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

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23 **Abstract**

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

42

43 **Keywords:** *Anthonomus pomorum*, biodiversity, complementary predation, ecosystem services,
44 insectivorous birds, parasitoids

45

46 **Key Message**

47

- 48 • The low input scenario of cider apple orchards in NW Spain facilitates understanding of
49 *Anthonomus pomorum* infestation and its biological control.
- 50 • Resource and habitat availability at local and landscape scales explained the prevalence of
51 *A. pomorum*.
- 52 • The co-occurring natural enemies of *A. pomorum*, parasitoids, birds and crawling
53 arthropods, potentially exert complementary control.

54 • Pest and natural enemy management through habitat measures is recommended instead
55 of pesticide use.

56

57 **Author Contribution Statement**

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

60

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66

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77

78 Introduction

79 Pest control in most farming systems currently relies on the use of pesticides (e.g. Parsa et al.
80 2014; Guedes et al. 2016), a situation which hampers the unravelling of the natural mechanisms
81 that regulate pest populations, given that not only pests but also their natural enemies may be
82 disrupted by pesticides (e.g. Monteiro et al. 2013; Markó et al. 2017). Low input farming is an
83 alternative production system which aims to optimize management and production with the
84 minimum use of external inputs, such as purchased fertilizers and pesticides (e.g. Gomiero et
85 al. 2011; Reganold and Wachter 2016). It may thus represent a suitable real world context
86 within which to understand the functioning of biological control. However, despite the suitability
87 of wildlife-friendly farming for globally important crops (e.g. Pywell et al. 2015), this issue has
88 seldom been addressed.

89 Apple is one of the major fruit crops in the world. With 84.10⁶ tons produced in 2014,
90 apple ranks 3rd in the global fruit production after bananas and watermelons (FAO 2017).
91 However, apple is threatened by numerous pests that can compromise crop viability, with
92 potential losses caused by pests in unsprayed orchards averaging 40-50% and even reaching
93 85% (Cross et al. 2015). Accordingly, European apple orchards normally receive 5-15
94 insecticide applications per year, at a cost of at least of 400€/ha (Cross et al. 2015).
95 Nevertheless, at both the regional and the local scale, there are examples of apple pests and
96 diseases which are successfully managed in low input contexts (e.g. Agnello et al. 2015; Walker
97 et al. 2017).

98 Cider apple orchards in Asturias, NW Spain, potentially provide an optimal system in
99 which to study apple production in a regional low input farming context. Asturias has a long
100 tradition of cider making, and most of its 10,000 ha of apple orchards are cultivated almost
101 exclusively to this end (INDUROT 2010). Apples are produced both in traditional extensive
102 orchards with large trees grown on seedling rootstock, and in semi-intensive orchards where
103 semi-dwarfing rootstock is used (Dapena et al. 2005). All are planted with selected local
104 cultivars tolerant to apple diseases, and, thus, the use of pesticide is very low, even, in some
105 cases, null. The orchards are embedded in a highly variegated landscape where patches of
106 semi-natural habitats, such as hedgerows and woodlands, are frequent. The low pressure of
107 pesticides and the surrounding landscape complexity favour biodiversity within cider apple

108 orchards and in their neighbourhood, including both apple pest insects and their natural
109 enemies (insects and vertebrates such as birds, e.g. Miñarro et al. 2005, 2009; García et al.
110 2018). Despite these characteristics, there is no information on how the low input context
111 actually affects the prevalence of pests or the effect of their antagonists.

112 The apple blossom weevil, *Anthonomus pomorum* L. (Coleoptera: Curculionidae), is a
113 common pest in Asturian cider apple orchards, and was a key pest in European apple orchards
114 before the extensive use of broad spectrum pesticides (Miles 1923; Regnier 1923). Linked to
115 reductions in both the application and the spectrum of pesticides over the last two decades, the
116 importance of *A. pomorum* as an apple pest has risen, particularly in organic farming systems
117 (e.g. Balázs et al. 1997; Cross et al. 1999; Oste-Lédée et al. 2001). According to their vital
118 requirements (Miles 1923), the size of populations of *A. pomorum* might be limited by
119 opportunities for both overwintering and egg-laying (Fig. 1). While it is known that adults
120 overwinter sheltered under the bark of apple trees (Miles 1923), most modern orchards are
121 grown on dwarfing rootstock that produce small trees with smooth bark and thus provide little
122 opportunity for winter shelter (Toepfer et al. 2000). As a result, in young and modern orchards,
123 adult weevils shelter in the trees surrounding the orchard (Brown et al. 1993; Toepfer et al.
124 2000). Another point to note is that apple trees naturally show biennial bearing: one year of
125 abundant blossom is followed by a year of scarce bloom (Jonkers 1979; Samach and Smith
126 2013), and as such, following a satiation process (Kelly 1994; Kelly and Sork 2002), apple pest
127 incidence would decrease in years of heavy blossom, whereas the limited availability of
128 blossom would constraint weevil egg-laying in years of scarce blossom. In addition, populations
129 of apple blossom weevils may also be limited by the occurrence of their natural enemies (Fig.
130 1). Weevils are attacked by several parasitoid species, mainly during their larval stage inside
131 the blossom (Miles 1923; Cross et al. 1999; Mody et al. 2011; Knuff et al. 2017). In their turn,
132 parasitoids have several resource requirements (floral resources for adults, shelter habitat,
133 other hosts) at both the orchard and the landscape scale (Gillespie et al. 2016). Besides
134 parasitoids, biological control by generalist predators (i.e. birds and crawling arthropods, Cross
135 et al. 1999) is also exerted during the weevil adult stage, both in early spring, when
136 overwintering adult weevils start to feed and mate, and, after the summer emergence, when
137 they feed on tree leaves (Fig. 1). Despite these findings, to our knowledge no study has

138 addressed the simultaneous roles of resource availability and predator pressure on apple weevil
139 incidence.

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

148

149 **Materials and Methods**

150 **Study site and orchard and landscape features**

151 The observational study was conducted between 2015 and 2017 in 23 cider-apple orchards
152 distributed over a 600 km² study area in Asturias (43° 21' to 43° 30' N, 5° 20' to 5° 45' W) (Figs.
153 2A and 2B). Orchards were located from 10 to 385 m a.s.l. and their size varied from 0.5 to 20.6
154 ha. Minimum distance between orchards was 1.2 km (Fig. 2B). Trees were grown on semi-
155 dwarfing rootstock, with a density of ca. 500 trees/ha in all but two cases, where trees were
156 grown on seedling rootstock with 250 trees/ha. All orchards comprised several cultivars, but all
157 sampling was done on the local cultivar 'Regona' to homogenize sampling (given that weevil
158 infestation and parasitism rates depend on cultivar; Mody et al. 2015; Knuff et al. 2017).

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

168 or pirimicarb against aphids. Only one orchard applied a broad-spectrum insecticide (lambda
169 cyhalothrin).

170 In 2015, 22 orchards were studied but the following year 4 sites had to be discarded
171 because of the scarcity of blossom, meaning that only 18 were surveyed in 2016. Seventeen of
172 the orchards were sampled in both years. In each orchard, eight trees (target trees) were
173 marked before full bloom. Sampling was conducted shortly after full flowering of the target
174 cultivar 'Regona', which varied notably among sites (between April 30th and May 16th in 2015
175 and May 19th and June 14th in 2016).

