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Top-down and bottom-up regulation of codling moth populations in cider apple orchards

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ABSTRACT

The success of biological control by natural enemies in agricultural crops relies on an understanding of the trophic interactions between natural enemies, pests and host plants. Top-down and bottom-up trophic effects, together with potential landscape and local-scale factors, may regulate pest populations. For two years, we analyzed codling moth populations (*Cydia pomonella*), their crop damage and their parasitoid communities in 26 low-input cider apple orchards in northern Spain. Codling moth abundance was estimated from overwintering larvae sampled with cardboard traps on trees, parasitism was estimated from parasitoids emerged from lab-reared moth larvae, and pest damage was assessed in apples before ripening. Codling moth abundance differed between orchards across years, and was positively correlated with apple production and the cover of apple plantations in the surrounding landscape. The effects of the apple production on codling moth abundance suggest bottom-up pest regulation. Apple damage in individual orchards reached 71%, but decreased with apple production, indicating codling moth satiation. Seven parasitoid species were recorded on codling moth larvae. Parasitism rate in individual orchards reached 42.5% of codling moth larvae. The number of parasitized larvae per orchard was positively related to parasitoid richness, but also to codling moth abundance, suggesting simultaneous top-down and bottom-up effects between parasitoids and pest. This study highlights the need to tackle the whole parasitoid-pest-plant system in order to better manage codling moth damage in orchards. The conservation of complementary parasitoid species through biodiversity-friendly actions should be combined with the control of apple production at the orchard- and landscape scale.

1. Introduction

The biological control of agricultural pests by natural enemies can offer effective solutions for avoiding crop damages while reducing the negative environmental and health impacts of chemical pesticides (Landis et al., 2000; Crowder and Jabbour 2014; Demestihas et al., 2017). Among these natural enemies, parasitoids are considered a highly effective group for biological control, thanks to their high diversity and specialization degree (Mason and Huber 1993; Godfray 1994). By impairing and eventually killing individual hosts (Godfray 1994), parasitoids can limit pest populations (Waage and Hassell 1982; Gerling et al., 2001), ultimately reducing crop damages and providing an ecosystem service valued at billions of dollars annually (Losey and Vaughan 2006; Crowder and Jabbour 2014). Importantly, the richness of parasitoid assemblages may be important in modulating their potential for biological control, as different species may render additive and complementary roles in hampering pests (Straub and Snyder 2006; Peralta et al., 2014). In fact, several studies have evidenced the positive effects of parasitoid richness on both the magnitude and the temporal stability of parasitism rates (Ives et al., 2005; Snyder et al., 2006; Tylianakis et al., 2006).

Pest population dynamics are frequently regulated not only by the top-down forces expected in natural enemy-pest interactions but also by bottom-up forces via their host plants, with the availability of food resources (i.e. crops) limiting pest population growth (Singer and Stireman 2005; Walker et al., 2008; Vidal and Murphy 2018). Consequently, a crop management system which decreases the access of pests to specific food resources, as for example by increasing within-crop species or

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genetic diversity, may lead to reduced pest damage (Root 1973; Smith and McSorley 2000). Establishing effective measures for the parasitoid-based biological control of crop pests therefore requires an integrative understanding of both top-down and bottom-up mechanisms simultaneously operating in all three levels of parasitoid-pest-plant interactions (Singer and Stireman 2005; Peralta et al., 2014).

Interactions between parasitoids, pests and crops may be shaped by the environmental heterogeneity inherent to agroecosystems at different (i.e. local and landscape) scales. The habitats adjacent to crop fields may be a source of complementary or alternative food sources for parasitoids (Bianchi and Wäckers 2008; Gillespie et al., 2016), or even pests in cases where they are fields of the same crop type (Ricci et al., 2009). Furthermore, spillover of insects to crops may be affected by not only the quality, but also the connectivity of surrounding habitats (Dennis et al., 2003; Hiebeler and Morin 2007). Thus, by affecting the population size of parasitoids and pests, local- and landscape-scale habitat variability may affect their trophic interactions, and hence the relative strength of both top-down and bottom-up relationships (Hunter and Price 1992; Maalouly et al., 2013; Šigut et al., 2018).

