Journal of Pest Science (2018) 91:1047–1061
https://doi.org/10.1007/s10340-018-0976-y

ORIGINAL PAPER

Unravelling pest infestation and biological control in low-input orchards: the case of apple blossom weevil

Marcos Miñarro[1] · **Daniel García**[2]

Received: 7 December 2017 / Revised: 22 February 2018 / Accepted: 26 March 2018 / Published online: 29 March 2018

Abstract

Low-input farming is an alternative production system that provides a great opportunity to disentangle the natural mechanisms regulating crop pests, since neither pests nor their natural enemies are disrupted by pesticides. Here, we use a key apple pest in Europe, the apple blossom weevil (*Anthonomus pomorum*), as a model case to unravel the factors driving pest infestation and its biological control in a low-input context, namely the cider apple orchards of NW Spain. We applied a holistic approach based on the complete life cycle of the pest and combined large-scale observation (23 orchards) with small-scale experimental assessment. Weevil attack (0.4–37.4% of flowers) increased with the proportion on apple trees in the immediate orchard neighbourhood and with semi-natural woody habitat in the surrounding landscape and decreased with tree distance to orchard edge and apple bloom level. Thus, the prevalence of the pest depended on the availability of the various resources required for foraging, egg-lying and overwintering. Three types of natural enemies supplied complementary pest control by preying on weevils at different stages in their life cycle: seven parasitoid species attacked immature weevils (6.4–81.5%), while the additive effects of birds and crawling arthropods were evident in terms of the removal of adult weevils (31–44%). We conclude that the effective biological control of *A. pomorum* can be achieved in low-input systems to maintain the pest at non-harmful levels, through combined management of the pest, its habitat and its natural enemies.

Keywords *Anthonomus pomorum* · Biodiversity · Complementary predation · Ecosystem services · Insectivorous birds · Parasitoids

Key message

- The low-input scenario of cider apple orchards in NW Spain facilitates understanding of *Anthonomus pomorum* infestation and its biological control.
- Resource and habitat availability at local and landscape scales explained the prevalence of *A. pomorum*.
- The co-occurring natural enemies of *A. pomorum*, parasitoids, birds and crawling arthropods, potentially exert complementary control.
- Pest and natural enemy management through habitat measures is recommended instead of pesticide use.

Introduction

Pest control in most farming systems currently relies on the use of pesticides (e.g. Parsa et al. 2014; Guedes et al. 2016), a situation which hampers the unravelling of the

---

Communicated by Y. Gao.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10340-018-0976-y) contains supplementary material, which is available to authorized users.

✉ Marcos Miñarro
mminarro@serida.org

[1] Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA), Apdo. 13, 33300 Villaviciosa, Asturias, Spain

[2] Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, y Unidad Mixta de Investigación en Biodiversidad (CSIC-Uo-PA), C/Catedrático Rodrigo Uría s/n, 33006 Oviedo, Asturias, Spain

natural mechanisms that regulate pest populations, given that not only pests but also their natural enemies may be disrupted by pesticides (e.g. Monteiro et al. 2013; Markó et al. 2017). Low-input farming is an alternative production system which aims to optimize management and production with the minimum use of external inputs, such as purchased fertilizers and pesticides (e.g. Gomiero et al. 2011; Reganold and Wachter 2016). It may thus represent a suitable real-world context within which to understand the functioning of biological control. However, despite the suitability of wildlife-friendly farming for globally important crops (e.g. Pywell et al. 2015), this issue has seldom been addressed.

Apple is one of the major fruit crops in the world. With 84×10^{-6} tons produced in 2014, apple ranks third in the global fruit production after bananas and watermelons (FAO 2017). However, apple is threatened by numerous pests that can compromise crop viability, with potential losses caused by pests in unsprayed orchards averaging 40–50% and even reaching 85% (Cross et al. 2015). Accordingly, European apple orchards normally receive 5–15 insecticide applications per year, at a cost of at least of 400 €/ha (Cross et al. 2015). Nevertheless, at both the regional and the local scales, there are examples of apple pests and diseases which are successfully managed in low-input contexts (e.g. Agnello et al. 2015; Walker et al. 2017).

Cider apple orchards in Asturias, NW Spain, potentially provide an optimal system in which to study apple production in a regional low-input farming context. Asturias has a long tradition of cider making, and most of its 10,000 ha of apple orchards are cultivated almost exclusively to this end (INDUROT 2010). Apples are produced both in traditional extensive orchards with large trees grown on seedling rootstock and in semi-intensive orchards where semi-dwarfing rootstock is used (Dapena et al. 2005). All are planted with selected local cultivars tolerant to apple diseases, and thus, the use of pesticide is very low, even, in some cases, null. The orchards are embedded in a highly variegated landscape where patches of semi-natural habitats, such as hedgerows and woodlands, are frequent. The low pressure of pesticides and the surrounding landscape complexity favour biodiversity within cider apple orchards and in their neighbourhood, including both apple pest insects and their natural enemies (insects and vertebrates such as birds, e.g. Miñarro et al. 2005, 2009; García et al. 2018). Despite these characteristics, there is no information on how the low-input context actually affects the prevalence of pests or the effect of their antagonists.

The apple blossom weevil, *Anthonomus pomorum* L. (Coleoptera: Curculionidae), is a common pest in Asturian cider apple orchards and was a key pest in European apple orchards before the extensive use of broad-spectrum pesticides (Miles 1923; Regnier 1923). Linked to reductions in both the application and the spectrum of pesticides over the last two decades, the importance of *A. pomorum* as an apple pest has risen, particularly in organic farming systems (e.g. Balázs et al. 1997; Cross et al. 1999; Oste-Lédée et al. 2001). According to their vital requirements (Miles 1923), the size of populations of *A. pomorum* might be limited by opportunities for both overwintering and egg-laying (Fig. 1). While it is known that adults overwinter sheltered under the bark of apple trees (Miles 1923), most modern orchards are grown on dwarfing rootstock that produce small trees with smooth bark and thus provide little opportunity for winter shelter (Toepfer et al. 2000). As a result, in young and modern orchards, adult weevils shelter in the trees surrounding the orchard (Brown et al. 1993; Toepfer et al. 2000). Another point to note is that apple trees naturally show biennial bearing: 1 year of abundant blossom is followed by a year of scarce bloom (Jonkers 1979; Samach and Smith 2013), and as such, following a satiation process (Kelly 1994; Kelly and Sork 2002), apple pest incidence would decrease in years of heavy blossom, whereas the limited availability of blossom would constraint weevil egg-laying in years of scarce blossom. In addition, populations of apple blossom weevils may also be limited by the occurrence of their natural enemies (Fig. 1). Weevils are attacked by several parasitoid species, mainly during their larval stage inside the blossom (Miles 1923; Cross et al. 1999; Mody et al. 2011; Knuff et al. 2017). In their turn, parasitoids have several resource requirements (floral resources for adults, shelter habitat, other hosts) at both the orchard and the landscape scales (Gillespie et al. 2016). Besides parasitoids, biological control by generalist predators (i.e. birds and crawling arthropods, Cross et al. 1999) is also exerted during the weevil adult stage, both in early spring, when overwintering adult weevils start to feed and mate, and after the summer emergence, when they feed on tree leaves (Fig. 1). Despite these findings, to our knowledge no study has addressed the simultaneous roles of resource availability and predator pressure on apple weevil incidence.

Here, we combine large-scale observation with small-scale experimental assessment to understand the multiple factors driving apple weevil infestation in a low-input context, the cider apple plantations of NW Spain. We apply a life cycle-based, holistic approach oriented to developing integrative strategies for biological control. Specifically, we aim to answer the following questions: (1) How important is apple blossom weevil as a pest in low-input apple orchards? (2) How important are natural enemies (parasitoids, predatory birds and crawling arthropods) in controlling this pest? and (3) What are the determinants of weevil infestation and biological control at both the local and the landscape scales?

