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4   **Animal biodiversity in cider apple orchards: simultaneous**

5   **environmental drivers and effects on insectivory and pollination.**

6

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15

16   **Abstract**

17   Making agriculture more sustainable requires a greater understanding of animal-

18   mediated ecosystem services. The beneficial effects of pest-control and pollination

19   provided by, respectively, insectivorous birds and pollinator insects are essential for

20   many crops. Improving these ecosystem services simultaneously in the same crop

21   system means, first, identifying the drivers of animal biodiversity that operate in

22   agricultural landscapes, and second, revealing the relationships between biodiversity

23   and the two services. Here, for two years, we addressed how landscape and small-scale

24   orchard features affected bird and insect biodiversity (abundance and species richness)

25   in cider apple orchards in northern Spain. We examined the effects of bird and insect

26   biodiversity on the magnitude of, respectively, insectivory and pollination. Bird

27   biodiversity was positively affected by the cover of apple canopy within orchards,

28   whereas that of pollinators responded positively to the cover of semi-natural woody

29   habitats and eucalyptus plantations in the surrounding landscape, and also on the level

30   of bloom at the orchard scale. Insectivory, estimated from sentinel model and exclusion

31   experiments, was positively affected by increased abundance and richness of birds

32   across orchards. Similarly, fruit set responded positively to higher abundance and

33   richness of wild bees, whereas seed set mostly depended on the abundance of wild

34   pollinators. Our findings suggest simultaneous positive effects of animal biodiversity on

35   pest-control and pollination in apple orchards, with no sign of trade-offs between

36   biodiversity groups or between ecosystem functions. A multi-scaled management of

37   orchard-level features (apple canopies and surrounding hedgerows for birds, and apple

38   bloom and ground cover for pollinators) and landscape-level ones (surrounding cover of

39   semi-natural woody habitats, moderate for birds, high for pollinators) is encouraged for

40   the simultaneous enhancement of pest-control and pollination. Biodiversity-farming

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41 win-win scenarios are possible in cider apple orchards by simultaneously promoting

42 multiple animal-mediated ecosystem services.

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44 **Keywords:** biological control, ecological functions, ecosystem services, fruit set,

45 insectivorous birds, landscape composition, orchard management, wild bees.

46

47 **1. Introduction**

48 Sustainable agriculture faces the challenge of ensuring food production while reducing

49 environmental impact and biodiversity loss (Foley et al., 2011; Bommarco et al., 2013).

50 The ecosystems within which farming is integrated (i.e. agroecosystems) can harbor

51 variable levels of biodiversity which, in turn, may provide crop-beneficial ecosystem

52 services (Kremen and Miles, 2012; Tscharntke et al., 2012a). In fact, different groups of

53 animals, plants or microorganisms are involved in a wide array of services, such as

54 biological control of crop pests (Maas et al., 2013; Cross et al., 2015), pollination

55 (Kleijn et al., 2015; Rader et al., 2016), maintenance of soil fertility (Edwards, 2004)

56 and water purification (Gharabaghi et al., 2006). Understanding how to simultaneously

57 foster different biodiversity groups to maximize multiple ecosystem services related to

58 the same crop is, therefore, a pivotal question in sustainable agriculture (Shennan, 2008;

59 Tscharntke et al., 2012a).

60   Birds and insects are two animal groups targeted as being highly relevant in

61 sustainable agriculture (Power, 2010; Shackelford et al., 2013). On the one hand,

62 insectivorous birds provide generalist biological control by preying upon different types

63 of arthropod pests across annual and perennial crops, in both temperate and tropical

64   regions (Karp and Daily, 2014; Rey Benayas et al., 2017). On the other hand, flower

65   visiting insects are the necessary pollinators of many crops, from annual crops to tree-

66   fruit productions, where they increase crop yield, fruit quality and harvest stability (

67   Klein et al., 2007; Garibaldi et al., 2013). Despite these findings, most studies provide

68   segregated information for insectivorous birds and for pollinator insects with respect to

69   various crops. The few studies that do target both biodiversity groups simultaneously

70   have successfully shown the occurrence of combined ecological effects (e.g. Classen et

71   al., 2014), although they have followed small-scale approaches, insufficient to predict

72   the combined role of the two biodiversity groups across the environmental gradients of

73   real agroecosystems. In this context, the importance of insectivorous birds and

74   pollinator insects can be only truly understood through the positive effects animal

75   biodiversity has on ecosystem functions (hereafter B-EF link) (Kremen, 2005; Duncan

76   et al., 2015). Namely, higher bird abundance has been associated with stronger pest

77   control (Jedlicka et al., 2011), as has higher bird richness (Bael et al., 2008) and

78   functional diversity (Philpott et al., 2009). In the case of flower visiting insects, richer

79   assemblages, especially of wild bees, are known to increase pollination services

80   (Mallinger and Gratton, 2015). Nevertheless, in order to manage the B-EF link in

81   agroecosystems, we need first to understand the factors that modulate the biodiversity of

82   pest predators and pollinators. In this sense, both the structure of the landscape

83   surrounding a farming site, as well as the in situ agricultural practices, can be

84   approached as environmental drivers of biodiversity at different spatial scales

85   (Shackelford et al., 2013).

86   Landscape structure may affect bird and pollinator biodiversity in agroecosystems

87   by containing semi-natural habitats that support animals with external resources (i.e.

88   beyond those provided by the crop itself) such as shelter, food, breeding areas, and

89 nesting places (Tscharntke et al., 2012b; Heath et al., 2017; Alomar et al., 2018). This

90 leads to positive relationships between the amount and spatial configuration of semi-

91 natural habitats around agroecosystems and the abundance and richness of different

92 animal groups (Tscharntke et al., 2012b; Kennedy et al., 2013). The small-scale features

93 of farming sites and their immediate surroundings (e.g. hedgerows and farm fringes),

94 which frequently depend on farming management, may also be seen as modulators of

95 resource availability for animals (Kennedy et al., 2013; Rey Benayas et al., 2017). For

96 instance, vegetated margins (Quinn et al., 2014) or dense ground cover (Rey et al.,

97 2019) both increase bird and insect biodiversity, whereas frequent tillage impacts

98 negatively on the persistence of bee populations (Ullmann et al., 2016). In sum,

99 identifying common or differential responses of pest-predators and pollinators to

100 landscape or within-farm features is essential for targeting the management practices

101 that foster multiple ecosystem services in agroecosystems (Manning et al., 2019).

102   In this study, we assess the environmental drivers of biodiversity, and the effects

103 of biodiversity on the provision of multiple ecosystem services, for different animal

104 groups in a given agroecosystem. We evaluate the ecological function of insectivorous

105 birds as pest enemies, and that of wild insects as pollinators, in cider apple orchards of

106 Asturias (N Spain), along a gradient of environmental variability at local (i.e. within

107 orchards) and landscape (i.e. around orchards) scale. Cider apple crop is a key

108 agroecosystem across the whole Cantabrian region in Spain (Pereira-Lorenzo et al.,

109 2007), and is highly variable in terms of management regimens and landscape contexts,

110 and may harbor rich assemblages of insectivorous birds (García et al., 2018) and

111 pollinator insects (Miñarro and García, 2018). Specifically, we aim here to answer the

112 following questions: (1) What are the local and landscape features driving the

113 biodiversity (abundance and richness) of insectivorous birds and pollinator insects? (2)

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114 Does the biodiversity of birds and pollinator insects affect, respectively, pest control

115 and crop pollination services? Based on our results we propose agricultural and

116 landscape management actions for promoting multi-functional animal biodiversity and

117 its derived ecosystem services.

118

119 **2. Methods**

120 *2.1. Study system*

121 The study was conducted in the cider apple (*Malus x domestica* Borkh.) crop area of

122 central Asturias (N Spain) (**Fig. 1A**). In this region, cider is a valuable traditional

123 product, strongly ingrained in society, and linked to tourism, gastronomy and leisure.

124 Cider apple annual yield reaches 50,000 tons. The majority of cider apple orchards are

125 comprised of local cultivars that are grown on seedling rootstocks, but new orchards are

126 also being grown on semi-dwarfing rootstock. Both systems typically have a density of

127 between 250 and 500 trees/ha. Orchards are embedded in a highly variegated traditional

128 landscape (**Fig. 1D**), containing a fine-grained mosaic of orchards, livestock pastures,

129 annual crops (e.g. corn), other fruit (e.g. blueberry, kiwi) and timber (mainly

130 eucalyptus) plantations, human infrastructures, and semi-natural woody vegetation

131 patches (temperate broad-leaved forest, riparian forest and heathland patches). At the

132 small scale of their immediate neighborhoods, apple orchards are typically surrounded,

133 either totally or partially, by natural woody vegetation in the form of hedgerows and/or

134 small forest patches which are mostly unmanaged by farmers (**Fig. 1C**; for a

135 comprehensive description of hedgerows and small forest patches see García et al.,

136 2018).