Codling moth (*Cydia pomonella* (L.), Lepidoptera: Tortricidae) is one of the most detrimental and economically serious pests in apple (*Malus* x *domestica* Borkh) orchards worldwide (Blommer 1994; Beers et al., 2003). In the absence of management, codling moth, a multivoltine species that may attack the fruit several times before harvesting, can lead to an almost complete loss of apple crops (Mills 2005). Its control is mostly based on broad-spectrum insecticides and mating disruption (Reyes et al., 2007; Witzgall et al., 2008). Although a varied assemblage of parasitoids has been described for codling moth in apple orchards (e.g. Athanassov et al., 1997; Cross et al., 1999; Mills 2005), in general, their effect on biological control in intensive orchards is considered ineffective due to their insufficiency (Thorpe et al., 2016) or dependency on the environmental context (Maalouy et al., 2013). Nevertheless, little is in fact known of the potential for biological control of codling moths in low-input orchards, where use of pesticides is minimal so there is consequently less disruption of natural enemies. Such a less disturbed scenario may allow to unravel the functioning of the parasitoid-codling moth-apple interaction.

In the present study, we explored parasitoid top-down and apple bottom-up effects on codling moth abundance and the damage it caused in low-input cider apple orchards in northern Spain. Both trophic forces were evaluated taking into account the potential effects of landscape- and local-scale factors. Specifically, we sought to explore: (1) codling moth abundance and its associated damage to apple production across years and orchards; (2) the bottom-up effects of the host apple plant on codling moth abundance and its associated damage; (3) the composition of the parasitoid assemblage attacking the codling moth across years and orchards; and (4) the top-down effects of parasitoid richness, and the bottom-up effects of codling moth abundance, on parasitized codling moth larvae. We then interpreted these findings in terms of management recommendations for promoting pest control by natural enemies.

2. Materials and methods

2.1. Study system and spatial sampling design

The study was conducted in the cider apple crop area of Asturias (N Spain) (Fig. A1). In this region, cider is a valuable traditional product, which is strongly ingrained in society, linked to tourism, gastronomy, leisure and an important source of income. The majority of cider apple orchards are relatively small (most cover between 0.5 and 4 ha), are extensively or semi-extensively managed and comprised of local cultivars. Extensive traditional orchards of randomly distributed cultivars are grown on seedling rootstocks (100–250 trees/ha), but new orchards are grown on semi-dwarfing rootstocks with cultivars distributed in rows (500–650 trees/ha). Apple trees in these production systems have large, dense canopies, reaching frequently more than 5 m high. Apple orchards in Asturias experience notable biennial bearing, with heavy yields in the odd years and lower yields in the even ones.

Orchards are embedded in a highly variegated traditional landscape, containing a fine-grained mosaic of land-uses, such as orchards, livestock pastures, other fruit plantations (e.g. blueberry, kiwifruit), timber (mainly eucalyptus) plantations, semi-natural woody vegetation patches (e.g. temperate broad-leaved forest, riparian forest), and human infrastructures. At the small scale of their immediate neighbourhoods, apple orchards are typically surrounded, either totally or partially, by natural woody vegetation in the form of hedgerows. Farmers use local cultivars tolerant to most common apple diseases (e.g. canker, scab, powdery mildew) and have high tolerance to pests, as most of them are not perceived as severe threats to productivity (Martínez-Sastre et al., 2020). As a consequence, farmers control pests according to their own perceptions and following personal schemes and, as a result, the use of pesticides in these orchards is very low, and often even null. We were able to collect data on sprayings from some of the orchards studied, and the total annual number of pesticide sprayings per orchard ranged from 0 to 2 (except in one organic orchard that sprayed six times; four of which with granulosis virus against codling moth). In non-organic orchards spraying against codling moth was with difubenzuron sprayings. Only one orchard applied a broad-spectrum insecticide (lambda-cyhalothrin). Nevertheless, the high number of codling moth recorded in almost all the orchards suggests limited and weak control of codling moth by farmers. In the region, the codling moth has two generations, the second being incomplete (Miñarro 2006).

Sampling was conducted in the years 2015 and 2016 in 26 semi-extensive cider apple orchards distributed over 600 km^2 (Fig. A1). Orchards were chosen to represent a gradient of variability in the environmental conditions within apple orchards (i.e. tree trunk diameter, orchard size, canopy cover) and in the surrounding landscape (i.e. cover of semi-natural habitats, pastures, apple orchards). In each orchard, we established a 25 m radius sampling station within the plantation, close but at least 25 m away from the orchard edge. Each sampling station comprised around 100 trees of which ten were randomly selected (hereafter, focal trees) among those with medium to high apple load and with the criterion of comprising trees from several cultivars, in order to minimize a potential cultivar effect on the results.

2.2. Sampling of codling moth and parasitoids and estimation of crop damage and production

We sampled codling moth larvae using traps made of 10 cm wide corrugated cardboard bands wrapped around the trunk of selected trees (40 cm above the ground and always under the first branch) (Fig. B1). The traps intercept larvae when they are moving from apples to the ground, and they use the spaces provided by the corrugated cardboard as shelter for pupation and overwintering. We covered all traps with a plastic mesh until collection, to protect them from moisture and animals (e.g. snails). Traps were installed in mid-July and collected in mid-December, and then stored at 5 °C until mid-February allowing larvae to diapause.

