



Animal biodiversity in cider apple orchards: Simultaneous environmental drivers and effects on insectivory and pollination



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ARTICLE INFO

Keywords:

Biological control
Ecological functions
Ecosystem services
Fruit set
Insectivorous birds
Landscape composition
Orchard management
Wild bees

ABSTRACT

Making agriculture more sustainable requires a greater understanding of animal-mediated ecosystem services. The beneficial effects of pest-control and pollination provided by, respectively, insectivorous birds and pollinator insects are essential for many crops. Improving these ecosystem services simultaneously in the same crop system means, first, identifying the drivers of animal biodiversity that operate in agricultural landscapes, and second, revealing the relationships between biodiversity and the two services. Here, for two years, we addressed how landscape and small-scale orchard features affected bird and insect biodiversity (abundance and species richness) in cider apple orchards in northern Spain. We examined the effects of bird and insect biodiversity on the magnitude of, respectively, insectivory and pollination. Bird biodiversity was positively affected by the cover of apple canopy within orchards, whereas that of pollinators responded positively to the cover of semi-natural woody habitats and eucalyptus plantations in the surrounding landscape, and also on the level of bloom at the orchard scale. Insectivory, estimated from sentinel model and exclusion experiments, was positively affected by increased abundance and richness of birds across orchards. Similarly, fruit set responded positively to higher abundance and richness of wild bees, whereas seed set mostly depended on the abundance of wild pollinators. Our findings suggest simultaneous positive effects of animal biodiversity on pest-control and pollination in apple orchards, with no sign of trade-offs between biodiversity groups or between ecosystem functions. A multi-scaled management of orchard-level features (apple canopies and surrounding hedgerows for birds, and apple bloom and ground cover for pollinators) and landscape-level ones (surrounding cover of semi-natural woody habitats, moderate for birds, high for pollinators) is encouraged for the simultaneous enhancement of pest-control and pollination. Biodiversity-farming win-win scenarios are possible in cider apple orchards by simultaneously promoting multiple animal-mediated ecosystem services.

1. Introduction

Sustainable agriculture faces the challenge of ensuring food production while reducing environmental impact and biodiversity loss (Foley et al., 2011; Bommarco et al., 2013). The ecosystems within which farming is integrated (i.e. agroecosystems) can harbor variable levels of biodiversity which, in turn, may provide crop-beneficial ecosystem services (Kremen and Miles, 2012; Tscharntke et al., 2012a). In fact, different groups of animals, plants or microorganisms are involved in a wide array of services, such as biological control of crop pests (Maas et al., 2013; Cross et al., 2015), pollination (Kleijn et al., 2015; Rader et al., 2016), maintenance of soil fertility (Edwards, 2004) and water purification (Gharabaghi et al., 2006). Understanding how to simultaneously foster different biodiversity groups to maximize

multiple ecosystem services related to the same crop is, therefore, a pivotal question in sustainable agriculture (Shennan, 2008; Tscharntke et al., 2012a).

Birds and insects are two animal groups targeted as being highly relevant in sustainable agriculture (Power, 2010; Shackelford et al., 2013). On the one hand, insectivorous birds provide generalist biological control by preying upon different types of arthropod pests across annual and perennial crops, in both temperate and tropical regions (Karp and Daily, 2014; Rey Benayas et al., 2017). On the other hand, flower visiting insects are the necessary pollinators of many crops, from annual crops to tree-fruit productions, where they increase crop yield, fruit quality and harvest stability (Klein et al., 2007; Garibaldi et al., 2013). Despite these findings, most studies provide segregated information for insectivorous birds and for pollinator insects with respect

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to various crops. The few studies that do target both biodiversity groups simultaneously have successfully shown the occurrence of combined ecological effects (e.g. Classen et al., 2014), although they have followed small-scale approaches, insufficient to predict the combined role of the two biodiversity groups across the environmental gradients of real agroecosystems. In this context, the importance of insectivorous birds and pollinator insects can be only truly understood through the positive effects animal biodiversity has on ecosystem functions (hereafter B-EF link) (Kremen, 2005; Duncan et al., 2015). Namely, higher bird abundance has been associated with stronger pest control (Jedlicka et al., 2011), as has higher bird richness (Bael Van et al., 2008) and functional diversity (Philpott et al., 2009). In the case of flower visiting insects, richer assemblages, especially of wild bees, are known to increase pollination services (Mallinger and Gratton, 2015). Nevertheless, in order to manage the B-EF link in agroecosystems, we need first to understand the factors that modulate the biodiversity of pest predators and pollinators. In this sense, both the structure of the landscape surrounding a farming site, as well as the in situ agricultural practices, can be approached as environmental drivers of biodiversity at different spatial scales (Shackelford et al., 2013).

Landscape structure may affect bird and pollinator biodiversity in agroecosystems by containing semi-natural habitats that support animals with external resources (i.e. beyond those provided by the crop itself) such as shelter, food, breeding areas, and nesting places (Tschamtko et al., 2012b; Heath et al., 2017; Alomar et al., 2018). This leads to positive relationships between the amount and spatial configuration of semi-natural habitats around agroecosystems and the abundance and richness of different animal groups (Tschamtko et al., 2012b; Kennedy et al., 2013). The small-scale features of farming sites and their immediate surroundings (e.g. hedgerows and farm fringes), which frequently depend on farming management, may also be seen as modulators of resource availability for animals (Kennedy et al., 2013; Rey Benayas et al., 2017). For instance, vegetated margins (Quinn et al., 2014) or dense ground cover (Rey et al., 2019) both increase bird and insect biodiversity, whereas frequent tillage impacts negatively on the persistence of bee populations (Ullmann et al., 2016). In sum, identifying common or differential responses of pest-predators and pollinators to landscape or within-farm features is essential for targeting the management practices that foster multiple ecosystem services in agroecosystems (Manning et al., 2019).