176

177 *Landscape features*

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

194

195 *Orchard features*

196 We measured *bloom level* as an indicator of the number of flowers in the orchard. This variable
197 would be expected to differ between cultivars, across sites and between years (due to the

198 natural biennial bearing of apple trees). We recorded bloom level when the target cultivar
199 ('Regona') was in full bloom, by walking perpendicular to tree rows in order to avoid a cultivar
200 effect (as rows contain a single cultivar) and covering the full extent of the orchard. For 30
201 randomly-chosen trees per orchard and year, we scored the number of flowers per tree by using
202 a semi-quantitative scale: 0, 0 flowers; 1, 1-10 flowers; 2, 11-50 flowers; 2.5, 51-100 flowers; 3,
203 101-500 flowers; 3.5, 501-1000 flowers; 4, 1001-5000 flowers; 4.5, 5001-10000 flowers; 5, more
204 than 10000 flowers. We calculated *bloom level* per orchard and year by averaging this estimate
205 across trees. We used the size of apple trees as an indicator of within-orchard resources for
206 weevils, both for overwintering (shelter) and breeding (blossom), and to this end we randomly
207 selected 10 trees from within an area with a 25-m radius centred on the midpoint of the target
208 trees, and measured tree canopy length and width. We calculated *canopy size* by multiplying
209 canopy length by canopy width for each tree, and averaged this estimate across trees per
210 orchard. Finally, we measured the density of flowers in the orchard groundcover (*groundcover*
211 *density*) since adult parasitoids feed on nectar (Gillespie et al. 2016) and thus flower density
212 could be an indicator of trophic resources for parasitoids (Simon et al. 2010). This was visually
213 assessed over 150-200-m transects, in 50x50 cm ground quadrats placed at 10-m intervals (14
214 intervals per transect in 2015, and 20 in 2016). Groundcover is managed differently in tree rows
215 than between rows, leading to small-scale differences in plant composition (e.g. Miñarro 2012).
216 Thus, half of the quadrats were in tree rows and half between rows. *Groundcover density* was
217 estimated as the number of flowers per square metre by averaging the density of flowers across
218 quadrats.

219

220 **Weevil infestation**

221 On each target tree, a 1-m length branch (100-150 flowers) at a height of 1-1.5 m was randomly
222 selected and the number of weevil infested flowers on it were counted. Weevil attacked flowers,
223 known as 'capped blossoms', are easily identifiable because their petals turn brown and dry,
224 and remain closed (Fig. 1). The number of flower clusters per branch was also counted and
225 multiplied by the average number of flowers per cluster, as estimated from 30 'Regona' clusters
226 in three different orchards each year (6.50 flowers per cluster in 2015, and 5.92 in 2016). For
227 each tree, the *weevil attack* was calculated as the percentage of capped blossoms as regards

228 the total number of flowers. We calculated *weevil abundance*, an indicator of the total number of
229 weevils per ha produced at each site, by multiplying weevil attack by the estimated number of
230 flowers per ha, the latter being calculated as the product of the number of trees per ha
231 multiplied by the average number of flowers per tree (estimated from bloom level sampling, by
232 replacing bloom level by a central value of the abundance class: 0 bloom level = 0 flowers; 1
233 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;
234 and 5 = 10000).

235

236 **Parasitism on weevils**

237 Fifteen capped blossoms were collected from each target tree (totalling 120 capped blossoms
238 per site) and taken to the laboratory. The sample from each tree was stored separately at room
239 temperature in a plastic Petri dish with lab paper at the bottom for moisture absorption. Petri
240 dishes were examined at 48-72-h intervals, and the emergence of weevils and parasitoids
241 recorded. After emergence, weevils and parasitoids were frozen and stored in Eppendorf tubes
242 at -20°C. Parasitoids were identified by Vladimir Žikić (Braconidae), Hossein Lotfalizadeh
243 (Chalcidoidea) and David Luna (Ichneumonidae). *Parasitoid richness* was calculated as the
244 number of emerged parasitoid species from each orchard, and *parasitoid attack*, i.e. the
245 percentage of weevils attacked by parasitoids, as the percentage of emerged parasitoids in
246 relation to the sum of emerged weevils and parasitoids.

247

248 **Predation on adult weevils**

249 We experimentally assessed the removal of adult weevils in the field by different predators and
250 in different seasons throughout the weevil life-cycle. The experiment was conducted in spring
251 2017 in one of the study orchards (located in Camoca, 43° 27' N, 5° 28' W). The experiment
252 was first set up in March-April, when adult weevils feed on the apple trees and oviposit in
253 blossoms after overwintering, and it was then replicated in May-June, when a new-cohort of
254 adults emerge and feed on trees (Oste-Lédée 2001; Fig. 1). In each season, 10 trees of similar
255 size, separated from each other by at least 5 m, and belonging to four different rows in the
256 orchard, were selected. For each tree, four branches of similar length and diameter and at a
257 height of approximately 1.5 m, were selected and a 25-cm apple twig with a row of 10 adult

258 weevils stuck with epoxy glue to it, was tied with wire to the upper part of each branch (Fig. S1).
259 The weevils were from the pool of adults emerging from the capped blossoms collected each
260 year (see above). The experimental weevils (branches) of each tree were assigned, in a full
261 factorial design, to one of two treatments simulating their access by two different types of
262 potential predators: birds and crawling arthropods. Bird access was prevented by covering the
263 weevils with a 50-cm long cylindrical (6-cm radius) cage of 10-mm pore plastic mesh, held
264 parallel to the branch and closed at both ends with wire strips (Fig. S1B). Crawling arthropod
265 access was prevented by a ring of sticky paste (Tanglefoot Company, Grand Rapids, Michigan)
266 applied to the base of the branch, at least 50-cm away from the weevils (Fig. S1C). Any
267 physical contact of these branches with other branches in the tree was avoided at the moment
268 of branch selection, in order to prevent other access opportunities for crawling arthropods.
269 Thus, each tree harboured the four combinations of treatments: bird access (no mesh, sticky
270 ring), arthropod access (mesh, no sticky ring), bird and arthropod access (no mesh, no sticky
271 ring), and bird and arthropod exclusion (mesh, sticky ring). Weevils were surveyed 14 days after
272 the experiment was set up, and the number of weevils removed was calculated (considering not
273 only those weevils completely removed but also those weevils whose body remains suggested
274 picking at by birds or chewing by arthropods) along with the number of intact remaining weevils.
275 A *predation rate* per twig was estimated as the proportion of weevils removed with respect to
276 the initial number of weevils.

277

278 **Statistical analysis**

279 Differences between years in the variables studied (e.g. weevil attack, parasitoid richness,
280 bloom level) were measured by means of paired t-tests (for variables showing a Gaussian
281 distribution), and Wilcoxon's tests (for variables departing from normality). We quantified the
282 effects of landscape structure and orchard features on weevils and parasitism by means of
283 Generalized Linear Mixed Models (GLMMs; Bolker et al. 2009), considering the following as
284 response variables: weevil attack, weevil abundance, parasitoid richness and parasitoid attack,
285 all based on data for each orchard and year. All but one response variable conformed to a
286 normal distribution after log-transformation, and consequently GLMMs included a Gaussian
287 distribution (identity link), while models including parasitoid richness had a Poisson distribution

288 (log link). As the main predictor variables we considered: the proportion of woody vegetation at
289 R1000 and R125, the proportion of apple at R1000 and R125, distance to edge, canopy size,
290 bloom level and groundcover density. Predictor variables were standardized prior to their
291 inclusion in the models. The proportion of woody vegetation at R125 was significantly correlated
292 (Pearson's $|r| > 0.64$, $N = 23$, see *Results*) with that at R1000 and with the proportion of apple at
293 R125, and thus it was excluded from models in order to avoid collinearity effects. All other
294 predictors were included in the early full models, but, to avoid model over-parametrization,
295 those terms that were non-significant ($P > 0.05$) were excluded in a backwards stepwise
296 procedure in order to select a simpler model. All models, nonetheless, included *year* as a
297 categorical fixed factor –in order to control for the effects of temporal autocorrelation in the data
298 set- as well as *orchard identity* as a random factor, given that almost all orchards were
299 replicated across seasons (Bolker et al. 2009). Analyses were performed with the *lmer*
300 (Gaussian) and *glmer* (Poisson) functions in the *lme4* package in R environment (Zuur et al.
301 2009).