137   Orchards are relatively small (most cover between 0.5 and 4 ha). To reduce

138 competition with trees, weeds in the tree-row are managed by mowing, shallow tillage

139 or herbicide application, depending on the orchard. In all orchards, alleys are

140 periodically cleaned using a shredder, but still maintain a natural ground cover, rich in

141 wild plants that flower throughout the year.

142   Among the arthropod pests present in Asturian cider apple orchards (Miñarro et

143 al., 2011), the most prevalent are the codling moth (*Cydia pomonella* L.), the rosy apple

144 aphid (*Dysaphis plantaginea* Passerini), green aphids (*Aphis* spp.) and the apple

145 blossom weevil (*Anthonomus pomorum* L.). Growers frequently tolerate moderate

146 levels of pests and diseases, as aesthetic damage is not relevant for cider apples and,

147 thus, pests are not perceived as severe threats to productivity. Furthermore, orchards are

148 based on local cultivars tolerant to common apple diseases (scab, canker and powdery

149 mildew). Consequently, the use of pesticides is not generalized and, when used, they are

150 applied at low intensity. The low degree of agricultural intensification in some orchards

151 and in the surrounding landscape allows for a high diversity of arthropods within

152 orchards, including crop pests as well as their natural enemies (e.g. birds, spiders,

153 earwigs, hoverfly larvae, predatory beetles) or mutualists (e.g. aphid-tending ants) (

154 Miñarro et al., 2011; García et al., 2018).

155   Previous studies in these orchards have registered a rich (53 species) assemblage

156 of wild birds, from which 54.7% of species were classified as having a predominantly

157 insectivorous diet and a tree-dwelling habit (García et al., 2018). The most common

158 insectivorous birds are robin (*Erithacus rubecula*), tits (Paridae), thrushes (Turdidae),

159 warblers (Sylviidae and Phylloscopidae), wren (Troglodytes troglodytes), and

160 woodpeckers (Picidae). The low use of pesticides, as well as the permanence of

161 flowering ground-cover most of the year, facilitates a high diversity of pollinators in

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162   Asturian apple orchards (Miñarro and García, 2018): 82 species of floral visitors being

163   recorded, of which honeybee (61%) was the dominant flower visitor, followed by

164   hoverflies (21%, 21 species), wild bees (7%, 39 species), flies (6%, 8 species)

165   bumblebees (3%, 4 species), beetles (1.3%, 8 species) and butterflies (0.4%). Pollinators

166   determine cider apple production quantitatively, as fruit set requires cross pollination

167   and hence relies almost completely on insect vectors (Miñarro and García 2018).

168

169   *2.2.   Spatial design of sampling*

170   Between 2015 and 2017, sampling was conducted in 26 cider apple orchards distributed

171   over 600 km^2 in the central part of the cider apple area in Asturias (N Spain) (**Fig. 1B**).

172   Minimum distance between orchards was 1.3 km (average distance in km: 8.02±0.94).

173   Orchards were chosen to represent a gradient of variability in the environmental

174   conditions within apple orchards and in the surrounding landscape (i.e. presence of

175   semi-natural habitats; García et al., 2018). For the monitoring of insectivorous birds and

176   insectivory, in each orchard, we established a sampling station within the plantation, 25

177   m away from the orchard edge, which was the center of a 25-m radius sampling plot

178   (R25 plot, hereafter; **Fig. 1C**). This guaranteed that sampling corresponded exclusively

179   to apple plantation habitat, and excluded different surrounding habitats (e.g. hedgerows)

180   even in the smallest orchard. To monitor flower visiting insects and measure

181   pollination, in each orchard we selected five focal trees of the local cultivar "Regona"

182   (target trees, hereafter) within a given row (as rows contain a single cultivar and each

183   orchard has several cultivars) (**Fig. 1C**), at least 15 m away from the edge (to avoid

184   potential edge effects; Campbell et al., 2017), and in front of a row of a different

185   cultivar (to enhance cross pollination; Ramírez and Davenport, 2013). In order to

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186   conduct additional surveys in relation to pollinators, two 150-200 m transects were set

187   up along two additional "Regona" rows (**Fig. 1C**).

188

189   *2.3.   Landscape structure and orchard features*

190   Landscape structure was quantified by means of a Geographic Information System of

191   the study area (GIS, ArcGIS9.3) based on 1:5000- scale orthophotographs (2014). We

192   delimited a circular plot of 1000-m radius (R1000 plot, hereafter), centered on the R25

193   plot of each orchard, within which we distinguished, by carefully digitizing landscape

194   patches, six general types of cover: 1) semi-natural woody habitats (including forest,

195   heathland, hedgerows, isolated trees within pastures or plantations); 2) timber (mainly

196   eucalyptus) plantations; 3) fruit tree plantations (apple, kiwi and blueberry); 4) pastures

197   (meadows), 5) other habitats (mainly water courses) and 6) urbanized ground (roads,

198   buildings, gardens around houses) (**Fig. 1D**). We estimated the availability of each

199   cover type around each orchard from the percentage of cover in each R1000 plot.

200   As orchard features have the potential to affect bird biodiversity, we measured,

201   based on the GIS mentioned above, orchard size and the amount of cover provided by

202   apple tree canopy in each R25 plot (apple canopy cover; from a layer of apple canopy

203   projection). In order to describe the vertical complexity of apple canopy, we randomly

204   selected 25 trees within the R25 plots. We held a 5-m long, scaled pole vertically 50 cm

205   from the trunk of each of these trees, and counted the number of contacts of apple

206   branches or leaves with the pole. We also measured canopy height from the lowest to

207   the tallest branch. We calculated apple canopy thickness by multiplying the number of

208   pole-canopy contacts by canopy height, and averaged this estimate across all 25 trees

209   per orchard. Orchard features can also affect pollinator biodiversity, and so, in addition

210   to orchard size and apple tree canopy cover, we included bloom level as an indicator of

211   the number of apple flowers in the orchard. We recorded bloom level when the target

212   cultivar ("Regona") was in full bloom, by walking perpendicular to tree rows (in order

213   to avoid a cultivar effect) and covering the full extent of the orchard. For 30 randomly

214   chosen trees per orchard and year, we scored the number of flowers per tree by using a

215   semi-quantitative scale: 0 (0 flowers); 1 (1–10 flowers); 2 (11–50 flowers); 2.5 (51–100

216   flowers); 3 (101–500 flowers); 3.5 (501–1000 flowers); 4 (1001–5000 flowers); 4.5

217   (5001–10,000 flowers); 5 (more than 10,000 flowers). We calculated bloom level per

218   orchard and year by averaging this estimate across trees. Finally, during apple bloom we

219   also measured the density and the richness of flowers on the ground cover variables

220   (ground cover density and ground cover richness respectively), as these flowers may

221   attract pollinators (Rosa García and Miñarro, 2014). This was visually assessed over

222   150–200 m transects, in 50×50 cm ground quadrants placed at 10 m intervals (14

223   intervals per transect in 2015 and 20 in 2016). Half of the quadrats were placed in tree

224   rows and half between rows (as ground cover is differently managed in the two areas).

225   Ground cover density was estimated as the number of flowers per square meter by

226   averaging the density of flowers across quadrats.

227

228   *2.4.   Animal assemblages in cider apple orchards*

229   *Insectivorous birds*

230   Bird biodiversity was evaluated by censuses in the R25 plot of each orchard. During 30

231   minutes, all individual birds heard or seen were counted and identified at the species

232   level. Due to the small size and the homogeneous habitat structure of the plots (with

233   regularly distributed trees and continuous herbaceous cover) we did not expect any

234 differences in detectability among bird species. When possible, we discarded repeated

235 observations attributable to the same individual birds which had remained in the plot

236 during a given slot (e.g. individuals that appear intermittently at the same perching site

237 within short time periods; see also García et al., 2018). Censuses were performed every

238 two weeks during Autumn-Winter (September to December) and Spring-Summer (April

239 to July) for two consecutive annual periods (2015-2016 and 2016-2017, years

240 hereafter), resulting in 36 censuses per orchard (9 censuses per season and year). From

241 all species detected, we selected for analysis only the forest insectivorous birds

242 (insectivorous birds henceforth), i.e. those with a frequent tree-dwelling behavior and an

243 insect-based diet (**Table A1**; for details about species classification see García et al.,

244 2018). We estimated the abundance and richness of insectivorous birds (bird abundance

245 and bird richness henceforth) per orchard, season and year, as the cumulative number

246 of, respectively, bird individuals and bird species recorded in the R25 plots. We assume

247 that bird abundance metric might, despite our efforts, include some repeated counting of

248 individual birds, and thus it must be considered as an estimate of bird activity in

249 functional terms, rather than a measure of bird population sizes.