In this study, we assess the environmental drivers of biodiversity, and the effects of biodiversity on the provision of multiple ecosystem services, for different animal groups in a given agroecosystem. We evaluate the ecological function of insectivorous birds as pest enemies, and that of wild insects as pollinators, in cider apple orchards of Asturias (N Spain), along a gradient of environmental variability at local (i.e. within orchards) and landscape (i.e. around orchards) scale. Cider apple crop is a key agroecosystem across the whole Cantabrian region in Spain (Pereira-Lorenzo et al., 2007), and is highly variable in terms of management regimens and landscape contexts, and may harbor rich assemblages of insectivorous birds (García et al., 2018) and pollinator insects (Miñarro and García, 2018). Specifically, we aim here to answer the following questions: (1) What are the local and landscape features driving the biodiversity (abundance and richness) of insectivorous birds and pollinator insects? (2) Does the biodiversity of birds and pollinator insects affect, respectively, pest control and crop pollination services? Based on our results we propose agricultural and landscape management actions for promoting multi-functional animal biodiversity and its derived ecosystem services.

2. Methods

2.1. Study system

The study was conducted in the cider apple (*Malus x domestica* Borkh.) crop area of central Asturias (N Spain) (Fig. 1A). In this region,

cider is a valuable traditional product, strongly ingrained in society, and linked to tourism, gastronomy and leisure. Cider apple annual yield reaches 50,000 tons. The majority of cider apple orchards are comprised of local cultivars that are grown on seedling rootstocks, but new orchards are also being grown on semi-dwarfing rootstock. Both systems typically have a density of between 250 and 500 trees/ha. Orchards are embedded in a highly variegated traditional landscape (Fig. 1D), containing a fine-grained mosaic of orchards, livestock pastures, annual crops (e.g. corn), other fruit (e.g. blueberry, kiwi) and timber (mainly eucalyptus) plantations, human infrastructures, and semi-natural woody vegetation patches (temperate broad-leaved forest, riparian forest and heathland patches). At the small scale of their immediate neighborhoods, apple orchards are typically surrounded, either totally or partially, by natural woody vegetation in the form of hedgerows and/or small forest patches which are mostly unmanaged by farmers (Fig. 1C; for a comprehensive description of hedgerows and small forest patches see García et al., 2018).

Orchards are relatively small (most cover between 0.5 and 4 ha). To reduce competition with trees, weeds in the tree-row are managed by mowing, shallow tillage or herbicide application, depending on the orchard. In all orchards, alleys are periodically cleaned using a shredder, but still maintain a natural ground cover, rich in wild plants that flower throughout the year.

Among the arthropod pests present in Asturian cider apple orchards (Miñarro et al., 2011), the most prevalent are the codling moth (*Cydia pomonella* L.), the rosy apple aphid (*Dysaphis plantaginea* Passerini), green aphids (*Aphis* spp.) and the apple blossom weevil (*Anthonomus pomorum* L.). Growers frequently tolerate moderate levels of pests and diseases, as aesthetic damage is not relevant for cider apples and, thus, pests are not perceived as severe threats to productivity. Furthermore, orchards are based on local cultivars tolerant to common apple diseases (scab, canker and powdery mildew). Consequently, the use of pesticides is not generalized and, when used, they are applied at low intensity. The low degree of agricultural intensification in some orchards and in the surrounding landscape allows for a high diversity of arthropods within orchards, including crop pests as well as their natural enemies (e.g. spiders, earwigs, hoverfly larvae, predatory beetles) or mutualists (e.g. aphid-tending ants) (Miñarro et al., 2011; García et al., 2018).

Previous studies in these orchards have registered a rich (53 species) assemblage of wild birds, from which 54.7 % of species were classified as having a predominantly insectivorous diet and a tree-dwelling habit (García et al., 2018). The most common insectivorous birds are robin (*Erithacus rubecula*), tits (Paridae), thrushes (Turdidae), warblers (Sylviidae and Phylloscopidae), wren (*Troglodytes troglodytes*), and woodpeckers (Picidae). The low use of pesticides, as well as the permanence of flowering ground-cover most of the year, facilitates a high diversity of pollinators in Asturian apple orchards (Miñarro and García, 2018): 82 species of floral visitors being recorded, of which honeybee (61 %) was the dominant flower visitor, followed by hoverflies (21 %, 21 species), wild bees (7%, 39 species), flies (6%, 8 species) bumblebees (3%, 4 species), beetles (1.3 %, 8 species) and butterflies (0.4 %). Pollinators determine cider apple production quantitatively, as fruit set requires cross pollination and hence relies almost completely on insect vectors (Miñarro and García, 2018).

2.2. Spatial design of sampling

Between 2015 and 2017, sampling was conducted in 26 cider apple orchards distributed over 600 km² in the central part of the cider apple area in Asturias (N Spain) (Fig. 1B). Minimum distance between orchards was 1.3 km (average distance in km: 8.02 ± 0.94). Orchards were chosen to represent a gradient of variability in the environmental conditions within apple orchards and in the surrounding landscape (i.e. presence of semi-natural habitats; García et al., 2018). For the monitoring of insectivorous birds and insectivory, in each orchard, we established a sampling station within the plantation, 25 m away from the