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

316

317 **Results**

318 **Weevil infestation**

319 Weevil attack ranged from 0.43 to 37.40%, depending on the site and the year (Fig. 3A). Weevil
320 attack in 2016 (mean \pm SE: 14.72 \pm 2.18) was almost double that of 2015 (8.00 \pm 1.26) (paired
321 t-test: $t = -4.77$; $df = 16$; $P < 0.001$), and in both years it correlated positively across orchards
322 (Pearson's correlation: $r = 0.74$; $P < 0.001$; $N = 17$). Weevil abundance (i.e. number of weevils
323 per ha) also varied widely, ranging from 314 to 63777, though no yearly differences were
324 detected (2015: 14160.27 \pm 3369.16; 2016: 10601.56 \pm 4059.26; Wilcoxon's paired test: $|z| = -$
325 1.207; $P = 0.227$; Fig. 3B), and no relationship was found for weevil abundance between years
326 (Spearman's correlation: $r_s = 0.43$; $P = 0.08$; $N = 17$).

327

328 **Parasitism on weevils**

329 A total of 470 parasitoids, belonging to seven species, emerged from capped blossoms.
330 *Scambus pomorum* (Hymenoptera: Ichneumonidae) was the most abundant (66.38%), followed
331 by *Pteromalus semotus* (Hymenoptera: Pteromalidae) (21.06%), *Bracon variator* (Hymenoptera:
332 Braconidae) (8.94%), *Bracon discoideus* (Hymenoptera: Braconidae) (2.55%), *Baryscapus*
333 *pospelovi* (Hymenoptera: Eulophidae) (0.64%), *Baryscapus adalia* (Hymenoptera: Eulophidae)
334 (0.21%) and *Scambus calobatus* (Hymenoptera: Ichneumonidae) (0.21%) (Table 1). The four
335 most abundant species occurred in both years and showed the same ranking of abundance
336 (Table 1). The most abundant parasitoid, *S. pomorum*, occurred in all 23 sites, whereas the
337 other species each occurred in between 1 and 15 sites (Table 1). Parasitoid richness per site
338 ranged from 1 to 5, averaging 2.04 \pm 0.22 in 2015 and 2.33 \pm 0.23 in 2016 (Fig. 3C). Differences
339 between years were not significant (Wilcoxon's paired test: $|z| = -0.535$; $P = 0.593$) and, indeed,
340 parasitoid richness in 2015 and 2016 correlated positively across orchards (Spearman's
341 correlation: $r_s = 0.56$; $P = 0.01$; $N = 17$).

342 Parasitoid attack affected between 6.40 and 81.50 % of immature weevils, depending
343 on the site and the year (Fig. 3D). On average, one third of weevils were attacked each year
344 (2015: 34.13 \pm 5.04; 2016: 32.40 \pm 4.50), and differences between years was not significant
345 (Wilcoxon's paired test: $|z| = -0.213$; $P = 0.831$). Parasitoid attack in 2015 and 2016 correlated
346 positively across orchards (Pearson's correlation: $r = 0.63$; $P = 0.006$; $N = 17$).

347

348 **Determinants of weevil infestation and parasitism**

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

359 Regarding orchard features, bloom level was significantly higher in 2015 (mean \pm SE =
360 2.59 ± 0.09 , min-max = 1.88-3.38) than in 2016 (mean \pm SE = 1.57 ± 0.18 , min-max = 0.38-
361 3.15; Wilcoxon's paired test: $|z| = -3.243$; $P = 0.001$) (Fig. S2). Sites varied considerably in
362 canopy size (mean \pm SE = 9.52 ± 0.82 , min-max = 4.20-23.95), and greatly in terms of density
363 of flowers in the groundcover (mean \pm SE = 26.41 ± 3.97 , min-max = 0.00-125.70), with no
364 significant differences between years (Wilcoxon's paired test: $|z| = -1.160$; $P = 0.246$).

365 Both landscape and orchard features affected weevil attack, with percentage of flowers
366 attacked by weevils increasing with proportion of semi-natural woody vegetation around apple
367 orchards at R1000, and with proportion of apple cover at R125 (Table 2; Figs. 4A and 4B). In
368 addition, weevil attack diminished with distance to the nearest edge (Table 2; Fig. 4C). As
369 regards orchard features, bloom level negatively affected weevil attack, with the proportion of
370 capped blossoms decreasing significantly in those orchards with higher quantities of flowers
371 (Table 2; Fig. 4D).

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

377 Parasitoid richness and parasitoid attack were not affected by either landscape
378 structure or orchard features, and parasitoid attack was also independent of weevil attack and

379 abundance. However, parasitoid richness was positively affected by weevil abundance, that is,
380 orchards with a higher weevil abundance also hosted more parasitoid species (Table 2).

381 **Predation on adult weevils** 382

383 Removal of weevils from experimental branches increased significantly when access to
384 predators, either birds or crawling arthropods was permitted (Fig. 5; Table 3). Indeed, predation
385 rate was the highest on open branches, where weevils were exposed to both types of predators
386 at the same time (between 31 and 44% of weevils, depending on the season), and was lowest
387 (2-13%) for branches with both plastic mesh and sticky ring exclusions. Thus birds and crawling
388 arthropods exerted an additive but independent (no significant effect of bird x arthropod
389 interaction was found; Table 3) predatory effect on adult weevils. There were also seasonal
390 differences in the proportion of weevils removed: overall predation rate was higher in May-June
391 (mean \pm SE = 0.29 ± 0.04) than in March-April (0.14 ± 0.04 ; Fig. 5; Table 3). Finally, there was
392 also seasonal variation in the strength of arthropod access effect on weevil removal in that it
393 was lower in June (Fig. 5; Table 3).

394

395 **Discussion**

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

410 issues, and in conclusion suggest management guidelines for apple blossom weevil that take
411 into account its habitat and its natural enemies.

412

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

414 The apple blossom weevil attacked flowers in all 23 orchards studied and can therefore be
415 considered to be widespread in the region. The range of weevil attack (0.4-37.4%) found in this
416 work is similar to the observed in other European countries: France (0.3-43%; FREDON 2006),
417 Germany (0-13%; Knuff et al. 2017), Hungary (0-45%; Brown et al. 1993) and Switzerland (0-
418 50%; Hausmann et al. 2004a). Despite this considerable range in rate of weevil attack, we
419 found there to be temporal consistency, i.e. orchards with a high attack rate one year also had a
420 high attack rate the following year.

421 Although the weevil attacks apple blossoms, preventing the flowers from becoming fruit,
422 this reproductive loss does not necessarily translate into a detrimental effect on apple crop size
423 since many healthy flowers also fail to become fruit. In fact, average fruit-set in apple is below
424 50% (e.g. Garratt et al. 2014; Földesi et al. 2015), and in the context of the current work it is
425 interesting to consider how many flowers need to be attacked by weevils before there are net
426 negative effects on yield. A manipulative experiment on two apple cultivars ('Golden Delicious'
427 and 'Royal Gala') which removed 1-3 of the five flowers per cluster found that when at least
428 three flowers remained, fruit set and yield were similar in non-manipulated and manipulated
429 clusters (Miranda et al. 2005). Yield reduction was only observed when two or fewer flowers per
430 cluster remained. Another factor that reduces yield variability is that fruits are heavier when crop
431 loads are smaller, due to the reduced competition among fruit (Miranda et al. 2005; Meland
432 2009). Crop load in its turn affects return bloom in the subsequent year: high fruit load in apple
433 inhibits floral induction and therefore fruit production the following year (Meland 2009; Samach
434 and Smith 2013). As such, weevil attack could even have a thinning effect on blossoms, by
435 diminishing the number of fruits per cluster, thus contributing to stabilizing yields across years
436 and buffering biennial bearing, a key problem in regions like Asturias, where annual apple
437 yields, both at the individual orchard and at the regional scale, can vary more than five-fold
438 between consecutive years (Dapena et al. 2005). Such variability means that apple growers do

439 not obtain regular crop yields or economic returns, and cider producers lack regular supplies
440 and are frequently forced to rely on providers from outside the region.

