

Ground-covers affect the activity density of ground-dwelling predators and their impact on the Mediterranean fruit fly, *Ceratitis capitata*

J. Cruz-Miralles[®] · M. Guzzo[®] · M. V. Ibáñez-Gual[®] · Ó. Dembilio[®] · J. A. Jaques[®]

Received: 25 August 2022 / Accepted: 7 November 2022 / Published online: 12 November 2022 © The Author(s) 2022

Abstract Three developmental stages of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), can be found in the soil (late third instar larvae, pupae, and teneral adults). These stages are susceptible to predation by generalist ground-dwelling predators. Our objectives have been to investigate the association between ground cover management (bare soil, a seeded cover of *Festuca arundinacea* and a mulch of straw), the emergence success of *C. capitata*, and the activity density of the most important groups of ground-dwelling predators (spiders, beetles, ants and earwigs). As expected, *C. capitata* emergence was lower in a seeded cover of *Festuca arundinacea* (FA) and a mulch of straw (M) (10.2%) relative to bare soil (BS) (13.2%). This

Handling Editor: Eric Riddick.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10526-022-10168-0.

J. Cruz-Miralles · M. Guzzo · J. A. Jaques (⊠) Departament de Biologia, Bioquímica i Ciències Naturals, Escola Tècnica Superior de Tecnologia i Ciències Experimentals (ESTCE), Universitat Jaume I, Campus del Riu Sec, Av. Vicent Sos Baynat S/N, 12071-Castelló de la Plana, Spain e-mail: jacas@uji.es

J. Cruz-Miralles e-mail: cruzj@uji.es

M. Guzzo e-mail: guzzo@uji.es was related to higher diversity and activity density of ground-dwelling predators in FA and M compared to BS. The contribution of the ground-dwelling predators considered in this study to this reduction highlights the key role of beetles, earwigs and, to a lesser extent, ants, while the contribution of the most abundant group of ground-dwelling predators, spiders, remains unclear. Ground covers appear as a strong and sustainable conservation biological control method that should be taken into consideration for the management of *C. capitata* populations.

Keywords Tephritidae \cdot Medfly \cdot Ground-dwelling predator \cdot Mulch of straw \cdot Bare soil \cdot *Festuca arundinacea*

M. V. Ibáñez-Gual Departament de Matemàtiques, Universitat Jaume I, ESTCE, Campus del Riu Sec, Av. Vicent Sos Baynat S/N, 12071-Castelló de la Plana, Spain e-mail: mibanez@uji.es

Ó. Dembilio

Empresa de Transformación Agraria S.A., S.M.E., M.P. (TRAGSA), Av. Industria 26, 46980-Paterna, Spain e-mail: odembili@tragsa.es

Introduction

The Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Diptera: Tephritidae), is a highly invasive agricultural pest which has been reported on more than 300 plant species including fruits, vegetables and nuts (CABI 2019). Adult females cause fruit rotting after oviposition and the consequent larval activity on the fleshy mesocarp of mature fruits often resulting in complete yield loss. In temperate areas, most severe damage occurs in stone fruit, as well as citrus, where this species seeks refuge during winter (Jacas et al. 2010). Economic costs include direct crop losses, control and prevention of C. capitata infestation, both pre- and post-harvest, and limited or loss of access-free export markets. Total damage caused by tephritids in all production, harvesting, packing, and marketing worldwide were estimated to amount to more than two billion dollars annually (Enkerlin 2005).

Until recently, the control of C. capitata has been mostly based on the use of insecticides, which can be used as bait (together with a food attractant) or as cover sprays. Because no single measure can effectively control C. capitata infestations, these treatments have been often combined with alternative non-chemical methods including: (1) cultural practices like fruit bagging (CABI 2019) or removal and destruction of infested fruit (Chueca et al. 2013), (2) pheromone trapping, with different techniques like mass trapping or lure-and-kill (Navarro-Llopis et al. 2015), (3) biological control, either classical, augmentative, or conservation (Argov and Gazit 2008; Monzó et al. 2011), and (4) the sterile insect technique (Kouloussis et al. 2017), often in the context of area-wide control programs (Enkerlin et al. 2017; Pla et al. 2021). Unacceptable eco-toxicological sideeffects of pesticides, including the development of insecticide resistance in C. capitata (Guillem-Amat et al. 2020), has led to an increasingly reduced number of active substances available to target this pest. Thus, there is a clear need to develop more sustainable methods to control C. capitata. In this context, conservation biological control, aiming at enhancing the impact of resident natural enemies on C. capitata, should play an increasingly important role.