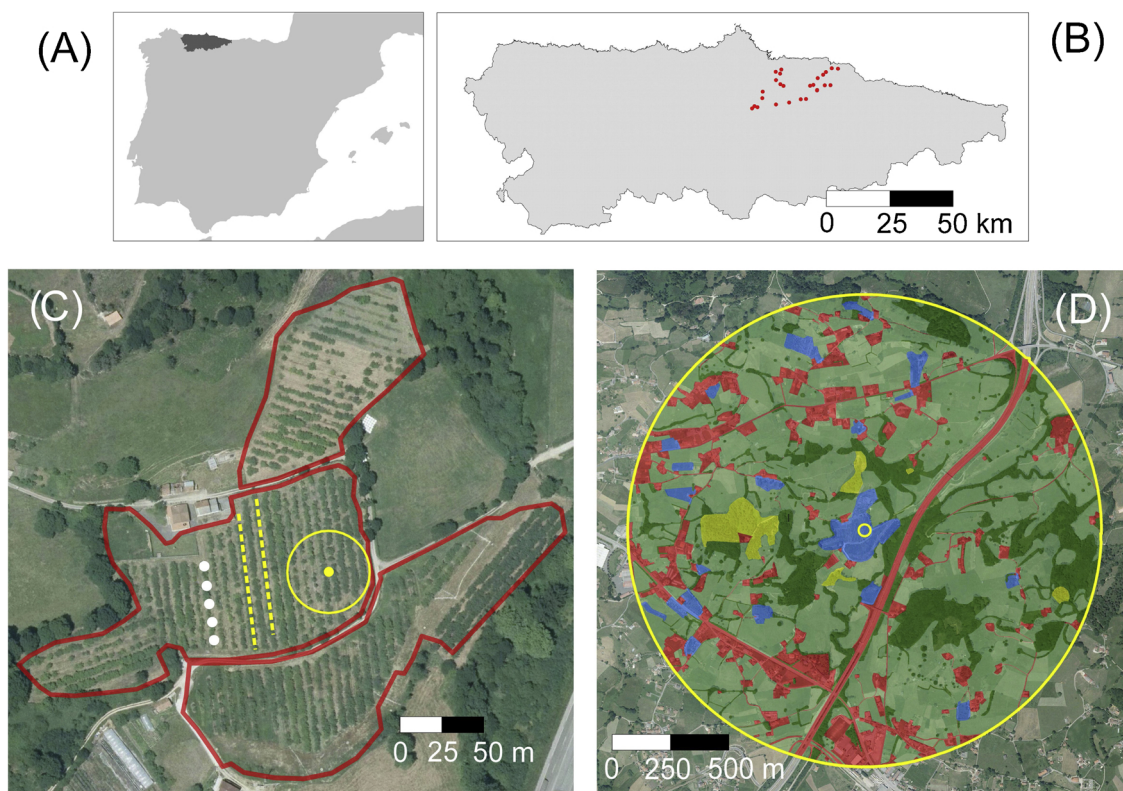


Fig. 1. Schematic representation of study sites and spatial design, showing: A) the region of study (Asturias province in dark gray within the Iberian Peninsula); B) the twenty-six study sites; C) an example of a study orchard, detailing a pollinator sampling station with 5 focal trees in a row of “Regona” 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). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

orchard edge, which was the center of a 25-m radius sampling plot (R25 plot, hereafter; Fig. 1C). This guaranteed that sampling corresponded exclusively to apple plantation habitat, and excluded different surrounding habitats (e.g. hedgerows) even in the smallest orchard. To monitor flower visiting insects and measure pollination, in each orchard we selected five focal trees of the local cultivar “Regona” (target trees, hereafter) within a given row (as rows contain a single cultivar and each orchard has several cultivars) (Fig. 1C), at least 15 m away from the edge (to avoid potential edge effects; Campbell et al., 2017), and in front of a row of a different cultivar (to enhance cross pollination; Ramírez and Davenport, 2013). In order to conduct additional surveys in relation to pollinators, two 150–200 m transects were set up along two additional “Regona” rows (Fig. 1C).

2.3. Landscape structure and orchard features

Landscape structure was quantified by means of a Geographic Information System of the study area (GIS, ArcGIS9.3) based on 1:5000-scale orthophotographs (2014). We delimited a circular plot of 1000-m radius (R1000 plot, hereafter), centered on the R25 plot of each orchard, within which we distinguished, by carefully digitizing landscape patches, six general types of cover: 1) semi-natural woody habitats (including forest, heathland, hedgerows, isolated trees within pastures or plantations); 2) timber (mainly eucalyptus) plantations; 3) fruit tree plantations (apple, kiwi and blueberry); 4) pastures (meadows), 5) other habitats (mainly water courses) and 6) urbanized ground (roads, buildings, gardens around houses) (Fig. 1D). We estimated the availability of each cover type around each orchard from the percentage of cover in each R1000 plot.

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

measured, based on the GIS mentioned above, orchard size and the amount of cover provided by apple tree canopy in each R25 plot (apple canopy cover; from a layer of apple canopy projection). In order to describe the vertical complexity of apple canopy, we randomly selected 25 trees within the R25 plots. We held a 5-m long, scaled pole vertically 50 cm from the trunk of each of these trees, and counted the number of contacts of apple branches or leaves with the pole. We also measured canopy height from the lowest to the tallest branch. We calculated apple canopy thickness by multiplying the number of pole-canopy contacts by canopy height, and averaged this estimate across all 25 trees per orchard. Orchard features can also affect pollinator biodiversity, and so, in addition to orchard size and apple tree canopy cover, we included bloom level as an indicator of the number of apple flowers in the orchard. We recorded bloom level when the target cultivar (“Regona”) was in full bloom, by walking perpendicular to tree rows (in order to avoid a cultivar effect) and covering the full extent of the orchard. For 30 randomly chosen trees per orchard and year, we scored the number of flowers per tree by using a semi-quantitative scale: 0 (0 flowers); 1 (1–10 flowers); 2 (11–50 flowers); 2.5 (51–100 flowers); 3 (101–500 flowers); 3.5 (501–1000 flowers); 4 (1001–5000 flowers); 4.5 (5001–10,000 flowers); 5 (more than 10,000 flowers). We calculated bloom level per orchard and year by averaging this estimate across trees. Finally, during apple bloom we also measured the density and the richness of flowers on the ground cover (variables ground cover density and ground cover richness respectively), as these flowers may attract pollinators (Rosa García and Miñarro, 2014). This was visually assessed over 150–200 m transects, in 50 × 50 cm ground quadrants placed at 10 m intervals (14 intervals per transect in 2015 and 20 in 2016). Half of the quadrats were placed in tree rows and half between rows (as ground cover is differently managed in the two areas). Ground cover

density was estimated as the number of flowers per square meter by averaging the density of flowers across quadrats.