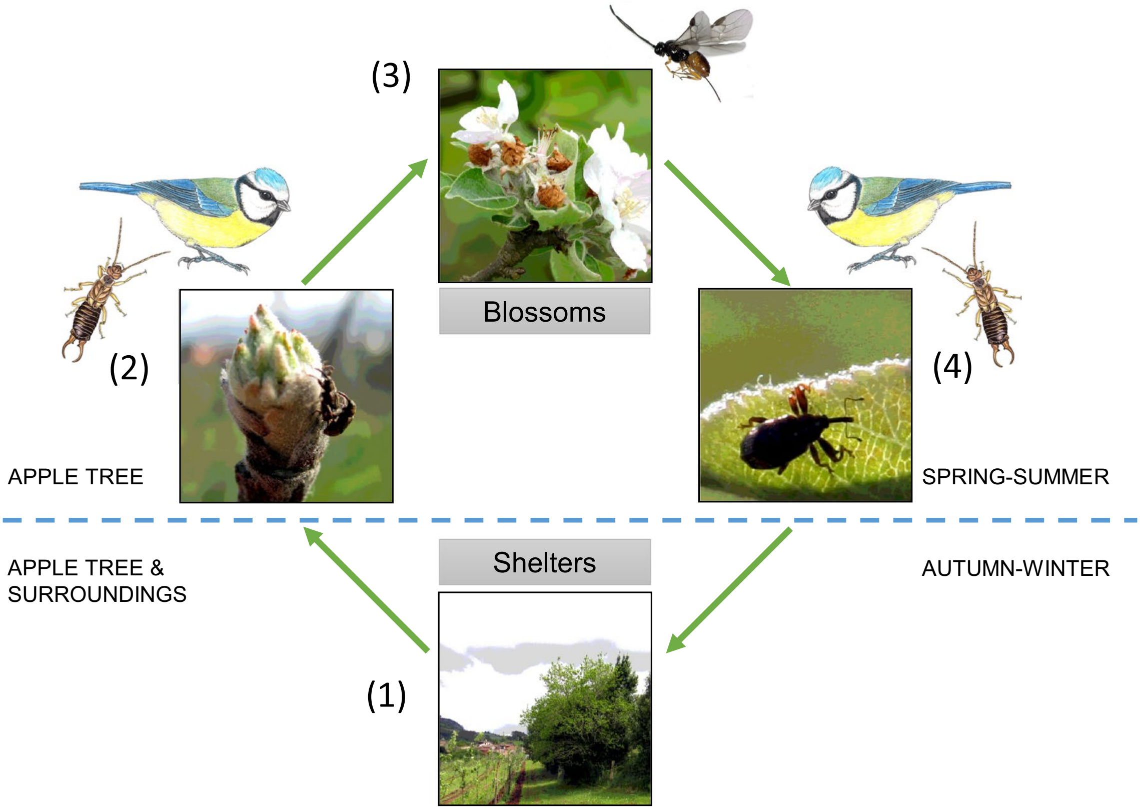

Fig. 1 Diagrammatic representation of the life cycle of the apple blossom weevil and some potential determinants of weevil populations in Asturian cider apple orchards (natural enemies, shelters, bloom). (*1*) Weevil overwinters as an adult, preferably hidden under the bark of old apple trees or other trees in the close vicinity (Brown et al. 1993; Toepfer et al. 2000). Lack of such winter shelters could limit weevil populations. (*2*) In early spring, adults leave the winter quarters and feed on apple trees by piercing the opening buds and sucking the juices. They alternate feeding and resting for several days until copulation and oviposition take place. These adults could be attacked by predators like birds or crawling arthropods. (*3*) When the flower is in D–E (56–57), females oviposit inside the flower buds (Toepfer et al. 2000; Knuff et al. 2017) and the hatched larvae feed on the reproductive parts of the flower. Weevils need flowers for reproduction and thus the number of blossoms could be a factor limiting weevil populations. At this point, larvae may be attacked by parasitoids. (*4*) Finally, the larvae pupate inside the blossom and then the young adults appear. The new generation of adults feed on the underside of apple leaves for several days before seeking winter quarters. At this stage, they may again be attacked by predators. Photographs by Marcos Miñarro and drawings by Daniel García

Materials and methods

Study site and orchard and landscape features

The observational study was conducted between 2015 and 2016 in 23 cider apple orchards distributed over a 600-km^2 study area in Asturias (43° 21′ to 43° 30′N, 5° 20′ to 5° 45′W) (Fig. 2a, b). Orchards were located from 10 to 385 m a.s.l., and their size varied from 0.5 to 20.6 ha. Minimum distance between orchards was 1.2 km (Fig. 2b). Trees were grown on semi-dwarfing rootstock, with a density of ca. 500 trees/ha in all but two cases, where trees were grown on seedling rootstock with 250 trees/ha. All orchards are comprised of several cultivars, but all sampling was performed on the local cultivar ‘Regona’ to homogenize sampling (given that weevil infestation and parasitism rates depend on cultivar; Mody et al. 2015; Knuff et al. 2017).

Three of the orchards were organic, whereas the rest followed IPM guidelines, and no orchard was sprayed against apple blossom weevil. As regards other pests, narrow-spectrum insecticides against the rosy apple aphid (*Dysaphis plantaginea* Passerini) and/or the codling moth (*Cydia pomonella* L.) were applied in some orchards. Fungicides are also rarely applied in the area, as the cultivars grown are tolerant to the main apple diseases (scab, canker and powdery mildew). Total annual number of pesticide sprayings per orchard ranged from 0 to 2 (except one organic orchard with six sprayings; four of which were of granulosis virus against codling moth). Sprayings in non-organic orchards were mainly made with copper oxychloride and oil in winter and, in some cases, one or two diflubenzuron sprayings against codling moth or pirimicarb against aphids. Only one orchard applied a broad-spectrum insecticide (lambda-cyhalothrin).

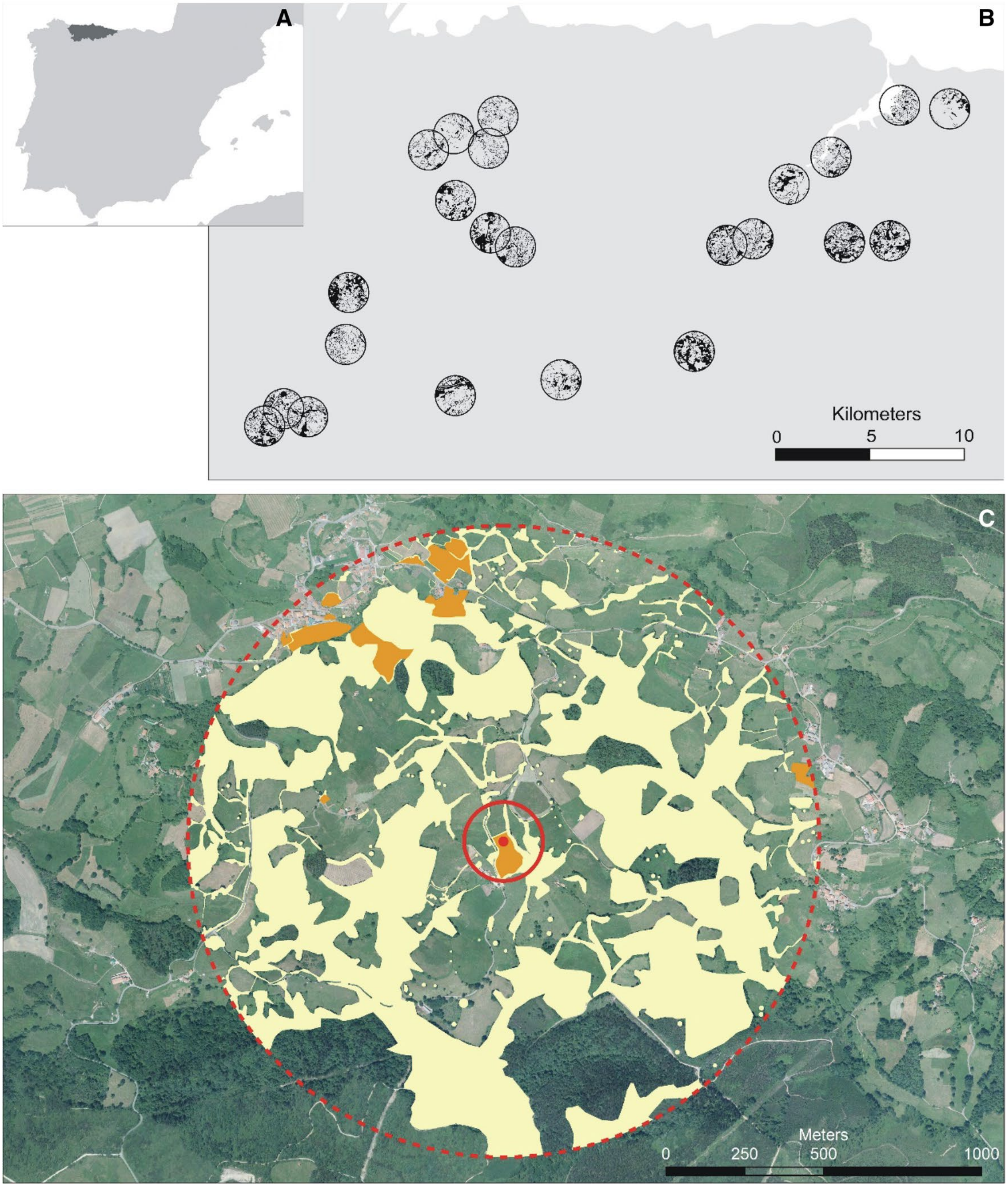

Fig. 2 Schematic representation of study sites and spatial design depicting **a** the region of study (Asturias province in dark grey within the Iberian Peninsula); **b** the study sites, highlighting the landscape-scale gradient of cover of woody vegetation (dark grey patches) around each site (1000-m-radius plots); **c** an example of cover of woody vegetation (pale yellow patches) and apple orchards (orange patches) in the 1000-m-radius plot (red dashed line) and the 125-m-radius plot (red line) around one of the orchards. (Color figure online)

In 2015, 22 orchards were studied, but the following year four sites had to be discarded because of the scarcity of blossom, meaning that only 18 were surveyed in 2016. Seventeen of the orchards were sampled in both years. In each orchard, eight trees (target trees) were marked before full bloom. Sampling was conducted shortly after full flowering of the target cultivar ‘Regona’, which varied notably among sites (between April 30th and May 16th in 2015 and May 19th and June 14th in 2016).