We counted codling moth larvae collected, differentiating between males and females by the presence or absence of male gonads, visible through the tegument (MacLellan 1972). In addition, we identified a group of codling moth larvae that were conspicuously small (hereafter, small size larvae). In such larvae, development has been blocked due to parasitism (Reed-Larsen and Brown 1990). In addition to the codling moth larvae cocoons, ectoparasitoid cocoons were also identified in the cardboard traps and were counted, collected and stored in individual vials for rearing.

In each orchard, the average number of codling moth larvae per tree per orchard (hereafter, *CM abundance*) was estimated across cardboard traps from the sum of alive codling moth larvae (females, males and small size larvae), dead codling moth larvae (killed by various unknown causes), ectoparasitoid cocoons (as each ectoparasitoid comes from a codling moth larva), and marks indicating pecking by birds. Although signs of pecking were scarce, we estimated the number of larvae that could have been eliminated by birds. For that, we calculated the number of larvae per unit area in the undamaged part of the cardboard trap and then estimated the number of bird-predated larvae by considering the size of the area damaged by pecks.

To estimate apple damage rate caused by codling moth (hereafter, *CM damage*) per orchard and year, we randomly collected from each focal tree 10 apples from the tree canopy and 10 apples from the ground below the tree around one week before harvest. All apples were cut in half *in situ* to look for signs of codling moth damage (e.g. larvae inside, galleries, frass), allowing us to calculate the average percentage of apples damaged per tree.

We quantified apple production per orchard per year, estimated as the average number of apples of the focal trees within each sampling station. Number of apples per tree were estimated before harvest from the average number of apples on 10 branches extrapolated to the total number of branches per tree.

In order to determine the level of parasitism (i.e. the number of larvae attacked by parasitoids) we selected, from the codling moths collected from traps in each orchard, a subsample of 50 females, 50 males and 50 small size larvae per orchard. The three types of larvae were placed in different plastic containers with new corrugated cardboard bands for shelter, and reared at 25 ± 1 °C and a 16 h/8 h light/dark photophase. Samples were monitored periodically for the emergence of both codling moth and parasitoid adults. Emerged parasitoids were kept individually in Eppendorf tubes at −20 °C until species identification (Athanassov et al., 1997; Graham 1969; Peters and Baur 2011).

We estimated the total number of parasitized codling moth larvae per orchard (hereafter, *number of parasitized larvae*). For this, firstly, we extrapolated the proportion of parasitoids emerged from the reared male and female codling moth subsamples (number of parasitoid emerged/parasitoid emerged + codling moth emerged) (Miñarro and Dapena 2004; Maalouly et al., 2013) to the number of female and male codling moth larvae counted in that orchard. Secondly, all small size larvae were also considered as parasitized codling moth (Reed-Larsen and Brown 1990), irrespective of parasitoid emergence or not from each subsample after rearing. We quantified the total number of parasitized codling moth larvae per orchard as the cumulative number of estimated male and female parasitized larvae, plus the number of small size larvae, plus the number of recorded ectoparasitoids. We also estimated a *parasitism rate*, i.e., the percentage of parasitized larvae in relation to the total number of overwintering codling moth larvae per orchard. Finally, the richness of parasitoids per orchard and year (hereafter, *parasitoid richness*) was estimated as the cumulative number of parasitoid species emerged from larvae samples and the ectoparasitoid species found in each orchard.

2.3. Landscape and local-scale features

Landscape structure was quantified by means of a Geographic Information System of the study area (GIS, ArcGIS9.3) based on 1:5000-scale orthophotographs (2014). Different types of cover were digitized in order to include four main habitats assumed to potentially affect codling moth and parasitoids: (1) semi-natural woody vegetation, (2) pastures and meadows, (3) apple plantations and (4) exotic tree plantations (mainly eucalyptus). Semi-natural woody vegetation included forest patches of variable size, hedgerows, and isolated trees, but excluded scrubland patches. We estimated the availability of the different habitats within a 1 km-radius circular plot centered on the sampling station of each orchard. This spatial scale fits with the long flight distances of parasitoids and codling moth adults (Yu et al., 2009; Pajač et al., 2011).

