundance of natural enemies and *P. oleae* adults was subjected to a
171 logistic regression approach in order to detect differences between managements. We
172 used this method instead of mean or median comparison because it is a more suitable
173 method to detect statistical differences due to the nature of our experimental unit (see
174 Peng et al., 2002).
175
176 We used two approaches to assess the differences in egg predation between the tilled
177 and mowed managements. Firstly, we fitted a generalized linear mixed model (GLMM)
178 using a Poisson tendency to test whether or not the relationship between the abundance
179 of natural enemies and the amount of the predation changed in the two types of
180 managements. We used a GLMM approach because our experimental unit (orchard)
181 changed throughout the years of study, in some of the re-sampled orchards farmers
182 passed from a tilled to a mowed management. Then, to control for such inter-annual
183 variation and site-management variation we included in the model year and site as
184 nested random effects. The number of predated eggs was included as the dependent
185 variable and the type of management and the total abundance of natural enemies were
186 included as fixed effects (see Table A.2 in supplementary data). Secondly, we assessed
187 the effectiveness of predation by analysing the potential damage of the pest (number of
188 olives with any kind of eggs laid × 100 / total of observed olives) and the rate of egg
189 hatching (number of hatched eggs × 100 / all observed eggs minus the predated ones)
190 (for more detail on these parameters see Ramos et al., 1987; Ramos and Ramos, 1990).

191 Then, we subjected the data after this transformation to a logistic regression approach in
192 order to compare both parameters and detect differences between managements.
193
194 Finally, non-metric multidimensional scaling (NMDS) was used to assess the overall
195 pattern of species composition of the natural enemies. Data used for the NMDS were
196 square-root transformed and subjected to Wisconsin double standardization (Legendre
197 and Gallagher, 2001). The Bray-Curtis dissimilarity distance was used to compute the
198 resemblance matrix amongst sites. Species scores, representing the different natural
199 enemy taxa were added to the final NMDS plot as weighted averages. Based on the
200 NMDS, smooth surfaces were generated with the data of *P. oleae* adult abundance and
201 predated eggs to explore associations between families of natural enemies and *P. oleae*.
202 Smooth surfaces result from fitting thin plate splines in two dimensions using
203 generalized additive models. The function selects the degree of smoothing by
204 generalized cross-validation and interpolates the fitted values on the NMDS plot
205 represented by lines ranking in a gradient (Oksanen et al., 2018) (see Table A.3 in
206 supplementary data). This method allowed us to indirectly relate different levels of the
207 abundance of predated eggs and adults of *P. oleae* with the abundance and
208 correspondence of different families of natural enemies.
209
210 Analyses were computed in the R software v.3.6.2 (R Developmental Core Team,
211 2019). Accordingly, the "lme4" package (Bates et al., 2020) was used to fit GLMM and
212 the "vegan" package (Oksanen et al., 2018) was used to compute NMDS and smooth
213 surfaces. Package lme4 was used because whilst other packages are more mature and
214 better documented, lme4 is fastest, offers built-in facilities for likelihood profiling and

parametric bootstrapping and especially it offers tools for crossed designs (Bates, 2010; Bates et al., 2018).

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, $p = 0.031$).

240

241 GLMM analysis showed that there is a positive relationship between the abundance of
242 natural enemies and the amount of predated eggs in both managements (Fig. 3). Both
243 effects, natural enemy abundance and management, were statistically significant (Table
244 2). The relationship tended to be high in the mowed orchards and this pattern appeared
245 at the lowest abundance of natural enemies (Fig. 3). Furthermore, there are differences
246 in the effectiveness of predation of *P. oleae* eggs between managements, i.e., in mowed
247 orchards the potential damage of the pest was significantly higher (Wald $\chi^2 = 8.996$, df
248 $= 1$, $p = 0.002$) but egg hatching was significantly lower (Wald $\chi^2 = 5.295$, df = 1, $p =$
249 0.021) than tilled orchards.