250

251 *Pollinators*

252 The biodiversity of apple flower visitors was surveyed during bloom in the spring of

253 2015 and 2016. Each orchard was surveyed at three different times (between 11 and

254 13h, 13 and 15h, and 15 and 17h) by different observers under standard climatic

255 conditions (i.e. total of 75 min per orchard per year). In each orchard, in one 0.5-m

256 radius area of the canopy of each target tree, and for a period of 5 min, we visually

257 recorded each insect visiting a flower, estimating the number of visits and the total

258   number of flowers in the selected area. We were only able to reliably identify the most

259   easily recognized species (e.g. *Apis mellifera*, *Bombus species*, *Andrena pilipes*,

260   *Episyrphus balteatus*, *Oxythyrea funesta*, etc.). Most pollinators were, thus, assigned to

261   one of the following groups: bumblebees, wild bees (categorized according to body size

262   as either large, medium or small, when, respectively, bigger than, similar to or smaller

263   than honeybees), hoverflies (predatory hoverflies with aphidophagous larvae, *Eristalis*

264   hoverflies), flies (Diptera other than hoverflies), beetles and butterflies. In order to

265   better assess species richness, we also made a separate assessment of apple pollinators

266   by capturing all pollinators we observed along "Regona" tree transects in an additional

267   10-min period during each survey event (i.e. a sum of 30 min per orchard per year).

268   Captures were made by sweep netting complemented by a slow approach to the insect

269   which was captured in a vial. All captured specimens were identified at the species level

270   in the laboratory (**Table A2**).

271   We estimated two variables of abundance and richness for apple pollinators per

272   orchard and year: 1) abundance and richness of wild pollinators, i.e. the cumulative

273   number of, respectively, pollinator individuals and pollinator species excluding

274   honeybee; and 2) abundance and richness of wild bees (i.e. solitary bees and

275   bumblebees). Although honeybee *Apis mellifera* is a dominant floral visitor in cider

276   apple in Asturias (Miñarro and García, 2018), its occurrence and abundance are highly

277   variable across orchards and highly dependent on the local management of hives,

278   making it somewhat independent of environmental gradients. Therefore, we excluded

279   this species from our analysis, focusing exclusively on wild pollinators. These have

280   been recognized globally as crucial crop pollinators (Garibaldi et al., 2013; Rader et al.,

281   2016), frequently more efficient, at least in qualitative terms, than honeybee (Thomson

282   and Goodell; 2001 Garibaldi et al., 2013). Wild bees have, in fact, been found to have

283 an important role in apple pollination (Mallinger and Gratton, 2015; Martins et al.,

284 2015) and to respond differentially to landscape and local features (Martins et al., 2015;

285 Joshi et al., 2016).

286

287 *2.5.   Estimates of ecological function*

288 *Bird insectivory*

289 We estimated bird insectivory in apple trees through two complementary methods: 1)

290 observations of bird attack on a sentinel pest, mimicked by plasticine caterpillar models

291 (sentinel model experiment, hereafter); and 2) measurements of the removal of

292 arthropods from apple trees through the comparison of branches which were

293 manipulated to exclude birds with unmanipulated branches (exclusion experiment,

294 hereafter).

295   As a sentinel pest, we recreated the caterpillar of codling moth (**Fig. B1A-B;** see

296 also Peisley et al., 2016, for a similar procedure). In Asturias, the codling moth is

297 bivoltine and, from July to the harvest time in October-November, the larvae seek

298 shelter, usually bark crevices in the trunk and main branches, for pupating and/or

299 overwintering (Miñarro, 2006). During this period, both by day and at night, larvae

300 move along upward and downward routes, avoiding smaller branches and leaves, from a

301 hatched egg to apple or from apples to shelters (MacLellan, 1960; Geier, 1963; Welter,

302 2009). During these displacements codling moth larvae may suffer predation by birds

303 (Solomon and Glen, 1979; Wearing and McCarthy, 1992; Welter, 2009). The caterpillar

304 models used in the experiment were 15-mm long and 3-mm diameter size, and were

305 molded with creamy pink (body) and brown (head) plasticine (**Fig. B1C**). Each model

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306   was presented to birds, in a posture imitating natural movement on a branch bearing

307   apples, pierced through its longitudinal axis with a green wire to attach it to the branch.

308   Sentinel model experiment was set up simultaneously in all orchards, and replicated in

309   mid-October 2015 and 2016, and mid July 2016. For each experiment, we deployed 10

310   caterpillar models on branches of similar diameter and height, across 10 trees of similar

311   size and apple crop within the R25 plot of each orchard (i.e. 100 caterpillar models per

312   plot; **Fig. 1C**). These numbers of caterpillar models per tree and per plot was lower than

313   the average number of codling moth larvae found in the same trees in the study plots

314   (mean number of larvae per tree: 2015: 31.52 ± 2.20, min-max: 0-189; 2016: $38.38 \pm$

315   2.32, min-max: 0-206, authors' unpublished data). Caterpillar models were examined 7

316   days after set up, recording whether they showed signs of bird attack (beak marks) on

317   their surface or had been partially removed (Peisley et al., 2016) (**Fig. B1D-E**). The

318   ground under the branches where models were attached was also inspected for models

319   which might have fallen 'naturally'. The negligible number of models fallen under

320   branches, the type of damage (no signs of rodent teeth marks were detected), and the

321   detection of bird attack on the models through camera trapping (authors' unpublished

322   data), make model removal almost completely attributable to birds (see also Geier,

323   1963; Garfinkel and Johnson, 2015; Peisley et al., 2016). For each tree in each orchard,

324   we estimated the number of attacked caterpillar models as those showing signs of attack

325   or having been removed.

326   The bird exclusion experiment was performed in April-June of 2017 in all study

327   orchards. Two large branches of similar length and diameter, but located on opposite

328   sides of a tree, at approximately 1.5-m height, were selected in 5 trees within the R25

329   plot of each orchard. In April, access to one branch by birds was excluded (excluded

330   treatment) by means of cylindrical (80-cm long and 16-cm radius) cage of wire mesh

14

331   (12 mm pore), held parallel to the main branch with tensors and covered at both ends by

332   3-mm pore plastic mesh. The other branch (open treatment) was left unaltered except

333   for being labeled. In June, we sampled the whole arthropod assemblage on exclusion

334   and open branches using a beating method. Three taps per branch were given with a

335   stick, and all the arthropods which fell from the branch were collected in a plastic tray

336   (80 x 50 x 8 cm) held below the branch. Beating samples were inspected in the

337   laboratory for arthropod collection, and arthropod samples were kept frozen at -18º C.

338   The total biomass of arthropods per branch and tree was estimated from the wet weight

339   of frozen samples, applying the same time frame after collection to all samples, and

340   using a precision balance with 0.1 mg accuracy.

341

342   *Pollination*

343   We estimated the contribution of pollinator insects to yield and fruit quality by

344   measuring fruit set (number of flowers to set) and seed set (number of seeds) on three

345   trees per orchard. At the beginning of the flowering period (end of April), 3 similar

346   "Regona" target trees per orchard were selected, and 40 recently opened flowers per tree

347   were marked with colored wire. Twenty randomly selected flowers were kept

348   unmanipulated, potentially allowing for self-pollination and cross-pollination through

349   insect and wind vectors (open-pollination treatment). The other 20 flowers were

350   supplemented with pollen collected previously from different cultivars (hand-

351   pollination treatment). These flowers were saturated with pollen, meaning that fruit set

352   and seed set in the hand-pollination treatment would be the maximum possible for the

353   corresponding tree. In July, when fruits were large enough to distinguish seeds, we

354   counted the number of fruits that had developed from all marked flowers in each

355   treatment. These fruits were harvested and taken to the laboratory to count the number

356   of well-developed seeds per fruit. To estimate fruit set we related the number of

357   developed fruits in the open-pollination treatment of each tree with that in the hand-

358   pollination treatment. In this way, we explored the effect of pollinators relative to the

359   maximum number of fruits potentially set under no pollen-limitation. We followed a

360   similar rationale with seed set, relating the number of well-developed seeds per fruit in

361   the open-pollination treatment of each tree with that in the hand-pollination treatment

362   (maximum 10 seed capsules per fruit). The proportion of fruit set per tree was estimated

363   as the ratio of open-pollinated fruits relative to the hand-pollinated fruits. A similar

364   approach was used for calculating the proportion of seed set per tree.

365

366   *2.6.   Statistical analysis*

367   We sought to represent the general trends of variability in landscape structure around

368   apple orchards across the study site. To do this, we applied a Principal Component

369   Analysis (PCA, performed with the PCA function in the *FactorMineR* R package;

370   Husson et al., 2008) to the six general cover types in R1000 plot across orchards (**Table**

371   **C1**). The first three principal components accounted for more than 82.2% of the

372   variation in our landscape data: PC1 (42.4% of variance explained) described a gradient

373   covering from pasture-dominated landscapes to landscapes dominated by timber

374   (mainly eucalyptus) plantations; PC2 (25.4%) gradient extended from urbanized

375   landscapes to landscapes dominated by semi-natural woody habitat; and PC3 (14.4%)

376   represented a gradient of increased proportions of other habitat types (mainly water

377   courses) and fruit plantations around the orchards. These three principal components

378   were used in the subsequent analyses as independent measures of landscape structure.

