



Do hedgerows influence the natural biological control of woolly apple aphids in orchards?

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Abstract

The provision of refuges for natural enemies could be a key aspect for the management of the woolly apple aphid [*Eriosoma lanigerum* (Hausmann, 1802)] (Hemiptera: Aphididae) in apple orchards. The present study assesses the effects of *Pyracantha coccinea* (Rosaceae) (firethorn) adjacent to apple orchards as this extra-orchard habitat would positively affect the abundance of natural enemies and control of *E. lanigerum*. Abundances were evaluated for the pest, the parasitoid, *Aphelinus mali* (Haldeman, 1851) (Hymenoptera: Aphelinidae) (during two seasons) and generalist predators (only during the second season). The assessments were conducted at different distances from *P. coccinea* located at the edge of the apple orchards. Additionally, parasitism rates by *A. mali* were examined using a categorical and two quantitative methods. Results indicate that *P. coccinea* hedges promoted an early colonization by *A. mali* in apple orchards especially during the first season. However, parasitism rates by *A. mali* were not affected at the beginning of the season, but as the season progressed, the rates increased on the apple trees in comparison with the hedges. Additionally, during the second season, the interaction between certain natural enemies had a stronger effect on the population growth rates of *E. lanigerum* in orchards with *P. coccinea* compared to control orchards. Based on these results, we conclude that *P. coccinea* hedges may promote the early colonization by *A. mali* in the orchards and have a positive effect on the abundance of spiders, but had no effect on coccinellid, carabids, earwigs and syrphids.

Keywords Woolly apple aphid · *Aphelinus mali* · *Eriosoma lanigerum* · Generalist predators · Parasitism · Apple orchards

Key message

- *Pyracantha coccinea* hedges may promote the early colonization of *Aphelinus mali* in apple orchards.
- By the end of the season, parasitism by *A. mali* was greater at the centre of the apple orchards compared to the hedges with *P. coccinea*.
- Spider population increased close to the *P. coccinea*.

- Natural enemy interactions had a stronger effect on the population growth of *Eriosoma lanigerum* in apple orchards with *P. coccinea*.

Introduction

Landscape simplification and agricultural intensification, which is the increased use of the same area or resources for agricultural production (Giller et al. 1997), have reduced biodiversity at the agroecosystem scale (Altieri 1999; Landis et al. 2000; Tscharntke et al. 2005), affecting natural enemy populations and pest suppression (Letourneau et al. 2015). Studies have suggested that heterogeneous landscapes with greater biodiversity should offer hosts, alternative food sources and refuges, which could improve the fecundity, longevity and survival of natural enemies (Bianchi et al. 2006; Duarte et al. 2018; Rega et al. 2018). However, the literature has also indicated that the increase in biodiversity does not necessarily increase the biological control function of the

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natural enemies, since the increase in the number of species interacting can often cause unpredictable effects on natural enemy performance (Letourneau et al. 2009; Cardinale et al. 2012). Therefore, evidence of the role of landscape on the biological control of a particular crop–pest system is needed. As a response, conservation biological control (CBC), which is the intentional provision of favourable conditions, such as refuges and alternative hosts for natural enemies with low pesticide input, has emerged as an important strategy for pest control (Landis et al. 2000; Eilenberg et al. 2001; Begg et al. 2016; Gillespie et al. 2016). Natural enemy activity is affected by the landscape structure and composition (Tylianakis et al. 2004; Lavandero et al. 2005; Grez et al. 2010; Gurr et al. 2011; Woltz et al. 2012; Veres et al. 2013; Raymond et al. 2015), and to implement CBC, one must evaluate each system and identify non-crop resources which could potentially enhance natural enemy function. Therefore, not only structural complexity but also landscape composition is key for the success of CBC. Evidence of natural enemies migrating to the target crop systems from these extra-crop refuges and then foraging and consuming prey is required to ensure a proper herbivore population control (Lavandero et al. 2004) and to fully address the consequences of the landscape composition in surrounding agricultural ecosystems.

The role of adjacent vegetation in annual crops or orchards has been studied in diverse agroecological settings (Altieri and Schmidt 1986; Corbett and Rosenheim 1996; Horton and Lewis 2000; Tylianakis et al. 2004; Lavandero et al. 2005; Miliczky and Horton 2005; Gurr et al. 2011; Veres et al. 2013), showing that adjacent vegetation could affect the abundance, persistence and reproduction of natural enemies. For example, parasitoids such as *Anagrus* spp. are positively affected by adjacent habitats with non-rice vegetation as sources of alternative hosts for overwintering and development (Corbett and Rosenheim 1996; Gurr et al. 2011); *Diadegma semiclausum* (Förster 1869) decreased parasitism rates in the absence of flower strips and also, decreased in abundance as distance from the flowers increased (Lavandero et al. 2005); and *Aphidius rhopalosiphi* (De Stefani Perez 1902) decreased parasitism on *Metopolophium dirhodum* (Walker 1849) with distance to the floral patches adjacent to cultivated wheat (Tylianakis et al. 2004). In the same way, the main generalist predators (carabids, coccinellids, spiders and hoverflies) present in agroecosystems are known to migrate from woodland and herbaceous habitats to the crops (Symondson et al. 2002; Rand et al. 2006). Therefore, the absence of these habitats as a result of agricultural expansion may negatively affect these predators. Abundance of coccinellids, for instance, has been found to rise with increasing semi-natural vegetation surrounding crops (Woltz et al. 2012; Raymond et al. 2015); however, this could depend upon the species of

coccinellid as well as on the orientation and height of the adjacent vegetation (Grez et al. 2010). Shrubs, as adjacent non-orchard habitats, gather large populations of important predators (Horton and Lewis 2000), and these are usually less disrupted, allowing natural enemies to build up their populations when food or hosts are not available in the crop (Miliczky and Horton 2007). Additionally, these non-cultivated habitats allow natural enemies to overwinter and to colonize the crops earlier in the season to control newly emerged pests compared to those crops in more homogenous landscapes (Geiger et al. 2009; Raymond et al. 2015). However, Derocles et al. (2014) indicated that there exist some plant–pest–natural enemy systems that show no connectivity between parasitoids from crop and non-crop resources. Therefore, the knowledge on the specific needs of natural enemies and the effect of the composition of the surrounding landscapes is of great interest to enhance the biological control service that is provided by these organisms.

Apple orchards, as woody and non-annual crops, may be considered as a more temporally stable, resilient and complex environment for natural enemies (Simon et al. 2010; Letourneau et al. 2015). However, fruit orchard management is characterized by high pesticide inputs which could reduce natural enemies that protect the crop from pest outbreaks (Simon et al. 2010). *Pyracantha coccinea* (Rosaceae) is a common shrub planted as a hedge-row all over the world (De Villalobos et al. 2010) and is commonly infested by the aphid *Eriosoma lanigerum* (Hausmann 1802) (Hemiptera: Aphididae) (Blackman and Eastop 2006; Lavandero et al. 2011; Ortiz-Martínez et al. 2013). In Chile, this shrub has been shown to host the introduced *E. lanigerum* and many of its natural enemies, including the parasitoid *Aphelinus mali* (Haldeman 1851) (Hymenoptera: Aphelinidae), which was introduced to control *E. lanigerum* in 1920 (Howard 1929; Rojas 2005). This aphid, introduced from North America, provoked huge economic losses in apple orchards until the introduction of *A. mali*. Although *A. mali* is one of the most important natural enemies of *E. lanigerum* worldwide (Howard 1929; Asante and Danthanarayana 1993), this parasitoid has the disadvantage of having fewer generations per year (4–5 generations per year) compared to its host (10–11 generations per year) (Mols and Boers 2001), and it is highly susceptible to insecticide applications (Cohen et al. 1996). In addition, studies have demonstrated that *P. coccinea* may be a suitable refuge for *A. mali* in apple orchards as this parasitoid prefers parasitizing aphids from apple trees irrespective of the aphid host plant (*P. coccinea* or apple tree) (Lavandero et al. 2011; Ortiz-Martínez et al. 2013). Additionally, there are generalist predators belonging to different insect groups such as syrphids, coccinellids, carabids, earwigs, and spiders, that may feed on *E. lanigerum* (Asante 1995; Short and

Bergh 2004; Nicholas et al. 2005; Gontijol et al. 2012; Lordan et al. 2015b). These natural enemies frequent apple orchards, but the knowledge on their distribution, abundance and effect on the biological control of *E. lanigerum* is limited to a few studies and, to the best of our knowledge, the effect of *P. coccinea* on the abundances of these natural enemies has never been studied.