250

251 The results of the NMDS, which represents the relationship and structure of the
252 communities of natural enemies and their association with egg predation and the
253 abundance of adults of *P. oleae*, are shown in Figure 4. Accordingly, the families
254 Araneidae, Linyphiidae, Liocranidae, Oxiopidae, Salticidae, Theridiidae, Thomisidae,
255 Uloboridae (order Araneae); Coccinelidae, Malachiidae, Staphylinidae (order
256 Coleoptera); Anthocoridae, Lygaeidae, Miridae, Nabidae, Reduviidae (order
257 Hemiptera); Braconidae, Elasmidae, Formicidae, Pteromalidae, Scelionidae (order
258 Hymenoptera); Chrysopidae (order Neuroptera); Mantidae (order Mantodea);
259 Raphidiidae (order Raphidioptera); and Aeolothripidae (order Thysanoptera) were
260 associated with elevated egg predation (Fig. 4A). However, the families Corinidae,
261 Oxiopidae, Salticidae (order Araneae); Cantharidae, Coccinelidae (order Coleoptera);
262 Lygaeidae (order Hemiptera); Encyrtidae, Eulophidae, Ichneumonidae (order
263 Hymenoptera); and Coniopterygidae (order Neuroptera) were associated with a low
264 abundance of *P. oleae* adults (Fig. 4B). In this type of analysis, an association of a

265 family of natural enemies with a high number of predated eggs implies that these taxa
266 could be involved in egg predation (or egg damage), increasing predation rates.
267 Conversely, an association with a low or intermediate abundance of adults of *P. oleae*
268 means that such taxa could be feeding on adults, decreasing their abundance to a lower
269 rate.
270
271 Based on the NMDS, trophic status, size, and the morphological features of each family,
272 the families that are more likely to damage the eggs of *P. oleae* are: Coccinelidae,
273 Staphylinidae (order Coleoptera); Anthocoridae, Miridae, Nabidae, Reduviidae (order
274 Hemiptera); Braconidae, Formicidae (order Hymenoptera); Chrysopidae (order
275 Neuroptera) and Aeolothripidae (order Thysanoptera). However, we have ruled out the
276 families that had (1) a low abundance in both managements (Coccinelidae,
277 Staphylinidae, Nabidae, Reduviidae), and (2) no predatory form of feeding (parasitoids:
278 Braconidae). Hence, only Aeolothripidae, Anthocoridae, Chrysopidae, Formicidae, and
279 Miridae are the families that could explain the differences in egg predation between the
280 tilled and mowed orchards.
281
282 4. Discussion
283 In this study we have assessed the effectiveness of the biological control of *P. oleae* in
284 organic olive orchards in terms of egg predation by natural enemies. As expected, the
285 presence of ground cover within the orchards positively affected the predation of eggs
286 laid by the antophagous generation of *P. oleae*, and thus, egg predation was more
287 effective in mowed orchards than in tilled orchards.
288

289 Organic orchards are very balanced and stable systems (Vossen, 2007). The orchards
290 that we measured were very similar in their agricultural practices and in their landscape
291 structure (with the exception of the ground cover management). This was reflected in
292 the composition and abundance of families of natural enemies. Both local and large-
293 scale factors can affect the abundance of natural enemies and pests in olive orchards,
294 such as less pesticide application or microclimate conditions and landscape diversity or
295 patch size, respectively (Boccaccio and Petacchi, 2009; Rodríguez et al., 2009; Ortega
296 and Pascual, 2014; Villa et al., 2016a; 2020; Morente et al., 2018; Álvarez et al.,
297 2019a). This may explain why the structure of the arthropod community tended not to
298 differ in our study. Nonetheless, it has been shown that the abundance of natural
299 enemies is positively affected by ground cover (Lousão et al., 2007; Cárdenas et al.,
300 2012; Rodríguez et al., 2012; Álvarez et al. 2019a). When analysing the relationship
301 between egg predation and natural enemy abundance in both managements, mowed
302 orchards tended to have higher predation as the abundance of natural enemies increased.
303 Interestingly, the highest differences in predated eggs between mowed and tilled
304 orchards appeared especially when the levels of natural enemies were low. This implies
305 that the differences in predation were caused by a subtle, but still higher abundance of
306 natural enemies.
307
308 On the other hand, previous studies on olive orchards showed that the presence of
309 ground cover had no effect on the abundance of *P. oleae* adults when tilled and mowed
310 orchards were compared (Paredes et al., 2013b; Paredes et al., 2015a). Nonetheless, it
311 has been found that certain plant species in the ground cover could promote an increase
312 in the abundance of *P. oleae* (Villa et al., 2016c). Our results follow such a tendency,
313 ground cover may increase the abundance of adults of *P. oleae*. Based on the former