Landscape features

Orchards were selected in order to cover a gradient of variability in their environmental conditions, based on preliminary surveys of features within orchards and the structure of their surrounding landscape. For the latter, a geographic information system of the study area (GIS, ArcGIS9.3) based on 1:5000-scale orthophotographs (2014) was used, from which a layer of cover was carefully digitized that included all semi-natural woody vegetation assumed to be suitable for weevils to overwinter (i.e. forest patches of variable size, hedgerows, and isolated trees within pastures). We estimated the availability of semi-natural woody vegetation at the large scale around each apple orchard (Fig. 2c), i.e. within a circular plot of 1-km radius (hereafter R1000) centred on the midpoint of the set of target trees (*prop. woody vegetation R1000*), and at the small scale, i.e. within a 125-m-radius (hereafter R125) plot (*prop. woody vegetation R125*). The GIS also included a layer pertaining to cover of apple plantations, from which we applied a similar multi-scaled procedure to estimate *prop. apple R1000* and *prop. apple R125* (Fig. 2c). We assumed that apple plantation cover also represented food and shelter availability for weevils in the landscape surrounding the target trees. We also estimated *distance to edge* as the distance from the centre of the set of target trees to the nearest woody edge.

Orchard features

We measured *bloom level* as an indicator of the number of flowers in the orchard. This variable would be expected to differ between cultivars, across sites and between years (due to the natural biennial bearing of apple trees). We recorded bloom level when the target cultivar ('Regona') was in full bloom, by walking perpendicular to tree rows in order to avoid a cultivar effect (as rows contain a single cultivar) and covering the full extent of the orchard. For 30 randomly chosen trees per orchard and year, we scored the number of flowers per tree by using a semi-quantitative scale: 0, 0 flowers; 1, 1–10 flowers; 2, 11–50 flowers; 2.5, 51–100 flowers; 3, 101–500 flowers; 3.5, 501–1000 flowers; 4, 1001–5000 flowers; 4.5, 5001–10,000 flowers; 5, more than 10,000 flowers. We calculated *bloom level* per orchard and year by averaging this estimate across trees. We used the size of apple trees as an indicator of within-orchard resources for weevils, both for overwintering (shelter) and for breeding (blossom), and to this end we randomly selected 10 trees from within an area with a 25-m radius centred on the midpoint of the target trees and measured tree canopy length and width. We calculated *canopy size* by multiplying canopy length by canopy width for each tree and averaged this estimate across trees per orchard. Finally, we measured the density of flowers in the orchard groundcover (*groundcover density*) since adult parasitoids feed on nectar (Gillespie et al. 2016), and thus, flower density could be an indicator of trophic resources for parasitoids (Simon et al. 2010). This was visually assessed over 150–200-m transects, in 50 × 50 cm ground quadrats placed at 10-m intervals (14 intervals per transect in 2015 and 20 in 2016). Groundcover is managed differently in tree rows than between rows, leading to small-scale differences in plant composition (e.g. Miñarro 2012). Thus, half of the quadrats were in tree rows and half between rows. *Groundcover density* was estimated as the number of flowers per square metre by averaging the density of flowers across quadrats.

Weevil infestation

On each target tree, a 1-m-length branch (100–150 flowers) at a height of 1–1.5 m was randomly selected and the number of weevil infested flowers on it was counted. Weevil-attacked flowers, known as 'capped blossoms', are easily identifiable because their petals turn brown and dry and remain closed (Fig. 1). The number of flower clusters per branch was also counted and multiplied by the average number of flowers per cluster, as estimated from 30 'Regona' clusters in three different orchards each year (6.50 flowers per cluster in 2015 and 5.92 in 2016). For each tree, the *weevil attack* was calculated as the percentage of capped blossoms as regards the total number of flowers. We calculated *weevil abundance,* an indicator of the total number of weevils per ha produced at each site, by multiplying weevil attack by the estimated number of flowers per ha, the latter being calculated as the product of the number of trees per ha multiplied by the average number of flowers per tree (estimated from bloom-level sampling, by replacing bloom level by a central value of the abundance class: 0 bloom level = 0 flowers; 1 bloom level = 5.5 flowers; 2 = 30.5; 2.5 = 75.5; 3 = 300.5; 3.5 = 750.5; 4 = 3000.5; 4.5 = 7500.5; and 5 = 10,000).

Parasitism on weevils

Fifteen capped blossoms were collected from each target tree (totalling 120 capped blossoms per site) and taken to the laboratory. The sample from each tree was stored separately at room temperature in a plastic Petri dish with laboratory paper at the bottom for moisture absorption. Petri dishes were examined at 48–72-h intervals, and the emergence of weevils and parasitoids recorded. After emergence, weevils and parasitoids were frozen and stored in Eppendorf tubes at − 20 °C. We identified Ichneumonids based on Fitton et al. (1988), whereas other families were identified by expert taxonomists (Vladimir Žikić (Braconidae), Hossein Lotfalizadeh (Chalcidoidea)) based on specific expertise. *Parasitoid richness* was calculated as the number of emerged parasitoid species from each orchard, and *parasitoid attack*, i.e. the percentage of weevils attacked by parasitoids, as the percentage of emerged parasitoids in relation to the sum of emerged weevils and parasitoids.

Predation on adult weevils

We experimentally assessed the removal of adult weevils in the field by different predators and in different seasons throughout the weevil life cycle. The experiment was conducted in spring 2017 in one of the study orchards (located in Camoca, 43° 27′N, 5° 28′W). The experiment was first set up in March–April, when adult weevils feed on the apple trees and oviposit in blossoms after overwintering, and it was then replicated in May–June, when a new cohort of adults emerge and feed on trees (Oste-Lédée et al. 2001; Fig. 1). In each season, 10 trees of similar size, separated from each other by at least 5 m, and belonging to four different rows in the orchard, were selected. For each tree, four branches of similar length and diameter and at a height of approximately 1.5 m were selected and a 25-cm apple twig with a row of 10 adult weevils stuck with epoxy glue to it was tied with wire to the upper part of each branch (Fig. S1). The weevils were from the pool of adults emerging from the capped blossoms collected each year (see above). The experimental weevils (branches) of each tree were assigned, in a full factorial design, to one of two treatments simulating their access by two different types of potential predators: birds and crawling arthropods. Bird access was prevented by covering the weevils with a 50-cm-long cylindrical (6-cm radius) cage of 10-mm pore plastic mesh, held parallel to the branch and closed at both ends with wire strips (Fig. S1B). Crawling arthropod access was prevented by a ring of sticky paste (Tanglefoot Company, Grand Rapids, Michigan) applied to the base of the branch, at least 50 cm away from the weevils (Fig. S1C). Any physical contact of these branches with other branches in the tree was avoided at the moment of branch selection, in order to prevent other access opportunities for crawling arthropods. Thus, each tree harboured the four combinations of treatments: bird access (no mesh, sticky ring), arthropod access (mesh, no sticky ring), bird and arthropod access (no mesh, no sticky ring) and bird and arthropod exclusion (mesh, sticky ring). Weevils were surveyed 14 days after the experiment was set up, and the number of weevils removed was calculated (considering not only those weevils completely removed but also those weevils whose body remains suggested picking at by birds or chewing by arthropods) along with the number of intact remaining weevils. A *predation rate* per twig was estimated as the proportion of weevils removed with respect to the initial number of weevils.

Statistical analysis

Differences between years in the variables studied (e.g. weevil attack, parasitoid richness, bloom level) were measured by means of paired t tests (for variables showing a Gaussian distribution) and Wilcoxon's tests (for variables departing from normality). We quantified the effects of landscape structure and orchard features on weevils and parasitism by means of generalized linear mixed models (GLMMs; Bolker et al. 2009), considering the following as response variables: weevil attack, weevil abundance, parasitoid richness and parasitoid attack, all based on data for each orchard and year. All but one response variable conformed to a normal distribution after log transformation, and consequently, GLMMs included a Gaussian distribution (identity link), while models including parasitoid richness had a Poisson distribution (log link). As the main predictor variables we considered: the proportion of woody vegetation at R1000 and R125, the proportion of apple at R1000 and R125, distance to edge, canopy size, bloom level and groundcover density. Predictor variables were standardized prior to their inclusion in the models. The proportion of woody vegetation at R125 was significantly correlated (Pearson's $|r| > 0.64$, $N = 23$, see "Results" section) with that at R1000 and with the proportion of apple at R125, and thus, it was excluded from models in order to avoid collinearity effects. All other predictors were included in the early full models, but, to avoid model over-parametrization, those terms that were non-significant ($P > 0.05$) were excluded in a backwards stepwise procedure in order to select a simpler model. All models, nonetheless, included *year* as a categorical fixed factor—in order to control for the effects of temporal autocorrelation in the data set—as well as *orchard identity* as a random factor, given that almost all orchards were replicated across seasons (Bolker et al. 2009). Analyses were performed with the *lmer* (Gaussian) and *glmer* (Poisson) functions in the *lme4* package in R environment (Zuur et al. 2009).