In the present study, apple orchards with *P. coccinea* at the edge were selected to evaluate the effects of this hedgerow on the natural enemies against the pest *E. lanigerum*. Additionally, the parasitism rates of *A. mali* were evaluated using various methodologies, to understand temporal and spatial effects on parasitoid efficiency to control *E. lanigerum*. We hypothesized that *P. coccinea*, as an adjacent habitat to the apple orchards, would positively affect the abundance of natural enemies of *E. lanigerum* and the biological control exercised by the natural enemies (parasitoid and generalist predators) against this aphid. Our predictions were: (1) that the abundance of natural enemies would decrease with increasing distance from *P. coccinea* hedges; (2) that the arrival time of the populations of *A. mali* would be positively affected by the presence of *P. coccinea* hedges; and (3) that the biological control on *E. lanigerum* populations by the main parasitoid and predators would increase in orchards with *P. coccinea* hedges.

Materials and methods

Field sites

All apple orchards studied were located in the Maule region of central Chile (see Fig. 1 and Table 1 in the supplementary material). The experiments were conducted during two seasons, 2016–2017 and 2017–2018 from November to April (from tight cluster to harvest). In the first season, eight apple orchards were selected with *P. coccinea* at the side of the field and there were no control orchards during this year, as the farthest distance from the *P. coccinea* (250 m) used in the experiments was thought to have less parasitoid activity, thus acting as a control (Tylianakis et al. 2004; Lavandero et al. 2005; Miliczky and Horton 2005). During the second season, 12 orchards were selected (six with *P. coccinea* and six without) (see Fig. 1 in the supplementary materials). Only orchards with *P. coccinea* taller than two metres and longer than ten metres with established *E. lanigerum* colonies were selected for the experiments. The experiments were conducted on the Granny Smith apple variety grafted on seedlings, and all orchards were 20–30 years old. Controls were selected based on a 500-m-wide buffer area without *P. coccinea* hedges.

Populations of *Eriosoma lanigerum*

The abundance of *E. lanigerum* was evaluated over the season at four apple trees for each of the distances to the *P. coccinea* hedge (20, 50 and 250 m) during the first year and at three apple trees for each of the distances to the *P. coccinea* hedges during the second year of sampling (during the second season the number of trees evaluated was reduced, since new measurements for natural enemies were added). In the control orchards without *P. coccinea*, only during the second season, three apple trees were evaluated for each of the distances from the edge (20, 50 and 250 m). For each tree, five branches of length approximately 50 cm and diameter 1.5 cm for standardization purposes were selected from the whole tree. The distance of 250 m from *P. coccinea* was expected to have no effect on parasitoid populations, since sampling distances were selected based on the assumption that parasitoid activity declines in the first 100 m from the adjacent non-crop habitats (Tylianakis et al. 2004; Lavandero et al. 2005; Miliczky and Horton 2005). Colonies of *E. lanigerum* on *P. coccinea* were evaluated during the season at six randomly selected points throughout the hedgerow, in which each point corresponded to a square of 50 × 50 cm. This evaluation was performed in an area, since the hedge does not have defined shoots like apple trees. This is largely due to the common periodic trimming of plant material performed for maintenance. For every branch of the apple trees and every selected point of the *P. coccinea* hedge, the colony length of *E. lanigerum* was measured. The number of *E. lanigerum* individuals per colony was then estimated by using the colony length and the mean of the number of aphids in six colonies of length 1 cm at different distances from *P. coccinea*. Samplings were performed every 15 days in all orchards.

Aphelinus mali: abundance, parasitism rates and life history

Parasitism by *A. mali* was assessed using three different methods to improve the understanding of the spatial–temporal effect on the control of *E. lanigerum*. The first method was using a categorical scale that allowed the estimation of *A. mali* abundance in the evaluated *E. lanigerum* colonies. The other two methods were with a direct count of mummies and aphids in exposed sentinel plants and collected colonies from the orchards.

Qualitative parasitism (categorical scale) and abundance

Together with the evaluations of the *E. lanigerum* populations, the percentage of parasitism by *A. mali* in each of the colonies found in the selected branches and *P. coccinea* points (see above) was assessed visually using a qualitative

scale (0 = 0%; 1 ≤ 10%; 2 = 10–50%; 3 = 51–90%; 4 ≥ 90%) as described by Lordan et al. (2015a). The mean value for each range of percentages was used to analyse the parasitism of these colonies (Lordan et al. 2015a). In addition, based on this scale, the number of mummies per colony was estimated with the estimated number of *E. lanigerum* calculated from above (see section entitled “Populations of *Eriosoma lanigerum*”). This variable represents the number of adult *A. mali* that may emerge from the mummies, since we have found that there is a mean of 94% of emergence from 327 mummies of *E. lanigerum* colonies randomly collected from the evaluated orchards. These mummies were kept separately in Eppendorf tubes (1.5 ml) under laboratory conditions (22 ± 2 °C; L:D/16:8 h) for 15 days, after which emergence was evaluated.

Quantitative parasitism

The parasitism rates were also evaluated by collecting *E. lanigerum* colonies at the centre of the orchards and at the *P. coccinea* hedges. Three colonies from three apple trees from the centre of the orchards and three colonies from three points of the *P. coccinea* were collected and placed in –20 °C to determine the number of aphids and mummies under a stereomicroscope (Olympus-SZ61, Olympus Corporation, Tokyo, Japan) in the laboratory. This sampling was performed twice in the eight apple orchards with *P. coccinea* during the first season, precisely when the abundance of *E. lanigerum* was highest in the season (February and March).

Sentinel plant traps

Parasitism rates were also examined with sentinel plant traps placed at eight apple orchards with *P. coccinea* during the first season.

One-month-old apple seedlings were transplanted to plastic bag pots of 15 cm of diameter using a 2:1 peat/vermiculite soil mixture. Two-week-old seedlings were sprayed with fungicides (first a mix of fluopyram and tebuconazole at 400 cc/ 400 l and 2 weeks later, tebuconazole only at 40 cc/100 l) to avoid fungal infections on the plants during the experiment. Plants were placed in a growth chamber (22 ± 2 °C; L:D/16:8 h) for 3 months, watered daily and a fertilizer rich in free amino acids was applied at 200 ml per 100 l of water. After this time, plants were transferred to a greenhouse (max: 41 °C; min: 11 °C) and infested with ten third and fourth instar of *E. lanigerum* individuals collected from a laboratory colony free of parasitoids. This source colony is kept under greenhouse conditions at the University of Talca. Leaves were cleaned manually with water and without disturbing aphids feeding on the stem twice a week to prevent the attack of *Tetranychus urticae* (Koch, 1836) in the greenhouse. Three four-month-old apple plants

previously infested with *E. lanigerum* in a greenhouse were used as sentinel plants and placed at the centre of the apple orchards (approximately at 200 m from the *P. coccinea*) and another three sentinel plants were placed below the *P. coccinea* during 5 days. This procedure was repeated three times in the season (beginning: November; mid: January and end of the season: March). Each of the apple plants contained a centimetre-long colony of *E. lanigerum*, in order to standardize the colony size for the parasitism rates estimate. Posterior to exposure, plants were caged individually and placed in a growth chamber at a controlled temperature (22 ± 2 °C) and photoperiod (L:D/16:8 h) for 10 days to allow parasitoid larvae to develop inside their aphid host. The parameters evaluated under a stereomicroscope in the laboratory were the number of *E. lanigerum* and the number of mummies, to allow calculation of the parasitism rates.