2.4. Animal assemblages in cider apple orchards

2.4.1. Insectivorous birds

Bird biodiversity was evaluated by censuses in the R25 plot of each orchard. During 30 min, all individual birds heard or seen were counted and identified at the species level. Due to the small size and the homogeneous habitat structure of the plots (with regularly distributed trees and continuous herbaceous cover) we did not expect any differences in detectability among bird species. When possible, we discarded repeated observations attributable to the same individual birds which had remained in the plot during a given slot (e.g. individuals that appear intermittently at the same perching site within short time periods; see also García et al., 2018). Censuses were performed every two weeks during Autumn-Winter (September to December) and Spring-Summer (April to July) for two consecutive annual periods (2015–2016 and 2016–2017, years hereafter), resulting in 36 censuses per orchard (9 censuses per season and year). From all species detected, we selected for analysis only the forest insectivorous birds (insectivorous birds henceforth), i.e. those with a frequent tree-dwelling behavior and an insect-based diet (Table A1; for details about species classification see García et al., 2018). We estimated the abundance and richness of insectivorous birds (bird abundance and bird richness henceforth) per orchard, season and year, as the cumulative number of, respectively, bird individuals and bird species recorded in the R25 plots. We assume that bird abundance metric might, despite our efforts, include some repeated counting of individual birds, and thus it must be considered as an estimate of bird activity in functional terms, rather than a measure of bird population sizes.

2.4.2. Pollinators

The biodiversity of apple flower visitors was surveyed during bloom in the spring of 2015 and 2016. Each orchard was surveyed at three different times (between 11 and 13 h, 13 and 15 h, and 15 and 17 h) by different observers under standard climatic conditions (i.e. total of 75 min per orchard per year). In each orchard, in one 0.5-m radius area of the canopy of each target tree, and for a period of 5 min, we visually recorded each insect visiting a flower, estimating the number of visits and the total number of flowers in the selected area. We were only able to reliably identify the most easily recognized species (e.g. *Apis mellifera*, *Bombus* species, *Andrena* pilipes, *Episyrphus balteatus*, *Oxythya funesta*, etc.). Most pollinators were, thus, assigned to one of the following groups: bumblebees, wild bees (categorized according to body size as either large, medium or small, when, respectively, bigger than, similar to or smaller than honeybees), hoverflies (predatory hoverflies with aphidophagous larvae, *Eristalis* hoverflies), flies (Diptera other than hoverflies), beetles and butterflies. In order to better assess species richness, we also made a separate assessment of apple pollinators by capturing all pollinators we observed along “Regona” tree transects in an additional 10-min period during each survey event (i.e. a sum of 30 min per orchard per year). Captures were made by sweep netting complemented by a slow approach to the insect which was captured in a vial. All captured specimens were identified at the species level in the laboratory (Table A2).

We estimated two variables of abundance and richness for apple pollinators per orchard and year: 1) abundance and richness of wild pollinators, i.e. the cumulative number of, respectively, pollinator individuals and pollinator species excluding honeybee; and 2) abundance and richness of wild bees (i.e. solitary bees and bumblebees). Although honeybee *Apis mellifera* is a dominant floral visitor in cider apple in Asturias (Miñarro and García, 2018), its occurrence and abundance are highly variable across orchards and highly dependent on the local management of hives, making it somewhat independent of environmental gradients. Therefore, we excluded this species from our analysis,

focusing exclusively on wild pollinators. These have been recognized globally as crucial crop pollinators (Garibaldi et al., 2013; Rader et al., 2016), frequently more efficient, at least in qualitative terms, than honeybee (Thomson and Goodell, 2001; Garibaldi et al., 2013). Wild bees have, in fact, been found to have an important role in apple pollination (Mallinger and Gratton, 2015; Martins et al., 2015) and to respond differentially to landscape and local features (Martins et al., 2015; Joshi et al., 2016).

2.5. Estimates of ecological function

2.5.1. Bird insectivory

We estimated bird insectivory in apple trees through two complementary methods: 1) observations of bird attack on a sentinel pest, mimicked by plasticine caterpillar models (sentinel model experiment, hereafter); and 2) measurements of the removal of arthropods from apple trees through the comparison of branches which were manipulated to exclude birds with unmanipulated branches (exclusion experiment, hereafter).

As a sentinel pest, we recreated the caterpillar of codling moth (Fig. B1A-B; see also Peisley et al., 2016, for a similar procedure). In Asturias, the codling moth is bivoltine and, from July to the harvest time in October–November, the larvae seek shelter, usually bark crevices in the trunk and main branches, for pupating and/or overwintering (Miñarro, 2006). During this period, both by day and at night, larvae move along upward and downward routes, avoiding smaller branches and leaves, from a hatched egg to apple or from apples to shelters (MacLellan, 1960; Geier, 1963; Welter, 2009). During these displacements codling moth larvae may suffer predation by birds (Solomon and Glen, 1979; Wearing and McCarthy, 1992; Welter, 2009). The caterpillar models used in the experiment were 15-mm long and 3-mm diameter size, and were molded with creamy pink (body) and brown (head) plasticine (Fig. B1C). Each model was presented to birds, in a posture imitating natural movement on a branch bearing apples, pierced through its longitudinal axis with a green wire to attach it to the branch. Sentinel model experiment was set up simultaneously in all orchards, and replicated in mid-October 2015 and 2016, and mid July 2016. For each experiment, we deployed 10 caterpillar models on branches of similar diameter and height, across 10 trees of similar size and apple crop within the R25 plot of each orchard (i.e. 100 caterpillar models per plot; Fig. 1C). These numbers of caterpillar models per tree and per plot was lower than the average number of codling moth larvae found in the same trees in the study plots (mean number of larvae per tree: 2015: 31.52 ± 2.20 , min-max: 0–189; 2016: 38.38 ± 2.32 , min-max: 0–206, authors' unpublished data). Caterpillar models were examined 7 days after set up, recording whether they showed signs of bird attack (beak marks) on their surface or had been partially removed (Peisley et al., 2016) (Fig. B1D-E). The ground under the branches where models were attached was also inspected for models which might have fallen ‘naturally’. The negligible number of models fallen under branches, the type of damage (no signs of rodent teeth marks were detected), and the detection of bird attack on the models through camera trapping (authors' unpublished data), make model removal almost completely attributable to birds (see also Geier, 1963; Garfinkel and Johnson, 2015; Peisley et al., 2016). For each tree in each orchard, we estimated the number of attacked caterpillar models as those showing signs of attack or having been removed.