We also used a GLMM (with a binomial error structure—logit link) to analyse the global influence of predator type on the probability of removal of adult weevils from experimental branches (binomial response variable). Fixed terms in the model were bird access, arthropod access and the interaction between both treatments, and season (considered here as a fixed factor due to the low number of levels within it, Bolker et al. 2009). Two- and three-order interactions between each treatment and season were included initially, but sequentially removed from the final model if they proved non-significant. Tree identity was included as a random factor. Model calculations were performed using the *glmer* function in the *lme4* package in R (Zuur et al. 2009). In order to assess paired comparisons between all combinations of treatments within a season, we fitted, separately for each season, a full GLMM which included predation rate as a binomial response, the treatment combination (which had four levels) as a single fixed predictor and tree identity as a random factor. We then estimated all paired contrasts between treatment combinations using the *glth* function in the *multcomp* package in R (Bretz et al. 2016).

Results

Weevil infestation

Weevil attack ranged from 0.43 to 37.40%, depending on the site and the year (Fig. 3a). Weevil attack in 2016 (mean ± SE: 14.72 ± 2.18) was almost double that of 2015 (8.00 ± 1.26) (paired *t* test: $t = -4.77$; df = 16; $P < 0.001$), and in both years it correlated positively across orchards (Pearson's correlation: $r = 0.74$; $P < 0.001$; $N = 17$). Weevil abundance (i.e. number of weevils per ha) also varied widely, ranging from 314 to 63,777, though no yearly differences were detected (2015: 14,160.27 ± 3369.16; 2016: 10,601.56 ± 4059.26; Wilcoxon's paired test: $|z| = -1.207$; $P = 0.227$; Fig. 3b), and no relationship was found for weevil abundance between years (Spearman's correlation: $r_s = 0.43$; $P = 0.08$; $N = 17$).

Parasitism on weevils

A total of 470 parasitoids, belonging to seven species, emerged from capped blossoms. *Scambus pomorum* (Hymenoptera: Ichneumonidae) was the most abundant (66.38%), followed by *Pteromalus semotus* (Hymenoptera: Pteromalidae) (21.06%), *Bracon variator* (Hymenoptera: Braconidae) (8.94%), *Bracon discoideus* (Hymenoptera: Braconidae) (2.55%), *Baryscapus pospelovi* (Hymenoptera: Eulophidae) (0.64%), *Baryscapus adalia* (Hymenoptera: Eulophidae) (0.21%) and *Scambus calobatus* (Hymenoptera: Ichneumonidae) (0.21%) (Table 1). The four most abundant species occurred in both years and showed the same ranking of abundance (Table 1). The most abundant parasitoid, *S. pomorum*, occurred in all 23 sites, whereas the other species each occurred in between 1 and 15 sites (Table 1). Parasitoid richness per site ranged from 1 to 5, averaging 2.04 ± 0.22 in 2015 and 2.33 ± 0.23 in 2016 (Fig. 3c). Differences between years were not significant (Wilcoxon's paired test: $|z| = -0.535$; $P = 0.593$), and indeed, parasitoid richness in 2015 and 2016 correlated positively across orchards (Spearman's correlation: $r_s = 0.56$; $P = 0.01$; $N = 17$).

Parasitoid attack affected between 6.40 and 81.50% of immature weevils, depending on the site and the year (Fig. 3d). On average, one-third of weevils was attacked each year (2015: 34.13 ± 5.04; 2016: 32.40 ± 4.50), and differences between years were not significant (Wilcoxon's paired

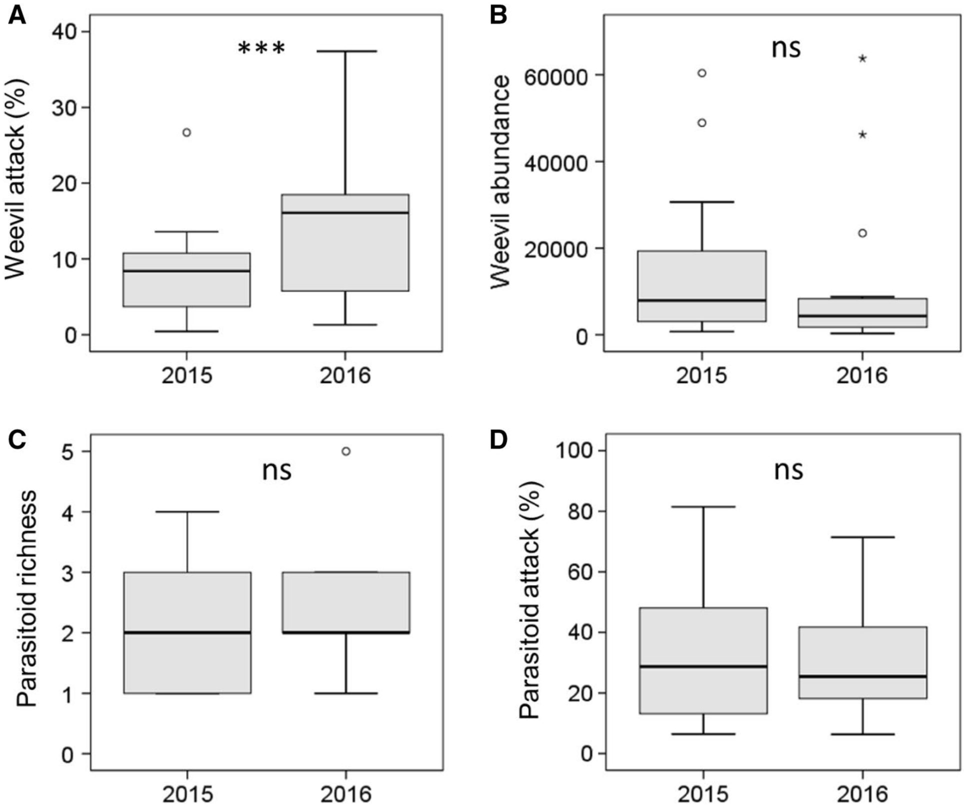

Fig. 3 Distribution of values of **a** weevil attack, **b** weevil abundance, **c** parasitoid richness and **d** parasitoid attack in different years. Boxplots indicate 25–75% quartiles (box boundaries), median (thick horizontal bar), largest and smallest observed values (whiskers), outliers (small circles) and extreme values (asterisks). Only weevil attack (percentage of capped blossoms) differed between years. Results of paired-test checks for statistical differences between years are also shown (***$P < 0.001$; ns: $P > 0.05$)

Table 1 Parasitoid species that attack apple blossom weevil

Parasitoid species	Family	Abundance			No. of sites where occurring		
		Total	2015	2016	Total	2015	2016
Scambus pomorum	Ichneumonidae	312	216	96	23	22	17
Pteromalus semotus	Pteromalidae	99	63	36	15	13	11
Bracon variator	Braconidae	42	17	25	9	6	8
Bracon discoideus	Braconidae	12	4	8	4	4	2
Baryscapus pospelovi	Eulophidae	3	–	3	2	–	2
Baryscapus adalia	Eulophidae	1	–	1	1	–	1
Scambus calobatus	Ichneumonidae	1	–	1	1	–	1
Total		470	300	170	23	23	23

Data on abundance and number of sites where each species occurred are shown for each year and for the total

test: $|z| = -0.213$; $P = 0.831$). Parasitoid attack in 2015 and 2016 correlated positively across orchards (Pearson's correlation: $r = 0.63$; $P = 0.006$; $N = 17$).

Determinants of weevil infestation and parasitism

The sites studied showed great variability in the proportion of semi-natural woody vegetation around apple orchards both in R1000 plots (mean ± SE = 0.23 ± 0.02, min–max = 0.10–0.42) and in R125 plots (mean ± SE = 0.20 ± 0.02, min–max = 0.03–0.50). Sites also varied greatly in the proportion of apple at both scales (R1000: mean ± SE = 0.08 ± 0.01, min–max = 0.02–0.15 and R125: mean ± SE = 0.39 ± 0.03, min–max = 0.13–0.67). No relationship was found between the proportion of semi-natural woody vegetation and the proportion of apple at R1000 (Pearson's correlation: $r = -0.07$; $P = 0.76$; $N = 23$), nor in the proportion of apple between scales (Pearson's correlation: $r = 0.19$; $P = 0.37$; $N = 23$). Sites also varied in the distance from target trees to edges (mean ± SE = 34.66 ± 2.65, min–max = 10.07–84.52), a feature that did not correlate with other landscape variables (Pearson's correlation: $|r| < 0.23$; $N = 23$ in all cases).