Three developmental stages of C. *capitata* can be found in the soil, namely late third instar larvae (LIII), which drop from fruit to the ground, burrow

in the soil, and form puparium, pupae, and teneral adults, which remain on the ground until they can fly. These stages are susceptible to predation by generalist ground-dwelling predators (Monzó et al. 2008). The establishment and management of an organic ground cover made of compost, straw or living grasses, is a common conservation biological control tool used to enhance the populations of these natural enemies but also other provisioning and regulating ecosystem services. Among organic ground covers, cover crops and straw mulching can be used in perennial crops like fruit orchards. They can also mitigate non-sustainable soil losses, frequent in many Mediterranean areas, associated with the expansion of drip irrigation on sloping terrain and the widespread use of glyphosate for weed control (Keestra et al. 2019). Cover crops often consist of inter-tree herbal strips, which may extend as a continuous cover across the orchard. They usually include Poaceae and Fabaceae selfregenerating species which selectively benefit natural enemies rather than their target phytophagous prey (Paredes et al. 2015). A cover crop based on the grass Festuca arundinacea L. (Poales: Poaceae) improved the natural control of mites (Aguilar-Fenollosa et al. 2011a), thrips (Aguilar-Fenollosa and Jacas 2013) and aphids (Gómez-Marco et al. 2015), and boosted the populations of ground-dwelling predators of C. capitata, including beetles of the families Carabidae and Staphylinidae and spiders of the family Lycosidae (Monzó et al. 2011), in citrus. Straw mulching has often been used with the main goal of suppressing weeds and preventing erosion (Prosdocimi et al. 2016). It can also boost the density of the grounddwelling predators (Johnson et al. 2004). Because this is the predator group of interest for a better control of C. capitata ground-dwelling stages, in this study we investigated the fate of late LIII of C. capitata associated with three soil management techniques (bare soil, a seeded cover of F. arundinacea, and a mulch of wheat straw) and the emergence of the resulting adults along the year. Further, we evaluated the effect of these techniques on the activity density of the main groups of generalist ground-dwelling predators. Our objectives were to investigate the association between ground cover management and (1) the emergence success of C. capitata; and (2) the abundance of the most important groups of ground-dwelling predators of C. capitata. We expected that enhanced activity of predators in a seeded cover of F. arundinacea and in a mulch of straw would reduce *C. capitata* successful development in these covers relative to bare soil.

Material and methods

Experimental orchard

Experiments were carried out from winter 2019 to autumn 2021 in a 1 ha citrus orchard located in Les Alqueries (province of Castelló, Spain, 39° 54'N, 00° 06'W). Trees were 20-year-old "Clemenules" mandarins [*Citrus clementina* Tanaka (Rutaceae)] grafted on citrange Carrizo (Poncirus trifoliata (L.) Rafinesque × Citrus sinensis (L.) Osbeck). Rows were 6 m apart from each other and followed a N-S orientation. Within rows, trees were spaced 4 m, dripirrigated, and maintained weed-free by herbicide treatments (glyphosate). Twenty-four adjacent trees in two consecutive rows (12 trees per row) in the middle of the orchard were removed in 2014 and replanted in late summer 2019 with two-year-old clementine trees (same scion-rootstock combination). These 24 trees were individually enclosed in an aluminum cage $(4 \times 4 \times 4 \text{ m})$ covered with a rigid nylon mesh $(10 \times 14 \text{ m})$ threads cm^{-2}) on all sides but one (the western side of the western row and the eastern side for the eastern row). These cages received one of the three ground management treatments considered in this study, which were randomly distributed within each of the rows (i.e., four cages per treatment per row).

The first treatment was bare soil (BS) by means of herbicide application (glyphosate+2-methyl-4-chlorophenoxyacetic acid-MCPA). The second treatment consisted of a homogeneous cover of F. arundinacea (FA; 'Fórmula Frutales y Cítricos', Semillas Fitó S.A., Barcelona, Spain), which was established in early autumn 2019 and subsequently mowed twice per season with grass clippings left in place. The third treatment consisted of a mulch of straw (M), which was also established in early autumn 2019 at a rate of 0.7 kg m⁻² and supplemented with the same amount of straw once per season. In all cases, the vicinity of the tree was maintained free of weeds, F. arundinacea, or straw by mechanical means. A datalogger (CEM, model DT-171; https://www.cem-instr uments.com/en/Product/detail/id/980), which continuously monitored temperature and RH values at 1-h intervals, was set in one of the cages. Daily rainfall measurements were obtained from the meteorological station of Vila-Real (http://riegos.ivia.es/lista do-de-estaciones/vila-real), located 5 km NW of the orchard.

Ceratitis capitata stock colony

The experiment was conducted using LIII (males and females) of Vienna 8^{D53-} GSS-Valencia genetic sexing strain obtained from a mass-rearing facility located in Caudete de las Fuentes (Valencia, Spain) (Pla et al. 2021). When LIII abandoned the diet in which they developed, they were collected in a container filled with water. These larvae were transferred to a 2 l container with water and kept at 12 °C until used in the experiments.