Life history of adult parasitoid

Mummies found in the sentinel plants were individually placed in Eppendorf tubes (1.5 ml) until parasitoid emergence. The number of days to emergence (from the arrival of the aphids to the laboratory until emergence) of *A. mali* was determined. Once the adults died, they were preserved in 70% alcohol and each individual was sexed.

Sampling of *Eriosoma lanigerum*'s predators

The abundances of the predators were determined using different traps and sampling methods in 12 apple orchards (six controls and six with *P. coccinea*), but only during the second season. Many natural enemies were encountered while conducting the experiments during the first season, and for this reason, the abundance measurement was added for the following season. Three traps (pitfall, yellow pan trap and corrugated cardboard) per distance were located between trees to avoid flooding of the traps during watering and their destruction by machinery. Carabids and spiders were monitored using pitfall traps (26 cm in diameter and 20 cm deep) dug into the soil and containing diluted glycerol (400 ml water with 10 ml glycerol) to preserve arthropods and soap to reduce surface tension. The abundances of syrphids and coccinellids were evaluated using yellow pan traps of 30 cm in diameter and 5 cm deep (placed at 20 cm above the ground with the same preservative and soap described above). Additionally, corrugated cardboard of 20 × 20 cm, placed at the base of the apple trunks was used to evaluate the abundance of earwigs (*Forficula* sp.) and spiders in the apple orchards. All these traps were placed at different distances (0 (beside the hedge/edge), 20, 50, 250 m) from the *P. coccinea* hedge/edge. The cardboard as well as the liquids in the pitfall and yellow pan traps were replaced every 2 weeks.

Estimation of biological control

The population growth rates of *E. lanigerum* were compared to the abundances of the main natural enemies (*A. mali*, syrphids and spiders) that in the present results showed to be affected by the presence of *P. coccinea*. This was calculated as a proxy for the biological control of *E. lanigerum*. The population growth rates for the whole season were calculated as below.

$$\Delta a = (E. lanigerum \text{ abundance}_{t} - E. lanigerum \text{ abundance}_{t-1}) / (E. lanigerum \text{ abundance}_{t-1})$$

This formula indicates the ratio between the contrast of the abundance of *E. lanigerum* at time “*t*” and time “*t*–1,” and the abundance of *E. lanigerum* at time “*t*–1,” as a proxy for the population growth rates of *E. lanigerum*. The population increase/decrease of *E. lanigerum* (Δa) was then estimated for each orchard and was correlated with the abundances of the natural enemy groups in the time series studied. The significance and the level of correlation were then used as an approximation of the effect of the increase/decrease of each of the natural enemy abundance on the reduction of the populations of *E. lanigerum*.

Statistical analysis

To evaluate the abundances of *E. lanigerum* and natural enemies separately on the *P. coccinea* and per distance in the orchard, generalized linear mixed models (GLMM) with a Poisson distribution were used with the sampling dates, distances (20, 50 and 250 m) and orchard types (with and without *P. coccinea*) as random factors. The same analyses were carried out for both seasons separately; however, orchard type was only included in the analysis performed for the data of the second season. Overdispersion and randomness of the residuals were first checked to select the adequate random effects structure (Harrison et al. 2018), and then, the most suitable models were selected according to the value of the Akaike information criterion (AIC) of each model (see Table 3 in the supplementary materials).

To assess the number of days until the corresponding 50% of the total accumulated population of *E. lanigerum* and *A. mali* (dependent variable) over the seasons and per distance, GLMMs with a Poisson distribution were used with the sampling dates, distances (20, 50 and 250 m) and orchard types (with and without *P. coccinea*) as random factors. As for the analyses of the abundances of *E. lanigerum* and its natural enemies, overdispersion and randomness of the residuals were checked to select an adequate random effects structure (Harrison et al. 2018), and then, the most suitable models were selected (Table 3 in the supplementary materials). The days until the corresponding 50% of the total accumulated

population were determined by the calculated area under the population abundance over a time curve for each distance and orchard during the whole sampling period and by linear interpolation. These values were then compared between different distances and for the second season, also between orchards types (with and without *P. coccinea*). The calculation of the accumulated total aphid population under the curve allows the aphid count at each sampling date to be transformed into a continuous variable at any time in

the season. In this case, the 50% of the total accumulated population was chosen to avoid the high variability caused by the low aphid population levels early in the season, giving a better overview of the population abundance in the season. The assumptions of normality and homoscedasticity were checked, and the data were analysed using an ANOVA per season.

To analyse all three methods used to assess the parasitism rates by *A. mali* (the ratio between the parasitized aphids (number of successes) and the total number of aphids in the colony) and the sex ratios of emerged parasitoids (the number of females or males per total of individuals), GLMMs were used with a binomial distribution with dates and distances as random factors. Overdispersion and randomness of the residuals were checked for all models to select an adequate random effects structure, and then, the most suitable models were selected (see Table 3 in the supplementary materials).

The correlation between the abundance of natural enemies (as explanatory variables) and the aphid population growth over time was evaluated using generalized estimating equations (GEE) (Liang and Zeger 1986). This analysis provides the significance of variables in explaining these repeated measurements, and although it does not directly predict a population change based on natural enemy abundance, it gives an idea of their possible effects on the aphid population. For this analysis, the sampled orchards were considered as the grouping factor with an autoregressive correlation (type ar1) and within-orchards observations as a function of the regular time intervals between observations (Zuur et al. 2009). Separated models were estimated for the abundance of the selected natural enemy groups (*A. mali*, syrphids and spiders), as these responded differently to the presence of *P. coccinea*. Then, the best suitable model was selected according to the value of the quasi-likelihood under the independence model criterion (QIC) of each model (Pan 2001). The correlations were analysed for the separate orchard types (control and orchards with *P. coccinea*).

All the statistical analyses were carried out using the software R v3.4.1 (R Development Core Team 2010) using the

lme4 package for mixed models, the *car* package to assess the significances between models in AIC values, the *geepack* package for the GEE function and the *MuMIn* package for GEE model selection.

Results

Populations of *Eriosoma lanigerum*

During the first season, there were significant differences among sampling dates ($\chi^2 = 51.631$; $P < 0.001$) as the estimated mean abundance of *E. lanigerum* increased throughout the season in the orchard, reaching its highest abundance in March at harvest time (Fig. 1a). However, the mean population of *E. lanigerum* did not vary significantly among the different distances from the *P. coccinea* ($\chi^2 = 1.568$; $P = 0.211$). During the first season, interactions between variables were not significant, and therefore, they were not included in the model (see Tables 2 and 3 in the supplementary material). When evaluating the time to reach 50% of the accumulated *E. lanigerum* population, results indicate that there were no significant differences between distances ($\chi^2 = 2.268$; $P = 0.132$). During the second season, *E. lanigerum* abundance also showed significant differences among sampling dates ($\chi^2 = 166.754$; $P < 0.001$) (Fig. 1b, c). However, the abundance of *E. lanigerum* did not vary

significantly between orchard types ($\chi^2 = 0.303$; $P = 0.582$) and among the different distances from the hedge/edge ($\chi^2 = 0.278$; $P = 0.598$). No significant interactions were found between distances and orchard types, sampling dates and distances, sampling dates and orchard types or in the three-way distances \times sampling dates \times orchard types interaction (see Tables 2 and 3 in the supplementary material). During the second season, the number of days to accumulate the 50% of the *E. lanigerum* populations showed significant differences between orchard types ($\chi^2 = 23.029$; $P < 0.001$) as *E. lanigerum* reached 50% of their accumulated total population earlier in orchards with *P. coccinea*.

During both seasons, the estimated mean abundance of *E. lanigerum* on the *P. coccinea* showed no significant differences among sampling dates (first season: $\chi^2 = 1.521$; $P = 0.218$; second season: $\chi^2 = 3.530$; $P = 0.060$) (Fig. 1a, b, c) (see Table 2 in the supplementary material).