Regarding orchard features, bloom level was significantly higher in 2015 (mean ± SE = 2.59 ± 0.09, min–max = 1.88–3.38) than in 2016 (mean ± SE = 1.57 ± 0.18, min–max = 0.38–3.15; Wilcoxon's paired test: $|z| = -3.243$; $P = 0.001$) (Fig. S2). Sites varied considerably in canopy size (mean ± SE = 9.52 ± 0.82, min–max = 4.20–23.95) and greatly in terms of density of flowers in the groundcover (mean ± SE = 26.41 ± 3.97, min–max = 0.00–125.70), with no significant differences between years (Wilcoxon's paired test: $|z| = -1.160$; $P = 0.246$).

Both landscape and orchard features affected weevil attack, with percentage of flowers attacked by weevils increasing with proportion of semi-natural woody vegetation around apple orchards at R1000 and with proportion of apple cover at R125 (Table 2; Fig. 4a, b). In addition, weevil attack diminished with distance to the nearest edge (Table 2; Fig. 4c). As regards orchard features, bloom level negatively affected weevil attack, with the proportion of capped blossoms decreasing significantly in those orchards with higher quantities of flowers (Table 2; Fig. 4d).

Weevil abundance was also positively affected by the proportion of semi-natural woody vegetation around apple orchards in R1000 and with the proportion of apple cover in R125 (Table 2). As would be expected, bloom level had a positive effect (Table 2) since weevil abundance was calculated based on estimated number of flowers. Finally, a marginal positive effect of canopy size on weevil abundance was also detected (Table 2).

Parasitoid richness and parasitoid attack were not affected by either landscape structure or orchard features, and parasitoid attack was also independent of weevil attack and abundance. However, parasitoid richness was positively affected by weevil abundance, that is, orchards with a higher weevil abundance also hosted more parasitoid species (Table 2).

Predation on adult weevils

Removal of weevils from experimental branches increased significantly when access to predators, either birds or crawling arthropods, was permitted (Fig. 5; Table 3). Indeed, predation rate was the highest on open branches, where weevils were exposed to both types of predators at the same time (between 31 and 44% of weevils, depending on the season), and was lowest (2–13%) for branches with both plastic mesh and sticky ring exclusions. Thus, birds and crawling arthropods exerted an additive but independent (no significant effect of bird x arthropod interaction was found; Table 3) predatory effect on adult weevils. There were also seasonal differences in the proportion of weevils removed: overall predation rate was higher in May–June

Table 2 Results of generalized linear mixed models evaluating the effects of landscape structure and orchard features on weevil attack (log), weevil abundance ($\log_{10}$) and parasitoid richness

Predictors	Estimate ± SE	*t*	*P*	Random factor	Variance estimate ± SD
Weevil attack (Gaussian, identity)					
Prop. woody vegetation R1000	0.39 ± 0.11	3.49	0.003	Orchard	0.17 ± 0.41
Prop. apple R125	0.28 ± 0.11	2.63	0.015		
Distance to edge	− 0.20 ± 0.08	− 2.52	0.017		
Bloom level	− 0.38 ± 0.06	− 6.19	< 0.0001		
Weevil abundance (Gaussian, identity)					
Prop. woody vegetation R1000	0.28 ± 0.07	4.20	0.001	Orchard	0.01 ± 0.08
Prop. apple R125	0.18 ± 0.07	2.67	0.016		
Bloom level	0.30 ± 0.06	5.30	< 0.0001		
Canopy size	0.14 ± 0.06	2.11	0.053		
Predictors	Estimate ± SE	*z*	*P*	Random factor	Variance estimate ± SD
Parasitoid richness (Poisson, log)					
Weevil abundance	0.22 ± 0.11	2.03	0.043	Orchard	0.00 ± 0.00

The estimate of variance by orchard, considered as a random factor, is also shown. Details of the family of error distribution and link function used are shown in brackets

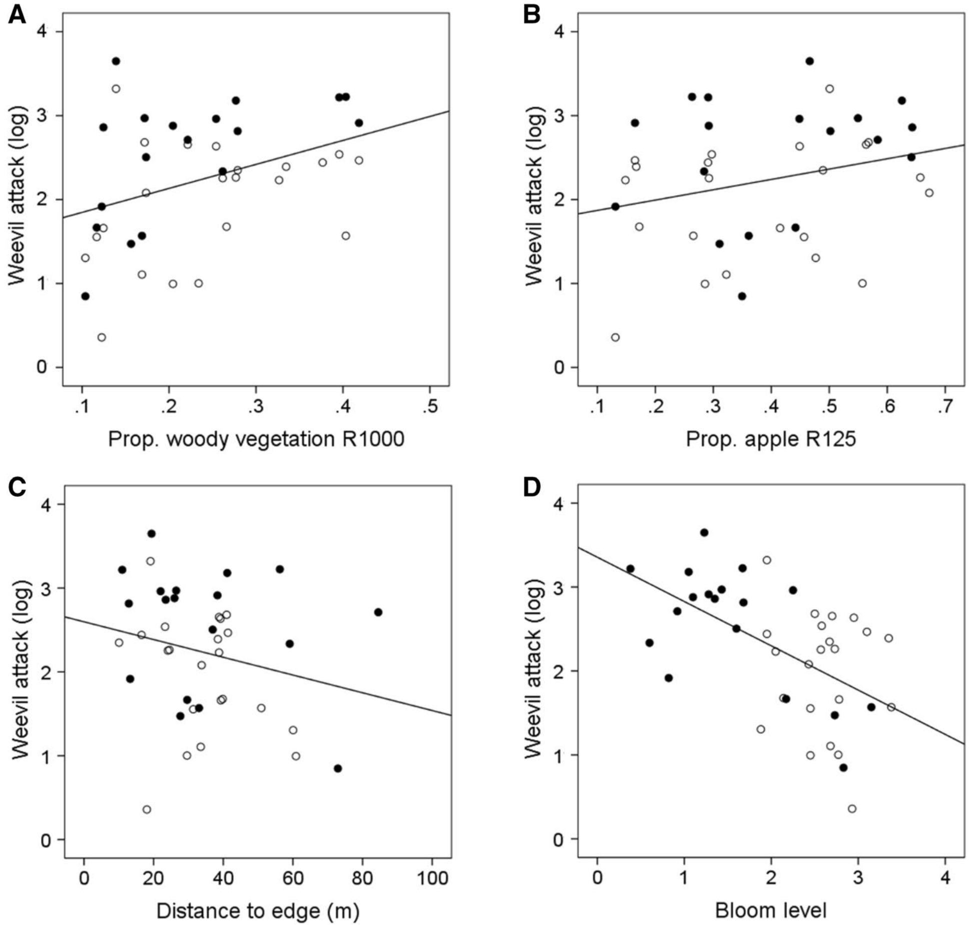

Fig. 4 Effects of landscape structure and orchard features on weevil attack. Effects of **a** the proportion of woody vegetation for the 1000-m-radius plot, **b** proportion of apple cover for the 125-m-radius plot, **c** distance from target trees to the nearest edge and **d** bloom level. Dots indicate different orchards, with different colours for different years (white: 2015; black: 2016). Linear fits predicted by linear regression models are shown

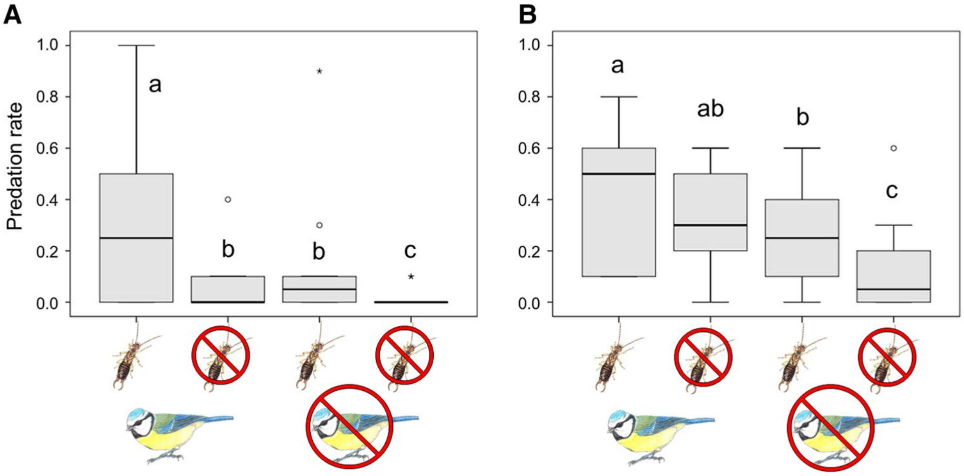

Fig. 5 Distribution of values of predation rate on adult weevils under different experimental treatments representing the access of different types of predators (birds, represented by a blue tit, and crawling arthropods, represented by an earwig). Panels represent different seasons: March–April (**a**) and May–June (**b**). Boxplots indicate 25–75% quartiles (box boundaries), median (thick horizontal bar), largest and smallest observed values (whiskers), outliers (small circles) and extreme values (asterisks). For each season, treatment levels with different letters above boxplots were significantly different. Drawings by Daniel García

Table 3 Results of the generalized linear mixed model evaluating the results of the experiment estimating the variability in the proportion of weevils removed by different types of predators (birds and arthropods and their interaction) from trees under different access treatments and between two seasons

Predictors	Estimate ± SE	*z*-value	*P*	Random factor	Variance estimate ± SD
Bird access	1.25 ± 0.35	3.59	< 0.001	Tree	0.98 ± 0.99
Arthropod access	2.51 ± 0.52	4.80	< 0.001		
Bird × arthropod	− 0.23 ± 0.42	− 0.55	0.580		
Season	2.44 ± 0.63	3.84	< 0.001		
Arthropod × season	− 1.64 ± 0.50	− 3.30	0.001		

The variance estimate for tree identity, considered as a random factor, is also shown. The model considered a binomial error distribution and a logit link

(mean ± SE = 0.29 ± 0.04) than in March–April (0.14 ± 0.04; Fig. 5; Table 3). Finally, there was also seasonal variation in the strength of arthropod access effect on weevil removal in that it was lower in June (Fig. 5; Table 3).