As local-scale features that can affect codling moth and parasitoids, we measured: (1) orchard size, (2) the amount of cover by apple tree canopy in each sampling station (hereafter, apple canopy cover; from a GIS layer of apple canopy projection), (3) apple tree trunk diameter (average from 25 trees within each sampling station), (4) the proportion of surrounding hedgerows and, (5) the proportion of apple plantations, both (4) and (5) being estimated within a circular plot of 125 m radius centered on the sampling station (hereafter, hedgerows R125 and apple plantation R125 respectively; from a GIS layer).

2.4. Statistical analysis

We compared CM abundance and CM damage among orchards by using Kruskall-Wallis tests (trees as sampling units) and between years with paired t-tests (orchards as sampling units). Parasitoid richness and parasitism rate per orchard were compared between years with paired Wilcoxon tests, whereas the number of parasitized larvae per orchard was compared between years with a paired *t*-test. All variables were checked for normality prior to tests, and CM abundance (sqrt) and number of parasitized larvae (log) were transformed. Analyses were performed using functions in the package *stats* (R Core Team 2013).

We sought to analyze the different trophic interactions between apple crop, codling moth and parasitoids, taking into account potential environment effects. To do this, we applied Generalized Linear Mixed Models (GLMMs; Bolker et al., 2009), considering CM abundance (sqrt), CM damage and number of parasitized larvae (log) as different response variables (all of which were checked for normality, and thus models considered Gaussian distribution and identity link). Trophic interactions were first analyzed by means of simple “trophic models”, searching for observational evidence of bottom-up and top-down forces. These simple trophic models included a specific pest-plant or parasitoid-pest interaction and the potential effects of landscape- or local-scale features. Hence, one model searched for bottom-up (plant→pest) effects on codling moth by checking the relationships between apple production per orchard (predictor) and CM abundance and CM damage (response variables). Another model searched for bottom-up (pest→parasitoids) and top-down (parasitoids→pest) effects between codling moth and parasitoids by checking the relationships between the number of parasitized larvae per orchard (response) and CM abundance (bottom-up predictor) and parasitoid richness (top-down predictor).

To evaluate the role of the environment, we widened the previous trophic models by incorporating, as additional predictors, landscape- and local-scale variables. Because of the large number of environmental variables, we did not include all variables at once in single extended models (Frost 2019; see Ricci et al., 2009, for a similar rationale). Thus, for each response variable, a “local-scale” extended model included, as additional predictors, orchard size, hedgerows R125, apple plantation R125, apple canopy cover, tree trunk diameter, and apple production. Similarly, a “landscape” extended model included, as additional predictors, the covers of apple plantation, semi-natural habitat, pastures and exotic trees. All main predictors were initially included in the full extended models, but, to avoid over-parameterization and overfitting, those terms that were non-significant ($P > 0.05$) were excluded in a backward stepwise procedure to select the simplest model, using likelihood ratio tests. Finally, we combined, for each trophic interaction, the selected “local-scale” and “landscape-scale” variables which were significant in a last GLMM.

All GLMMs included year as a fixed factor and orchard identity as a random factor given that all orchards were replicated across all years (Bolker et al., 2009). The marginal and conditional R^2 were calculated to assess the amount of variance explained by the fixed and random effects, respectively (Nakagawa and Schielzeth 2013). Means ± Standard Deviation (SD) are shown throughout the text. GLMMs were performed using the package *nlme* (Pinheiro et al., 2020).

All statistical analyses were performed using the software package R, version 3.5.3.

3. Results

3.1. Codling moth abundance and crop damage

A total of 16,536 larvae were collected from the cardboard traps (7618 in 2015, 8918 in 2016). CM abundance per cardboard trap ranged from 1 to 99 (32.43 ± 27.00) in 2015 and 1 to 89 (37.26 ± 25.87) in 2016. While CM abundance was not significantly different between years, it did vary significantly between orchards each year (Fig. C1A; Table D1).

Codling moth damage to apples varied significantly between orchards and years (Fig. C1B; Table D1). CM damage per orchard ranged from 1.50% to 49.00% in 2015 and from 14.58% to 70.93% in 2016. Damage, overall, was greater in 2016 (42.75% ± 16.39; mean ± SD) than in 2015 (21.40% ± 15.76).

3.2. Determinants of codling moth abundance and crop damage

The best model in terms of bottom-up effects on codling moth populations, after taking into account local- and landscape-scale factors (Table E1 and E2), showed a positive significant response of CM abundance to apple production, apple plantation R125 and year (2016) (Table 1, Fig. 1 A and B).

In contrast, the best model for bottom-up effects on codling moth damage to apples (Table E1 and E2) found a negative significant effect of apple production (Table 1, Fig. 1C), i.e. higher yields lead to lower damage rates. Again, a positive significant effect of year (2016) on CM damage was found (Table 1).