The bird exclusion experiment was performed in April–June of 2017 in all study orchards. Two large branches of similar length and diameter, but located on opposite sides of a tree, at approximately 1.5-m height, were selected in 5 trees within the R25 plot of each orchard. In April, access to one branch by birds was excluded (excluded treatment) by means of cylindrical (80-cm long and 16-cm radius) cage of wire mesh (12 mm pore), held parallel to the main branch with tensors and covered at both ends by 3-mm pore plastic mesh. The other branch (open treatment) was left unaltered except for being labeled. In June,

we sampled the whole arthropod assemblage on exclusion and open branches using a beating method. Three taps per branch were given with a stick, and all the arthropods which fell from the branch were collected in a plastic tray (80 × 50 × 8 cm) held below the branch. Beating samples were inspected in the laboratory for arthropod collection, and arthropod samples were kept frozen at -18 °C. The total biomass of arthropods per branch and tree was estimated from the wet weight of frozen samples, applying the same time frame after collection to all samples, and using a precision balance with 0.1 mg accuracy.

2.5.2. Pollination

We estimated the contribution of pollinator insects to yield and fruit quality by measuring fruit set (number of flowers to set) and seed set (number of seeds) on three trees per orchard. At the beginning of the flowering period (end of April), 3 similar “Regona” target trees per orchard were selected, and 40 recently opened flowers per tree were marked with colored wire. Twenty randomly selected flowers were kept unmanipulated, potentially allowing for self-pollination and cross-pollination through insect and wind vectors (open-pollination treatment). The other 20 flowers were supplemented with pollen collected previously from different cultivars (hand-pollination treatment). These flowers were saturated with pollen, meaning that fruit set and seed set in the hand-pollination treatment would be the maximum possible for the corresponding tree. In July, when fruits were large enough to distinguish seeds, we counted the number of fruits that had developed from all marked flowers in each treatment. These fruits were harvested and taken to the laboratory to count the number of well-developed seeds per fruit. To estimate fruit set we related the number of developed fruits in the open-pollination treatment of each tree with that in the hand-pollination treatment. In this way, we explored the effect of pollinators relative to the maximum number of fruits potentially set under no pollen-limitation. We followed a similar rationale with seed set, relating the number of well-developed seeds per fruit in the open-pollination treatment of each tree with that in the hand-pollination treatment (maximum 10 seed capsules per fruit). The proportion of fruit set per tree was estimated as the ratio of open-pollinated fruits relative to the hand-pollinated fruits. A similar approach was used for calculating the proportion of seed set per tree.

2.6. Statistical analysis

We sought to represent the general trends of variability in landscape structure around apple orchards across the study site. To do this, we applied a Principal Component Analysis (PCA, performed with the PCA function in the *FactorMineR* R package; Husson et al., 2008) to the six general cover types in R1000 plot across orchards (Table C1). The first three principal components accounted for more than 82.2 % of the variation in our landscape data: PC1 (42.4 % of variance explained) described a gradient covering from pasture-dominated landscapes to landscapes dominated by timber (mainly eucalyptus) plantations; PC2 (25.4 %) gradient extended from urbanized landscapes to landscapes dominated by semi-natural woody habitat; and PC3 (14.4 %) represented a gradient of increased proportions of other habitat types (mainly water courses) and fruit plantations around the orchards. These three principal components were used in the subsequent analyses as independent measures of landscape structure.

In order to evaluate the effects of landscape and orchard features on bird biodiversity, we used Generalized Linear Mixed Models (GLMM; Bolker et al., 2009), considering bird abundance and bird richness per orchard as two different response variables (both response variables were checked for normality, and thus models considered Gaussian distribution and identity link). In each model, we considered as main predictors the three principal components of landscape structure, apple canopy cover, apple canopy thickness and orchard size. Apple canopy cover and apple canopy thickness were positively correlated (Pearson's correlation: $r = 0.46$, $P = 0.02$, $N = 26$), although we considered this

correlation level weak to lead to collinearity constraints. Consequently, all the main predictors were initially included in full models, together with season (Autumn-Winter, Spring-Summer) and year (2015–2016, 2016–2017), which were considered as categorical fixed factors (Bolker et al., 2009). In order to avoid over-parameterization and over-fitting in these models, we pursued a step-wise deletion of non-significant ($p > 0.05$) fixed factors from full models, using likelihood ratio tests. A similar GLMM step-wise procedure was applied to evaluate the effects of landscape and orchard features on pollinator biodiversity. In this case, response variables (abundance and richness of wild pollinators and wild bees) were transformed (\log_{10}) to meet normality requirements. All bird and insect models included orchard identity as a random factor given that all orchards were replicated across seasons and/or years (Bolker et al., 2009).

We evaluated the effects of bird biodiversity on insectivory rate, first, by means of GLMMs using, as a response variable, the proportion of attacked caterpillar models per tree (sentinel model experiment), considering a binomial error distribution and a logit-link function. As fixed-effect main predictor, we considered, in separate models, bird abundance and bird richness per orchard. Each model also incorporated season and year as categorical fixed factors, as well as tree identity (nested within orchard, dataset considered different measurements made on the same tree in different seasons and years) and orchard identity as random factors. Second, based on the data of the exclusion experiment, we developed GLMMs considering arthropod biomass (\log_{10}) per branch as response variable (Gaussian distribution, identity link), and, in separate models, bird abundance and bird richness as fixed-effect main predictor. All models also included as predictor the experimental treatment (excluded vs. open; fixed factor) as well as tree identity (nested within orchard) and orchard identity as random factors. The main-effect and treatment interaction was removed from models after they have proven to be non-significant.

Similar GLMMs were used to analyze the effects of pollinator biodiversity on pollination rates. Namely, we considered, fruit set and seed set per tree as response variables with a binomial error distribution and a logit link function. These binomial variables considered the number of fruits or seeds in the open-pollination treatment as success, and the difference in the numbers in hand-pollination and open-pollination treatments as failures. As fixed-effect main predictors, we considered, in separate models, the abundance and the richness of wild bees and wild pollinators. All models also included year as categorical fixed factor, as well as tree identity (nested within orchard) and orchard identity as random factors. All GLMMs analyses were performed with *lme* function in the *nlme* R package (Pinheiro et al., 2014). Variance explained by the final complete models and by fixed effects was estimated from conditional and marginal R^2 values, respectively (Nakagawa and Schielzeth, 2013). Means are shown \pm Standard Error (SE) throughout the text.