C. capitata management

From December 2019 to September 2021, once per month, around 1500 LIII were transferred to Universitat Jaume I (UJI) facilities and split in groups of 100. Two of these groups were kept in the laboratory and 12 were further processed in the field. One of the two laboratory groups was introduced into a 10 cm in diameter Petri dish and wrapped in aluminum foil, while the other one was set on top of a 21.5 cm diameter and 19 cm high pot containing a mixture of vermiculite and peat (1:3; vol:vol) watered to field capacity. Both groups were transferred to a climatic cabinet at 25:20 °C and a 16:8 L:D photoperiod. Subsequently, pupariation and adult emergence were scored. These values were used to correct values recorded for field-released insects (see below). The remaining 12 groups of LIII were eventually released in the field, two per treatment and row, which were randomly assigned to the corresponding treatment cages. LIII were released in an emergence trap (see Supplementary Fig. S1) consisting of a 15 cm long and 12 cm diameter toilet soil pipe fitted with a rubber band to a bottomless transparent plastic bottle of the same diameter and 35 cm long, with a zenithal ventilation hole covered with a mesh. Prior to the release, a hole of the same dimensions as the soil pipe was dug by carefully extracting a soil cylinder. Then the pipe was put in place and the previously drilled soil cylinder introduced into the pipe. LIII were transferred to the surface of the soil cylinder within the trap, which was covered with the bottomless bottle to protect them from predation. Two days later, when LIII should have burrowed in the soil to pupate, the bottles were removed and the number of individuals (either larvae or pupae) remaining on the top of the soil cylinder within trap were counted. This figure was considered as representative of larval mortality (i.e., individuals either dead or fully exposed to predation). Then, the trap was left uncovered to allow full exposure of the buried individuals (late LIII) to natural enemies and abiotic conditions. Based on the temperatures measured in the orchard, the thermal constant and the lower development threshold of C. capitata (260 degree-days and 11 °C, respectively; Escudero-Colomar et al. 2008), the emergence date was estimated. Two to three days before reaching that date, the bottomless bottle was put in place again to capture the emerging flies. The bottle included a transparent plastic sheet sprayed with tangle-trap®. Traps were inspected every 2-3 days and adults found stuck on the glue were counted and removed. The whole trap was removed after seven days with no captures. Field larval mortality and adult emergence (%) were calculated based on the number of larvae and adults counted. These percentages were corrected with the corresponding laboratory values (Abbott 1925).

Pitfall traps

To identify potential above-ground predators of C. capitata, a pitfall trap was set in one cage per treatment (three traps in total). Traps consisted of a plastic jar (12.5 cm diam., 12 cm depth), with a plastic funnel fitted to its upper edge. A plastic container (250 ml) half filled with a 3:1 mixture of water and ethanol, and 1.25% antifreeze, was placed inside the plastic cup. The three cages were selected at the beginning of the experiment and were not considered when assigning the emergence traps. Traps were serviced every 15 days. Captures were transported to the laboratory where they were sorted out. Specimens were categorized into the following generalist soil predator groups: beetles (carabids and staphylinids), earwigs, ants, and spiders (mostly lycosids). Although some species of Carabidae and Staphylinidae are herbivorous (Maddison et al. 2009; Rischen et al. 2021), we counted all specimens within these families as generalist soil-dwelling predatory beetles. Other ground-dwelling coleopteran families where predation does not prevail (i.e., Silphidae, Tenebrionidae) were excluded from this category. Counts were expressed as activity density (specimens collected/ days of trap activity).

Statistical analysis

Corrected larval mortality and adult emergence were modeled using Generalized Linear Mixed Models (GLMM) with a binomial distribution of the error and a logit link function. Ground-predator functional group activity density values were modeled using GLMM with a Gaussian distribution of the error and identity link function. In all cases, treatment (BS, FA, or M) was used as a fixed factor and the dates when emergence traps were set as a random factor. Once differences between treatments were established, the same variables were further analyzed in each cover separately. For larval mortality and adult emergence we used General Linear Models (GLM) with a binomial distribution of the error and a logit link function. For larval mortality, mean temperature and mean RH during the two days following larval release were used as fixed factors. For adult emergence we used the same factors referred to the whole period extending from larval release to adult emergence (which ranged from about eight days in summer to three months in winter), as well as the accumulated rainfall and the maximum activity density of spiders, beetles, ants, and earwigs recorded during that period. When modeling each predator group, we used a GLM with a Gaussian distribution of the error and identity link function and considered the same variables as for adult emergence but excluded the predator group modeled. Because we expected a non-linear relationship between the abiotic factors taken into account, the models included the effect of linear and quadratic combinations of these variables. Due to the high number of covariates in the models, no interactions among factors were considered. Models were refined by progressively removing non-significant (P > 0.05)factors. Akaike information criterion (AIC) (Akaike 1974) was used to select the best model. When necessary, pairwise comparisons were made using Tukey post-hoc test (P < 0.05). The R software (R Core Team 2021) was used to fit the models. Package *lme4* (Bates et al. 2015) was used to fit both GLMMs and GLMs, and package *multcomp* (Hothorn et al. 2008) was used to perform the pairwise comparisons.