379   In order to evaluate the effects of landscape and orchard features on bird

380   biodiversity, we used General Linear Mixed Models (GLMM; Bolker et al., 2009),

381   considering bird abundance and bird richness per orchard as two different response

382   variables (both response variables were checked for normality, and thus models

383   considered Gaussian distribution and identity link). In each model, we considered as

384   main predictors the three principal components of landscape structure, apple canopy

385   cover, apple canopy thickness and orchard size. Apple canopy cover and apple canopy

386   thickness were positively correlated (Pearson's correlation: $r = 0.46$, $P = 0.02$, $N = 26$),

387   although we considered this correlation level weak to lead to collinearity constraints.

388   Consequently, all the main predictors were initially included in full models, together

389   with season (Autumn-Winter, Spring-Summer) and year (2015-2016, 2016-2017),

390   which were considered as categorical fixed factors (Bolker et al., 2009). In order to

391   avoid over-parameterization and over-fitting in these models, we pursued a step-wise

392   deletion of non-significant ($p>0.05$) fixed factors from full models, using likelihood

393   ratio tests. A similar GLMM step-wise procedure was applied to evaluate the effects of

394   landscape and orchard features on pollinator biodiversity. In this case, response

395   variables (abundance and richness of wild pollinators and wild bees) were transformed

396   ($\log_{10}$) to meet normality requirements. All bird and insect models included orchard

397   identity as a random factor given that all orchards were replicated across seasons and/or

398   years (Bolker et al., 2009).

399   We evaluated the effects of bird biodiversity on insectivory rate, first, by means of

400   GLMMs using, as a response variable, the proportion of attacked caterpillar models per

401   tree (sentinel model experiment), considering a binomial error distribution and a logit-

402   link function. As fixed-effect main predictor, we considered, in separate models, bird

403   abundance and bird richness per orchard. Each model also incorporated season and year

404   as categorical fixed factors, as well as tree identity (nested within orchard, dataset

405   considered different measurements made on the same tree in different seasons and

406   years) and orchard identity as random factors. Second, based on the data of the

407   exclusion experiment, we developed GLMMs considering arthropod biomass ($\log_{10}$) per

408   branch as response variable (Gaussian distribution, identity link), and, in separate

409   models, bird abundance and bird richness as fixed-effect main predictor. All models

410   also included as predictor the experimental treatment (excluded vs. open; fixed factor)

411   as well as tree identity (nested within orchard) and orchard identity as random factors.

412   The main-effect and treatment interaction was removed from models after the yhave

413   proven to be non-significant.

414   Similar GLMMs were used to analyze the effects of pollinator biodiversity on

415   pollination rates. Namely, we considered, fruit set and seed set per tree as response

416   variables with a binomial error distribution and a logit link function. These binomial

417   variables considered the number of fruits or seeds in the open-pollination treatment as

418   success, and the difference in the numbers in hand-pollination and open-pollination

419   treatments as failures. As fixed-effect main predictors, we considered, in separate

420   models, the abundance and the richness of wild bees and wild pollinators. All models

421   also included year as categorical fixed factor, as well as tree identity (nested within

422   orchard) and orchard identity as random factors. All GLMMs analyses were performed

423   with *lme* function in the *nlme* R package (Pinheiro et al., 2014). Variance explained by

424   the final complete models and by fixed effects was estimated from conditional and

425   marginal R^2 values, respectively (Nakagawa and Schielzeth, 2013). Means are shown $\pm$

426   Standard Error (SE) throughout the text.

427

3. Results

3.1. *Effect of landscape and local-scale orchard features on insectivorous bird and pollinator biodiversity*

The orchards studied showed wide variability in the structure of their surrounding landscape, as judged by the three main vectors obtained from the PCA (**Figure C1, Table C1**). Orchards also differed greatly in terms of local-scale features, as indicated by the variability in ground cover richness (mean = 7.16 ± 0.59, min-max = 0-19), ground cover density (mean = 29.65 ± 3.82, min-max = 0-125.7), bloom (mean = 2.14 ± 0.12, min-max = 0.38-3.38), apple canopy cover (mean = 0.43 ± 0.03, min-max = 0.18-0.73), and apple canopy thickness (mean = 17.4 ± 1.3, min-max = 6.5–29.0).

The step-wise approach applied led to a model of abundance of insectivorous birds that included significant effects of apple canopy cover within apple orchards, season and year, but no effect of PCA vectors representing landscape features (**Table 1, Table D1**). Namely, bird abundance increased in those orchards with higher apple canopy cover, and it was higher in Autumn-Winter and 2016-2017 (**Table 1, Fig. 2**). The bird richness model included the same set of significant predictors and trends as that of bird abundance, and, in addition, a positive significant effect of orchard size, indicating the occurrence of more bird species in bigger orchards (**Table 1, Table D1**).

In terms of all wild pollinators, we found significant biodiversity responses to landscape structure (**Table D1**). Namely, wild pollinator abundance was positively and significantly affected by both PC1 (**Table 2**) and PC2 (**Table 2, Fig. 3A**) (which represented, respectively, eucalyptus cover and semi-natural woody habitat cover), but negatively affected by PC3 (representing the cover of water courses and fruit plantations). Wild pollinator abundance was also significantly higher in 2016-2017

19

452   (**Table 2**). Wild pollinator richness was positively affected by PC1 (**Table 2**) and

453   orchard-scale bloom level (**Table 2, Fig. 3B**). In the case of wild bees, abundance was

454   negative and significantly affected by PC3 (representing the cover by water courses and

455   fruit plantations (**Table 2, Fig. 3C**). It also responded positively to PC2 (semi-natural

456   woody habitat cover), a predictor approaching significance, and whose inclusion in the

457   step-wise reduced model led to a negligible difference in likelihood ratio with an

458   increasingly purged model (**Table D1**). Wild bee richness was also positive and

459   significantly related to bloom magnitude within orchards (**Table 2, Fig. 3D**). No effects

460   of abundance and richness of flowers in the ground cover were detected (**Table D1**).

461

462   *3.2.   Effects of bird biodiversity on insectivory*

463   The sentinel model experiment suggested the high, but variable across orchards,

464   potential for avian predation on codling moth (mean attack rate on caterpillar models

465   per tree per orchard: 64.2% ±4.7; min-max: 24.3-94.3%). The proportion of attacked

466   caterpillar models per tree increased significantly in those orchards harboring a higher

467   abundance (**Table 3, Fig. 4A)** as well as a greater richness (**Table 3, Fig. 4B)** of

468   insectivorous birds.

469   The exclusion experiment demonstrated significant effects of insectivorous birds

470   on the abundance of arthropods in the cider apple orchards. The presence of

471   insectivorous birds significantly decreased the total biomass of arthropods on apple

472   branches, with excluded branches harboring 3.72 times more biomass than open

473   branches (**Table 3, Fig. 4C-D**). Interestingly, arthropod biomass was negatively

474   affected by bird abundance and richness irrespective of the experimental treatment

475   (**Table 3, Fig. 4C-D).** That is to say, a lower abundance of arthropods was found on the

476 open branches of apple trees in those orchards with higher abundance and richness of

477 insectivorous birds.

478

479 *3.3.   Effects of pollinator biodiversity on pollination*

480 The proportion of developed fruits per tree in the open-pollination treatment averaged

481 0.312 (±0.017) whereas in the hand-pollination treatment reached 0.503 (±0.017; **Table**

482 **E1**). The proportion of developed seeds per tree was also lower in the open-pollination

483 treatment (0.630±0.019) than in the hand-pollination treatment (0.808±0.011; **Table**

484 **E1**). Fruit set per tree, estimated as the quotient between the value of fruit set in open-

485 pollination treatment and that of the hand-pollination treatment, presented a positive

486 relationship with the richness and abundance of wild pollinators (**Table 4**). The

487 response of fruit set to pollinator biodiversity was much stronger in the case of wild

488 bees, with positive significant effects related to their abundance and richness, and fitted

489 by non-linear, saturating trends (**Table 4; Fig. 5A-B**). Apple seed set per tree, estimated

490 as the quotient between the value of seed set in the open-pollination treatment and that

491 of the hand-pollination treatment, was also significantly higher in those orchards

492 harboring higher abundances of all wild pollinators as well as wild bees (**Table 4**; **Fig.**

493 **5C-D**). However, the richness of wild pollinators had a negative and significant effect

494 on seed set (**Table 4**).

495

496 4. **Discussion**

497 In this work, we disentangle both the environmental drivers and the functional effects of

498 biodiversity in agroecosystems, focusing on different groups of wild animals (forest

21

499   insectivorous birds, and pollinator insects) responsible for distinct ecosystem services

500   (pest control and pollination) in the same crop, the cider apple in Asturias (N Spain).