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 (Fig. 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,

Table 1

Results of Generalized Linear Mixed Models evaluating the effects of landscape structure and orchard features on abundance and richness of birds. 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 , as well as variance (\pm SD) estimate for orchard identity, considered as a random factor, are also shown.

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

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 (Table 2). Wild pollinator richness was positively affected by PC1 (Table 2) and orchard-scale bloom level (Table 2, Fig. 3B). In the case of wild bees, abundance was negative and significantly affected by PC3 (representing the cover by water courses and fruit plantations (Table 2, Fig. 3C). It also responded positively to PC2 (semi-natural woody habitat cover), a predictor approaching significance, and whose inclusion in the step-wise reduced model led to a negligible difference in likelihood ratio with an increasingly purged model (Table D1). Wild bee richness was also positive and significantly related to bloom magnitude within orchards (Table 2, Fig. 3D). No effects of abundance and richness of flowers in the ground cover were detected (Table D1).

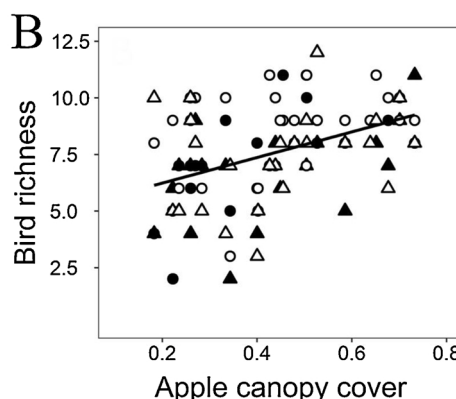
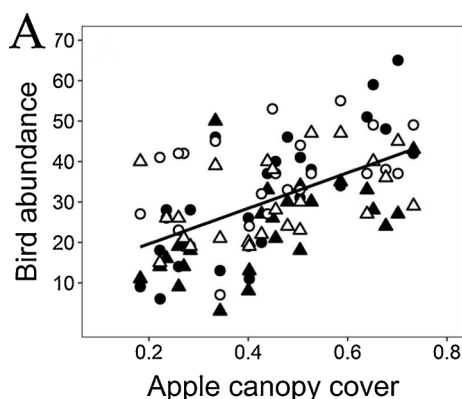


Fig. 2. Examples of significant effects of orchard features on the abundance and richness of insectivorous birds. Colors indicate different years, 2015–2016 (black) and 2016–2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles). Linear fits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

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 , as well as variance (\pm SD) estimate for orchard identity, considered as a random factor, are also shown.

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

3.2. Effects of bird biodiversity on insectivory

The sentinel model experiment suggested the high, but variable across orchards, potential for avian predation on codling moth (mean attack rate on caterpillar models per tree per orchard: 64.2 % \pm 4.7; min-max: 24.3–94.3 %). The proportion of attacked caterpillar models per tree increased significantly in those orchards harboring a higher abundance (Table 3, Fig. 4A) as well as a greater richness (Table 3, Fig. 4B) of insectivorous birds.

The exclusion experiment demonstrated significant effects of insectivorous birds on the abundance of arthropods in the cider apple

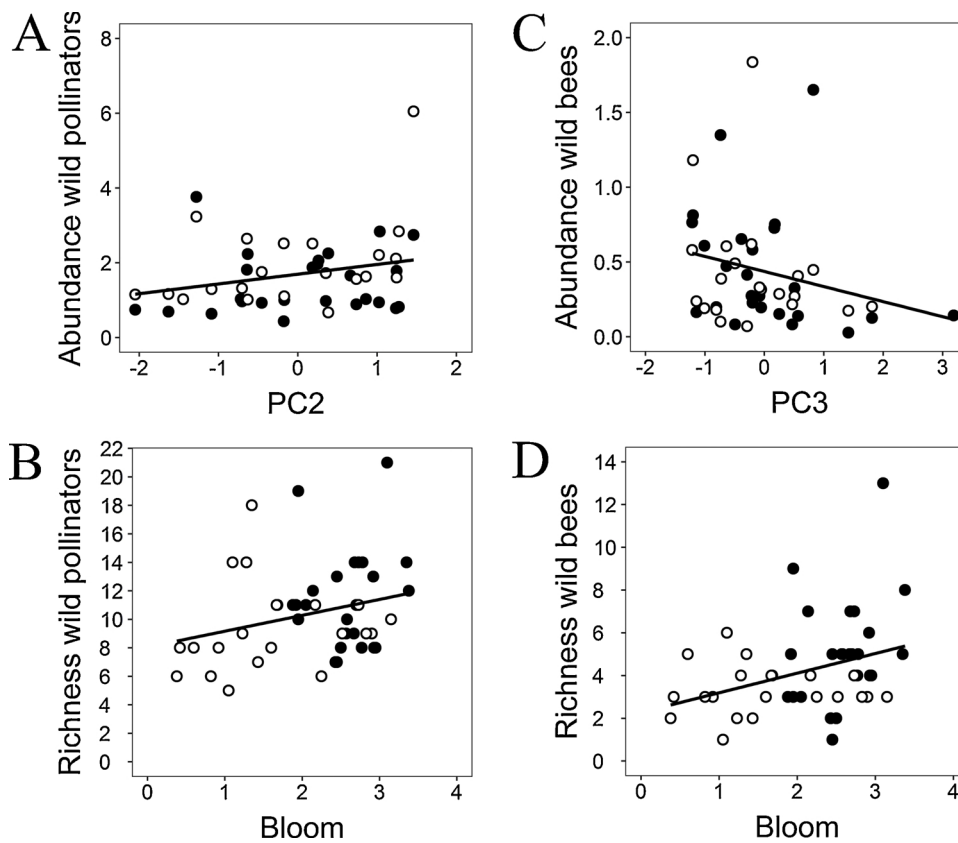


Fig. 3. Examples of significant effects of landscape and orchard features on the abundance and richness of pollinators. Dots indicate different orchards, with different colors for years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination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

Table 3

Generalized Linear Mixed Models evaluating the effects of bird abundance and richness on the attack of caterpillar models (sentinel model experiment) and on arthropod biomass (exclusion experiment). For sentinel model experiment response variable was fitted by considering a binomial error distribution (logit link). Exclusion experiment models included treatment (excluded vs. open) as a main predictor (fixed factor). Values of marginal and conditional (between parentheses) R^2 are shown, as well as the variance (\pm SD) estimate for tree identity (nested within orchard) and orchard identity, considered as random factors.