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

447

448 **How important are natural enemies in controlling apple blossom weevil?**

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

456 Overall we found seven species of parasitoids, with up to five species being found per
457 site. Thus the assemblage of larval parasitoids detected in our study was richer than that
458 described in previous studies (see for example Knuff et al. 2017; Mody et al. 2017). However,
459 equally high levels of richness have been found for other animal groups in the low-intensity
460 agroecosystem of Asturian cider apple orchards (e.g. Miñarro et al. 2005, 2009; García et al.
461 2018). Parasitoids were widespread across the study region, and, on average, attacked 30% of
462 developing weevils, and in some orchards this figure reached 81.5%. These values may be
463 considered high, for example compared to those reviewed by Cross et al. (1999), showing
464 weevil parasitism rates to usually be below 50%. This parasitoid complex, however, seems to
465 be ineffective in preventing apple tree damage in the current year because they attack the
466 weevils once they are already inside the blossoms, and as such the flowers are already
467 damaged. That said, they would however contribute to reducing the weevil population (one third
468 on average) from year to year. It should also be noted that the global effect of parasitoids on

469 weevil populations could be even larger than we have seen in this work, as adult weevils may
470 also be attacked (Zijp and Blommers 1992).

471 Birds and crawling arthropods preyed on adult weevils from both the overwintering and
472 the new generation. To this end they would prevent damage to the plant in both the current year
473 (by preventing weevil egg-laying) and the following year (by decreasing the extant weevil
474 population). Birds and arthropods have an additive predatory effect (e.g. for a case involving
475 birds and ants, see Singer et al. 2017). Our results accord with this in that, depending on the
476 season, 30-45% of weevils were removed when both types of predators were present, predation
477 rates which could be considered high enough to exert a regulation effect on weevil population
478 dynamics (see Prieditis 1975 for predation rates of around 57%). In spring and summer adult
479 weevils are active –feeding, crawling, mating and ovipositing (e.g. Miles 1923; Duan et al.
480 1996)– both during the day and at night when temperatures are above 5°C (Duan et al. 1996;
481 Hausmann et al. 2004b) and can be easily detected by predators. In addition, cases of bird
482 species preying on adults and also opening capped blossom to feed on immature stages of *A.*
483 *pomorum* have been frequently reported (e.g. Miles 1923; Zijp and Blommers 1992; Cross et al.
484 1999). The results of the present study on predation by birds are supported by those of another
485 experiment in the area which suggested that birds have a strong effect on reducing the
486 population of, among others pests, apple blossom weevil in cider apple orchards (García et al.
487 2018).

488 As well as birds, crawling arthropods also contributed to reducing weevil populations.
489 Ants can attack adult weevils as well as larvae in capped blossoms (Fig. S3), and have also
490 been reported as attacking other *Anthonomus* species in shrubs (Alves-Silva et al. 2014).
491 Spiders, earwigs, predatory bugs and other generalist predators, all of which are frequent in the
492 apple orchards studied (Miñarro et al. 2005, 2009), could also play their part in the predation
493 recorded in this study.

494

495 **What are the determinants of weevil infestation and biological control?**

496 Local and large-scale landscape features contributed to explaining the spatio-temporal
497 variation in weevil infestation across study years and orchards and the yearly bloom level is
498 mostly responsible for explaining the between-year differences in weevil attack. As commented

499 earlier, apple orchards in Asturias experience notable biennial bearing and in 2015, a year of
500 heavy bloom, weevil attack was lower than in the poor-bloom year 2016. This decrease in pest
501 attack rate associated with the poor year of biennial bearing could be the result of a predator
502 satiation process by which the scarce crops lead to a decrease in the populations of specialist
503 herbivores, which are then followed by abundant crops that would satiate the scarce predators,
504 which are unable to respond numerically or functionally to resource overyielding (Kelly 1994;
505 Kelly and Sork 2002). However, in our case, weevil abundance (i.e. the number of weevils per
506 ha) and, hence, the estimated amount of blossom damaged, remained steady across years,
507 indicating that changes in percentage of damage depended on yield dynamics (i.e. the total
508 number of flowers) rather than on changes in weevil population size. Thus, the results here
509 demonstrate that although biennial bearing led to a dilution of weevil attack, this reproductive
510 strategy did not seem to ultimately regulate the population size of apple blossom weevil. Indeed,
511 a similar dilution effect of high bloom levels was recorded at the orchard level as well as at the
512 larger scale: weevil attack diminished with increasing bloom level across orchards. On the
513 contrary, bloom level and weevil abundance were positively correlated since the latter was
514 calculated based on the former. One local factor not explicitly considered in our study but with
515 large potential influence on weevil populations is the apple genotype (e.g. Mody et al. 2015;
516 Knuff et al. 2017). We conducted our study on a single cultivar to control for potential cultivar
517 effects, but, anyway, there is still a possibility that weevil incidence on this target cultivar could
518 be affected by the presence of other cultivars. This was not the case in the present study, as
519 suggested by the lack of relationship between proportion of the target cultivar in the whole
520 orchard and weevil attack or weevil abundance ($r = -0.241$; $P = 0.134$ and $r_s = -0.209$; $P = 0.195$,
521 respectively). Nevertheless, further research on cultivar susceptibility are needed to offer a more
522 generalized response to the pest status and the drivers affecting *A. pomorum* in our
523 region. Weevil attack across orchards responded to habitat features related to the surrounding
524 availability of apple plantations and woody vegetation at different spatial scales (but see Markó
525 et al. 2017). At the fine scale, the cover of apple trees positively impacted on weevil attack:
526 orchards surrounded by other orchards suffered from higher levels of weevil infestation.
527 *Anthonomus pomorum* is a specialist pest that uses apple crop for feeding, mating, breeding
528 and overwintering (Miles 1923), and it therefore is able to respond to apple volatiles, and even

529 to visual cues of this tree (Hausmann et al. 2004c; Collatz and Dorn 2013) due to its
530 specialization, and thus an increase in weevil populations related to increased coverage of
531 apple trees is to be expected. At the large scale, woody vegetation cover around orchards also
532 had a positive effect on weevil attack since it offers winter shelter for adult weevils, which
533 frequently hide under the bark of trees (Brown et al. 1993; Toepfer et al. 2000). At the end of
534 winter, weevils travel from their woodland refuges to reproduce in apple orchards, where they
535 are sedentary, and tend to stay on the first apple tree they colonize or to only move short
536 distances, mainly along the row of trees (Toepfer et al. 1999). This type of colonization pattern
537 would explain why weevil infestation in this study decreased with distance to the orchard edge
538 (see also, for similar border effects, Brown et al. 1993; Toepfer et al. 1999). In sum, our results
539 suggest that surrounding semi-natural habitats provide a suitable resource for the whole life-
540 cycle of apple blossom weevil.

541 In contrast to the results for weevils, and unexpectedly, we did not detect any
542 environmental driver of parasitoid abundance and richness, contrarily to the landscape effect
543 detected in Swiss orchards, where weevil parasitism was higher in potted trees closer to the
544 forest edge (Mody et al. 2011). We neither detected effects of the size of the weevil population
545 on the level of parasitism attack, although we did find that abundance of weevils was positively
546 correlated with parasitoid richness. This could, however, be the result of a sampling effect since
547 the higher the host availability, the higher the probability of sampling more species attacking
548 that host. Despite it is well known that pesticides can negatively affect natural enemies (e.g.
549 Monteiro et al. 2013; Markó et al. 2017), we do not consider that pesticide usage could be an
550 important factor driving parasitoid assemblages in our study system, given the low pesticide
551 pressure in our orchards (0 to 2 sprayings with narrow-spectrum products). This work did not
552 evaluate the local and landscape determinants of other natural enemies of apple blossom
553 weevils, i.e. birds and crawling arthropods, which has been shown elsewhere. For example, bird
554 abundance and richness increase with apple tree canopy cover and with the availability of semi-
555 natural woody habitats (García et al. 2018) and the diversity of crawling predators like spiders,
556 ants, earwigs and predatory beetles is also influenced by landscape features (Lefebvre et al.
557 2016, 2017) as well as by local management strategies (Miñarro et al. 2009; Marliac et al.
558 2016).