Table 1 Statistics (*F*; *P*-value) of the GLMMs adjusted to larval mortality (AIC=3024.9) and adult emergence of *C. capitata* (AIC=2629.0), to spider, beetle, ant, and earwig activity density (AIC=944.4, 671.2, 857.7 and 329.7, respectively)

F	P-value	Mean ± SE		
		BS	М	FA
Larval mortality (%)				
99.78	< 0.001	$9.26 \pm 1.57^{\text{b}}$	$9.19 \pm 1.92^{\rm b}$	$15.06 \pm 1.51^{\mathrm{a}}$
Adult emergence (%)				
23.28	< 0.001	$13.17 \pm 1.85^{\mathrm{a}}$	10.46 ± 1.72^{b}	9.94 ± 1.66^{b}
Spider activity density (specimens per trap per day)				
84.56	< 0.001	3.63 ± 0.44^{c}	$10.45\pm0.87^{\rm a}$	7.26 ± 0.56^{b}
Beetle activity density (specimens per trap per day)				
80.23	< 0.001	$0.61 \pm 0.13^{\circ}$	$2.03\pm0.27^{\rm b}$	3.71 ± 0.37^{a}
Ant activity density (specimens per trap per day)				
17.38	< 0.001	1.44 ± 0.36^{b}	$2.38 \pm 0.30^{\rm b}$	3.06 ± 0.29^{a}
Earwig activity density (specimens per trap per day)				
26.07	< 0.010	0^{c}	1.12 ± 0.22^{a}	$0.39\pm0.07^{\rm b}$

Time was considered as a random factor and treatment (bare soil-BS, mulch of straw-M and *F. arundinacea* cover-FA) as a fixed factor; df were 2 and 237 for larval mortality and adult emergence, and 2 and 178 in all remaining cases except for earwigs, where df were 1 and 118. Within each row, means followed by the same letter are not different (Tukey's post-hoc test, P > 0.05)

Results

Mean daily values of temperature, RH and rainfall registered during the assays are shown in Supplementary Fig. S2 and S3. The mean temperature inside the cages ranged from 4.5 to 29.9 °C (mean: 18.0 °C). The absolute minimum and maximum temperatures ranged from -0.4 to 24.3 °C (mean 13.2 °C) and 6.0 to 37.9 °C (mean 23.5 °C), respectively. RH ranged from 32.6 to 97.9% (mean 68.8%). A total of 974.12 mm of rain were registered during the sampling period, with a mean of 40.0 mm per month, with four episodes of heavy rain (>40 mm in 24 h) on December 4, 2019; March 31, 2020; November 4, 2020; and April 22, 2021. Maximum and minimum mean monthly values of rainfall corresponded to November 2020 (126.0 mm) and February 2020 (0.6 mm), respectively.

Larval successful pupariation in the laboratory was 100%. As a consequence, field-collected data needed no correction. The GLMM fitted to these values showed significant differences between covers (Table 1). Highest mortality of *C. capitata* larvae

corresponded to FA (15.1%) and there were no significant differences between M and BS (9.2%). When the different covers were separately analyzed with GLMs considering temperature (T) and RH as random factors, the best fit included the linear and the quadratic forms of both factors with the exception of the linear form of RH in BS and its quadratic form in FA. Consequently, this factor was removed from the corresponding models (Supplementary Table S1). The relationship between T and RH and larval mortality was positive in all cases except for RH in M, where the relationship was negative. As a consequence, within the T range of this study, the higher the T, the higher larval mortality. The same applied to RH except in M, where the higher RH, the lower larval mortality.

Mean adult emergence under laboratory conditions was 92.1%, ranging from 82.0 to 99.0%. These values were used to correct the corresponding field monthly values. Although emergence traps set from December to February were maintained on site for up to three months, adult emergence was nil during these months on both seasons irrespective of the ground cover. These periods coincided with minimum temperatures mostly below 10 °C (Supplementary Fig. S2) and damp soil. As this situation precluded the establishment of an emergence date which could be used to close the period for the counting of grounddwelling predators, these periods had to be discarded for the GLMs relating adult emergence and predator activity density. A total of 759 predators were collected from December 2019 to September 2021; 347 specimens in M, 316 in FA and 96 in BS. The GLMMs fitted to adult emergence and to groundpredator group activity density showed that there were significant differences between covers (Table 1). Lowest adult emergence corresponded to M and FA (10.2%). Highest emergence occurred in BS (13.2%), where the activity density of spiders, beetles (carabids and staphylinids), ants and earwigs were lower than in the other two covers. Indeed, earwigs could not be found in BS. Activity density of spiders and earwigs were higher in M, as those of beetles and ants were in FA (Table 1). While spiders and beetles were active all year round, ants and earwigs were mostly absent during the coldest months. The GLMs used to explain adult emergence and predator activity density showed that the effect of the different factors



Fig. 1 Results of the GLMs explaining (1) adult *C. capitata* emergence as a function of the activity density of different ground-predator groups (spiders, beetles, earwigs and ants), as well as temperature (T), RH and rainfall (P), and (2) the activity density of each predator group as a function of those of the other predatory groups, T, RH and P in the three dif-

ferent ground covers treatments (bare soil-BS, mulch of straw-M and *F. arundinacea* cover-FA). Black and grey arrows and letters (T, RH, P) represent negative and positive correlations (P < 0.05), respectively (see Supplementary Tables S1-S6). Non-significant correlations are not shown

considered changed with the cover and species/group considered (Fig. 1).