Sentinel model experiment – Prop. attacked caterpillar models				
	Predictors	Estimate \pm SE/SD	z	P
Abundance model R^2 0.224 (0.471)	Intercept	-2.978 \pm 0.343		
	Bird abundance	0.015 \pm 0.006	2.736	0.006
	Season (Spring-Summer)	0.886 \pm 0.092	9.655	< 0.001
	Year (2016–2017)	2.688 \pm 0.092	29.011	< 0.001
	Tree [Orchard] (random factor)	0.27 \pm 0.519		
	Orchard (random factor)	2.992 \pm 1.412		
Richness model R^2 0.231 (0.487)	Intercept	-5.047 \pm 0.368		
	Bird richness	0.331 \pm 0.030	11.190	< 0.001
	Season (Spring-Summer)	1.125 \pm 0.083	13.530	< 0.001
	Year (2016–2017)	2.572 \pm 0.092	27.850	< 0.001
	Tree [Orchard] (random factor)	0.288 \pm 0.537		
	Orchard (random factor)	1.926 \pm 1.388		
Exclusion experiment - Biomass (mg) of arthropods (log)				
	Predictors	Estimate \pm SE/SD	t	P
Abundance model R^2 0.332 (0.503)	Intercept	4.556 \pm 0.296		
	Bird abundance	-0.031 \pm 0.009	-3.28	0.003
	Treatment (Open)	-1.398 \pm 0.118	-11.839	< 0.001
	Tree [Orchard] (random factor)	0.486 \pm 0.929		
	Orchard (random factor)	0.251 \pm 0.181		
Richness model R^2 0.324 (0.503)	Intercept	4.546 \pm 0.335		
	Bird richness	-0.123 \pm 0.043	-2.828	0.009
	Treatment (Open)	-1.398 \pm 0.118	-11.839	< 0.001
	Tree [Orchard] (random factor)	0.485 \pm 0.321		
	Orchard (random factor)	0.284 \pm 0.123		

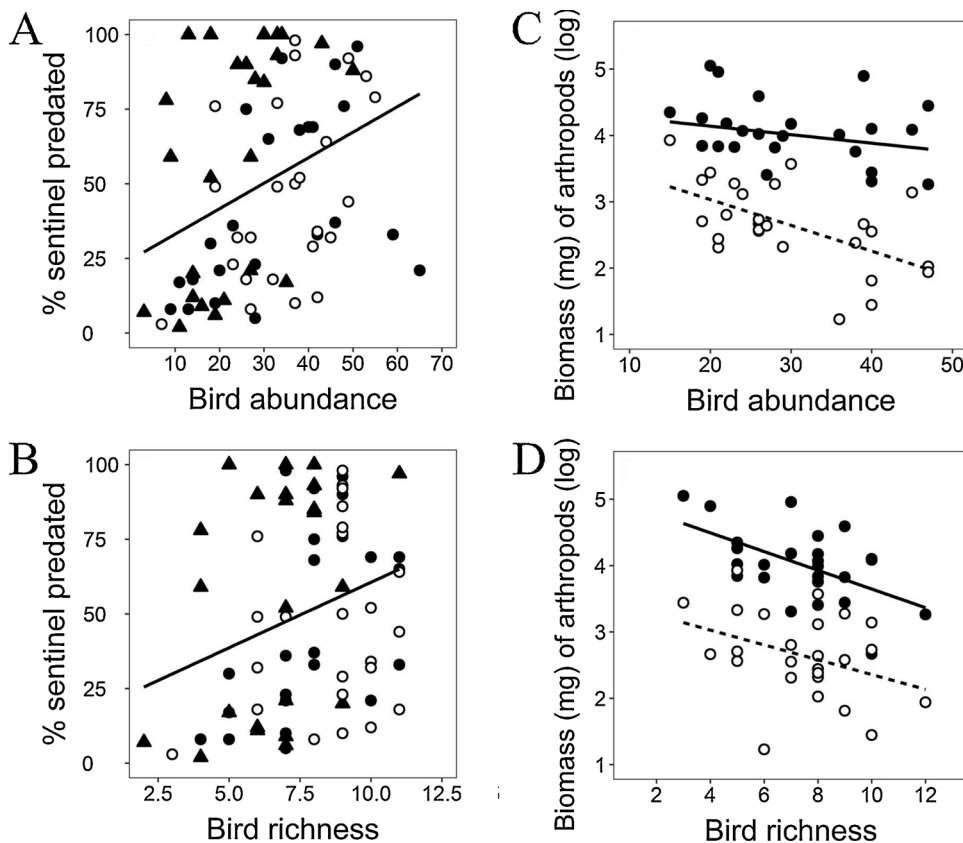


Fig. 4. Significant effects predicted by Generalized Linear Mixed Models of birds biodiversity on insectivory, estimated as the percentage of attacked caterpillar models (A-B), and the biomass (log) of arthropods in beating samples (C-D). In A-B, colors indicate different years, 2015-2016 (black) and 2016-2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles). In C-D, dots indicate different orchards, with different colors for exclusion (black) and open (white) treatments. Linear fits are shown for each combination of predictor and response variables.

orchards. The presence of insectivorous birds significantly decreased the total biomass of arthropods on apple branches, with excluded branches harboring 3.72 times more biomass than open branches (Table 3, Fig. 4C–D). Interestingly, arthropod biomass was negatively affected by bird abundance and richness irrespective of the experimental treatment (Table 3, Fig. 4C–D). That is to say, a lower abundance of arthropods was found on the open branches of apple trees in those orchards with higher abundance and richness of insectivorous birds.