501   We followed a two-step approach in which, first, we found that landscape structure and

502   local-scale orchard features influenced the biodiversity of pest predator birds and

503   pollinator insects within cider apple orchards. Specifically, bird biodiversity was

504   affected by within-orchard apple canopy cover, whereas pollinator biodiversity

505   depended on landscape structure and apple bloom within orchards. Second, our study

506   evidences positive effects of both bird and pollinator biodiversity on the magnitude of

507   the respective ecological functions (insectivory and pollination) supplied by each animal

508   group. Indeed, insectivory rates in orchards increased with both the abundance and

509   richness of birds, as did fruit set and seed set with those of pollinators, especially wild

510   bees. We thus found a consistent positive B-EF link across animal groups and functions

511   performing simultaneously in a given crop type. Although our methodological approach

512   to the complex inter-relationships among habitat structure, biodiversity and ecosystem

513   functions was not strictly integrative (e.g. Heath and Park, 2019), we discuss below the

514   determinants of animal biodiversity and its consequences, in relation to the preservation

515   of ecosystem services with potential benefits for cider apple production.

516

517   *4.1. Effects of landscape and local-scale orchard features on bird and pollinator*

518   *biodiversity*

519   Against expectations, our analysis did not detect any effect of landscape cover types on

520   the biodiversity of birds within apple orchards. Several studies have shown that

521   surrounding semi-natural woody vegetation promotes bird abundance and richness

522   within woody crops (Karp and Daily, 2014; Heath and Long, 2019; Rey et al., 2019). In

523   fact, our previous study in these cider apple orchards also evidenced positive effects of

524   semi-natural woody cover at the large scale (García et al., 2018). This discrepancy

525   between our previous and present results may be related to two analytical facts. First,

526   the response of within-orchard bird biodiversity to the availability of surrounding semi-

527   natural woody habitat may show non-linear trends, scarcely detected by the linear

528   model incorporating integrative landscape predictors here applied. In fact, a positive

529   response of bird biodiversity to semi-natural woody habitat availability emerges at low-

530   to-medium values of the habitat gradient, becoming null or even negative beyond a

531   threshold of 25-30% habitat availability (**Fig. F1; Table F1**; see also García et al.,

532   2018). Second, we also estimated bird biodiversity at a smaller extent (a 25-m radius

533   plot in each apple orchard) than in our previous analysis (50-m radius plot which

534   incorporated apple orchard and nearby habitats; García et al., 2018). The narrower

535   analytical grain used here for response variables probably weakened our ability to detect

536   clear landscape effects on local bird biodiversity (García et al., 2011).

537   In contrast, we found clear effects of orchard-scale features on bird abundance and

538   richness. Namely, apple canopy cover strongly affected bird biodiversity, with more

539   continuous and wider tree covers, rather than denser canopy volumes (no effect of

540   canopy thickness was found) benefiting bird abundance and richness within orchards.

541   Covering a longer period of time, these findings corroborate our previous results

542   (García et al., 2018) and suggest the importance of apple canopy cover for ensuring safe

543   foraging conditions for birds, as well as small-scale connectivity for them when moving

544   within orchards (Henry et al., 2007), or when using orchards as stepping stones between

545   habitat patches (Blitzer et al., 2012). Moreover, our results also evidenced that bigger

546   orchards also harbored richer assemblages of insectivorous birds, suggesting that they

547 operate as a suitable habitat that brings together species from large-scale, landscape bird

548 assemblages (Tscharntke et al., 2012b).

549   In the case of pollinators, we found that landscape structure did influence

550 biodiversity in cider apple orchards. The insects studied here responded to large-scale

551 environmental gradients, probably as a result of wide foraging ranges and their

552 capability for long-distance flights (Walther-Hellwig and Frankl, 2000; Gathmann and

553 Tscharntke, 2002). As judged by the effects of PC2 vector, the cover of surrounding

554 semi-natural woody habitats increased the abundance of wild pollinators, including wild

555 bees, in cider apple flowers (see similar patterns in Martins et al., 2015; Joshi et al.,

556 2016). These habitats often increase pollinator resource availability in the agricultural

557 landscape, in the form of flowers (Kennedy et al., 2013), refuges (Motzke et al., 2016),

558 or nesting sites (Kremen et al., 2007). Our analysis also suggests the positive effect of

559 timber plantations (which increase across the landscape at the expense of pastures) on

560 wild pollinator abundance and richness. Eucalyptus, the dominant timber in the region,

561 is a mast-flowering species that may represent a complementary food resource for

562 pollinators (Horskins and Turner, 1999; Fontúrbel et al., 2015), contributing to some

563 spillover of pollinators to apple orchards. However, contrary to what has been found in

564 other studies (Öckinger and Smith, 2007; Venturini et al., 2017), the availability of

565 surrounding pastures did not increase pollinator biodiversity in cider apple orchards.

566 Finally, the extension of other habitat types such as water courses (a supposedly

567 suboptimal habitat for pollinators) as well as that of fruit plantations (probably

568 representing habitat homogenization and a saturation effect; Samnegård et al., 2019),

569 negatively affected wild bee abundance.

570   We also found clear effects of local-scale orchard features on pollinator

571 biodiversity. Specifically, greater magnitudes of bloom in apple trees attracted more

572   wild pollinator and wild bee species (see also Westphal et al., 2003; Holzschuh et al.,

573   2013). However, in terms of the flower availability in the ground cover, our results

574   contrast with studies suggesting positive effects of this feature on crop pollinators (e.g.

575   Alomar et al., 2018; for other apple orchards see also Campbell et al., 2017; Samnegård

576   et al., 2019). The lack of ground cover effect shown here may be due to the high

577   contrast represented by the mass flowering of apple and the disperse flowering of

578   ground cover in Asturian orchards, with apple monopolizing generalist pollinators and

579   making them indifferent to other floral resources (Holzschuh et al., 2011; Joshi et al.,

580   2016).

581

582   *4.2. Effects of animal biodiversity on insectivory and pollination*

583   Our study shows birds and insects to be effective providers of respectively, insectivory

584   and pollination in cider apple orchards. More importantly, by addressing these

585   ecological functions across orchards, we evidence positive effects of abundance and

586   species richness of both animal groups on the magnitude of their respective functions.

587   We found, therefore, functional consequences of biodiversity across groups of

588   organisms co-occurring in a given agroecosystem.

589   Our results suggest the strong ability of insectivorous birds to reduce arthropod

590   load on cider apple trees. Namely, excluding birds from branches led to an almost four-

591   fold increase in arthropod biomass, a considerably higher figure than applying this

592   condition to other woody crops such as coffee (Karp and Daily, 2014) or cacao (Maas et

593   al., 2013). The positive effects of bird biodiversity on insectivory may emerge from

594   sampling (or dominance) effects (Maas et al., 2016), with richer orchards incorporating

595   abundant and highly effective insectivores (e.g. tits; Mols and Visser, 2002), and from

596   functional complementarity, with richer orchards including a birds with a greater variety

597   of traits and behaviors (i.e. flycatchers, foliage gleaners, bark gleaners; García et al.,

598   2018) which would lead to to additive predatory effects across bird species.

599   As in the case of insectivorous birds, we found evidence of a positive B-EF link

600   between wild insects and pollination in cider apple orchards, especially when focusing

601   on wild bees. Namely, abundance and richness of wild bees impacted positively on fruit

602   set (see also Mallinger and Gratton, 2015; Martins et al., 2015). The relationship

603   between fruit set and wild bee abundance and richnes showed a nonlinear, saturating

604   pattern, suggesting a dominant effect of abundant species at low richnes levels but

605   redundancy at higher richness levels, when maximum fruit set levels are attained

606   (Winfree, 2013). These positive patterns on fruit set were, however, somehow diluted

607   when all wild pollinators were considered. This may be due to the greater pollination

608   effectiveness of wild bees compared to other groups (Martins et al., 2015), facilitating

609   that they would better reflect dominance or complementarity effects across their

610   biodiversity gradients (Fontaine et al., 2005; Földesi et al., 2016). In other words, some

611   inefficient non-bee pollinators could have almost null effects on fruit set: having these

612   species or individuals in the pollinator assemblage would not necessarily mean

613   significant improvement in pollination function, even at low richness levels (Schwartz

614   et al., 2000). Concerning seed set, although wild pollinator abundance positively

615   affected this pollination parameter, our study shows a surprisingly negative effect of

616   wild pollinator richness (but see, for example, Martins et al., 2015; Campbell et al.,

617   2017). Such negative effects of richness could emerge from interspecific competition, as

618   the incorporation of some species may trigger negative interactions that reduce the

619   global effectiveness of the pollinator set (Valido et al., 2014; Agüero et al., 2018).