Adult C. capitata emergence was negatively related to temperature in all covers. It was also negatively related to RH in FA and to rainfall in M but the opposite was observed in the other two covers (Supplementary Table S2). Adult emergence was also negatively related to beetle and earwig activity density irrespective of the cover, and to ant captures in FA. However, adult emergence was positively related to ant captures in the other two covers, similar to what was observed for spiders regardless of the cover considered. Spider activity density was negatively related to temperature, RH and rainfall in all three covers and was positively related to beetles in BS and FA, and to ants in M and FA (Supplementary Table S3). Beetle activity density was negatively related to temperature and RH in BS and M but was positively related to these factors in FA. Rainfall had differing effects on beetles. The effect was positive in BS but negative in FA. In general, beetle activity density was positively related to those of other predators except for ants in FA (Supplementary Table S4). Ants positively responded to temperature, RH and rainfall irrespective of the cover. Their relationship with other predator groups was mostly positive except for beetles in FA (Supplementary Table S5). Finally, earwigs, which could not be found in BS, were positively affected by temperature and RH in M only and showed a positive relationship with beetles and ants in M and FA (Supplementary Table S6).

Discussion

Our results show that, as expected, *C. capitata* emergence was lower in FA and M relative to BS, and this could be related to higher diversity and activity density of ground-dwelling predators in FA and M compared to BS. Both adult emergence and predator activity density depended on the abiotic factors

589

considered (temperature, RH and rainfall). Although the responses to these factors barely changed for spiders (mostly negative) and ants (mostly positive) irrespective of the cover, they did so for predatory beetles (positive in FA but negative in the other two covers) and for *C. capitata* (positive for temperature in all covers but diverse for the RH and rainfall) (Fig. 1).

Different studies have demonstrated that ground covers (either a crop or a mulch) partially intercept or reflect the solar radiation, thus reducing the radiation absorption of soil, which results in lower soil and air temperature nearby compared to bare soil. Additionally, fluctuation magnitude of soil temperature in soils with a ground cover is smaller (Ni et al. 2018; Yang et al. 2018). Cover crops also reduce soil bulk density and improve soil structure and hydraulic properties (Koudahe et al. 2022). Yang et al. (2018) demonstrated that a mulch of straw increased soil moisture compared to bare soil, while Ni et al. (2018) found that water content in vegetated soils depended on the season. While it was lower by up to 50% compared to bare soil during the summer, during autumn water content could be up to 70% higher, a consequence of low soil temperature inducing lower root water uptake. Based on these studies, we can infer that (1) BS was most probably exposed to wider daily and seasonal thermal fluctuations and lower water content compared to FA and to M, and (2) M most probably increased soil moisture compared to the other two covers independently of the season while FA decreased it in summer and increased it in winter.

Increased water retention could justify why rainfall positively affected survival of late LIII larvae but negatively affected below-ground development of C. *capitata* immature stages in M, whereas the opposite occurred in FA and BS. Quesada-Moraga et al. (2012), using a parametric model describing the effect of temperature and soil moisture on the probability of C. capitata completing the preimaginal development at different temperature-soil moisture combinations [15-35 °C and 1-17.0% (wt:wt)], concluded that adult emergence increased with increasing temperature and soil moisture, ranging from 32.1% at 15.0 °C and 1.0% wt:wt to 90.7% at 25.0 °C and 5.0% wt:wt, with a maximum of 91.6% emergence at 23.5° and 7% wt:wt. These results are consistent with contrasting conclusions from Bento et al. (2010) and Eskafi and Fernández (1990) but also with our observations for adult emergence in M compared to FA and BS. Bento et al (2010) established that *C. capitata* emergence was higher in drier soils, whereas Eskafi and Fernández (1990) concluded otherwise.

Reasons leading to predatory beetles responding positively to temperature, RH and rainfall in FA but mostly negatively to the same factors in BS and M could be related to the response of preferred food sources, including aphids, thrips and leafhoppers, which are common in *F. arundinacea* covers (Aguilar-Fenollosa et al. 2011b; Aguilar-Fenollosa and Jacas 2013; Gómez-Marco et al. 2015), contrary to M and BS. Although mites and springtails are abundant in mulches (Reddy et al. 1994), preferred prey for beetles was most probably absent in both covers. This situation would also explain lower relative abundance of beetles in BS (12%) and M (22%) compared to FA (44%).