Aphelinus mali: abundance, parasitism rates and life history

Abundance of *Aphelinus mali*

During both seasons, populations of *A. mali* showed a peak at the end of the season (Fig. 1d, e, f) with significant differences among sampling dates (season 1: $\chi^2 = 60.331$; $P < 0.001$; season 2: $\chi^2 = 159.105$; $P < 0.001$). During the

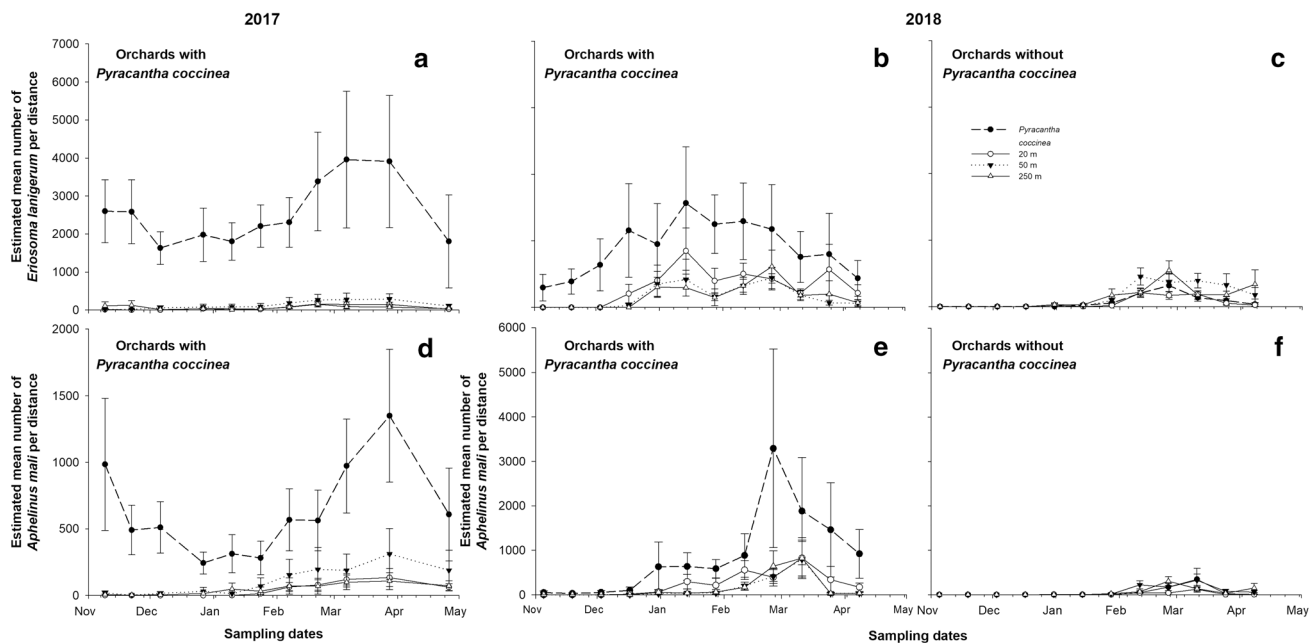


Fig. 1 The estimated mean number of *Eriosoma lanigerum* and *Aphelinus mali* per distance were evaluated for two seasons. During the first season (2017) only orchards were evaluated with *Pyracantha coccinea* (a, d) while in the second season (2018) orchards were assessed with and without *P. coccinea* (b, c, e, f). Colonies of *E. lanigerum* were sampled on the *P. coccinea* or first line of apple

trees (black dots with dash line), at 20 (white dots with solid line), 50 (black triangle with dotted line) and 250 m (white triangle with solid line) from the hedge/edge. The y-axes of the graphs corresponding to the estimated mean number of *A. mali* per distance (d, e, f), have different scales

first season, there was no significant interaction between distances and sampling dates (see Tables 2 and 3 in the supplementary material). During the second season, no significant interactions were found between distances and orchard types, sampling dates and distances, sampling dates and orchard types or sampling dates \times distances \times orchard types interaction (see Tables 2 and 3 in the supplementary material).

During the first season, *A. mali* populations reached 50% of the total accumulation significantly earlier closer to the *P. coccinea* hedge ($\chi^2 = 4.283$; $P = 0.039$) (Fig. 1d); however, in the second season, the time to accumulate the 50% of the *A. mali* population showed no significant differences between distances ($\chi^2 = 0.077$; $P = 0.782$) or between orchard types ($\chi^2 = 0.762$; $P = 0.383$) (see Table 2 in the supplementary material).

Results of *A. mali* abundance on the *P. coccinea* hedges show significant differences among sampling dates only for the second season (season 1: $\chi^2 = 3.599$; $P = 0.058$; season 2: $\chi^2 = 4.108$; $P = 0.043$).

Qualitative parasitism

The qualitative parasitism rates of observed colonies showed significant differences between sampling dates for the first season ($\chi^2 = 20.302$; $P < 0.001$); however, there were no significant differences among distances from the *P. coccinea* hedge ($\chi^2 = 0.684$; $P = 0.408$) (Fig. 2a).

During the second season, there were interactions between the orchard types (with or without *P. coccinea*) and distances from the hedge/edge ($\chi^2 = 9.934$; $P = 0.002$) as parasitism rates were greater close to the *P. coccinea* in orchards with the hedge. A significant interaction between the orchard types and sampling dates was also found ($\chi^2 = 9.795$; $P = 0.002$), since parasitism rates at the end of the season were higher in orchards with *P. coccinea* than in the control orchards (Fig. 2b, c). Parasitism showed significant differences between sampling dates during this season ($\chi^2 = 181.364$; $P < 0.001$) as parasitism increased throughout the season. However, interactions between distances and sampling dates ($\chi^2 = 2.613$; $P = 0.106$) or sampling dates \times distances \times orchard types ($\chi^2 = 0.853$; $P = 0.356$) were not significant (see Tables 2 and 3 in the supplementary material).

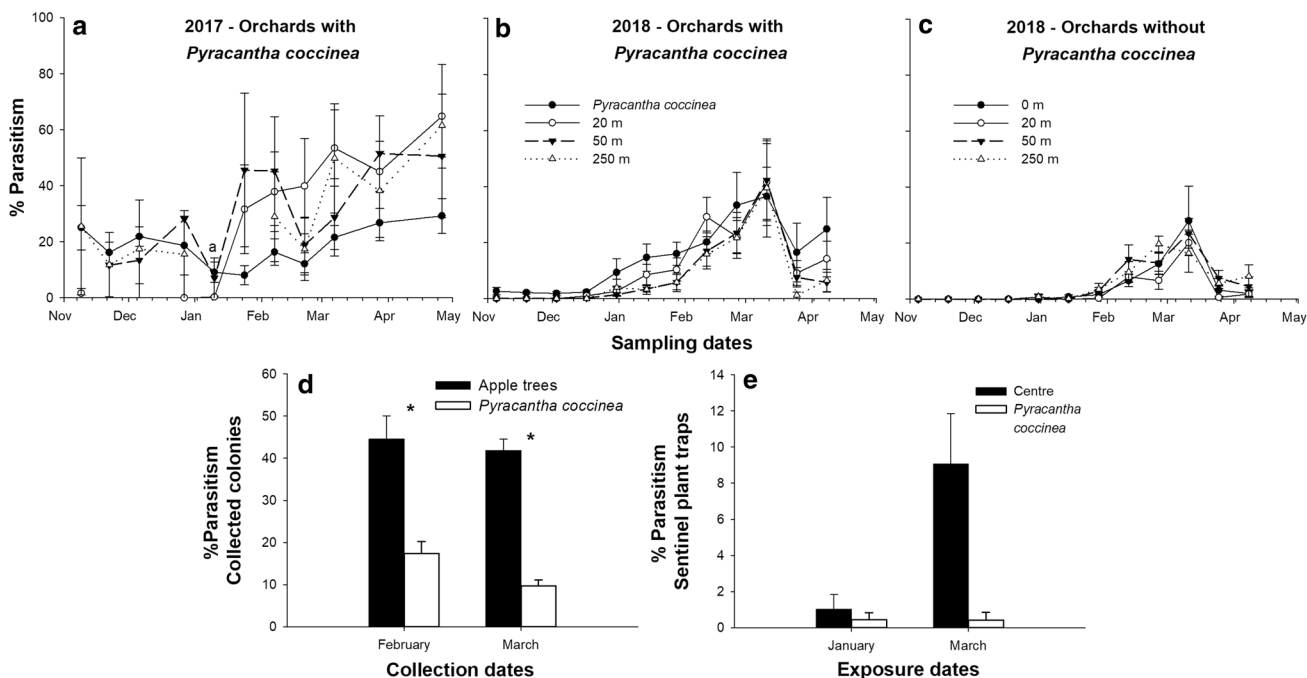


Fig. 2 Results (mean \pm SE) of the percentage of parasitism by *Aphelinus mali* on evaluated colonies of *Eriosoma lanigerum* (a, b, c) for two seasons (2017: a and 2018: b, c), for each of the distances (0 m: first line of trees in orchards without *Pyracantha coccinea*; 20 m; 50 m; and 250 m) from the hedge/edge in orchards with (a, b) or without (c) *P. coccinea* over time. The percentage of parasitism by *A. mali* was also evaluated collecting *E. lanigerum* colonies in the apple orchards and hedge (d), and using apple sentinel plant