559

560 **Implications for management**

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

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

581 Ecological intensification at the farm level to promote biological control has been
582 recommended (Bommarco et al. 2013). For example, nest boxes for insectivorous birds are
583 readily occupied and can promote the biological control of agricultural pests (Mols and Visser
584 2002; Benayas et al. 2017) and other measures favouring the biodiversity of natural enemies
585 (flower strips, hedgerows) have also been recommended (e.g. Wratten et al. 2012; Sidhu and
586 Joshi 2016).

587 Finally, insecticides are only to be considered necessary in cases of very high attack of
588 *A. pomorum*, usually reached in the poor bloom year, and always taking into account the border

589 effect, that is, reducing the spraying from the edge to the centre of the orchard. In such cases,
590 furthermore, the insecticide should be sprayed at bud burst, after adults have colonized the
591 orchard and before any significant oviposition occurs (Miles 1923), and it should preferably be
592 applied during warm weather, when adults are more active (Duan et al. 1996). Further applied
593 research should pinpoint to develop explicit practical guidelines for insecticide application under
594 prevision of high pest attack, including the economic thresholds for the occurrence of *A.*
595 *pomorum*.

596

597 References

- 598 Agnello A, Cox K, Dominguez L, Francescato P, Lordan J, Robinson T (2015) An Insect,
599 Disease and Weed Management Program for New York Organic Apples. *New York Fruit*
600 *Quarterly* 23(4):27-34.
- 601 Alves-Silva E, Bächtold A, Barônio GJ, Torezan-Silingardi HM, Del-Claro K (2015) Ant-
602 herbivore interactions in an extrafloral nectaried plant: are ants good plant guards against
603 curculionid beetles? *J Nat Hist* 49:841-851.
- 604 Balázs K, Molnár M, Bujaki G, Gonda I, Karacsony D, Bartha J (1997) Possibility and problems
605 of organic apple growing in Hungary. *Biol Agric Hortic* 15:223-232.
- 606 Benayas JMR, Meltzer J, de las Heras-Bravo D, Cayuela L (2017) Potential of pest regulation
607 by insectivorous birds in Mediterranean woody crops. *PLoS one* 12:e0180702.
- 608 Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White, JSS (2009)
609 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends*
610 *Ecol Evol* 24:127-135.
- 611 Bommarco R, Kleijn D, Potts SG (2013) Ecological intensification: harnessing ecosystem
612 services for food security. *Trends Ecol Evol* 28:230-238.
- 613 Bretz F, Hothorn T, Westfall P (2016) *Multiple comparisons using R*. CRC Press
- 614 Brown MW, Szentkiralyi F, Kozar F (1993) Spatial and temporal variation of apple blossom
615 weevil populations (Col., Curculionidae) with recommendations for sampling. *J Appl*
616 *Entomol* 115:8-13.

- 617 Collatz J, Dorn S (2013) A host-plant-derived volatile blend to attract the apple blossom weevil
618 *Anthonomus pomorum*—the essential volatiles include a repellent constituent. Pest Manag
619 Sci 69:1092-1098.
- 620 Cross JV, Solomon MG, Babandreier D et al (1999) Biocontrol of pests of apples and pears in
621 northern and central Europe: 2. Parasitoids. Biocontrol Sci Techn 9:277-314.
- 622 Cross JV, Fountain M, Markó V, Nagy C (2015) Arthropod ecosystem services in apple
623 orchards and their economic benefits. Ecol Entomol 40:82-96.
- 624 Dapena E, Miñarro M, Blázquez MD (2005) Organic cider-apple production in Asturias (NW
625 Spain). IOBC/wprs Bull 28(7):142-146.
- 626 Duan JJ, Weber DC, Hirs B, Dorn S (1996) Spring behavioral patterns of the apple blossom
627 weevil. Entomol Exp Appl 79:9-17.
- 628 FAO (2017) Food and Agriculture Organization of the United Nations,
629 <http://www.fao.org/faostat/en/#data/QC> (Accessed 24 August 2017).
- 630 Földesi R, Kovács-Hostyánszki A, Kőrösi Á et al (2016) Relationships between wild bees,
631 hoverflies and pollination success in apple orchards with different landscape contexts.
632 Agric Forest Entomol 18:68-75.
- 633 FREDON (2006) L'anthonome du pommier, un ravageur à surveiller de près. Fiche technique.
634 Fédération Régionale de Défense contre les Organismes Nuisibles. 4pp.
- 635 García D, Miñarro M, Martínez-Sastre R (2018) Birds as suppliers of pest control in cider apple
636 orchards: bird biodiversity filters and insectivore effect. Agric Ecosyst Environ 254:233-
637 243.
- 638 Garratt MP, Breeze TD, Jenner N, Polce C, Biesmeijer JC, Potts SG (2014) Avoiding a bad
639 apple: Insect pollination enhances fruit quality and economic value. Agric Ecosyst Environ
640 184:34-40.
- 641 Gillespie MA, Gurr GM, Wratten SD (2016) Beyond nectar provision: the other resource
642 requirements of parasitoid biological control agents. Entomol Exp Appl 159:207-221.

643 Gomiero T, Pimentel D, Paoletti MG (2011) Environmental impact of different agricultural
644 management practices: conventional vs. organic agriculture. *Critical Rev Plant Sci* 30:95-
645 124.

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

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

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

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

654 INDUROT (2010) Cartografía del manzano en el Principado de Asturias. Consejería de Medio
655 Rural y Pesca. Gobierno del Principado de Asturias, 67 pp.

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

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

658 Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol*
659 *Systemat* 33:427-447.

660 Knuff AK, Obermaier E, Mody K (2017) Differential susceptibility and suitability of domestic and
661 wild apple species for a florivorous weevil and its parasitoids. *J Appl Entomol* 141:285-
662 299.

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

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

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

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

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

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

679 Meland M (2009) Effects of different crop loads and thinning times on yield, fruit quality, and
680 return bloom in *Malusx domestica* Borkh. 'Elstar'. *J Hortic Sci Biotech* 84:117-121.

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

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

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

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

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

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

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

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

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

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

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

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

711 Parveaud C-E, Brenner J, Stoeffel A, Corroyer N (2016) Anthonome du pommier en agriculture
712 biologique. Fiche technique. 6 pp.

713 Prieditis A (1975) Natural enemies of the apple blossom weevil (*Anthonomus pomorum*). Augu
714 Aizsardzibas Problemas, (84), 17-27.

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

718 Reganold JP, Wachter JM (2016) Organic agriculture in the twenty-first century. Nature Plants
719 2:15221.

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

722 Rusch A, Chaplin-Kramer R, Gardiner MM et al (2016) Agricultural landscape simplification
723 reduces natural pest control: a quantitative synthesis. *Agric Ecosyst Environ* 221:198-
724 204.

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

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

729 Simon S, Bouvier JC, Debras JF, Sauphanor B (2010) Biodiversity and pest management in
730 orchard systems. A review. *Agronomy for Sustainable Development* 30:139-152.

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

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

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

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

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

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

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

745 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and*
746 *Extensions in Ecology with R*. Springer, New York.

747

748 **Table 1.** Parasitoid species that attack apple blossom weevil. Data on abundance and number
 749 of sites where each species occurred are shown for each year and for the total.

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

750

751 **Table 2.** Results of Generalized Linear Mixed Models evaluating the effects of landscape
 752 structure and orchard features on weevil attack (log), weevil abundance (log₁₀), and parasitoid
 753 richness. The estimate of variance by orchard, considered as a random factor, is also shown.
 754 Details of the family of error distribution and link function used are shown in brackets.

Weevil attack (Gaussian, identity)					
Predictors	Estimate ± SE	t	P	Random factor	Variance Estimate ± SD
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)					
Predictors	Estimate ± SE	t	P	Random factor	Variance Estimate ± SD
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		
Parasitoid richness (Poisson, log)					
Predictors	Estimate ± SE	z	P	Random factor	Variance Estimate ± SD
Weevil abundance	0.22 ± 0.11	2.03	0.043	Orchard	0.00 ± 0.00

755

756

757 **Table 3.** Results of the Generalized Linear Mixed Model evaluating the results of the
 758 experiment estimating the variability in the proportion of weevils removed by different types of
 759 predators (birds and arthropods and their interaction) from trees under different access
 760 treatments and between two seasons. The variance estimate for tree identity, considered as a
 761 random factor, is also shown. The model considered a binomial error distribution and a logit link.