620

5. Conclusions and implications for management

Our results evidence strong potential, on the basis of animal biodiversity, for the compatible provision of two important ecosystem services, pest control and pollination, in cider apple crops. We must acknowledge that the insectivorous birds studied here may also provoke ecosystem disservices, by consuming beneficial insects (pollinators and other natural enemies such as spiders) or even damaging fruit (e.g. Pejchar et al., 2018; Gonthier et al. 2019). However, in this sense, we did not find signs of negative trade-offs either between biodiversity groups (**Table G1**) or between insectivory and pollination (**Table G1**), suggesting no strong effects of predatory birds on pollinator assemblages and pollination. Moreover, our previous studies evidence the strong capacity of birds to control cider apple pests even when intraguild predation occurs (i.e. towards arthropods acting as natural enemies; García et al., 2018; Miñarro and García, 2018). And finally, although birds occasionally damage apples (by picking at the pulp) crop losses are usually negligible in Asturian orchards, probably due to the early harvest and the high availability of wild fleshy-fruits in surrounding hedgerows for frugivorous birds (authors unpublished data). We thus suggest that the combined activity of insectivorous bird and pollinator insects will have positive net effects on apple crops (see also Peisley et al., 2016). In this sense, it is likely that lower pest damage and enhanced pollination will benefit apple farmers in the form of higher yield (Mols and Visser, 2002; Mallinger and Gratton, 2015), increased harvest quality (Garratt et al., 2014; Peisley et al., 2016), and increased profitability (due to decreased expenditure on insecticides; Cross et al., 2015). Future studies should include the relationship between the ecological variables measured here and explicit yield parameters in order to properly assess the ultimate agronomic role of biodiversity on cider apple farming. These should also include assessments of negative effects, both direct and indirect, of birds on fruit

646 production, in order to explicitly quantify animal services in terms of the balance

647 between costs and benefits (Peisley et al., 2015). Nevertheless, our results suggest that

648 win-win solutions for biodiversity conservation and sustainable agricultural production

649 are possible in cider apple crop.

650   The present results suggest co-occurring agricultural benefits of two different

651 biodiversity groups, opening the door to simultaneous management. This is a

652 challenging task, as even single biodiversity groups, such as vertebrate pest enemies,

653 require integrative and multi-scaled management plans to be implemented (Lindell et

654 al., 2018). Nevertheless, here we have identified several, albeit none of which were

655 clearly common, environmental drivers of bird and insect assemblages. This hinders the

656 identification of simple strategies for the simultaneous improvement of pest predation

657 and pollination. In other words, different measures at landscape and orchard scales are

658 needed in order to enhance simultaneously the biodiversity of bird and that of insect. At

659 the landscape scale, maintaining semi-natural woody habitats (i.e. shrubs, hedgerows,

660 mixed forests), by conserving extant patches (i.e. avoiding losses due to land

661 consolidation programs) or even allowing rewilding (i.e. ecological succession in

662 abandoned fields towards shrubland and secondary forest), but also allowing some

663 eucalyptus plantations, would enhance wild pollinators. At least moderate levels of

664 landscape-scale forest cover also seem to be beneficial to bird biodiversity, which also

665 benefits from woody hedgerows and small forest patches in orchard boundaries (García

666 et al., 2018). These large-scale and out-of-orchard features may not be open to

667 management by apple farmers, and thus should be considered in land management plans

668 that also involve municipal and regional public administrations. At the orchard scale,

669 maintaining wide apple canopy cover would promote insectivorous birds. This measure

670 may indirectly ensure wider flowering canopies and therefore the bloom that fosters the

671   biodiversity of pollinators. However, bloom promotion may be in conflict with the

672   interest of stabilizing yield across years (Asturian apple varieties show bi-annual

673   masting, a production problem generally treated with chemicals and pruning). The

674   trade-off between bloom and masting control, mediated by apple canopy cover, needs

675   further study to assess management thresholds. Finally, even with no evidence of any

676   direct effect on apple pollination, we would still encourage farmers to maintain well-

677   developed and diverse ground covers in order to promote indirect benefits, such as the

678   provision of habitat for other natural enemies of apple pests (e.g. hoverflies or parasitoid

679   wasps; Rosa and Miñarro, 2014), as well food and shelter resources outside of the apple

680   blossom season for apple pollinators.

681

Author contributions

683   DG and MM designed the study. All authors collected the data. RMS performed the

684   analysis with input from DG. RMS drafted the manuscript and all authors contributed to

685   interpretation and writing.

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1011 **Table 1**. Results of Generalized Linear Mixed Models evaluating the effects of

1012 landscape structure and orchard features on richness and abundance of birds. Presented

1013 models are those selected by a step-wise deletion of non-significant fixed predictors

1014 (Table D1). Values of marginal and conditional (between parentheses) R^2 are shown, as

1015 well as variance (±SD) estimate for orchard identity, considered as a random factor, are

1016 also shown.

1017

Bird abundance			
$\mathbf{R^2}$ = 0.380 (0.589)			
Predictors	**Estimate ± SE/SD**	**t**	**P**
Intercept	11.36 ± 4.32		
Apple canopy cover	45.52 ± 9.04	5.03	<0.001
Season (Spring-Summer)	-7.18 ± 1.65	-4.36	<0.001
Year (2016-2017)	4.51 ± 1.65	2.74	0.007
Orchard (random factor)	6.06 ± 8.20		
Bird richness			
$\mathbf{R^2}$ 0.291 (0.420)			
Predictors	**Estimate ± SE/SD**	**t**	**P**
Intercept	4.14 ± 0.83		
Apple canopy cover	7.12 ± 1.54	4.63	<0.001
Orchard size	0.13 ± 0.06	2.14	0.044
Season (Spring-Summer)	-1.07 ± 0.33	-3.26	0.002
Year (2016-2017)	0.82 ± 0.33	2.50	0.015
Orchard (random factor)	0.81 ± 1.63		

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Table 2. Results of Generalized Linear Mixed Models evaluating the effects of landscape structure and orchard features on pollinator biodiversity. Presented models are those selected by a step-wise deletion of non-significant fixed predictors (Table D1). Values of marginal and conditional (between parentheses) R^2 are shown, as well as variance (±SD) estimate for orchard identity, considered as a random factor, are also shown.

Wild pollinator abundance			
R^2 0.344 (0.344)			
Predictors	**Estimate ± SE**	**t**	**P**
Intercept	0.102 ± 0.039		
PC 1	0.074 ± 0.029	2.57	0.017
PC 2	0.073 ± 0.029	2.50	0.021
PC 3	-0.081 ± 0.032	-2.56	0.018
Year (2016-2017)	0.130 ± 0.059	2.22	0.039
Orchard (random factor)	7.515 ± 0.197		
Wild pollinator richness			
R^2 0.284 (0.540)			
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.872 ± 0.046		
PC 1	0.061 ± 0.020	3.03	0.006
Bloom	0.060 ± 0.019	3.12	0.006
Orchard (random factor)	0.071 ± 0.095		
Wild bee abundance			
R^2m 0.189 (0.327)			
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	-0.514 ± 0.051		
PC 2	0.104 ± 0.051	2.03	0.054
PC 3	-0.144 ± 0.056	-2.58	0.017
Orchard (random factor)	2.696 ± 0.347		
Wild bee richness			
R^2 0.113 (0.184)			
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.372 ± 0.089		
Bloom	0.095 ± 0.039	2.44	0.024
Orchard (random factor)	0.060 ± 0.203		

Table 3. Generalized Linear Mixed Models evaluating the effects of bird abundance

1032 and richness on the attack of caterpillar models (sentinel model experiment) and on

1033 arthropod biomass (exclusion experiment). For sentinel model experiment response

1034 variable were fitted by considering a binomial error distribution (logit link) and for

1035 exclusion experiment models included treatment (excluded vs. open) as a main predictor

1036 (fixed factor). Values of marginal and conditional (between parentheses) R2 are shown,

1037 as well as the variance (±SD) estimate for tree identity (nested within orchard) and

1038 orchard identity, considered as random factors.

Sentinel model experiment – Prop. attacked caterpillar models

	Predictors	Estimate ± SE/SD	z	P
Abundance model R^2 0.224 (0.471)	Intercept	-2.978 ± 0.343		
	Bird abundance	0.015 ± 0.006	2.736	0.006
	Season (Spring-Summer)	0.886± 0.092	9.655	<0.001
	Year (2016-2017)	2.688 ± 0.092	29.011	<0.001
	Tree [Orchard] (random factor)	0.27 ± 0.519		
	Orchard (random factor)	2.992 ± 1.412		
Richness model R^2 0.231 (0.487)	Intercept	-5.047± 0.368		
	Bird richness	0.331± 0.030	11.190	<0.001
	Season (Spring-Summer)	1.125± 0.083	13.530	<0.001
	Year (2016-2017)	2.572 ± 0.092	27.850	<0.001
	Tree [Orchard] (random factor)	0.288 ± 0.537		
	Orchard (random factor)	1.926 ± 1.388		

Exclusion experiment - Biomass (mg) of arthropods (log)

	Predictors	Estimate ± SE/SD	t	P
Abundance model R^2 0.332 (0.503)	Intercept	4.556 ± 0.296		
	Bird abundance	-0.031 ± 0.009	-3.28	0.003
	Treatment (Open)	-1.398 ± 0.118	-11.839	<0.001
	Tree [Orchard] (random factor)	0.486 ± 0.929		
	Orchard (random factor)	0.251 ± 0.181		
Richness model R^2 0.324 (0.503)	Intercept	4.546 ± 0.335		
	Bird richness	-0.123 ± 0.043	-2.828	0.009
	Treatment (Open)	-1.398 ± 0.118	-11.839	<0.001
	Tree [Orchard] (random factor)	0.485 ± 0.321		
	Orchard (random factor)	0.284 ± 0.123		

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Table 4. Generalized Linear Mixed Models evaluating the effects of the abundance and richness of wild pollinators and wild bees on fruit set and seed set. Models included the variance (±SD) estimate for tree identity (nested within orchard) and orchard identity, considered as random factors. Response variables were fitted by considering a binomial error distribution (logit link).