Discussion

In this work, we studied the role of the pest apple blossom weevil in the cider apple orchards of NW Spain. The environmental setting of these orchards, together with their low-intensity management practices, provided a low-input context that enabled us to apply a holistic study approach based on the whole life cycle of the pest. Moreover, we combined large-scale observational approaches with small-scale experiments to gain insight into both patterns of weevil infestation and the mechanisms of its biological control. We found predictable relationships between weevil infestation and orchard and landscape features which evidence the importance of resource availability at different scales on the prevalence of this pest. We also found evidence for the occurrence of complementary natural enemies (parasitoids, birds and crawling arthropods), which acted as local suppliers of pest control, although we failed to detect the regional drivers of this predatory assemblage. We would encourage the use of this type of integrative approach to aid understanding of the relevance of other kind of pests whose populations are simultaneously affected by resource and predator availability at different scales (see also Martin et al. 2015, 2016). In the following sections, we detail and discuss these issues and in conclusion suggest management guidelines for apple blossom weevil that take into account its habitat and its natural enemies.

How important is apple blossom weevil in Asturian low-input apple orchards?

The apple blossom weevil attacked flowers in all 23 orchards studied and can therefore be considered to be widespread in the region. The range of weevil attack (0.4–37.4%) found in this work is similar to the observed in other European countries: France (0.3–43%; FREDON 2006), Germany (0–13%; Knuff et al. 2017), Hungary (0–45%; Brown et al. 1993) and Switzerland (0–50%; Hausmann et al. 2004a). Despite this considerable range in rate of weevil attack, we found there to be temporal consistency, i.e. orchards with a high attack rate 1 year also had a high attack rate the following year.

Although the weevil attacks apple blossoms, preventing the flowers from becoming fruit, this reproductive loss does not necessarily translate into a detrimental effect on apple crop size since many healthy flowers also fail to become fruit. In fact, average fruit set in apple is below 50% (e.g. Garratt et al. 2014; Földesi et al. 2016), and in the context of the current work it is interesting to consider how many flowers need to be attacked by weevils before there are net negative effects on yield. A manipulative experiment on two apple cultivars (‘Golden Delicious’ and ‘Royal Gala’), which removed 1–3 of the five flowers per cluster, found that when at least three flowers remained, fruit set and yield were similar in non-manipulated and manipulated clusters (Miranda et al. 2005). Yield reduction was only observed when two or fewer flowers per cluster remained. Another factor that reduces yield variability is that fruits are heavier when crop loads are smaller, due to the reduced competition among fruit (Miranda et al. 2005; Meland 2009). Crop load in its turn affects return bloom in the subsequent year: high fruit load in apple inhibits floral induction and therefore fruit production the following year (Meland 2009; Samach and Smith 2013). As such, weevil attack could even have a thinning effect on blossoms, by diminishing the number of fruits per cluster, thus contributing to stabilizing yields across years and buffering biennial bearing, a key problem in regions like Asturias, where annual apple yields, both at the individual orchard and at the regional scale, can vary more than fivefold between consecutive years (Dapena et al. 2005). Such variability means that apple growers do not obtain regular crop yields or economic returns, and cider producers lack regular supplies and are frequently forced to rely on providers from outside the region.

The arguments above cast doubts on the notion that apple blossom weevil has a serious economic impact in Asturian apple orchards. That said, more research to quantify the real effect of weevil attack on fruit set, yield and the (de-) stabilization of biennial fruit production is needed in order to better understand the importance of this pest and to establish suitable action thresholds, which currently range from 10 to 40 adults on 100 beaten branches before flowering occurs (Oste-Lédée et al. 2001; FREDON 2006; Parveaud et al. 2016).

How important are natural enemies in controlling apple blossom weevil?

We applied different approaches and spatiotemporal scales to studying the different natural enemies of apple blossom weevils. This multi-scale approach may, we acknowledge, hamper the establishment of direct comparisons between enemy types in terms of how they exert biological control over populations of *A. pomorum* in cider apple orchards. Nevertheless, our results evidence that parasitoids, birds and crawling arthropods are all active and co-occurring predators of *A. pomorum* and suggest that they could exert complementary roles in supplying the ecosystem service of pest control (see also Martin et al. 2015).

Overall, we found seven species of parasitoids, with up to five species being found per site. Thus, the assemblage of larval parasitoids detected in our study was richer than that described in previous studies (see, for example, Knuff et al. 2017; Mody et al. 2017). However, equally high levels of richness have been found for other animal groups in the low-intensity agroecosystem of Asturian cider apple orchards (e.g. Miñarro et al. 2005, 2009; García et al. 2018). Parasitoids were widespread across the study region and on average attacked 30% of developing weevils, and in some orchards this figure reached 81.5%. These values may be considered high, for example compared to those reviewed by Cross et al. (1999), showing weevil parasitism rates to usually be below 50%. This parasitoid complex, however, seems to be ineffective in preventing apple tree damage in the current year because they attack the weevils once they are already inside the blossoms, and as such the flowers are already damaged. That said, they would, however, contribute to reducing the weevil population (one-third on average) from year to year. It should also be noted that the global effect of parasitoids on weevil populations could be even larger than we have seen in this work, as adult weevils may also be attacked (Zijp and Blommers 1992).

Birds and crawling arthropods preyed on adult weevils from both the overwintering and the new generation. To this end, they would prevent damage to the plant in both the current year (by preventing weevil egg-laying) and the following year (by decreasing the extant weevil population). Birds and arthropods have an additive predatory effect (e.g. for a case involving birds and ants, see Singer et al. 2017). Our results accord with this in that, depending on the season, 30–45% of weevils were removed when both types of predators were present, predation rates which could be considered high enough to exert a regulation effect on weevil population dynamics (see Prieditis 1975 for predation rates of around 57%). In spring and summer, adult weevils are active—feeding, crawling, mating and ovipositing (e.g. Miles 1923; Duan et al. 1996)—both during the day and at night when temperatures are above 5 °C (Duan et al. 1996; Hausmann et al.

2004b) and can be easily detected by predators. In addition, cases of bird species preying on adults and also opening capped blossom to feed on immature stages of *A. pomorum* have been frequently reported (e.g. Miles 1923; Zijp and Blommers 1992; Cross et al. 1999). The results of the present study on predation by birds are supported by those of another experiment in the area which suggested that birds have a strong effect on reducing the population of, among others pests, apple blossom weevil in cider apple orchards (García et al. 2018).

As well as birds, crawling arthropods also contributed to reducing weevil populations. Ants can attack adult weevils as well as larvae in capped blossoms (Fig. S3) and have also been reported as attacking other *Anthonomus* species in shrubs (Alves-Silva et al. 2015). Spiders, earwigs, predatory bugs and other generalist predators, all of which are frequent in the apple orchards studied (Miñarro et al. 2005, 2009), could also play their part in the predation recorded in this study.

What are the determinants of weevil infestation and biological control?