314 results one could assume that ground cover does not promote biological control by
315 itself. However, we showed that egg hatching of *P. oleae* is lower in orchards with a
316 ground cover, and thus, less hatching implies that there are potentially less larvae of *P.*
317 *oleae* that could damage olives. Therefore, we can assume that the effects of the ground
318 cover to control *P. oleae* lead towards the predation of eggs rather than attacking the
319 adults.
320
321 Regarding the predators, our results are in agreement with previous studies that have
322 recorded the role of predator heteropterans, such as Anthocoridae and several species of
323 Miridae as major predators of olive pests (Mazomenos et al., 1994; Cantero, 1997;
324 López-Villalta, 1999; Morris et al., 1999; Alvarado et al., 2004; Paredes et al., 2013a;
325 2015b). The fact that these groups are positively affected by the presence of ground
326 cover suggests their sensitivity to perturbation. However, it has been shown that
327 predator heteropterans are more sensitive to the presence of native adjacent vegetation
328 rather than ground cover, although some species such as *Deraeocoris punctum*
329 (Rambur), have shown the opposite (Paredes et al., 2013a) implying that differences at
330 species level are important. These inconsistencies may be the result of the movement of
331 the natural enemies across habitats within and outside olive orchards. For example,
332 Álvarez et al. (2019a) showed that predators and parasitoids move from ground cover to
333 adjacent vegetation and olive trees, respectively, but omnivores move from adjacent
334 vegetation to ground cover and olive trees, specifically when the ground cover withers.
335 In addition, there is evidence that *Anthocoris nemoralis* (Fabricius), (Plata et al., 2017)
336 and some lacewings (Chrysopidae) (Porcel et al., 2017) move from ground cover to
337 adjacent vegetation.
338

339 Lacewing larvae, for example, have been described as one of the main natural enemies
340 that attack *P. oleae* (Bento et al., 1999; Torres, 2006; Villa et al., 2016b). Lacewing
341 larvae are positively affected by ground cover (Villa et al., 2016b). Interestingly, in our
342 study this group did not differ between the tilled and mowed orchards, although we
343 mainly sampled adults which are very stable geographically (Alcalá-Herrera et al.,
344 2019). This could be explained by the fact that winged adults have high ranges of
345 movement (Rusch et al., 2010) and it is possible that they move across the region from
346 one orchard to another to lay their eggs. Nevertheless, in our analysis lacewings were
347 related with high levels of egg predation, which supports the hypothesis that this group
348 is of great importance in the biological control of *P. oleae*.
349
350 Another family that showed interesting patterns was Aeolothripidae. In our analysis it
351 showed an important interaction with egg predation, but this family was present only in
352 the mowed orchards. The role of Aeolotrhipidae as a natural enemy of olive pests has
353 been poorly documented (reviewed by Torres, 2006). It is known that Aeolothripidae
354 attack other Thysanoptera, however, it also has been suggested that some genera of
355 Aeolothripidae can feed on the eggs of lepidopterans (Lewis, 1973). Moreover, some
356 species of European *Aeolothrips* sp. can feed on mites, larvae, and eggs of psyllids and
357 whiteflies, as well as on aphids (Trdan et al., 2005). Thus, the role of Aeolothripidae in
358 the predation of the eggs of *P. oleae* should be investigated more thoroughly.
359
360 In the case of the omnivores, it is known that ants are important predators of *P. oleae*
361 (Morris et al., 1999; 2002). Our results showed that ants had the highest abundance
362 within olive orchards, however, we did not found differences in the abundance of ants
363 between mowed and tilled orchards. This is of great importance, because a predator that