traps (e). Colony collection was conducted in February and March at the apple trees of the centre (black bars) and at the *P. coccinea* (white bars) (d). Sentinel plants were exposed two times in the season (January and March) at the centre (black bars) and under the *P. coccinea* (white bars) (e). Asterisks above the bars indicate significant differences based on Tukey–HSD test ($P < 0.05$). All data on the y-axes are not on the same scale

Quantitative parasitism and sentinel plant traps

The quantitative parasitism estimated with the collected colonies from apple trees and from the *P. coccinea* hedge (Fig. 2d) showed significantly greater parasitism rates on the apple trees of the centre of the orchards (approximately 200 m from the *P. coccinea*) compared to the colonies collected on the *P. coccinea* hedges ($\chi^2 = 160.112$; $P < 0.001$). Additionally, parasitism of colonies collected showed a significant interaction between plants (apple trees or *P. coccinea* hedges) and time of collection ($\chi^2 = 10.530$; $P = 0.001$).

Parasitism rates estimated using sentinel plants (Fig. 2e) showed no significant differences between plants placed at the centre of the orchards and plants located under the *P. coccinea* hedges ($\chi^2 = 3.631$; $P = 0.057$). In addition, parasitism rates on sentinel plants showed no significant differences between exposure dates (January and March) ($\chi^2 = 0.543$; $P = 0.461$).

Life history of adult parasitoid

The number of days to emergence (Fig. 3a) of the adult parasitoids from parasitized aphids on the sentinel plants did not differ significantly between collection times and locations (centre or under the *P. coccinea*) (collection times: $\chi^2 = 0.016$; $P = 0.900$; locations: $\chi^2 = 0.643$; $P = 0.423$). Results regarding the emerged adults indicate that there were differences between collection times ($\chi^2 = 18.167$; $P < 0.001$) for the abundance of females, and between collection times ($\chi^2 = 29.793$; $P < 0.001$) and locations ($\chi^2 = 10.868$; $P < 0.001$) for the abundance of males (Fig. 3b). However, the sex ratio showed no significant differences between plant locations ($\chi^2 = 0.419$; $P = 0.517$) and collection times

($\chi^2 = 0.523$; $P = 0.470$) (see Tables 2 and 3 in the supplementary material).

Sampling of *Eriosoma lanigerum*'s predators

The predatory groups responded differently to the presence of *P. coccinea* and the peak of abundance for each predator varied during the season (Fig. 4). Additionally, the total abundance of natural enemies, excluding earwigs (*Forficula* sp.), tend to decrease with the distance to the edge, especially with *P. coccinea* at the edge of the orchard (Fig. 5).

The population of syrphids showed a significant interaction between distances and sampling dates ($\chi^2 = 14.076$; $P < 0.001$) as abundance of syrphids was greater closer to the edge at the beginning of the season independent of the orchard type (Table 2 in the supplementary material). However, there were no interactions between sampling dates and orchards types ($\chi^2 = 0.814$; $P = 0.367$), distances and orchard types ($\chi^2 = 0.956$; $P = 0.328$) or in the three-way distances \times sampling dates \times orchard types interaction ($\chi^2 = 1.246$; $P = 0.264$) (see Tables 2 and 3 in the supplementary material).

The abundance of spiders showed a significant increase in mid-December indicated by the significant differences between sampling dates ($\chi^2 = 29.184$; $P < 0.001$) (Fig. 4b). In addition, the presence of *P. coccinea* affected the populations of spiders, with more spiders close to the *P. coccinea* hedge, in contrast to the control orchards, where a greater abundance was observed farther from the edge ($\chi^2 = 11.411$; $P < 0.001$) (Fig. 5b). Interactions between sampling dates and orchard types ($\chi^2 = 3.486$; $P = 0.062$), distances and sampling dates ($\chi^2 = 0.417$; $P = 0.519$) or

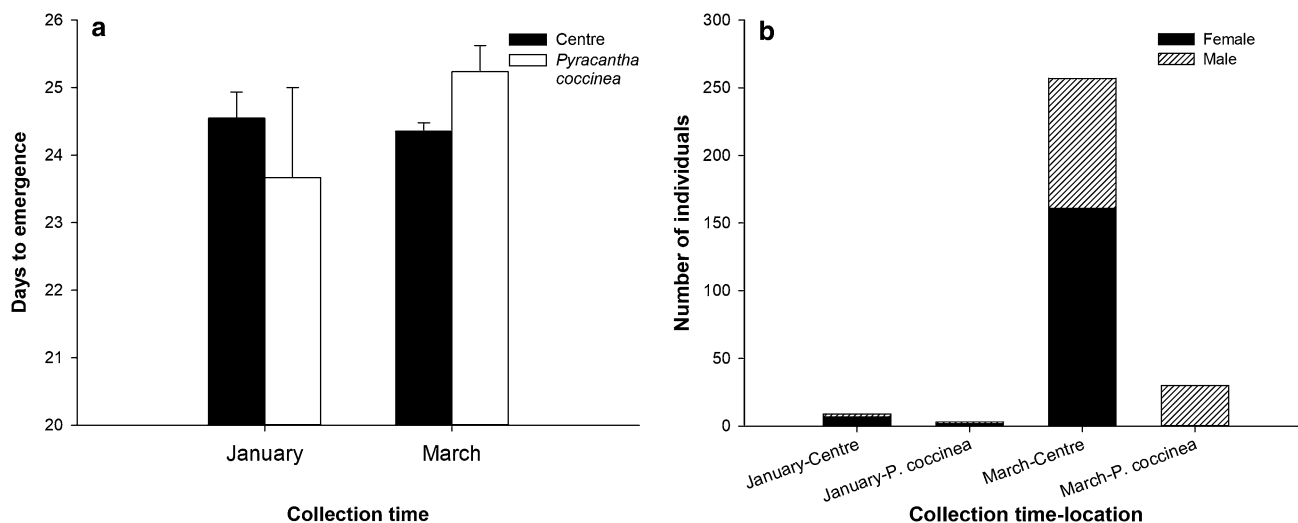


Fig. 3 Results (mean \pm SE) of the days to emergence (from collection to emergence) (a) and sexed adults (females and males) (b) of *Aphelinus mali* emerged from colonies of *Eriosoma lanigerum* located on

sentinel plant traps exposed at the centre (black bars) and under the *Pyracantha coccinea* (white bars) in apple orchards