Ants were the most abundant group of predators found by Urbaneja et al. (2006) in a similar study carried out in a citrus orchard with bare soil. Ants represented 83% of total catches, a value much higher than those found in our study (28, 21 and 17% in BS, M and FA, respectively). All the other groups of predators found by Urbaneja et al. (2006) represented less than 9%. This value is much lower than those found in our study, except for earwigs, as they could not be found in BS (Table 1). This could be related to lack of proper shelters to breed and thrive in this cover. Indeed, earwig population density in different agroecosystems has been shown to depend on the intensity of soil management (Moerkens et al. 2008; Huth et al. 2011). Interestingly, mean C. capitata adult emergence recorded along the year by Urbaneja et al. (2006) ranged from 13.8 to 31.6%, with nil values during the coldest months (November through February) and also in May, which coincide with our findings in BS. These authors pointed at ants as partly responsible for C. capitata predation. However, our results supported a negative relationship between ant activity density and adult emergence in FA only (Fig. 1). Although such a negative relationship could include predation as well as other interactions (i.e., competition, risk avoiding behavior), the setup of our experiments (use of sentinel larvae on top of soil) makes predation the most likely explanation for our observations. In our study, beetles and earwigs were negatively related to C. capitata emergence irrespective of the ground management (Fig. 1), which points at these two groups of predators as key for the natural regulation of C. capitata ground-dwelling stages. Surprisingly, the activity density of the most abundant predator group in our study, spiders, was not negatively related to C. capitata emergence in any of the three ground covers. This could be due to spiders feeding mostly on either LIII before burial or teneral adult flies but not on buried pupae. Although late LIII were taken into consideration in our assays, adults were excluded from potential predators, as the emergence traps were covered a few days before adult emergence. Indeed, Monzó et al. (2008) proved that Pardosa cribata Simon (Araneae, Lycosidae), the most abundant ground-dwelling spider in citrus in eastern Spain, could prey on both LIII and adults but not on pupae. These authors also showed a preference of P. cribata for adult fruit flies. Spiders were not negatively related to any other group of predators either (Fig. 1) and this could be interpreted as spiders most probably feeding on other arthropod groups not properly captured in pitfall traps, like aphids, thrips or leafhoppers in FA or mites and springtails in M, or even other spiders (Picchi et al. 2016). FA showed the most complex relationships between the arthropods considered in this study (Fig. 1), with three predatory groups (beetles, ants and earwigs) negatively related to C. capitata emergence and including the only case of intra-guild negative interactions, identified in this study (ants and beetles). Interestingly, both beetles and ants responded positively to temperature, RH and rainfall in FA, which could trigger an increase in the magnitude of those negative interactions. Such a situation did not repeat in the other two covers (dissimilar response to abiotic factors for ants and beetles in M and BS).

To sum up, our results demonstrate that bare soil, which is the ground cover management technique most widely used in Spanish fruit orchards (including citrus) in the Mediterranean area, is the least favorable for the conservation biological control of *C. capitata*. Lowest predator abundance was coupled with a 29.2% increased *C. capitata* adult emergence compared to the other two covers. Therefore, the implementation of a cover of either *F. arundinacea* or a mulch of straw should be considered as a tool to increase the impact of ground-dwelling predators on *C. capitata*. Although this increase in damage in a particular orchard and time, overall, the use of a cover of either a mulch of straw or *F. arundinacea* should

contribute to reduced damage caused by C. capitata, especially when this measure is applied to a large area in combination with others (area-wide IPM). The contribution of the different mortality factors considered in this study to this reduction highlights the key role of beetles, earwigs and, to a lesser extent, ants, while the contribution of the most abundant group of ground-dwelling predators, spiders, deserves further research. Although a detailed economic analysis would be needed, a cover of F. arundinacea, which can also favor the conservation along the year of natural enemies of other important fruit pests, like mites, thrips, and aphids (Aguilar-Fenollosa et al. 2011a, b, c; Aguilar-Fenollosa and Jacas 2013; Gómez-Marco et al. 2015; Gómez-Martínez et al. 2018), appears as a strong and sustainable conservation biological control method that should be taken into consideration for the management of C. capitata in fruit orchards.

Acknowledgements We thank M. Piquer (UJI) and A. Benages (COCALNI, Cooperativa Citrícola de Les Alqueries) for technical support and provision of the experimental orchard, respectively. Financial support has been provided by the European Union's Horizon 2020 Program for Research and Innovation grant number 818184 (FF-IPM) and PRIMA grant number 1812 (PLANT-B).

Author contributions JAJ and JCM conceived and designed research. JCM and MG conducted the experiments. OD contributed *C. capitata* larvae. JAJ, JCM, MG and MVI analyzed data. JAJ prepared the first draft of the manuscript, which was read, modified and eventually approved by all authors.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. Financial support has been provided by the European Union's Horizon 2020 Program for Research and Innovation grant number 818184 (FF-IPM) and PRIMA grant number 1812 (PLANT-B).

Data availability Raw data will be available at UJI public repository (http://repositori.uji.es/xmlui/).

Declarations

Competing interest Except for JAJ, who is member of the editorial board of BioControl, the authors have no additional competing interest to disclose.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included