	Fruit set				Seed set			
Wild pollinator abundance	R^2 0.022 (0.101)	**Estimate ± SE/SD**	**z**	**P**	R^2 0.034 (0.058)	**Estimate ± SE/SD**	**z**	**P**
	Intercept	0.178±0.230			Intercept	1.178 ± 0.162		
	Abundance wild pollinators	0.110 ± 0.060	1.850	0.064	Abundance wild pollinators	0.354 ± 0.043	8.265	<0.001
	Year (2016)	0.296 ± 0.077	3.865	0.001	Year (2016)	-0.022 ± 0.052	-0.429	0.668
	Tree [Orchard] (random factor)	1.482 ± 1.217			Tree [Orchard] (random factor)	0.964 ± 0.982		
	Orchard (random factor)	0.657 ± 0.811			Orchard (random factor)	0.239 ± 0.489		
Wild pollinator richness	R^2 0.022 (0.096)	**Estimate ± SE/SD**	**z**	**P**	R^2 0.021 (0.057)	**Estimate ± SE/SD**	**z**	**P**
	Intercept	0.051 ±0.302			Intercept	2.995 ± 0.223		
	Richness wild pollinators	0.024 ± 0.019	1.272	0.203	Richness wild pollinators	-0.118 ± 0.014	-8.667	<0.001
	Year (2016)	0.420 ± 0.067	6.281	<0.001	Year (2016)	0.077 ± 0.045	1.706	0.088
	Tree [Orchard] (random factor)	1.467 ± 1.211			Tree [Orchard] (random factor)	0.087 ± 0.295		
	Orchard (random factor)	0.604 ± 0.777			Orchard (random factor)	0.094 ± 0.306		
Wild bee abundance	R^2 0.038 (0.175)	**Estimate ± SE/SD**	**z**	**P**	R^2 0.019 (0.053)	**Estimate ± SE/SD**	**z**	**P**
	Intercept	-0.338 ± 0.264			Intercept	1.340 ± 0.155		
	Abundance wild bees	1.629 ± 0.135	12.063	<0.001	Abundance wild bees	0.845 ± 0.084	10.063	<0.001
	Year (2016)	0.276 ± 0.063	4.401	<0.001	Year (2016)	0.097 ± 0.044	2.198	0.028
	Tree [Orchard] (random factor)	1.530 ± 1.237			Tree [Orchard] (random factor)	0.984 ± 0.992		
	Orchard (random factor)	1.159 ± 1.077			Orchard (random factor)	0.231 ± 0.481		
Wild bee richness	R^2 0.028 (0.092)	**Estimate ± SE/SD**	**z**	**P**	R^2 0.014 (0.047)	**Estimate ± SE/SD**	**z**	**P**
	Intercept	0.001 ± 0.235			Intercept	-0.909 ± 0.255		
	Richness wild bees	0.066 ± 0.022	2.990	0.003	Richness wild bees	-2.4e-5 ± 0.015	0.790	0.999
	Year (2016)	0.475 ± 0.068	6.997	<0.001	Year (2016)	0.227 ± 0.047	1.911	<0.001
	Tree [Orchard] (random factor)	1.462 ± 1.209			Tree [Orchard] (random factor)	0.937 ± 0.968		
	Orchard (random factor)	0.580 ± 0.762			Orchard (random factor)	0.187 ± 0.433		

Figure captions

Figure 1. Schematic representation of study sites and spatial design, showing: A) the region of study (Asturias province in dark gray within the Iberian Peninsula); B) the twenty-six study sites; C) an example of a study orchard, detailing a pollinator sampling station with 5 focal trees in a row of "Regona" apple trees (white points), two additional "Regona" rows selected for transects (yellow dashed line), and the 25-m radius plot around one bird sampling station (yellow circle); D) an example of land uses in the 1000-m radius plot around a sampling station: semi-natural cover vegetation (dark green patches), timber (mainly eucalyptus) plantation (yellow patches), fruit tree plantation (blue patches), pastures (pale green patches) and urbanized ground (red patches).

Figure 2. Examples of significant effects of orchard features on the abundance and richness of insectivorous birds. Colors indicate different years, 2015-2016 (black) and 2016-2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

Figure 3. Examples of significant effects of landscape and orchard features on the abundance and richness of pollinators. Dots indicate different orchards, with different colors for years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

1067   **Figure 4.** Significant effects predicted by Generalized Linear Mixed Models of birds

1068   biodiversity on insectivory, estimated as the percentage of attacked caterpillar models

1069   (A-B), and the biomass (log) of arthropods in beating samples (C-D). In A-B, colors

1070   indicate different years, 2015-2016 (black) and 2016-2017 (white). Seasons are

1071   indicated with different shapes for Autumn-Winter (circles) and Spring-Summer

1072   (triangles). In C-D, dots indicate different orchards, with different colors for exclusion

1073   (black) and open (white) treatments. Linear fits are shown for each combination of

1074   predictor and response variables.

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1076   **Figure 5.** Examples of significant effects predicted by Generalized Linear Mixed

1077   Models of pollinator insect biodiversity on pollination in terms of: (A) abundance and

1078   (B) richness of wild bees on fruit set; (C) abundance of wild bees and (D) abundance of

1079   wild pollinators on seed set. Fruit/seed set (represented in percentages) were estimated

1080   as the quotient between the value of fruit/seed set in open-pollination treatment and

1081   those in the hand-pollination treatment. Dots indicate different orchards, with different

1082   colors for years, 2015 (black) and 2016 (white). Non-linear trends are fitted for fruit set