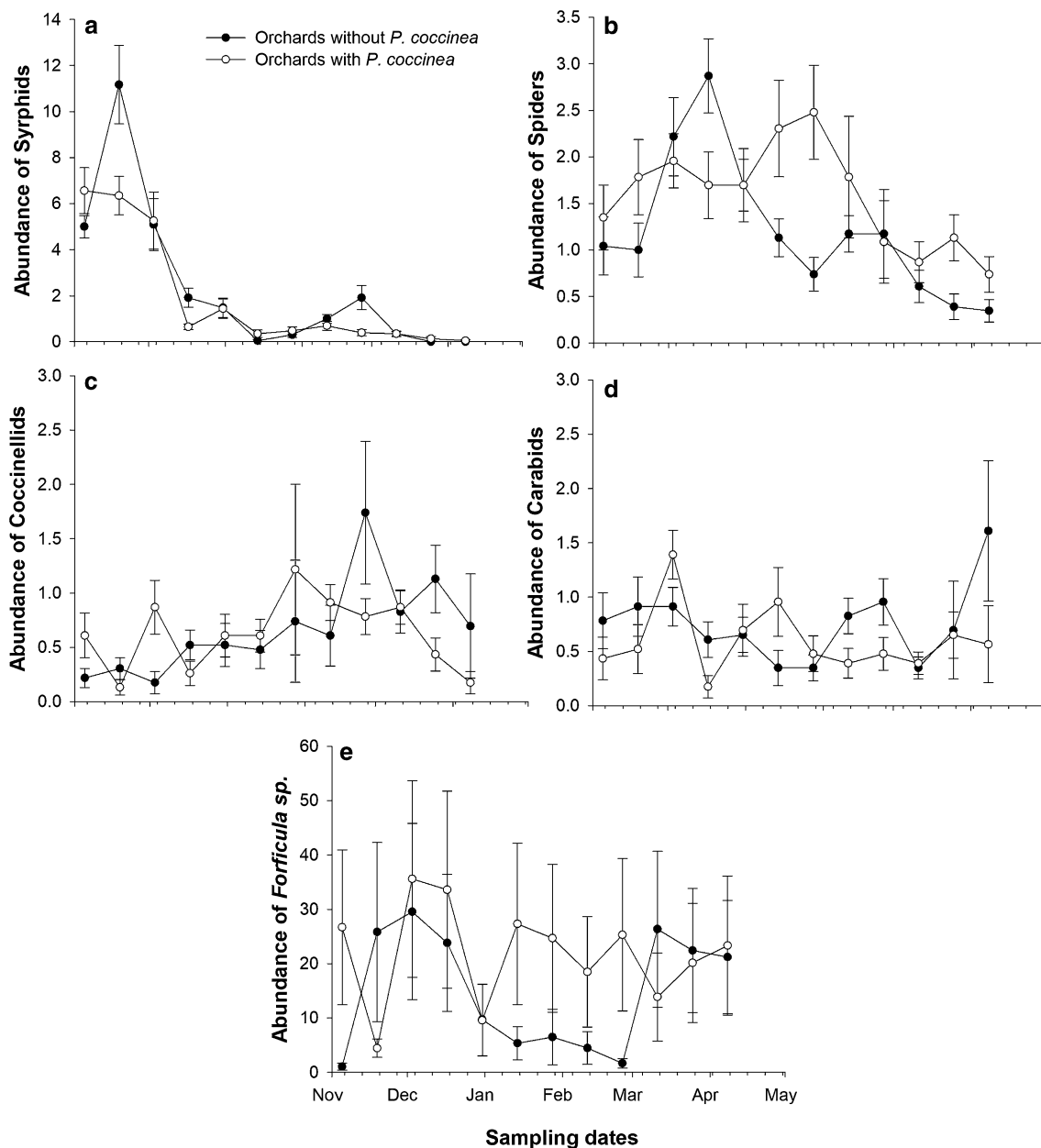


Fig. 4 Results (mean±SE) of the total abundance of different natural enemies (syrphids: **a**; spiders: **b**; coccinellids: **c**; carabids: **d**; and *Forficula* sp.: **e**) encountered in apple orchards with (white dots with

solid line) and without (black dots with solid line) *Pyracantha coccinea* during the second season. All data on the y-axes are not on the same scale

three-way interaction ($\chi^2 = 0.461$; $P = 0.497$) were not significant (see Tables 2 and 3 in the supplementary material).

The population of coccinellids showed significant differences between sampling dates ($\chi^2 = 8.620$; $P = 0.003$) (Fig. 4c). However, there were no differences between distances to the edge/hedge ($\chi^2 = 1.320$; $P = 0.251$) and between type of orchards ($\chi^2 = 0.313$; $P = 0.576$) (Fig. 5c) (see Tables 2 and 3 in the supplementary material).

The population of carabid beetles was rather low and showed no significant differences between distances

($\chi^2 = 1.607$; $P = 0.205$), sampling dates ($\chi^2 = 0.705$; $P = 0.401$) or orchard types ($\chi^2 = 0.202$; $P = 0.654$) (see Tables 2 and 3 in the supplementary material; Figs. 4d and 5d).

The population of *Forficula* sp. showed significant differences among sampling dates ($\chi^2 = 5.507$; $P = 0.019$) (Fig. 4e). However, results showed no significant differences between distances ($\chi^2 = 1.644$; $P = 0.2$) or orchard types ($\chi^2 = 0.017$; $P = 0.896$) (see Tables 2 and 3 in the supplementary material).

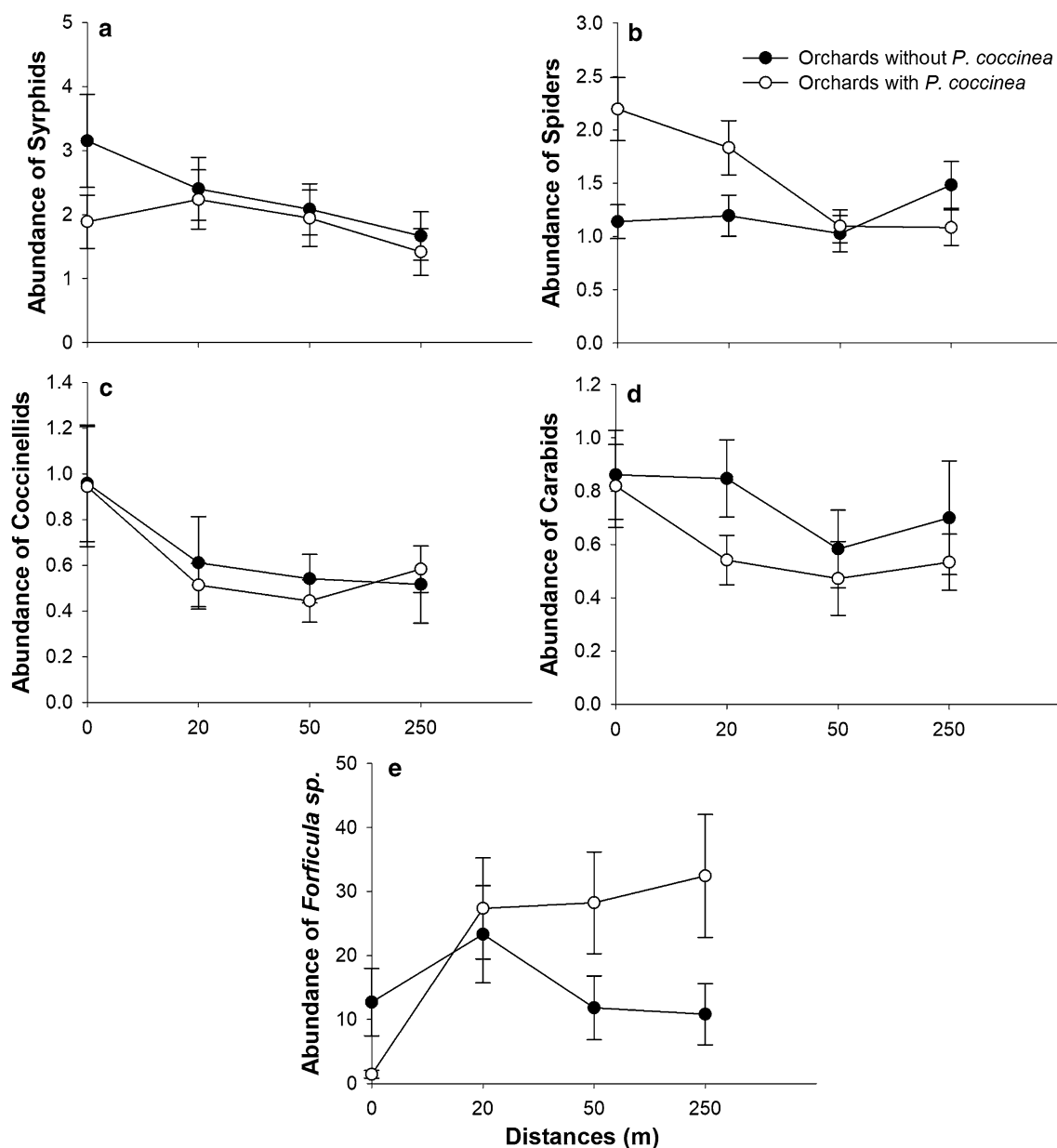


Fig. 5 Results (mean \pm SE) of the total abundance of different natural enemies (syrphids: **a**; spiders: **b**; coccinellids: **c**; carabids: **d**; and *Forficula* sp.: **e**) encountered in apple orchards with (white bars) and

without (black bars) *Pyracantha coccinea* for each of the evaluated distances. All data on the y-axes are not on the same scale

Estimation of biological control

The results of the GEE analysis suggest that the abundance of *A. mali* had a strong effect on *E. lanigerum* growth rates as *A. mali* was a variable in almost all the best models (Table 1).