Local- and large-scale landscape features contributed to explaining the spatiotemporal variation in weevil infestation across study years and orchards, being the yearly bloom level mostly responsible for explaining the between-year differences in weevil attack. As commented earlier, apple orchards in Asturias experience notable biennial bearing and in 2015, a year of heavy bloom, weevil attack was lower than in the poor bloom year 2016. This decrease in pest attack rate associated with the poor year of biennial bearing could be the result of a predator satiation process by which the scarce crops lead to a decrease in the populations of specialist herbivores, which are then followed by abundant crops that would satiate the scarce predators, which are unable to respond numerically or functionally to resource overyielding (Kelly 1994; Kelly and Sork 2002). However, in our case, weevil abundance (i.e. the number of weevils per ha) and, hence, the estimated amount of blossom damaged, remained steady across years, indicating that changes in percentage of damage depended on yield dynamics (i.e. the total number of flowers) rather than on changes in weevil population size. Thus, the results here demonstrate that although biennial bearing led to a dilution of weevil attack, this reproductive strategy did not seem to ultimately regulate the population size of apple blossom weevil. Indeed, a similar dilution effect of high bloom levels was recorded at the orchard level as well as at the larger scale: weevil attack diminished with increasing bloom level across orchards. On the contrary, bloom level and weevil abundance were positively correlated since the latter was calculated based on the former. One local factor not explicitly considered in our study but with large potential influence on weevil populations is the apple genotype (e.g. Mody et al. 2015; Knuff et al. 2017). We conducted our study on a single cultivar to control for potential cultivar effects, but, anyway, there is still a possibility that weevil incidence on this target cultivar could be affected by the presence of other cultivars. This was not the case in the present study, as suggested by the lack of relationship between proportion of the target cultivar in the whole orchard and weevil attack or weevil abundance ($r = -0.241$; $P = 0.134$ and $r_s = -0.209$; $P = 0.195$, respectively). Nevertheless, further research on cultivar susceptibility is needed to offer a more generalized response to the pest status and the drivers affecting *A. pomorum* in our region.

Weevil attack across orchards responded to habitat features related to the surrounding availability of apple plantations and woody vegetation at different spatial scales (but see Markó et al. 2017). At the fine scale, the cover of apple trees positively impacted on weevil attack: orchards surrounded by other orchards suffered from higher levels of weevil infestation. *Anthonomus pomorum* is a specialist pest that uses apple crop for feeding, mating, breeding and overwintering (Miles 1923), and it therefore is able to respond to apple volatiles, and even to visual cues of this tree (Hausmann et al. 2004c; Collatz and Dorn 2013) due to its specialization, and thus, an increase in weevil populations related to increased coverage of apple trees is to be expected. At the large scale, woody vegetation cover around orchards also had a positive effect on weevil attack since it offers winter shelter for adult weevils, which frequently hide under the bark of trees (Brown et al. 1993; Toepfer et al. 2000). At the end of winter, weevils travel from their woodland refuges to reproduce in apple orchards, where they are sedentary, and tend to stay on the first apple tree they colonize or to only move short distances, mainly along the row of trees (Toepfer et al. 1999). This type of colonization pattern would explain why weevil infestation in this study decreased with distance to the orchard edge (see also, for similar border effects, Brown et al. 1993; Toepfer et al. 1999). In sum, our results suggest that surrounding semi-natural habitats provide a suitable resource for the whole life cycle of apple blossom weevil.

In contrast to the results for weevils, and unexpectedly, we did not detect any environmental driver of parasitoid abundance and richness, contrarily to the landscape effect detected in Swiss orchards, where weevil parasitism was higher in potted trees closer to the forest edge (Mody et al. 2011). We neither detected effects of the size of the weevil population on the level of parasitism attack, although we did find that abundance of weevils was positively correlated with parasitoid richness. This could, however, be the result of a sampling effect since the higher the host availability, the higher the probability of sampling more species attacking that host. Despite it is well known that pesticides can negatively affect natural enemies (e.g. Monteiro et al. 2013; Markó et al. 2017), we do not consider that pesticide usage could be an important factor driving parasitoid assemblages in our study system, given the low pesticide pressure in our orchards (0–2 sprayings with narrow-spectrum products). This work did not evaluate the local and landscape determinants of other natural enemies of apple blossom weevils, i.e. birds and crawling arthropods, which has been shown elsewhere. For example, bird abundance and richness increase with apple tree canopy cover and with the availability of semi-natural woody habitats (García et al. 2018), and the diversity of crawling predators like spiders, ants, earwigs and predatory beetles is also influenced by landscape features (Lefebvre et al. 2016, 2017) as well as by local management strategies (Miñarro et al. 2009; Marliac et al. 2016).

Implications for management

Our results on the pest status of *A. pomorum* in cider apple orchards seem to support the notion that low-input management can be acceptable. Bearing in mind that apple blossom weevil is not seen as a serious agronomic threat in Asturias, we would also suggest that farmers should also consider the present system to have a capacity for biological control (thanks to the functional diversity of predators) that is sufficient to keep the pest at non-harmful levels. Moreover, levels of this pest are predictable between years, i.e. the percentage of flowers damaged will depend on the damage the previous year. This has two management implications. First, it allows growers to predict the level of damage to their orchard and make management decisions accordingly. Second, if good population control is achieved, further control measures will probably not be required for some years, until weevil density peaks again.

Landscape management is also to be recommended, although it is recognized that management at such a large scale is usually beyond the grower's scope. Semi-natural habitats around apple orchards provide a suitable environment for the apple blossom weevil, whereas no such relation was found for parasitoids. On the contrary, woody landscape complexity is known to favour biodiversity of insectivorous birds in these same orchards, and such birds can contribute greatly to the control of other apple pests (García et al. 2018). Furthermore, it is generally assumed that landscape complexity, in general, facilitates the ecosystem service of pest control by natural enemies (Tscharntke et al. 2012; Rusch et al. 2016). Thus, the results of different services and disservices provided by the landscape in this agroecosystem should be balanced to take the most appropriate management decisions.

Ecological intensification at the farm level to promote biological control has been recommended (Bommarco et al. 2013). For example, nest boxes for insectivorous birds are readily occupied and can promote the biological control of agricultural pests (Mols and Visser 2002; Benayas et al. 2017) and other measures favouring the biodiversity of natural enemies (flower strips, hedgerows) have also been recommended (e.g. Wratten et al. 2012; Sidhu and Joshi 2016).

Finally, insecticides are only to be considered necessary in cases of very high attack of *A. pomorum,* usually reached in the poor bloom year, and always taking into account the border effect, that is, reducing the spraying from the edge to the centre of the orchard. In such cases, furthermore, the insecticide should be sprayed at bud burst, after adults have colonized the orchard and before any significant oviposition occurs (Miles 1923), and it should preferably be applied during warm weather, when adults are more active (Duan et al. 1996). Further applied research should pinpoint to develop explicit practical guidelines for insecticide application under prevision of high pest attack, including the economic thresholds for the occurrence of *A. pomorum*.

Author contribution statement

MM and DG conceived and designed the research, conducted the experiments, analysed the data and wrote the manuscript, which both authors have approved.

Acknowledgements We thank Kent Twizell, David Luna, Carlos Guardado, Alejandro González and Alejandro Núñez for technical support; the technicians from Campoastur S. Coop. Asturiana for helping us with orchard selection; the orchard owners for allowing us to work on their orchards; and Vladimir Žikić, Hossein Lotfalizadeh and David Luna for identification of the parasitoid species.

Funding This study was funded by grants INIA-RTA2013-00139-C03-01 (Ministerio de Economía, Industria y Competitividad (MinECo) and Fondo Europeo de Desarrollo Regional) to MM, PCIN2014-145-C02-02 (MinECo; EcoFruit project BiodivERsA-FACCE2014-74) and CGL2015-68963-C2-2-R (MinECo) to DG. Funding sources had no involvement in study design, collection, analysis or interpretation of data, the writing of the report or the decision to submit the article for publication.

Compliance with ethical standards

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

Agnello A, Cox K, Dominguez L, Francescatto P, Lordan J, Robinson T (2015) An insect, disease and weed management program for New York organic apples. N Y Fruit Q 23(4):27–34

Alves-Silva E, Bächtold A, Barônio GJ, Torezan-Silingardi HM, Del-Claro K (2015) Ant–herbivore interactions in an extrafloral nectaried plant: are ants good plant guards against curculionid beetles? J Nat Hist 49:841–851

Balázs K, Molnár M, Bujaki G, Gonda I, Karacsony D, Bartha J (1997) Possibility and problems of organic apple growing in Hungary. Biol Agric Hortic 15:223–232

Benayas JMR, Meltzer J, de las Heras-Bravo D, Cayuela L (2017) Potential of pest regulation by insectivorous birds in Mediterranean woody crops. PLoS ONE 12:e0180702

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bommarco R, Kleijn D, Potts SG (2013) Ecological intensification: harnessing ecosystem services for food security. Trends Ecol Evol 28:230–238

Bretz F, Hothorn T, Westfall P (2016) Multiple comparisons using R. CRC Press, Boca Raton

Brown MW, Szentkiralyi F, Kozar F (1993) Spatial and temporal variation of apple blossom weevil populations (Col., Curculionidae) with recommendations for sampling. J Appl Entomol 115:8–13

Collatz J, Dorn S (2013) A host-plant-derived volatile blend to attract the apple blossom weevil *Anthonomus pomorum*–the essential volatiles include a repellent constituent. Pest Manag Sci 69:1092–1098

Cross JV, Solomon MG, Babandreier D et al (1999) Biocontrol of pests of apples and pears in northern and central Europe: 2. Parasitoids. Biocontrol Sci Technol 9:277–314

Cross JV, Fountain M, Markó V, Nagy C (2015) Arthropod ecosystem services in apple orchards and their economic benefits. Ecol Entomol 40:82–96

Dapena E, Miñarro M, Blázquez MD (2005) Organic cider-apple production in Asturias (NW Spain). IOBC/wprs Bull 28(7):142–146