364 is not affected by management and has high abundances could be used to enhance local
365 biological control strategies. Several studies have shown *Tapinoma* ants as the most
366 abundant type of ant within olive orchards, sometimes representing more than 50
367 percent of the relative abundance amongst omnivores within olive orchards (Morris et
368 al., 1998a; 1998b;1999; 2002; Morris and Campos, 1999; Redolfi et al., 1999; Pereira et
369 al., 2004; Rodriguez et al., 2005; Santos et al., 2007; Campos et al., 2011), which makes
370 it one of the strongest candidates for controlling *P. oleae*. Indeed, some species of the *T.*
371 *nigerrimum* complex are beneficial in olive orchards in the southern area of the Iberian
372 Peninsula (Seifert et al., 2017). Furthermore, it has been found that it is possible to
373 boost the abundance and trophic interactions of *Tapinoma* ants within the canopy of
374 olive trees with mature ground cover (Álvarez et al., 2019b) and less pesticide use
375 (Morente et al., 2018).
376
377 In addition, we found that the family Braconidae shows an important association with
378 predators upon egg predation. Only one species of Braconidae is known to parasitize the
379 eggs of *P. oleae*: *Chelonus eleaphilus* Silv (Arambourg, 1986). This species is a
380 poliembrionic parasite, i.e., females oviposit inside the eggs of their prey (Grbic et al.,
381 1998; Segoli et al., 2010). This species is one of the most important and specific
382 parasitoids of *P. oleae* in the circum-Mediterranean region. The fact that Braconidae
383 populations respond to ground cover management may be due to their need for flowers
384 to feed on (Nave et al., 2016). On the other hand, in our analysis Elasmidae and
385 Scelionidae showed a similar pattern to Braconidae, but Scelionidae had higher
386 abundances in mowed orchards. Some species of the family Scelionidae may attack
387 other natural enemies causing intra-guild predation, such as *Telenomus acrobater* Giard,

388 which has been described as parasitizing the eggs of lacewings (Alrouedchi, 1981;
389 Campos, 1986; Rodríguez et al., 2012).
390
391 Finally, it is important to point out that the NMDS showed interesting patterns. The fact
392 that the tendency of the variable "predated eggs" depends on the tendency of adult
393 abundance should be taken into account, i.e., the more *P. oleae* adults there are, the
394 more the eggs they can lay, and thus, be predated. This is why the panels in Figure 4,
395 are very similar. However, the families that are related with the predation on adults are
396 well defined. The spiders are the arthropods that are most likely to predate adults, which
397 is in agreement with previous studies (Paredes et al., 2015b). Interestingly, and
398 according to what we have mentioned, in the NMDS natural enemies assembled in
399 different groups that correspond to their trophic status. Consequently, several
400 assemblages might fulfil complementary functional roles determined by the way they
401 catch prey (Uetz et al., 1999; Straub et al., 2008). For example, it has been found that a
402 single assemblage of natural enemies, such as *A. nemoralis*, *Brachynotocoris* sp., and
403 *Pseudoloxops coccineus* (Meyer Dur), is better correlated with the control of *P. oleae*
404 (Paredes et al., 2015b). The assemblage of these species has been explained as the result
405 of the (complex) life cycle of *P. oleae* (Wilby et al., 2005) and their preference for eggs
406 (Paredes et al., 2015b). In addition, the arachnid families Araneidae and Linyphiidae,
407 which are orb-weaving and sheet-weaving spiders respectively, are most likely to play a
408 role in reducing the adults of *P. oleae* (Paredes et al., 2015b).
409
410 5. Conclusions
411 Overall, even though the arthropod communities in tilled and mowed orchards were
412 similar, when the orchards were mowed this positively affected key taxa that play an

important role predating *P. oleae* population. Hence, we agree that the establishment and maintenance of ground cover in organic olive orchards is of great significance because it promotes the biological control of *P. oleae* by means of egg predation, especially when there is a low abundance of natural enemies. The hypothesis is that an olive orchard with ground cover produces stronger and more 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.

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.

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657 Tables

658 Table 1. Relative abundance (RA), acronyms, presence in orchards: tilled (T) and

659 mowed (M), and trophic guilds of the families of natural enemies (*n* = 36) identified in

660 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

Table 2. Fixed effects of the fitted model (GLMM) explaining egg predation: type of management and natural enemy abundance.

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

666 Figure legends

667 Fig. 1. Panoramic view of tilled (left) and mowed (right) organic olive orchards (A).
668 Oviposition site of *Prays oleae* on an olive (B). Appearance of laid eggs of *P. oleae* on
669 an olive: live egg (C), hatched egg (D), and predated egg (E). Site and eggs are
670 indicated by triangles.