3.3. Codling moth parasitoid assemblage

We found seven parasitoid hymenoptera species from four families (Table 2). Three species accounted for 94.9% of individuals of the parasitoid assemblage and were widerspread across orchards: *Ascogaster quadridentata* (Wesmael) (1148 individuals, 66.3% of individuals, 20 orchards in 2015 and 22 in 2016); *Pristomerus vulnerator* (Panzer) (298 and 17.2% of individuals, 9 orchards in 2015 and 14 in 2016); *Trichomma enecator* (Rossius) (197 and 11.4%, 13 orchards in 2015 and 11 in 2016) (Figs. F1–F2). Less frequent species, which included *Liotryphon caudatus* (Ratzeburg) (45 individuals), *Nippocryptus vittatorius* (Jurine) (31), *Dibrachys cavus* (Walker) (5) and *Perilampus tristis* (Mayr) (8), accounted in total for 5.1% of individuals (Table 2, Fig. F2).

We found a total of 1732 parasitized larvae (641 in 2015, 1091 in 2016) (Table 2). The number of parasitized larvae ranged from 0 to 190 per orchard and year (35.44 ± 43.85) (Fig. F2). No differences in the number of parasitized larvae were detected between years (Table D1).

Table 1
Final Generalized Linear Mixed Models evaluating bottom-up effects on codling moth abundance and damage taking into account local- and landscape-scale factors (Gaussian distribution, identity link). The variance (±SD) estimate for orchard identity, considered as a random factor, is also shown.

CM abundance	R^{2}m 0.282; R^{2}c 0.630		
Predictors	Estimate± SE	t	p
Intercept	1.192 ± 1.132		
Apple production	0.003 ± <0.001	3.469	0.002
Apple plantationR125	3.993 ± 1.833	2.179	0.039
Year (2016)	1.805 ± 0.566	3.188	0.005
Orchard (random factor)	1.317 ± 1.360		
CM damage	**R^{2}m 0.400; R^{2}c 0.721**		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.343 ± 0.058		
Apple production	−0.001 ± <0.001	−2.727	0.013
Year (2016)	0.143 ± 0.043	3.320	0.003
Orchard (random factor)	0.111 ± 0.103		

Table 2
Number of codling moth larvae (percentage of relative abundance in brackets) parasitized by different parasitoid species per year and in total.

Species	Family	2015	2016	Total
Ascogaster quadridentata	Braconidae	318 (49.6%)	830 (76.1%)	1148 (66.3%)
Pristomerus vulnerator	Ichneumonidae	152 (23.6%)	146 (13.4%)	298 (17.2%)
Trichomma enecator	Ichneumonidae	128 (20.1%)	69 (6.4%)	197 (11.4%)
Liotryphon caudatus	Ichneumonidae	13 (2.0%)	32 (2.8%)	45 (2.6%)
Nippocryptus vittatorius	Ichneumonidae	26 (4.1%)	5 (0.5%)	31 (1.7%)
Perilampus tristis	Perilampidae	0 (0.0%)	8 (0.7%)	8 (0.5%)
Dibrachys cavus	Pteromalidae	4 (0.6%)	1 (0.1%)	5 (0.3%)
Total		641 (100%)	1091 (100%)	1732 (100%)

The number of parasitoid species found in 2015 and 2016 was 6 and 7, respectively. There were no significant differences between years in parasitoid richness (Table D1, Fig. F1), but parasitism rate was significantly higher in 2016 (14.55 ± 11.91%; range: 0–42.45%) than in 2015 (8.57 ± 7.15%; 0–24.12%) (Table D1; Fig. C1C).

3.4. Determinants of the number of parasitized larvae

The number of parasitized larvae per orchard was positively affected by parasitoid richness as well as CM abundance (Table 3, Fig. 2). No effects of local- or landscape-scale variables were detected (Table E1 and E2).

4. Discussion

In this work, we disentangle the trophic interactions between apple and codling moth and its parasitoids in cider apple orchards while simultaneously searching for landscape- and local-scale features that might affect these interactions. In the 26 cider-apple orchards monitored for two years, codling moth populations were able to reach high densities per tree, damaging up to 70.9% of the apple crop. Seven parasitoid species attacked codling moth, parasitism rates reaching 42.5%. By analyzing each trophic interaction we detected positive effects of resource availability (i.e. apple production and apple plantations) on codling moth abundance. However, damage by this pest proportionally decreased with apple production, suggesting the satiation of the pest under high resource availability. Moreover, codling moth parasitism increased with parasitoid richness and codling moth abundance. Our study thus suggests that simultaneous top-down and bottom-up forces across the interaction triad parasitoids-pest-plant could be important and even necessary to control codling moth in apple crops. We discuss below the possible consequences of these interactions in low-input systems, in relation to the promotion of biological control by parasitoids with potential benefits for cider apple production.