Duan JJ, Weber DC, Hirs B, Dorn S (1996) Spring behavioral patterns of the apple blossom weevil. Entomol Exp Appl 79:9–17

FAO (2017) Food and agriculture organization of the United Nations. http://www.fao.org/faostat/en/#data/QC. Accessed 24 Aug 2017

Fitton MG, Shaw MR, Gauld ID (1988) Pimpline ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). In: Handbooks for the identification of British insects, vol 7(1). Royal Entomological Society of London, London

Földesi R, Kovács-Hostyánszki A, Kőrösi Á et al (2016) Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. Agric For Entomol 18:68–75

FREDON (2006) L'anthonome du pommier, un ravageur à surveiller de près. Fiche technique. Fédération Régionale de Défense contre les Organismes Nuisibles

García D, Miñarro M, Martínez-Sastre R (2018) Birds as suppliers of pest control in cider apple orchards: bird biodiversity filters and insectivore effect. Agric Ecosyst Environ 254:233–243

Garratt MP, Breeze TD, Jenner N, Polce C, Biesmeijer JC, Potts SG (2014) Avoiding a bad apple: insect pollination enhances fruit quality and economic value. Agric Ecosyst Environ 184:34–40

Gillespie MA, Gurr GM, Wratten SD (2016) Beyond nectar provision: the other resource requirements of parasitoid biological control agents. Entomol Exp Appl 159:207–221

Gomiero T, Pimentel D, Paoletti MG (2011) Environmental impact of different agricultural management practices: conventional vs. organic agriculture. Crit Rev Plant Sci 30:95–124

Guedes RNC, Smagghe G, Stark JD, Desneux N (2016) Pesticide-induced stress in arthropod pests for optimized integrated pest management programs. Annu Rev Entomol 61:43–62

Hausmann C, Samietz J, Dorn S (2004a) Significance of shelter traps for spring monitoring of *Anthonomus pomorum* in apple orchards. Entomol Exp Appl 112:29–36

Hausmann C, Samietz J, Dorn S (2004b) Monitoring the dynamics of orchard colonisation by *Anthonomus pomorum* in spring. Entomol Exp Appl 110:207–216

Hausmann C, Samietz J, Dorn S (2004c) Visual orientation of overwintered *Anthonomus pomorum* (Coleoptera: curculionidae). Environ Entomol 33:1410–1415

INDUROT (2010) Cartografía del manzano en el Principado de Asturias. Consejería de Medio Rural y Pesca. Gobierno del Principado de Asturias

Jonkers H (1979) Biennial bearing in apple and pear: a literature survey. Sci Hortic 11:303–317

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9:465–470

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447

Knuff AK, Obermaier E, Mody K (2017) Differential susceptibility and suitability of domestic and wild apple species for a florivorous weevil and its parasitoids. J Appl Entomol 141:285–299

Lefebvre M, Franck P, Toubon JF, Bouvier JC, Lavigne C (2016) The impact of landscape composition on the occurrence of a canopy dwelling spider depends on orchard management. Agric Ecosyst Environ 215:20–29

Lefebvre M, Papaïx J, Mollot G et al (2017) Bayesian inferences of arthropod movements between hedgerows and orchards. Basic Appl Ecol 21:76–84

Markó V, Elek Z, Kovács-Hostyánszki A et al (2017) Landscapes, orchards, pesticides–Abundance of beetles (Coleoptera) in apple orchards along pesticide toxicity and landscape complexity gradients. Agric Ecosyst Environ 247:246–254

Marliac G, Mazzia C, Pasquet A, Cornic JF, Hedde M, Capowiez Y (2016) Management diversity within organic production influences epigeal spider communities in apple orchards. Agric Ecosyst Environ 216:73–81

Martin EA, Reineking B, Seo B, Steffan-Dewenter I (2015) Pest control of aphids depends on landscape complexity and natural enemy interactions. PeerJ 3:e1095

Martin EA, Seo B, Park CR, Reineking B, Steffan-Dewenter I (2016) Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecol Appl 26:448–462

Meland M (2009) Effects of different crop loads and thinning times on yield, fruit quality, and return bloom in *Malus* × *domestica* Borkh. 'Elstar'. J Hortic Sci Biotechnol 84:117–121

Miles HW (1923) Observations on the bionomics of the apple-blossom weevil, *Anthonomus pomorum,* Linn. Ann Appl Biol 10:348–369

Miñarro M (2012) Weed communities in apple orchards under organic and conventional fertilization and tree-row management. Crop Prot 39:89–96

Miñarro M, Hemptinne J-L, Dapena E (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. Biocontrol 50:403–414

Miñarro M, Espadaler X, Melero VX, Suárez-Álvarez V (2009) Organic versus conventional management in an apple orchard: effects of fertilization and tree-row management on ground-dwelling predaceous arthropods. Agric For Entomol 11:133–142

Miranda C, Santesteban LG, Royo JB (2005) Removal of the most developed flowers influences fruit set, quality, and yield of apple clusters. HortSci 40:353–356

Mody K, Spoerndli C, Dorn S (2011) Within-orchard variability of the ecosystem service 'parasitism': effects of cultivars, ants and tree location. Basic Appl Ecol 12:456–465

Mody K, Collatz J, Dorn S (2015) Plant genotype and the preference and performance of herbivores: cultivar affects apple resistance to the florivorous weevil *Anthonomus pomorum*. Agric For Entomol 17:337–346

Mody K, Collatz J, Bucharova A, Dorn S (2017) Crop cultivar affects performance of herbivore enemies and may trigger enhanced pest control by coaction of different parasitoid species. Agric Ecosyst Environ 245:74–82

Mols CM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. J Appl Ecol 39:888–899

Monteiro LB, Lavigne C, Ricci B, Franck P, Toubon JF, Sauphanor B (2013) Predation of codling moth eggs is affected by pest management practices at orchard and landscape levels. Agric Ecosyst Environ 166:86–93

Oste-Lédée S, Desprez MC, Emery D (2001) Anthonome du pommier (*Anthonomus pomorum* L.). Recherche de stratégie de lutte en verger de production biologique. L'Arboriculture Fruit 551:51–56

Parsa S, Morse S, Bonifacio A et al (2014) Obstacles to integrated pest management adoption in developing countries. PNAS 111:3889–3894

Parveaud C-E, Brenner J, Stoeffel A, Corroyer N (2016) Anthonome du pommier en agriculture biologique. Technical brochure

Prieditis A (1975) Natural enemies of the apple blossom weevil (*Anthonomus pomorum*). Augu Aizsardz Probl 84:17–27

Pywell RF, Heard MS, Woodcock BA, Hinsley S, Ridding L, Nowakowski M, Bullock JM (2015) Wildlife-friendly farming increases crop yield: evidence for ecological intensification. Proc R Soc B 282:20151740

Reganold JP, Wachter JM (2016) Organic agriculture in the twenty-first century. Nat Plants 2:15221

Regnier R (1923) De quelques grands ennemis du Pommier et de leurs Parasites. Revue de botanique appliquée et d'agriculture coloniale 3:169–185

Rusch A, Chaplin-Kramer R, Gardiner MM et al (2016) Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. Agric Ecosyst Environ 221:198–204

Samach A, Smith HM (2013) Constraints to obtaining consistent annual yields in perennials. II: environment and fruit load affect induction of flowering. Plant Sci 207:168–176

Sidhu CS, Joshi NK (2016) Establishing wildflower pollinator habitats in agricultural farmland to provide multiple ecosystem services. Front Plant Sci 7:363

Simon S, Bouvier JC, Debras JF, Sauphanor B (2010) Biodiversity and pest management in orchard systems. A review. Agron Sustain Dev 30:139–152

Singer MS, Clark RE, Lichter-Marck IH, Johnson ER, Mooney KA (2017) Predatory birds and ants partition caterpillar prey by body size and diet breadth. J Anim Ecol 86:1363–1371

Toepfer S, Gu H, Dorn S (1999) Spring colonisation of orchards by *Anthonomus pomorum* from adjacent forest borders. Entomol Exp Appl 93:131–139

Toepfer S, Gu H, Dorn S (2000) Selection of hibernation sites by *Anthonomus pomorum*: preferences and ecological consequences. Entomol Exp Appl 95:241–249

Tscharntke T, Tylianakis JM, Rand TA et al (2012) Landscape moderation of biodiversity patterns and processes eight hypotheses. Biol Rev 87:661–685

Walker JT, Suckling DM, Wearing CH (2017) Past, present, and future of integrated control of apple pests: the New Zealand experience. Annu Rev Entomol 62:231–248

Wratten SD, Gillespie M, Decourtye A, Mader E, Desneux N (2012) Pollinator habitat enhancement: benefits to other ecosystem services. Agric Ecosyst Environ 159:112–122

Zijp JP, Blommers LHM (1992) *Syrrhizus delusorius* and *Scambus pomorum*, two parasitoids of the apple blossom weevil. Proceed Exp Appl Entomol 3:46–50

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York