in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Abbott WS (1925) A Method of computing the effectiveness of an insecticide. J Econ Entomol 18:265–267
- Aguilar-Fenollosa A, Jacas JA (2013) Effect of ground cover management on Thysanoptera (thrips) in clementine mandarin orchards. J Pest Sci 86:469–481
- Aguilar-Fenollosa A, Ibañez-Gual MV, Pascual-Ruiz S, Hurtado M, Jacas JA (2011a) Effect of ground-cover management on spider mites and their phytoseiid natural enemies in clementine mandarin orchards (II): top-down regulation mechanisms. Biol Control 59:171–179
- Aguilar-Fenollosa A, Ibañez-Gual MV, Pascual-Ruiz S, Hurtado M, Jacas JA (2011b) Effect of ground-cover management on spider mites and their phytoseiid natural enemies in clementine mandarin orchards (I): bottom-up regulation mechanisms. Biol Control 59:150–170
- Aguilar-Fenollosa A, Pascual-Ruiz S, Hurtado M, Jacas JA (2011c) Efficacy and economics of ground cover management as a conservation biological control strategy against *Tetranychus urticae* in clementine mandarin orchards. Crop Prot 30:1328–1333
- Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723
- Argov Y, Gazit T (2008) Biological control of the Mediterranean fruit fly in Israel: introduction and establishment of natural enemies. Biol Control 46:502–507
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48
- CABI (Centre for Agriculture and Bioscience International) (2019) invasive species compendium. http://www.cabi. org/isc/. Accessed 23 April 2022
- Chueca P, Garcerá C, Urbaneja A, Moltó E (2013) A new mechanised cultural practice to reduce *Ceratitis capitata* Wied. Populations in area-wide IPM. Span J Agric Res 4:1129–1136
- de Bento FMM, Marques RN, Costa MLZ, Walder JMM, Silva AP, Parra JRP (2010) Pupal development of *Ceratitis capitata* (Diptera: Tephritidae) and *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) at different moisture values in four soil types. Environ Entomol 39:1315–1322
- Enkerlin WR (2005) Impact of fruit fly control programmes using the sterile insect technique. In: Dyck VA, Hendrichs J, Robinson AS (eds) Sterile insect technique. Principles and practice in area-wide integrated pest management. Springer, Dordrecht, pp 651–676
- Enkerlin W, Gutiérrez Ruelas J, Pantaleón R, Soto Litera C, Villaseñor Cortés A, Zavala López JL, Orozco Dávila D, Montoya Gerardo P, Silva Villarreal L, Cotoc Roldán E, Hernández López F, Arenas Castillo A, Castellanos

Domínguez D, Valle Mora A, Rendón Arana P, Cáceres Barrios C, Midgarden D, Villatoro Villatoro C, Lira Prera E, Zelaya Estradé O, Castañeda Aldana R, López Culajay J, Ramírez y Ramírez F, Liedo Fernández P, Ortíz Moreno G, Reyes Flores J, Hendrichs J (2017) The moscamed regional programme: review of a success story of areawide sterile insect technique application. Entomol Exp Appl 164:188–203

- Escudero-Colomar LA, Vilajeliu M, Batllori L (2008) Seasonality in the occurrence of the Mediterranean fruit fly [*Ceratitis capitata* (Wied.)] in the north-east of Spain. J Appl Entomol 132:714–721
- Eskafi FM, Fernández A (1990) Larval–pupal mortality of Mediterranean fruit fly (Diptera: Tephritidae) from interaction of soil, moisture, and temperature. Environ Entomol 19:1666–1670
- Gómez-Marco F, Tena A, Jacas JA, Urbaneja A (2015) Early arrival of predators control *Aphis spiraecola* (Hemiptera: Aphididae) colonies in citrus clementine. J Pest Sci 89:69–79
- Gómez-Martínez MA, Jaques JA, Ibáñez-Gual MV, Pina T (2018) When the ground cover brings guests: is Anaphothrips obscurus a friend or a foe for the biological control of Tetranychus urticae in clementines? J Pest Sci 91:613–623
- Guillem-Amat A, Ureña E, López-Errasqín E, Navarro-Llopis V, Batterham P, Sánchez L, Perry T, Hernández-Crespo P, Ortego F (2020) Functional characterization and fitness cost of spinosad-resistant alleles in *Ceratitis capitata*. J Pest Sci 93:1043–1058
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363
- Huth C, Schirra KJ, Seitz A, Louis F (2011) A beneficial species becomes a pest — the common earwig *Forficula auricularia* (Linnaeus 1758). IOBC/WPRS Bull 67:249–256
- Jacas JA, Karamaouna F, Vercher R, Zappalà L (2010) Citrus pest management in the northern Mediterranean basin (Spain, Italy and Greece). In: Ciancio A, Mukerji K (eds) Integrated management of arthropod pests and insect borne diseases. Integrated management of plant pests and diseases, Springer, Dordrecht, pp 3–27
- Johnson JM, Hough-Goldstein JA, Vangessel MJ (2004) Effects of straw mulch on pest insects, predators, and weeds in watermelons and potatoes. Environ Entomol 33:1632–1643
- Keestra SD, Rodrigo-Comino J, Novara A, Giménez-Morera A, Pulido M, Di Prima S, Cerdà A (2019) Straw mulch as a sustainable solution to decrease runoff and erosion in glyphosate-treated clementine plantations in Eastern Spain. An assessment using rainfall simulation experiments. CATENA 174:95–103
- Koudahe K, Allen SC, Djaman K (2022) Critical review of the impact of cover crops on soil properties. Intl Soil Water Conserv Res 10:343–354
- Kouloussis NA, Gerofotis CD, Ioannou CS, Iliadis IV, Papadopoulos NT, Koveos DS (2017) Towards improving sterile insect technique: exposure to orange oil compounds increases sexual signalling and longevity in *Ceratitis capitata* males of the Vienna 8 GSS. PLoS ONE 12(11):e0188092