Table 3
Final Generalized Linear Mixed Model evaluating bottom-up and top-down effects on number of parasitized larvae taking into account local-scale and landscape effects (Gaussian distribution, identity link). The variance (±SD) estimate for orchard identity, considered as a random factor, is also shown.

Number of parasitized larvae	R^{2}m 0.680; R^{2}c 0.680		
Predictors	Estimate± SE	t	p
Intercept	0.638 ± 0.258		
Parasitoid richness	0.701 ± 0.099	7.110	<0.001
CM abundance	0.014 ± 0.005	2.744	0.013
Orchard (random factor)	0.003 ± 0.803		

4.1. Codling moth abundance and crop damage

Average codling moth damage to apples per year was 21% in 2015 and 43% in 2016, and more than 30 larvae on average were trapped on each tree. These high values are inconceivable in intensive orchards producing dessert apples, where the abundance of codling moth is less than a few larvae per tree (Ricci et al., 2009; Monteiro et al., 2013) and apple damage is typically below the economic threshold of 1% (Cross et al., 1999). However, the high codling moth abundances and damage levels recorded in our cider orchards are not surprising taking into account the high tolerance level of local farmers to pests and the lack of regular applications of pest control techniques in the region.

The population of codling moth was stable across years but highly variable among orchards each year. Thus, orchards with a higher proportion of apple orchards in the immediate surroundings (125 m radius) and larger apple yields had higher numbers of codling moth. Both these factors can be considered an estimate for host density (i.e. availability of resources), at different spatial scales, and taken together suggest a bottom-up regulation of codling moth populations. We did not detect landscape effects at the larger scale (1 km radius), supporting the results of Ricci et al. (2009), who found major environmental effects on codling moth abundance at distances below 150 m.

Despite a stable codling moth population across years, apple damage in 2016 (42.7%) was double that of 2015 (21.3%). As commented earlier, apple orchards in Asturias experience notable biennial bearing, and 2015 was a year of heavier yields than 2016 (we counted 2.5 times more apples per tree in 2015 (689 ± 346) than in 2016 (270 ± 212); paired *t*-test for difference between years; $P < 0.001$). This decrease in pest attack rate associated with the year of high yield seems to be the result of a satiation process by which the population of the specialist herbivore is unable to respond numerically or functionally to resource overyielding (Kelly 1994; Kelly and Sork 2002). In our case, codling moth abundance and, hence, the estimated amount of apples damaged, remained stable across years, indicating that changes in percentage of damage depended on yield dynamics (i.e. the total number of apples) rather than on changes in pest population size. Thus, the results here demonstrate that although biennial bearing led to a dilution of codling moth attack, this reproductive strategy did not seem to ultimately regulate pest population size. A similar pattern was found in these orchards for the apple blossom weevil (*Anthonomus pomorum* L.), a specialist pest also totally dependent on apple trees (in this case flowers) for reproduction (Miñarro and García 2018). Anyway, the present study was restricted to two years, thus covering only one cycle of biennial fruit production. It would be interesting to see if the observed pattern is confirmed over a longer time.

4.2. Codling moth parasitism

The parasitoid richness in these low-input orchards was high in comparison with that recorded in more intensive orchards (e.g. Maalouly et al., 2013; 2015). We found a parasitoid assemblage of seven species attacking codling moth that was stable across years and sites. All the parasitoid species found are among those known to attack codling moth in Europe, with the three dominant parasitoids in the study area (*A. quadridentata, P. vulnerator, T. enecator*) also being the most frequent across European orchards (Athanassov et al., 1997; Cross et al., 1999; Mills 2005). *Dibrachys cavus* and *P. tristis* can also act as hyperparasitoids but their disturbing effect on overall parasitism is unlikely in the study area given their low occurrence in the sample (<1%). The community of codling moth parasitoids was highly heterogeneous not only in taxonomic but also in functional terms. As such, these seven species (belonging to different genus) represent a wide gradient of morphological, behavioural, and physiological variability observed in body size (e.g. the four ichneumonid species are clearly larger), adult emergence phenology (large species emerge before codling moth whereas small species emerge later (Miñarro and Dapena 2004)) or, interestingly, host stage attacked: egg (*A. quadridentata*), young larvae (*P. vulnerator, P. tristis*), older larvae (*T. enecator*) and cocoon (*L. caudatus, D. cavus*) (Athanassov et al., 1997; Mills 2005). This variability suggests high functional diversity and explicit niche segregation that can partially avoid spatial and temporal competition among parasitoid species and so enhance pest control (Finke and Snyder 2008; Cancino et al., 2014).