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

762

763

764 **Figure legends**

765 **Fig. 1.** Diagrammatic representation of the life cycle of the apple blossom weevil and some
766 potential determinants of weevil populations in Asturian cider apple orchards (natural enemies,
767 shelters, bloom). (1) Weevil overwinters as an adult, preferably hidden under the bark of old
768 apple trees or other trees in the close vicinity (Brown et al., 1993; Toepfer et al., 2000). Lack of
769 such winter shelters could limit weevil populations. (2) In early spring, adults leave the winter
770 quarters and feed on apple trees by piercing the opening buds and sucking the juices. They
771 alternate feeding and resting for several days until copulation and oviposition take place. These
772 adults could be attacked by predators like birds or crawling arthropods. (3) When the flower is in
773 D-E (56-57), females oviposit inside the flower buds (Toepfer et al., 2002; Knuff et al., 2017)
774 and the hatched larvae feed on the reproductive parts of the flower. Weevils need flowers for
775 reproduction and thus the number of blossoms could be a factor limiting weevil populations. At
776 this point larvae may be attacked by parasitoids. (4) Finally, the larvae pupate inside the
777 blossom and then the young adults appear. The new generation of adults feed on the underside
778 of apple leaves for several days before seeking winter quarters. At this stage they may again be
779 attacked by predators. Photos by Marcos Miñarro and drawings by Daniel García.

780
781 **Fig. 2.** Schematic representation of study sites and spatial design depicting (A) the region of
782 study (Asturias province in dark grey within the Iberian Peninsula); (B) the study sites,
783 highlighting the landscape-scale gradient of cover of woody vegetation (dark grey patches)
784 around each site (1000-m radius plots); (C) an example of cover of woody vegetation (pale
785 yellow patches) and apple orchards (orange patches) in the 1000-m radius plot (red dashed
786 line) and the 125-m radius plot (red line) around one of the orchards.

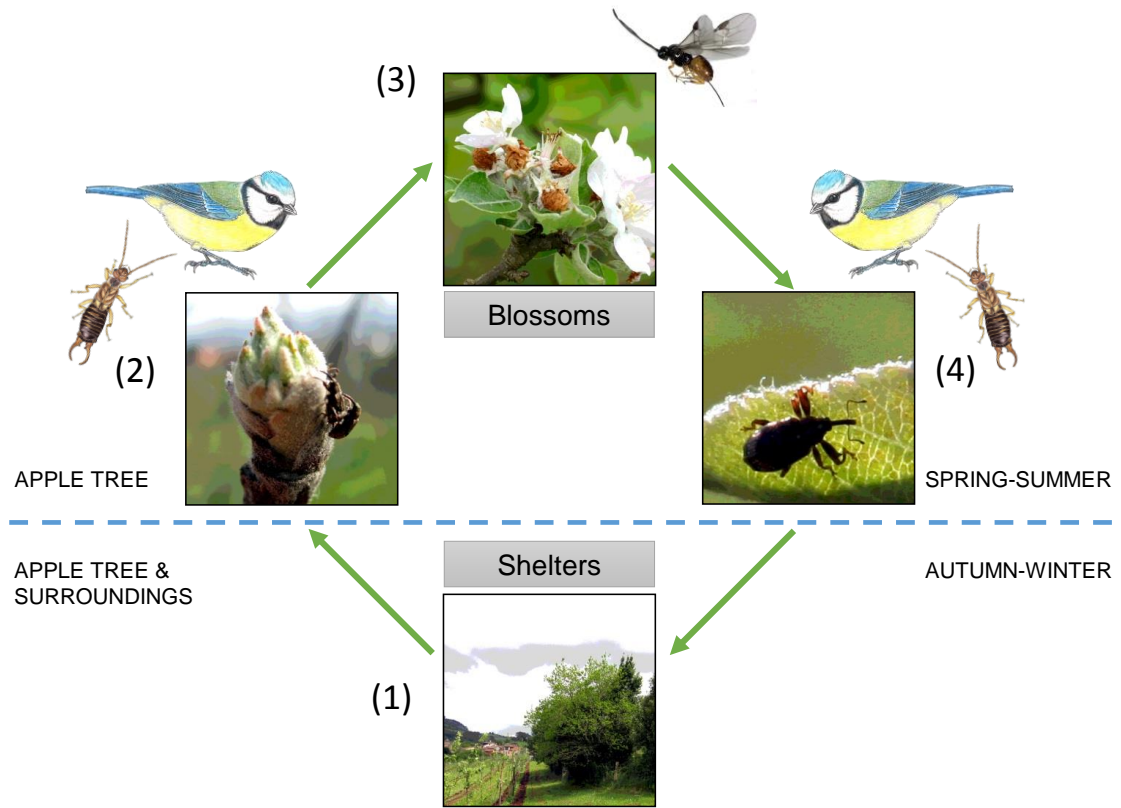
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788 **Fig. 3.** Distribution of values of (A) weevil attack, (B) weevil abundance, (C) parasitoid richness
789 and (D) parasitoid attack in different years. Boxplots indicate 25-75% quartiles (box
790 boundaries), median (thick horizontal bar), largest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

794 **Fig. 4.** Effects of landscape structure and orchard features on weevil attack. Effects of (A) the
795 proportion of woody vegetation for the 1000-m radius plot, (B) proportion of apple cover for the
796 125-m radius plot, (C) distance from target trees to the nearest edge and (D) bloom level. Dots
797 indicate different orchards, with different colours for different years (white: 2015; black: 2016).
798 Linear fits predicted by Linear Regression Models are shown.

799

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

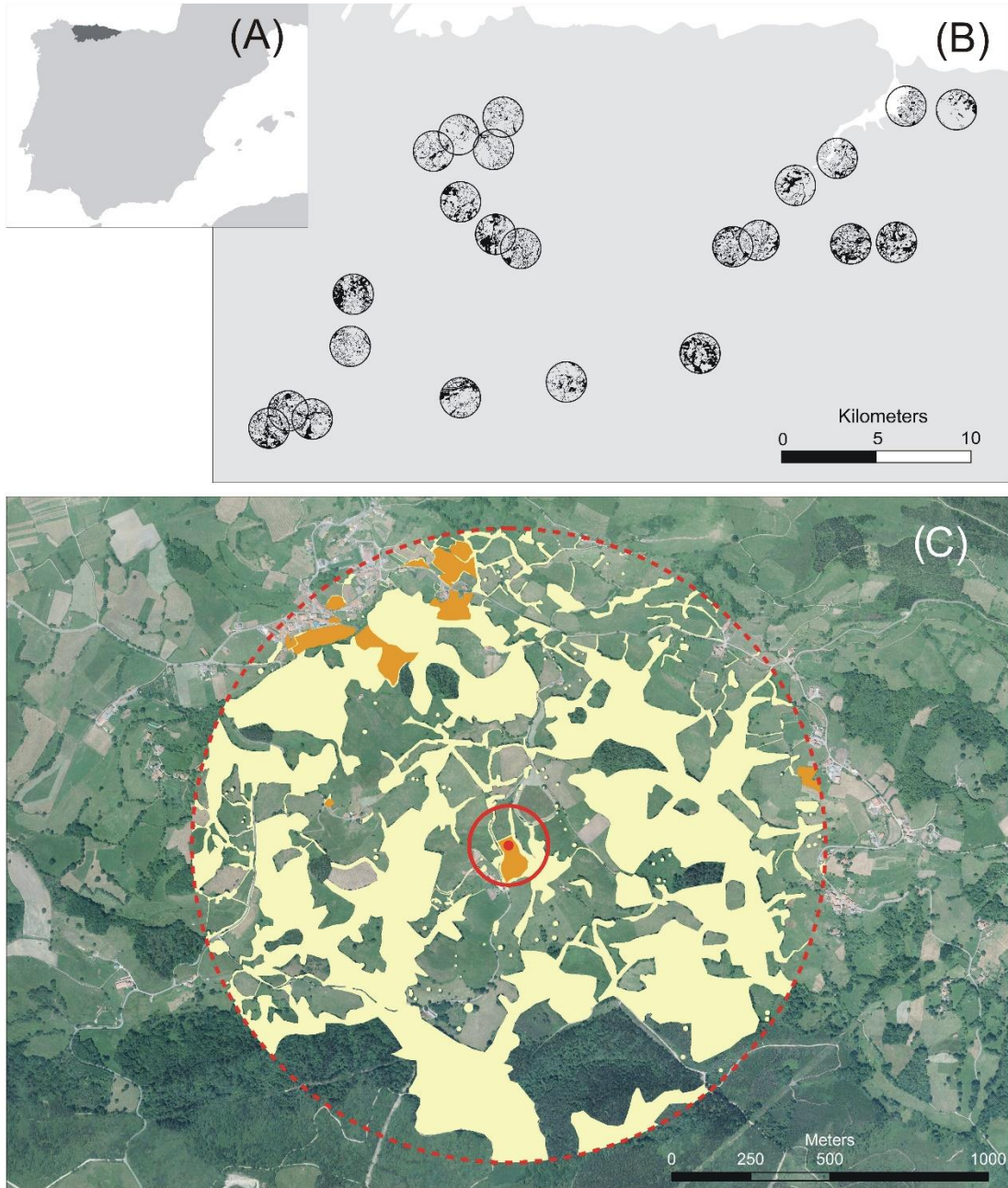
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809 **Fig. 1**