1083   combinations and linear trends for seed set combinations are shown.
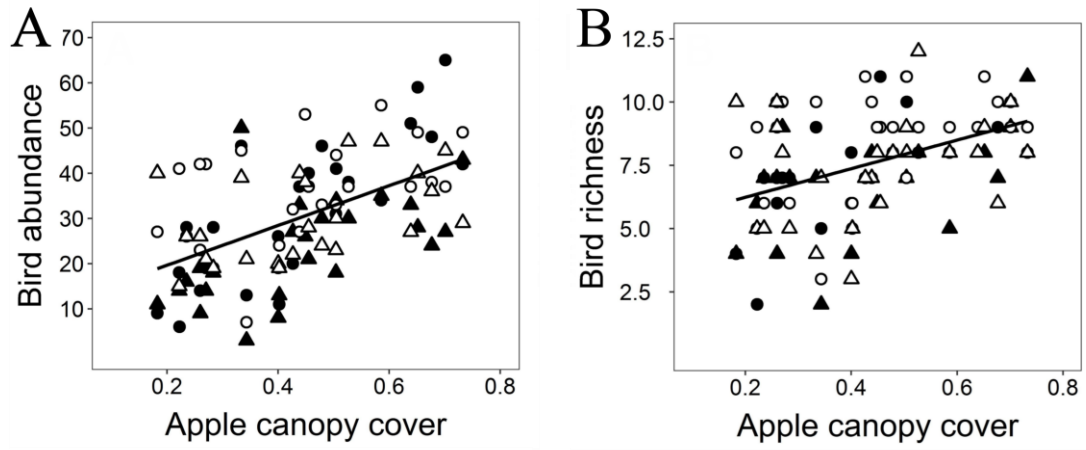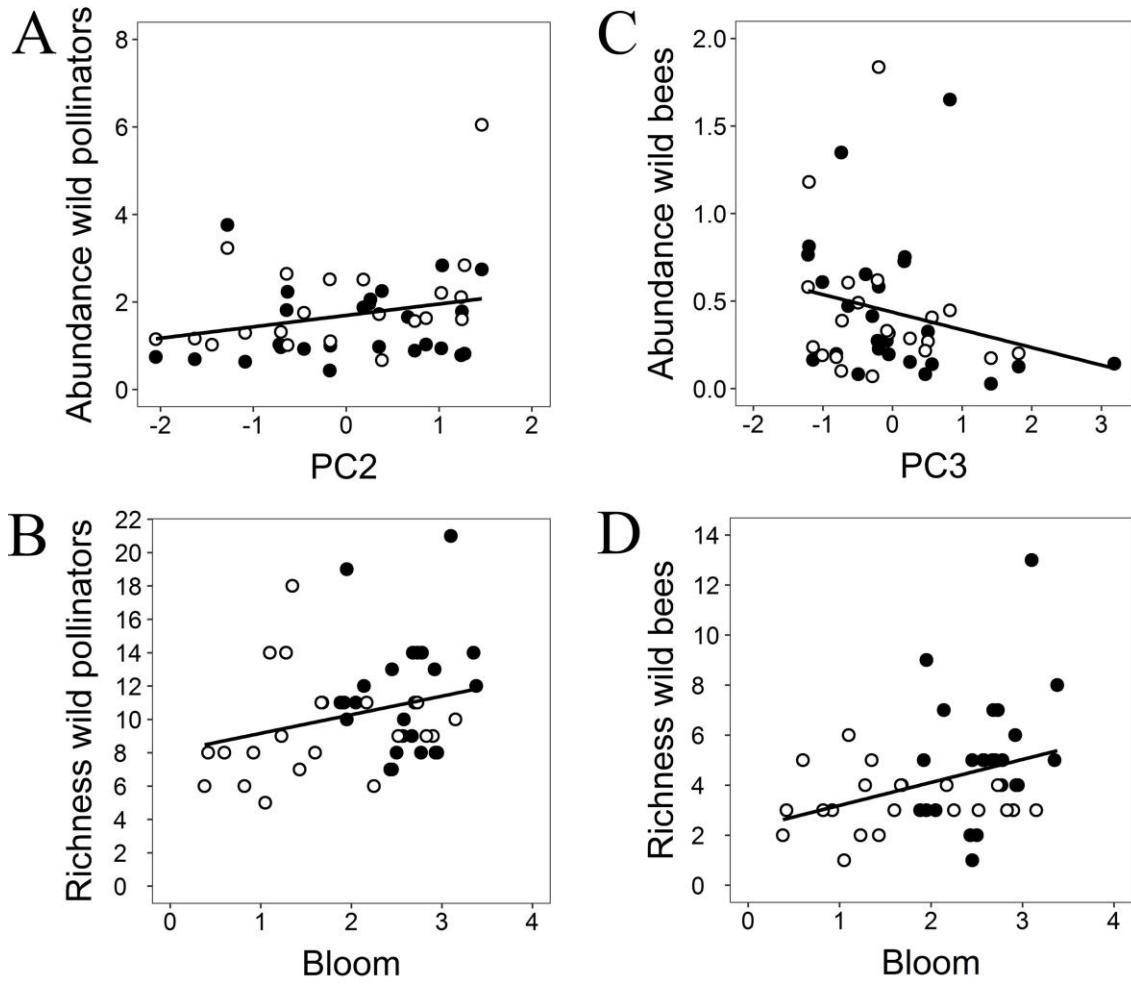
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1085   **Figure 1.**
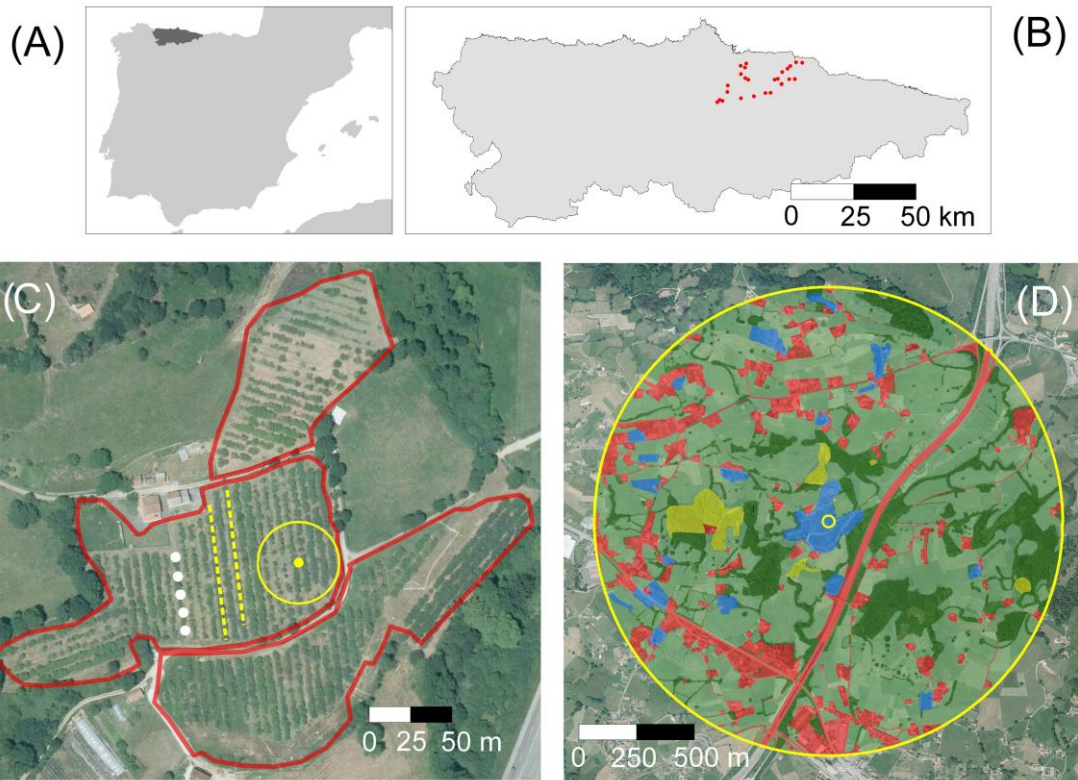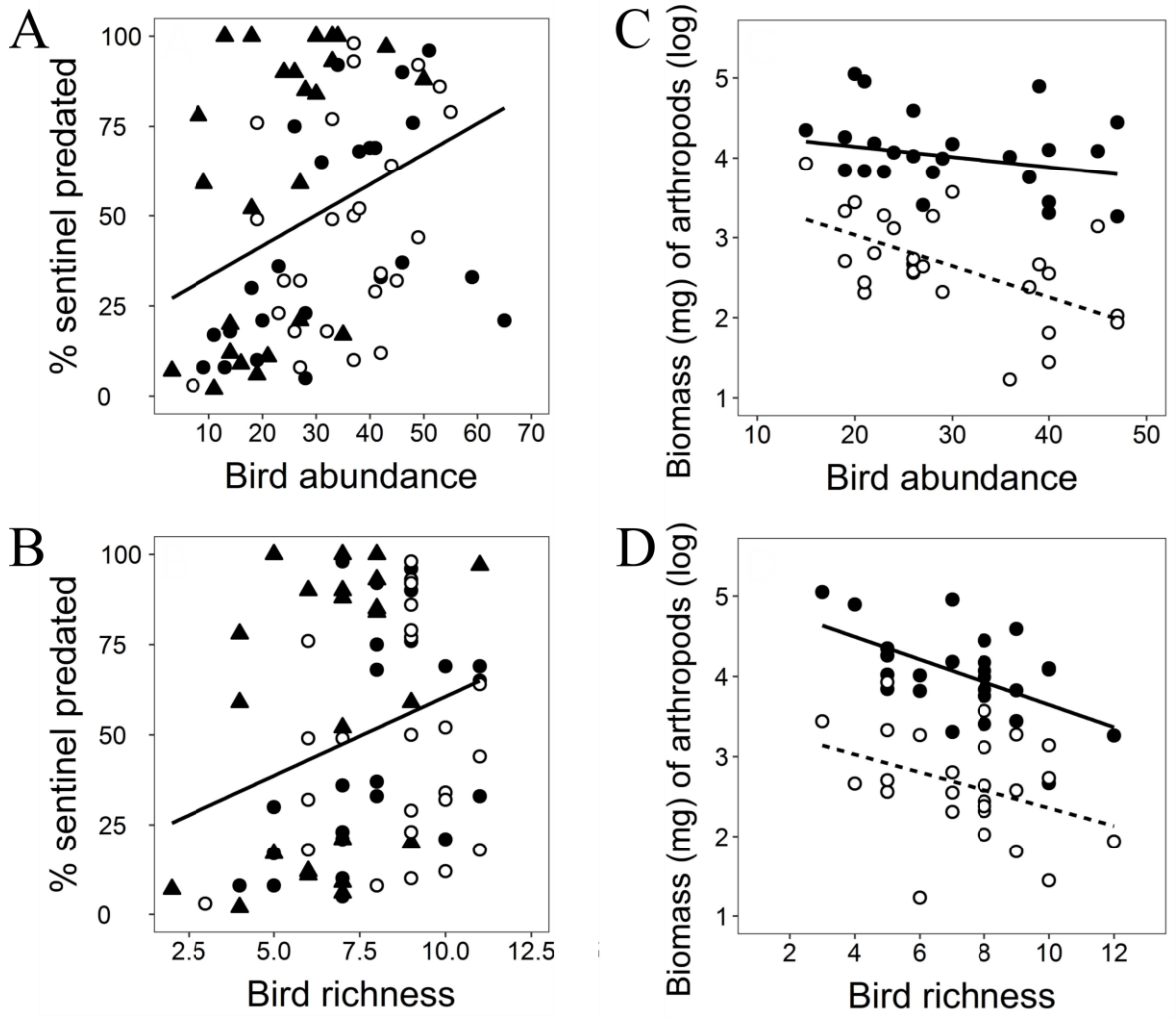
1089 **Figure 2.**

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Figure 3.

Figure 4.

1101   **Figure 5.**

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