671

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

677

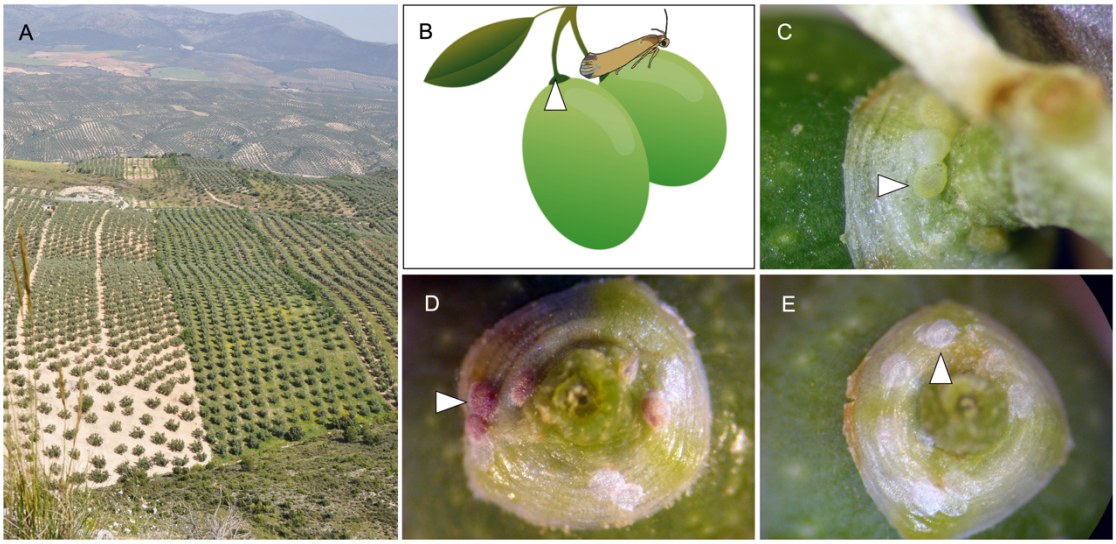
678 Fig. 3: Relation amongst variables according to GLMM analysis: egg predation, the
679 natural enemy (NE) abundance, and management.

680

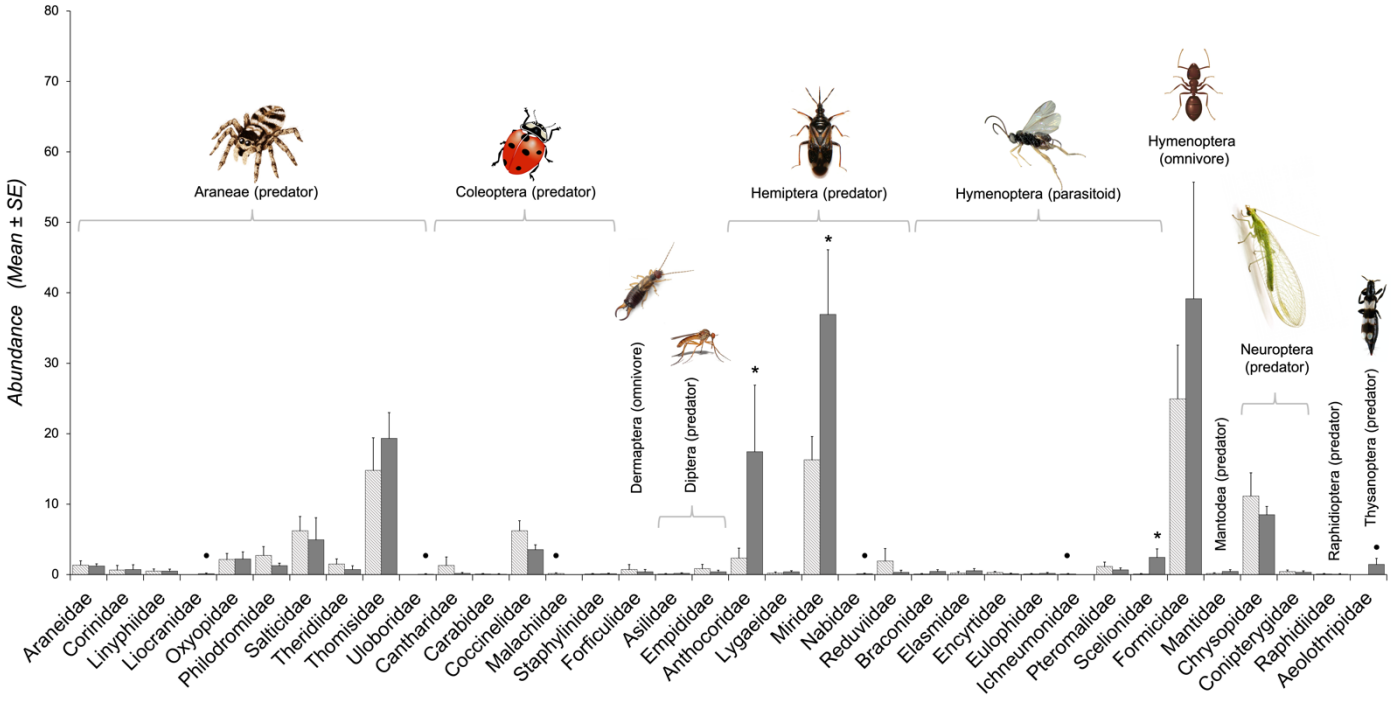
681 Figure 4: Non metric multi-dimensional scaling (NMDS) of the total abundance of
682 natural enemies. Proximity amongst families of natural enemies within the ordination
683 plot indicates that their abundances are positively related. Lines (smooth surfaces)
684 represent different levels, in the form of a gradient, of predated egg counts (A) and adult
685 abundance (B) of *P. oleae*, according to generalised additive models. See family
686 acronyms in Table 1.