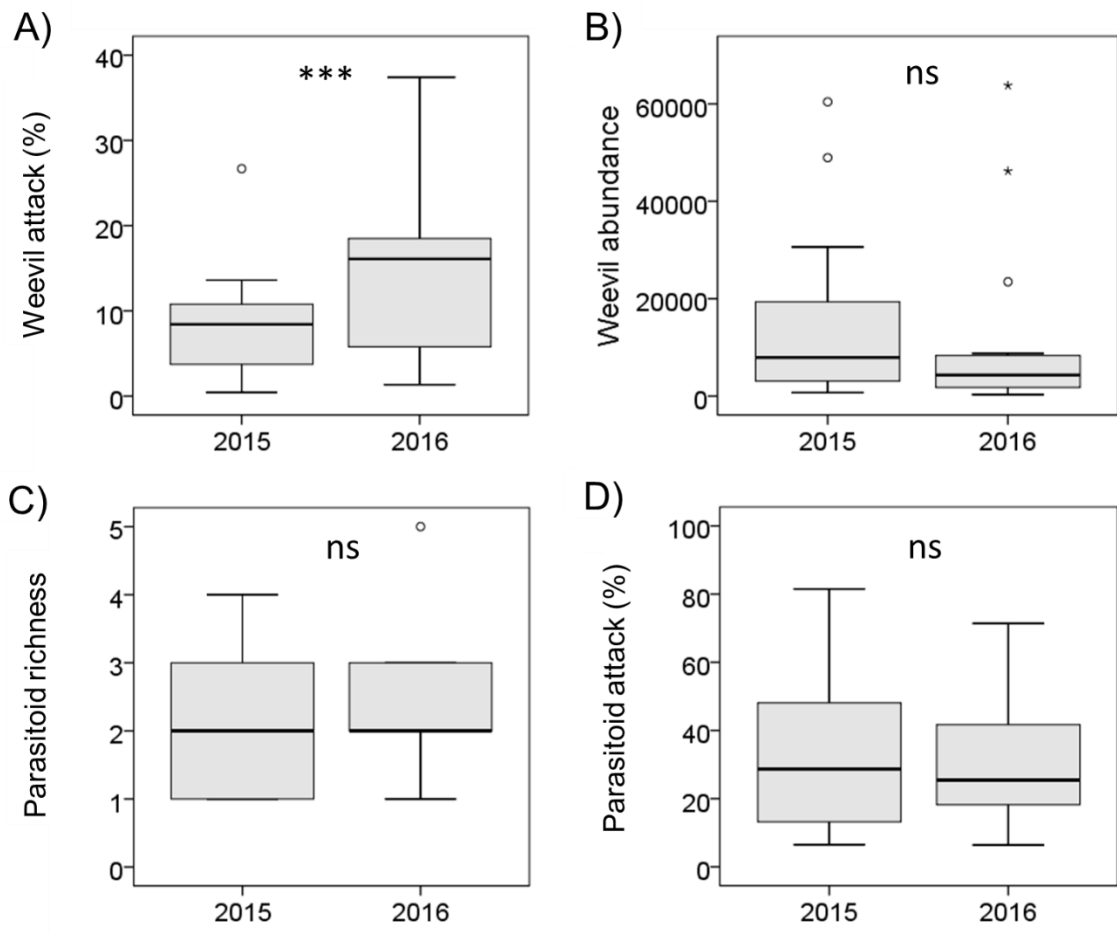
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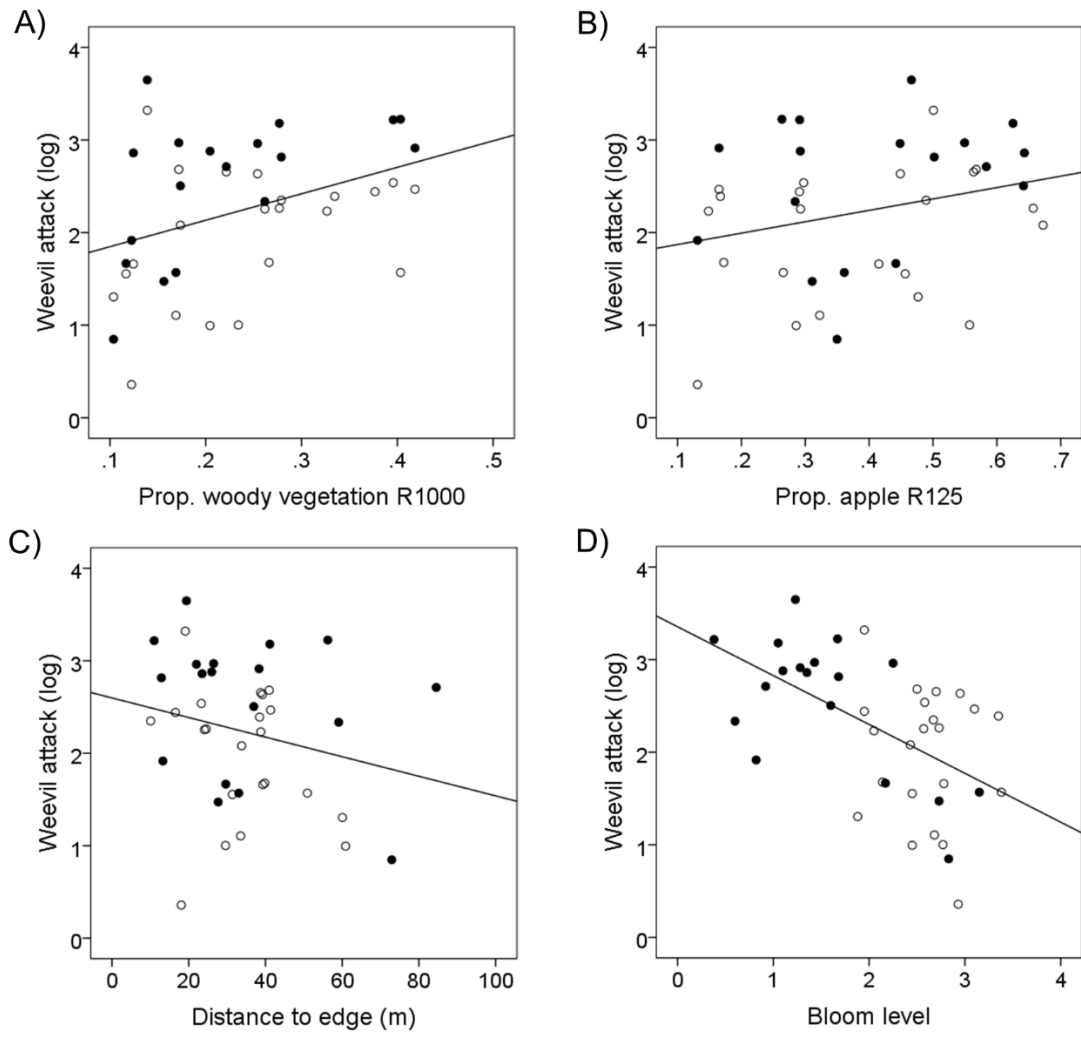
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812 **Fig. 2**