The number of parasitized larvae per orchard was positively related to not only parasitoid richness, but also to codling moth abundance, suggesting simultaneous top-down and bottom-up effects between parasitoids and pest. Regarding the top-down effects, we can assume that the biological control of codling moth increases as the result of the additive effects of the incorporation of different parasitoid species with complementary roles (Finke and Snyder 2008; Peralta et al., 2014). As mentioned above, such complementarity arises from the segregation of ecological niches between parasitoids in order that they can exploit the trophic resource (i.e. pest) while avoiding interspecific competition (Finke and Snyder 2008; Poisot et al., 2013). The bottom-up effects of pest abundance on number of parasitized larvae are not surprising given the high dependence of parasitoids on host abundance (Hassell 2000) and the fact that more available hosts would enable more parasitized larvae.

Parasitoids provided a parasitism rate that ranged from 0 to 42.5% across orchards and averaged 14.5% or 8.6%, depending on the year. This means a reduction of up to 42.5% in the number of emerged moths in the next generation. Studies in high-input orchards have reported very low parasitism rates (<5% on average) (Maalouly et al., 2013; Monteiro et al., 2013), probably as a consequence of pesticide use, not only in the orchard itself but also in surrounding ones (Ricci et al., 2009; Mates et al., 2012; Monteiro et al., 2013). This indicates that, as a general recommendation, the use and spectrum of pesticides should be reduced for the conservation of parasitoid communities.

4.3. Conclusions and implications for management

Populations of codling moth in the study area remained stable across years and were favoured by the host plant: number of apples at the orchard scale and cover of apple orchards at the surrounding-landscape scale. However, damage by this pest depended on yield dynamics and proportionally decreased with apple production, suggesting a satiation of the pest under high resource availability. In line with this, farmers should, evidently, first try to reduce codling moth populations, preferably with techniques compatible with biological control. Importantly, neighbouring farmers should coordinate their actions to reduce codling moth spreading between orchards. Second, farmers face the challenge of trying to increase and to stabilize apple yields in order to have a high and predictable percentage of apples undamaged every year as a consequence of the satiation process.

Our results show that, undoubtedly, parasitoids can exert a notable reduction in the codling moth population (up to 42% in certain orchards). This top-down effect is enhanced by parasitoid species richness providing more functionally diverse communities and, hence, apple crops should be managed accordingly to ensure such parasitoid diversity. We did not detect any landscape- or local factors driving parasitoid communities that allow us to make specific management recommendations. Nevertheless, it is well known that general biodiversity-friendly actions, such as promoting environmental heterogeneity, floral resources or alternative hosts at local- and landscape scales, help the conservation and promotion of parasitoid communities (MacFadyen et al., 2011; Gillespie et al., 2016).

Codling moth feeds directly on the commercial product (i.e. apples) and, consequently, the tolerance threshold for this pest in dessert apple crops is very low (usually <1% of damage; Cross et al., 1999). Although this threshold would evidently be higher in the case of cider apple, the high values of abundance and damage of codling moth reflect that biological control, by itself, is not strong enough to maintain codling moth populations and crop damage below reasonable thresholds. This