687

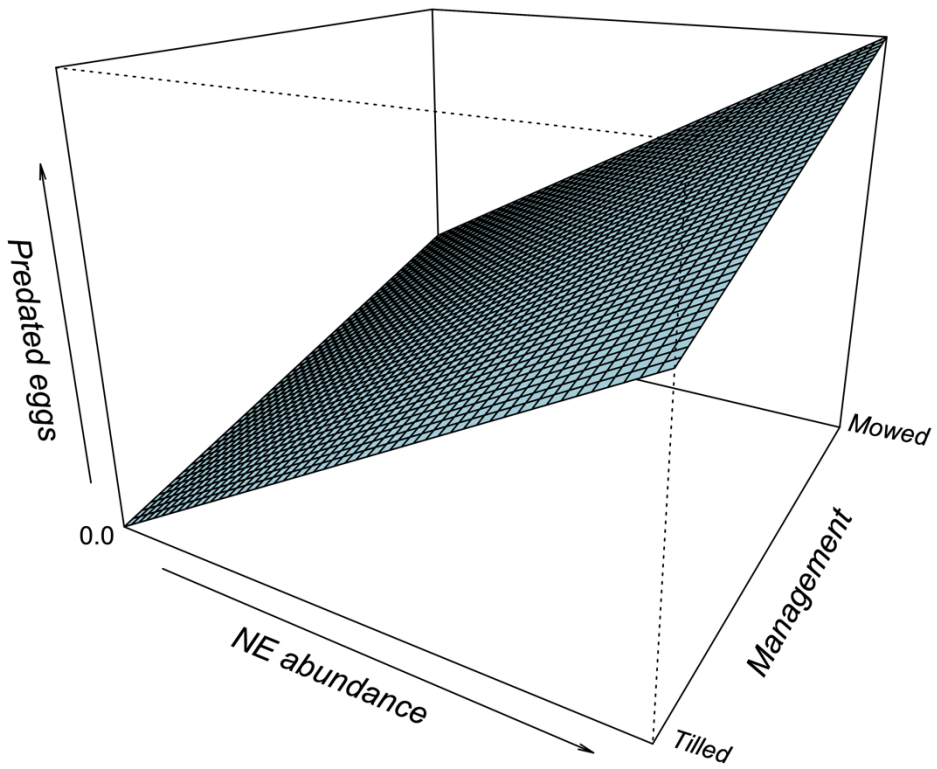
Fig. 1



691 Fig. 2

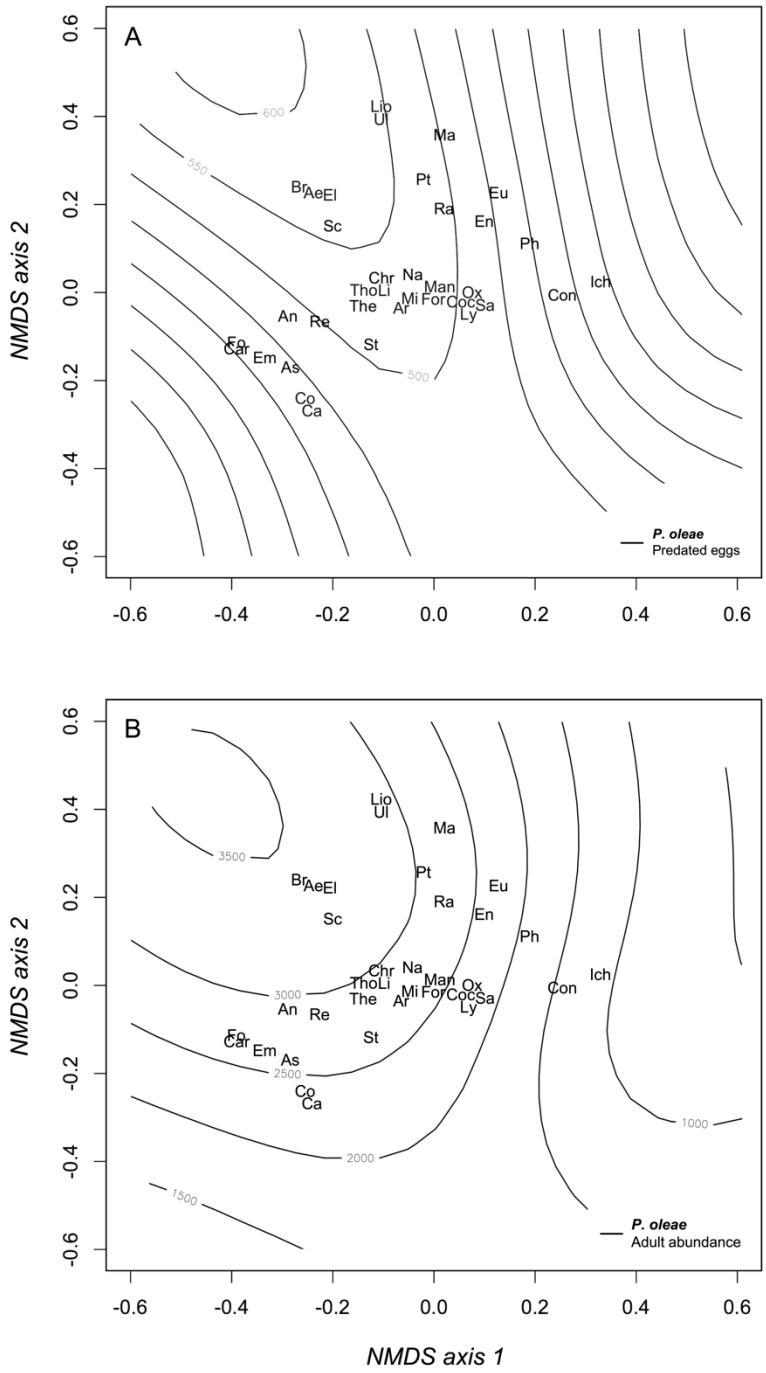

Abundance (Mean ± SE)
80
70
60
50
40
30
20
10
0
Araneae (predator)
Coleoptera (predator)
Hemiptera (predator)
Hymenoptera (parasitoid)
Hymenoptera (omnivore)
Dermaptera (omnivore)
Diptera (predator)
Neuroptera (predator)
Mantodea (predator)
Raphidioptera (predator)
Thysanoptera (predator)
Araneidae
Corinidae
Linyphidae
Liocranidae
Oxyopidae
Philodromidae
Salticidae
Theridiidae
Thomisidae
Uloboridae
Cantharidae
Carabidae
Coccinelidae
Malachiidae
Staphylinidae
Forficulidae
Asilidae
Empididae
Anthocoridae
Lygaeidae
Miridae
Nabidae
Reduviidae
Braconidae
Elasmidae
Encyrtidae
Eulophidae
Ichneumonidae
Pteromalidae
Scelionidae
Formicidae
Mantidae
Chrysopidae
Conipterygidae
Raphidiidae
Aeolothripidae

692 Fig. 3



693

694 Fig. 4


A
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An
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St
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Car
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As
Co
Ca
P. oleae
Predated eggs
B
3500
3000
2500
2000
1500
1000
NMDS axis 2
NMDS axis 1
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6

695