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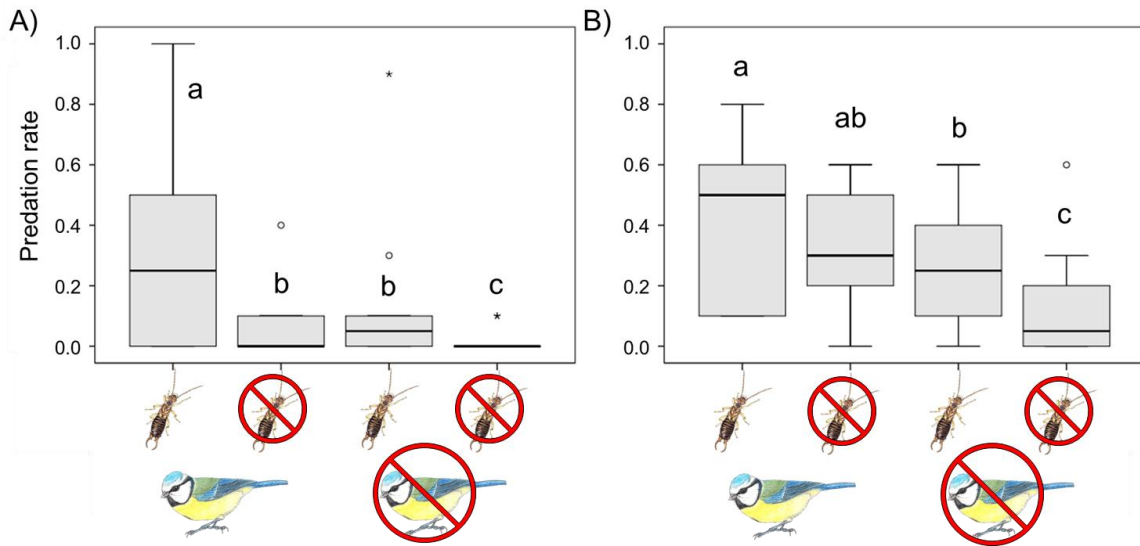
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 815 **Fig. 3**
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818 **Fig. 4**

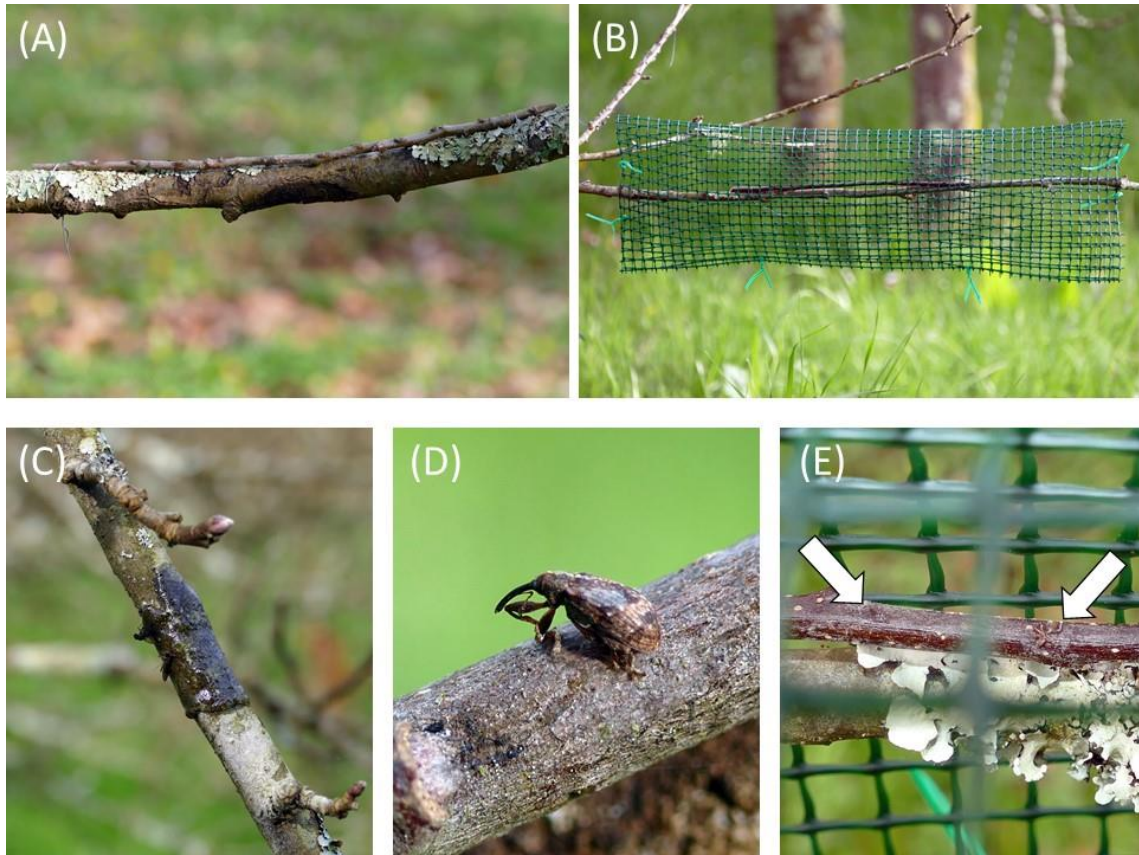
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821 **Fig. 5**

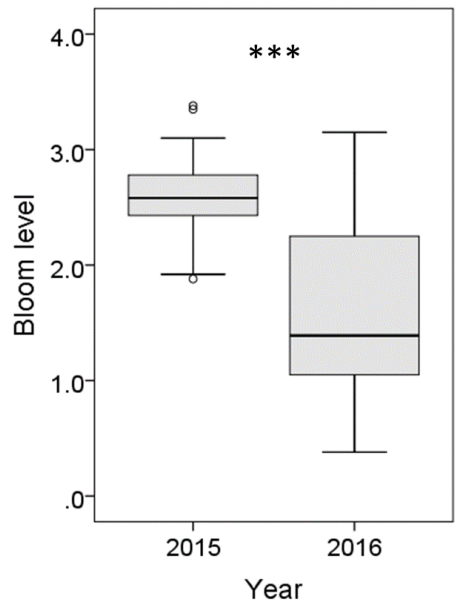
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825

826 **Fig. S1.** Details of the experiment of predation by birds and crawling arthropods on adult
827 weevils. A twig with ten adult weevils tied to an apple branch (A); Plastic mesh to prevent bird
828 access (B); Sticky ring to prevent the access of crawling arthropods to weevils (C); Adult weevil
829 glued to the twig (D); Remains of adult weevils after removal by arthropods (arrows show where
830 the weevils were glued) (E).

831



832

833 **Fig. S2.** Distribution of values of the bloom level (number of flowers) in 2015 and 2016. The
834 result of a Wilcoxon's paired test to check for statistical differences between years is also shown
835 (***: $P < 0.001$). Boxplots indicate 25-75% quartiles (box boundaries), median (thick horizontal
836 bar), largest and smallest observed values (whiskers) and outliers (small circles).

837



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839

840

Fig. S3. Photos of ants attacking a weevil larva (left) and a weevil adult (right) in Asturian (NW Spain) apple orchards. In the second photo, the ant finally threw the weevil off the branch.