During the first season, the abundance of *A. mali* had a negative effect on the aphid population growth rates of the colonies sampled on the *P. coccinea*. However, results indicate that inside of the orchard, abundance of *A. mali*

increased with increasing the growth rates of *E. lanigerum* (Table 1).

During the second season and based on the obtained results, different models were evaluated with the main natural enemies (*A. mali*, syrphids and spiders) that were shown to be affected by the presence of *P. coccinea* (see Table 2 in the supplementary material). In apple trees at the edge of the orchards without *P. coccinea*, the abundance of syrphids positively correlated with the growth rates of *E. lanigerum* indicating that the increase of *E. lanigerum* populations also increases the abundance of

Table 1 Results of GEE for the analysis of the correlation between the population growth rates of *Eriosoma lanigerum* and the abundances of natural enemies

Orchard type	Sampled area	Selected model ^a		Coefficient	<i>P</i> value ^b		
2017							
Orchards with <i>Pyracantha coccinea</i>	<i>Pyracantha coccinea</i>	AGR~AM	AM	-1.25E-04	<0.001***		
	Inside the orchard	AGR~AM	AM	1.76E-03	<0.001***		
2018							
Orchards without <i>Pyracantha coccinea</i>	Apple trees at 0 m from the edge	AGR~S	S	1.18E-03	<0.001***		
	Inside the orchard	AGR~AM	AM	4.16E-03	<0.001***		
Orchards with <i>Pyracantha coccinea</i>	<i>Pyracantha coccinea</i>	AGR~AM×S×A	AM	-3.90E-04	<0.001***		
			S	1.17E-01	<0.001***		
			A	-5.95E-01	<0.001***		
			AM×S	-2.09E-05	<0.001***		
			AM×A	1.46E-04	<0.001***		
			S×A	-1.61E-02	<0.001***		
			AM×S×A	1.09E-04	<0.001***		
			Inside the orchard	AGR~AM×S×A	AM	1.69E-04	<0.001***
				S	-2.84E-02	<0.001***	
				A	3.64E-02	<0.001***	
				AM×S	1.50E-04	<0.001***	
				AM×A	1.02E-03	<0.001***	
S×A	-2.48E-02	<0.001***					
		AM×S×A	-8.03E-04	<0.001***			

For each of the sampling periods (2017 and 2018), type of orchards (with or without *Pyracantha coccinea*) and sampled area, a model was selected based on the QIC (quasi-likelihood under the independence model criterion) values for GEE model selection. Based on the results, only natural enemies such as *Aphelinus mali*, syrphids and spiders were used in the models

^aAGR = aphid growth rate; AM = estimated mean value of *Aphelinus mali*; S = abundance of Syrphids; A = abundance of Spiders

^b*P* < 0.05*; *P* < 0.01**; *P* < 0.001***

syrphids. Similarly, inside of the control orchards *E. lanigerum* population growth rates had a positive effect on the abundance of *A. mali* (Table 1). On the other hand, in orchards with *P. coccinea* at the edge, the abundance of *A. mali* negatively affected the aphid population growth rates on the *P. coccinea* hedges whereas inside of the orchard, the relation was positive as in the control orchards. Likewise, spiders showed a negative effect on aphid population growth rates on *P. coccinea* hedges, but *E. lanigerum* growth rates were positively correlated to the abundance of spiders inside of the apple orchards. However, aphid population growth rates were positively correlated with the abundance of syrphids on the *P. coccinea* hedges and negatively inside of the orchards. Additionally, the model that included interactions between the different natural enemies showed a negative effect on the aphid population growth rates which in turn could suggest that all the natural enemies together performed a good control inside the orchards. However, the interaction between the natural enemies on *P. coccinea* hedges indicates a positive effect on *E. lanigerum* population growth (Table 1).

Discussion

In the present study, *P. coccinea* was evaluated in terms of its ability to affect the population abundance of *E. lanigerum* and its natural enemies as well as their influence on the control of *E. lanigerum*. We observed that *P. coccinea* affects the abundance and the dynamics of *E. lanigerum* and its natural enemies differently. In particular, for the specialist parasitoid *A. mali*, we observed that the build-up of its populations followed the populations of its host *E. lanigerum*, independent of the presence of *P. coccinea*. However, the population of the aphids on *P. coccinea* reached the 50% of its total population earlier than on the apple trees (between 21 and 32 days earlier), having a positive effect on the population build-up of *A. mali* close to the *P. coccinea*, where *A. mali* populations arrived to the 50% of the seasonal population significantly earlier, especially in the first season. In addition, by the end of the season, the parasitism of *E. lanigerum* by *A. mali* was greater on apple trees, most probably as a consequence of its dispersion into the orchard and of a numerical response caused by the greater aphid populations found at the centre of the orchard at this time of the season compared to the beginning of the season.

Non-cultivated habitats adjacent to the orchards are known to provide refuge from the disturbances encountered inside the production area and food for natural enemies (Miliczky and Horton 2007). These refuge sites would also allow early colonization by the natural enemies in the cultivated area, especially at the beginning of the season (Geiger et al. 2009; Raymond et al. 2015). In the present study, syrphids had greater abundances closer to the edge of the orchards at the beginning of the season independent of whether the adjacent habitat was structured by *P. coccinea* or by spontaneous vegetation. Syrphids are known to increase their abundance at the edges of the crops, especially if flowers are present (Cowgill et al. 1993; White et al. 1995). Thus, the increase of syrphids presented here may correspond with the flowering time of the plants at the edge/hedge of the orchards. Similarly, coccinellids are strongly affected by adjacent vegetation, increasing their abundance with increasing landscape heterogeneity (Woltz et al. 2012). However, some authors have suggested that the heterogeneity itself is not the only factor that changes the abundance, since the composition, orientation, height and permeability of the landscape have been shown to have an effect on some species irrespective of the landscape structure (Grez et al. 2010). This may have been the case of the coccinellids of the present study, as results indicated that these insects were not affected by the orchard type (with or without *P. coccinea*) or by the distance to the hedge/edge. Likewise, carabid populations are strongly affected by adjacent vegetation, specially wooded habitats (Dufлот et al. 2018). However, the rather low carabid populations found in the studied orchards may have hindered the identification of the possible effects of the adjacent habitats on their populations. On the other hand, the abundance of spiders seems to be directly affected by the presence of *P. coccinea*. Results here indicate that spider abundance is greater close to the *P. coccinea*, whereas in control orchards their populations are greater with increasing distances from the edge. It has been suggested that spiders have an affinity for woody and perennial vegetation such as shrubs (Schmidt and Tscharrntke 2005; Bianchi et al. 2006; Miliczky and Horton 2007) which could explain why spiders migrated to apple trees and away from the edges in orchards without *P. coccinea* hedges. The earwig population tended to decrease at the *P. coccinea* hedges with respect to the rest of the apple orchard. Despite the fact that earwigs are known to use shrubs as refuges (Bianchi et al. 2005), the *P. coccinea* may have different microclimatic conditions that avoid its proper development. Some authors have indicated that different types of vegetation create microclimatic conditions that influence the development of earwigs (Lamb and Wellington 1975; Helsen et al. 1998; Lordan et al. 2015b), suggesting that the density of the vegetation may affect their abundance. Therefore, apple trees with a greater canopy may constitute an ideal shelter allowing greater abundances of

earwigs, compared to *P. coccinea* or other type of adjacent vegetation that could allow less cover. Additionally, other predators attracted to the *P. coccinea* hedges may have fed on the earwigs, such as birds (Moerkens et al. 2009) or other generalist predators. In general, the results of this study show that the abundance of the generalist predators was influenced by the composition and structure of the orchard edges. This concurs with Rand et al. (2006) where authors explained that the natural enemies may have different preferences towards the composition of the vegetation in the edge. In the present study, for example, spiders were positively affected by the *P. coccinea*, but coccinellids, syrphids, earwigs and carabids were unaffected. However, only the abundance of adult stages was considered in this study, which could have biased our results. Therefore, for future research, the use of exclusion cages would provide a better understanding of the control exercised by predators on *E. lanigerum* populations without the presence of the parasitoids.