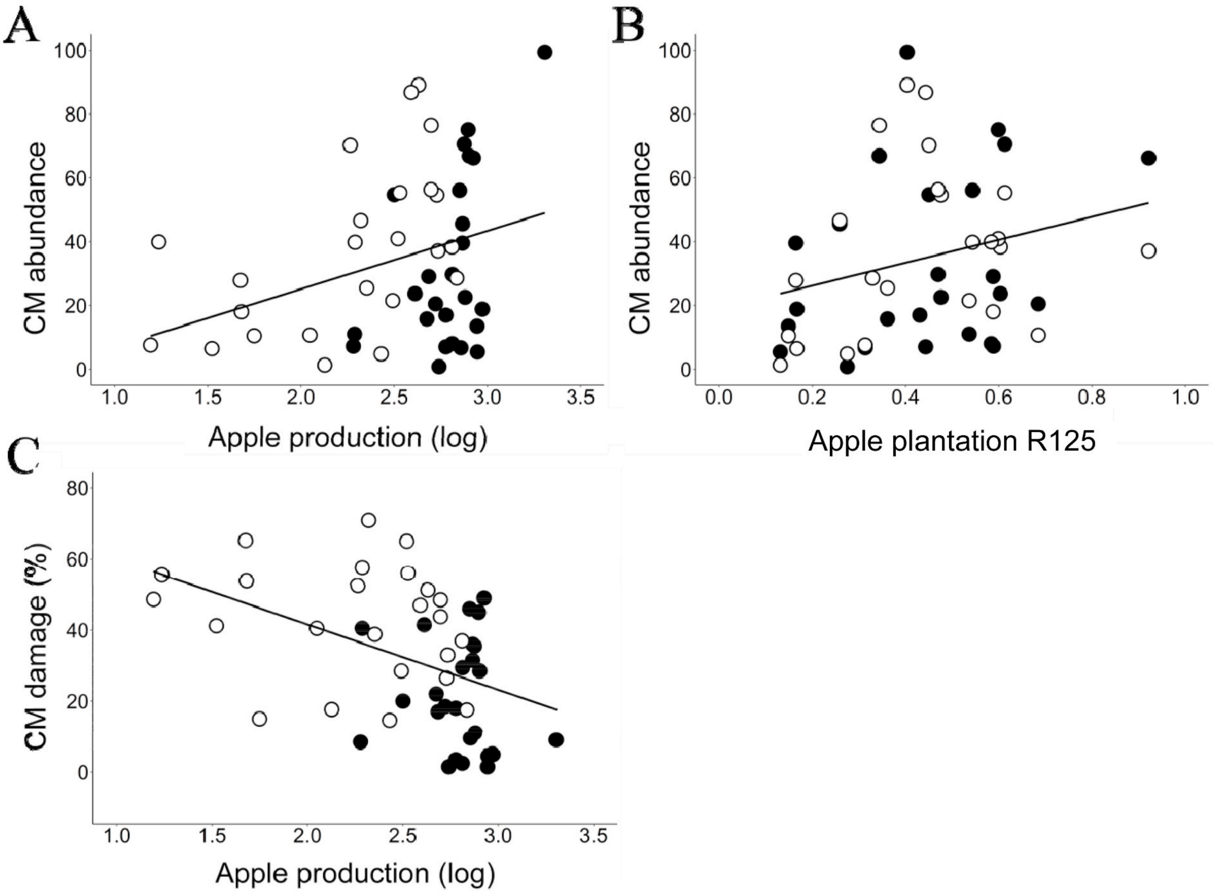

Fig. 1. Significant effects of apple production and local-scale variables on codling moth abundance and codling moth damage. Colours indicate different years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

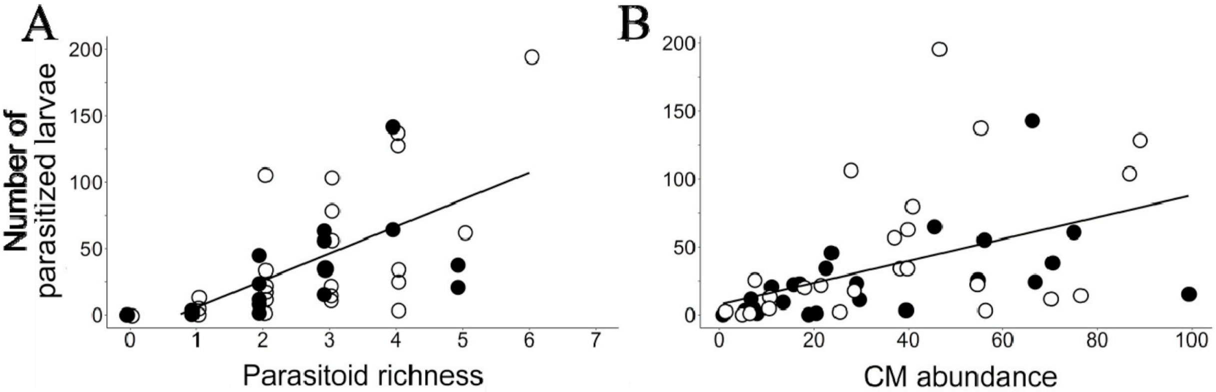

Fig. 2. Significant effects of codling moth abundance (A) and parasitoid richness (B) on the number of parasitized larvae. Colours indicate different years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

happens even despite the high biodiversity not only of parasitoids but also of generalist predators, both arthropods (Miñarro et al., 2011) and birds (García et al., 2018), attacking codling moth in these low-input cider orchards. Thus the promotion of biological control should be combined with other control strategies compatible with natural enemies (e.g. mating disruption, granulosis virus or cultural practices like post-harvest recovery of attacked fruit; Judd et al., 2005; Witzgall et al., 2008; Wearing et al., 2012) to ensure the most effective and sustainable control of this key pest.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2021.105545.

Author contributions

MM and DG designed the study. All authors contributed to data collection. RMS analyzed the data and wrote the manuscript, with guidance from DG and MM. MM, DG and RP revised the manuscript.

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