- Maddison DR, Moore W, Baker MD, Ellis TM, Ober KA, Cannone JJ, Gutell RR (2009) Monophyly of terrestrial adephagan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). Zool Scr 38(1):43–62
- Moerkens R, Leirs H, Peusens G, Gobin B (2008) Are populations of European earwigs, *Forficula auricularia*, density dependent? Entomol Exp Appl 130:198–2006
- Monzó C, Mollá Ó, Castañera P, Urbaneja A (2008) Activitydensity of *Pardosa cribata* in Spanish citrus orchards and its predatory capacity on *Ceratitis capitata* and *Myzus persicae*. Bio Control 54:393–402
- Monzó C, Sabater-Muñoz B, Urbaneja A, Castañera P (2011) The ground beetle *Pseudophonus rufipes* revealed as predator of *Ceratitis capitata* in citrus orchards. Biol Control 56:17–21
- Navarro-Llopis V, Primo J, Vacas S (2015) Bait station devices can improve mass trapping performance for the control of the Mediterranean fruit fly. Pest Manag Sci 71:923–927
- Ni J, Cheng Y, Wang Q, Wang Wang Ng C, Garg A (2018) Effects of vegetation on soil temperature and water content: field monitoring and numerical modelling. J Hydrol 571:494–502
- Paredes D, Cayuela L, Gurr G, Campos M (2015) Is ground cover vegetation an effective biological control enhancement strategy against olive pests? PLoS ONE 10(2):e0117265
- Picchi MS, Bocci G, Petacchi R, Entling MH (2016) Effects of local and landscape factors on spiders and olive fruit flies. Agric Ecosyst Environ 222:138–147
- Pla I, García de Oteyza J, Tur C, Martínez MA, Laurín MC, Alonso E, Martínez M, Martín A, Sanchis R, Navarro MC, Navarro MT, Argilés R, Briasco M, Dembilio O, Dalmau V (2021) Sterile insect technique programme against Mediterranean fruit fly in the Valencian community (Spain). Insects 12:415
- Prosdocimi M, Tarolli P, Cerdà A (2016) Mulching practices for reducing soil water erosion: a review. Earth-Sci Rev 161:191–203
- Quesada-Moraga E, Valverde-García P, Garrido-Jurado I (2012) The effect of temperature and soil moisture on the development of the preimaginal Mediterranean fruit Fly (Diptera: Tephritidae). Environ Entomol 41:966–970
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (Austria). https://www.r-project.org/
- Reddy MV, Reddy VR, Yule DF, Cogle AL, George PJ (1994) Decomposition of straw in relation to tillage, moisture, and arthropod abundance in a semi-arid tropical Alfisol. Biol Fert Soils 17:45–50
- Rischen T, Frenzel T, Fischer K (2021) Biodiversity in agricultural landscapes: different non-crop habitats increase diversity of ground-dwelling beetles (Coleoptera) but

support different communities. Biodivers Conserv 30:3965-3981

- Urbaneja A, Garcia-Marí F, Tortosa D, Navarro C, Vanaclocha P, Bargues L, Castañera P (2006) Influence of ground predators on the survival of the Mediterranean fruit fly pupae, *Ceratitis capitata*, in Spanish citrus orchards. Bio-Control 51:611–626
- Yang YH, Ding JL, Zhang YH, Wu J, Zhang J, Pan X, Giao C, Wang Y, He F (2018) Effects of tillage and mulching measures on soil moisture and temperature, photosynthetic characteristics and yield of winter wheat. Agric Water Manage 201:299–308

Joaquín Cruz-Miralles is an associate lecturer of Crop Production and Agricultural Entomology at the Department of Biology, Biochemistry and Natural Sciences of Universitat Jaume I (Spain). His areas of expertise include agricultural entomology and acarology, biological control, chemical ecology, zoophytophagy, and plant defence induction.

Michela Guzzo is a doctoral candidate at the Department of Biology, Biochemistry and Natural Sciences of Universitat Jaume I (Spain). Her research is focused on the understanding of the relationships between plants, pests and their natural enemies in citrus and the design of more sustainable protection practices in this crop.

M. Victoria Ibañez is a professor of probability and statistics at the Department of Mathematics of Universitat Jaume I (Spain). Her areas of expertise include spatial statistics, stochastic processes, image analysis, and statistical shape analysis. Research on more theoretical topics is accompanied by basic research applied to the fields of plant protection and health sciences.

Óscar Dembilio is a researcher at the public company TRAGSA (Spain). His areas of expertise include integrated pest management on different crops, focusing on biological control using the sterile insect technique against the medfly, *Ceratitis capitata*.

Josep A. Jaques is a full professor of crop production and agricultural entomology at the Department of Biology, Biochemistry and Natural Sciences of Universitat Jaume I (Spain). His areas of expertise include insect and mite biology, population ecology, pest management systems with emphasis on biological control, and pest risk analysis. His research is focused on the understanding of the relationships between plants, herbivorous, and carnivorous arthropods in different crops and their application to develop more sustainable crop protection practices.