Parasitoids are also predicted to benefit from adjacent vegetation (Miliczky and Horton 2005) by increasing their abundance when close to extra-orchard habitats. In this study, although the estimated abundance of *A. mali* was influenced by the abundance of the pest, it was not affected by the distance to the *P. coccinea*. The actual movement of the parasitoid was not considered in the present study; however, previous work conducted by Lavandero et al. (2011) studied dispersal of *A. mali* through population genetic analyses between different areas in Chile and between host plants (apple trees and *P. coccinea*). This study showed that *A. mali* moves between host plants since the gene flow between regions and hosts plants lacked genetic differentiation. Additionally, it has been shown that *A. mali* prefers apple trees as a host plant, especially if this was its natal host plant (Ortiz-Martínez et al. 2013). However, aphids with apple trees as a host plant in the same study showed a significant preference for its natal host, but those aphids from the *P. coccinea* showed no significant preference between host plants (Ortiz-Martínez et al. 2013). This could indicate that some of the aphids from the firethorn may move to apple trees, but results by Lavandero et al. (2011) demonstrated that there is a highly significant genetic differentiation between host plants (apple trees and firethorn), clearly separating aphid genetics from different host plants and reducing the probability of movement between *P. coccinea* and apple trees. Indeed, the early arrival of the pest to the *P. coccinea*, as suggested by our data, could also create conditions for the early infection of the apple trees. However, the high genetic differentiation described above and the tendency of crawlers to disperse from the roots to the shoots observed throughout the season (and vice versa) mainly suggests that they move between trees that touch each other and from the root system of apple trees (Lordan et al. 2015a).

We present evidence of the variation of natural enemy abundances during the season caused by a non-crop resource (*P. coccinea* hedges). At the beginning of the season (in the spring), pollen feeders such as syrphids are expected to be more abundant (Cowgill et al. 1993; White et al. 1995) and foraging at the edges of the apple orchards. The presence of flowering *P. coccinea* at the first sampling date (at the beginning of November) may have had an effect on the abundance of syrphids compared to the control orchards without *P. coccinea*; however, 2 weeks later, when flowering of *P. coccinea* finished, the abundance of syrphids shifted. On the other hand, earwigs in the control orchards followed the expected seasonal changes with two peaks of great abundances, one at the beginning and another at the end of the season (Lamb and Wellington 1975). However, the population of earwigs in apple orchards with *P. coccinea* remained without observing the expected rapid decline of the population that normally occurs when nymphs moult to the adult stage (Lamb and Wellington 1975; Moerkens et al. 2009; Lordan et al. 2015b). In the middle of the season, spiders were the predominant generalist predators studied here, independent of the presence of *P. coccinea*. However, by the end of the season, coccinellids and *A. mali* increased their abundances. Although *P. coccinea* may not promote the establishment of coccinellids, it may be an important resource for the early colonization of *A. mali* in apple orchards as a consequence of the earlier infestation of *E. lanigerum* on *P. coccinea*. The early arrival of the host on the *P. coccinea* may have increased earlier in the season the intensity of chemical signals that the parasitoid uses for foraging on its host. Parasitoid foraging may be affected by different cues from the host and by the plant–host interaction (De Moraes et al. 1998; Soler et al. 2007; Erb et al. 2010). Not only through volatiles (De Moraes et al. 1998; Erb et al. 2010) but also through the hosts excretions that provide specific information that allows parasitoids to find their host. This is the case of the aphidiid primary parasitoids [*A. rhopalosiphii*, *Aphidius picipes* (Nees, 1811), *Aphidius ervi* (Haliday, 1834) and *Praon volucre* (Haliday, 1833)], where foraging can be modulated when they are exposed to honeydew of cereal aphids (Budenberg 1990). Further research to understand the cues that *A. mali* uses to forage for its host should be considered, as it has been found for other herbivore-parasitoid systems (Mehrnejad and Copland 2006; Leroy et al. 2009).

The natural enemies in the orchards can vary with the local geographical conditions, the landscape structure and composition and the crop management (Simon et al. 2010). Thus, the main natural enemies of *E. lanigerum* may change depending on the studied area. As examples, syrphids have been highlighted as important natural enemies in the USA (Short and Bergh 2004; Gontijol et al. 2012); as well as *A. mali* in China (Zhou et al. 2014) and the earwigs together with *A. mali* in Australia and New Zealand (Nicholas et al. 2005; Wearing et al. 2010). In Chile, *A. mali* has been

reported as the major natural enemy of *E. lanigerum* in apple orchards; however, other potential natural enemies such as syrphids, coccinellids, earwigs, carabids and spiders also play a role. In the current study, various methods to estimate the parasitism rates of *A. mali* were used in the orchards with *P. coccinea*. Significant effects on parasitism rates between distances were observed when using the qualitative method (especially in orchards with *P. coccinea*) and between host plants in the quantitative sampling method. The quantitative bioassay using sentinel plants is known to be useful to compare parasitism rates in field conditions. However, this bioassay is laborious and takes only a snapshot of the parasitoid activity (Letourneau et al. 2015), which will depend on the overall host density and the duration of the exposure in the orchards. On the other hand, studying the parasitism rates through a qualitative scale results in less precise estimations, but, it takes into account the host density of the colonies that are present in the orchards. In any case, it is recognized that both methods are reasonable for estimating parasitism rates (Letourneau et al. 2015; Lordan et al. 2015b), but caution should be exercised when interpreting the results. In this study, although only the direct biological control service of *A. mali* was measured, the link between the aphid population growth and the main generalist predators was assessed indirectly using the generalized estimating equations (GEE) analysis. These analyses indicated that the interactions between these generalist predators negatively affect *E. lanigerum* population growth inside of the orchards with *P. coccinea* hedges. These links were stronger in orchards with *P. coccinea* compared to control orchards, suggesting an effect on the biological control in those orchards with *P. coccinea*. Future research should include the direct study of predation by these generalist predators on *E. lanigerum* colonies as well as of any effects of intraguild predation on the pest consumption and the dynamics using molecular approaches.

In conclusion, the presence of *P. coccinea* at the edge of the apple orchards positively affected the abundance and biological control service by some potential natural enemies of *E. lanigerum*. These are the cases for *A. mali* where *P. coccinea* promoted the early build-up of this parasitoid and for the spider populations that increase close to the *P. coccinea*. In addition, results indicated that *P. coccinea* did not promote *E. lanigerum* dispersion to the apple trees as the aphid population showed no significant differences between distances, which in turn, supports the findings by Lavandero et al. (2011) where populations of *E. lanigerum* showed high genetic differentiation between *P. coccinea* and apple trees. Therefore, the use of this hedgerow adjacent to apple orchards seems to be more beneficial for the control of this pest than detrimental. However, further research should be conducted to ensure that *P. coccinea* does not promote other pests into the orchards before including this as a pest management tool for apple orchards.

Author contribution statement

APC and BL designed research. APC and DA conducted the experiments. APC and BL analysed data, wrote the manuscript and acquired funding. All authors have read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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