3.3. Effects of pollinator biodiversity on pollination

The proportion of developed fruits per tree in the open-pollination treatment averaged $0.312 (\pm 0.017)$ whereas in the hand-pollination treatment reached $0.503 (\pm 0.017)$; Table E1). The proportion of developed seeds per tree was also lower in the open-pollination treatment (0.630 ± 0.019) than in the hand-pollination treatment (0.808 ± 0.011 ; Table E1). Fruit set per tree, estimated as the quotient between the value of fruit set in open-pollination treatment and that of the hand-pollination treatment, presented a positive relationship with the abundance and richness of wild pollinators (Table 4). The response of fruit set to pollinator biodiversity was much stronger in the case of wild bees, with positive significant effects related to their abundance and richness, and fitted by non-linear, saturating trends (Table 4; Fig. 5A–B). Apple seed set per tree, estimated as the quotient between the value of seed set in the open-pollination treatment and that of the hand-pollination treatment, was also significantly higher in those orchards harboring higher abundances of all wild pollinators as well as wild bees (Table 4; Fig. 5C–D). However, the richness of wild pollinators had a negative and significant effect on seed set (Table 4).

4. Discussion

In this work, we disentangle both the environmental drivers and the

functional effects of biodiversity in agroecosystems, focusing on different groups of wild animals (forest insectivorous birds, and pollinator insects) responsible for distinct ecosystem services (pest control and pollination) in the same crop, the cider apple in Asturias (N Spain). We followed a two-step approach in which, first, we found that landscape structure and local-scale orchard features influenced the biodiversity of pest predator birds and pollinator insects within cider apple orchards. Specifically, bird biodiversity was affected by within-orchard apple canopy cover, whereas pollinator biodiversity depended on landscape structure and apple bloom within orchards. Second, our study evidences positive effects of both bird and pollinator biodiversity on the magnitude of the respective ecological functions (insectivory and pollination) supplied by each animal group. Indeed, insectivory rates in orchards increased with both the abundance and richness of birds, as did fruit set and seed set with those of pollinators, especially wild bees. We thus found a consistent positive B-EF link across animal groups and functions performing simultaneously in a given crop type. Although our methodological approach to the complex inter-relationships among habitat structure, biodiversity and ecosystem functions was not strictly integrative (e.g. Heath and Park, 2019), we discuss below the determinants of animal biodiversity and its consequences, in relation to the preservation of ecosystem services with potential benefits for cider apple production.

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

Against expectations, our analysis did not detect any effect of landscape cover types on the biodiversity of birds within apple orchards. Several studies have shown that surrounding semi-natural woody vegetation promotes bird abundance and richness within woody crops (Karp and Daily, 2014; Heath and Long, 2019; Rey et al., 2019). In fact, our previous study in these cider apple orchards also evidenced positive effects of semi-natural woody cover at the large scale (García et al.,

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

2018). This discrepancy between our previous and present results may be related to two analytical facts. First, the response of within-orchard bird biodiversity to the availability of surrounding semi-natural woody habitat may show non-linear trends, scarcely detected by the linear model incorporating integrative landscape predictors here applied. In fact, a positive response of bird biodiversity to semi-natural woody habitat availability emerges at low-to-medium values of the habitat gradient, becoming null or even negative beyond a threshold of 25–30 % habitat availability (Fig. F1; Table F1; see also García et al., 2018). Second, we also estimated bird biodiversity at a smaller extent (a 25-m radius plot in each apple orchard) than in our previous analysis (50-m radius plot which incorporated apple orchard and nearby habitats; García et al., 2018). The narrower analytical grain used here for response variables probably weakened our ability to detect clear landscape effects on local bird biodiversity (García et al., 2011).

In contrast, we found clear effects of orchard-scale features on bird abundance and richness. Namely, apple canopy cover strongly affected bird biodiversity, with more continuous and wider tree covers, rather than denser canopy volumes (no effect of canopy thickness was found) benefiting bird abundance and richness within orchards. Covering a longer period of time, these findings corroborate our previous results (García et al., 2018) and suggest the importance of apple canopy cover for ensuring safe foraging conditions for birds, as well as small-scale connectivity for them when moving within orchards (Henry et al., 2007), or when using orchards as stepping stones between habitat patches (Blitzer et al., 2012). Moreover, our results also evidenced that bigger orchards also harbored richer assemblages of insectivorous birds, suggesting that they operate as a suitable habitat that brings together species from large-scale, landscape bird assemblages (Tschardt et al., 2012b).

In the case of pollinators, we found that landscape structure did influence biodiversity in cider apple orchards. The insects studied here responded to large-scale environmental gradients, probably as a result of wide foraging ranges and their capability for long-distance flights (Walther-Hellwig and Frankl, 2000; Gathmann and Tschardt, 2002).

As judged by the effects of PC2 vector, the cover of surrounding semi-natural woody habitats increased the abundance of wild pollinators, including wild bees, in cider apple flowers (see similar patterns in Martins et al., 2015; Joshi et al., 2016). These habitats often increase pollinator resource availability in the agricultural landscape, in the form of flowers (Kennedy et al., 2013), refuges (Motzke et al., 2016), or nesting sites (Kremen et al., 2007). Our analysis also suggests the positive effect of timber plantations (which increase across the landscape at the expense of pastures) on wild pollinator abundance and richness. Eucalyptus, the dominant timber in the region, is a mast-flowering species that may represent a complementary food resource for pollinators (Horskins and Turner, 1999; Fontúrbel et al., 2015), contributing to some spillover of pollinators to apple orchards. However, contrary to what has been found in other studies (Öckinger and Smith, 2007; Venturini et al., 2017), the availability of surrounding pastures did not increase pollinator biodiversity in cider apple orchards. Finally, the extension of other habitat types such as water courses (a supposedly suboptimal habitat for pollinators) as well as that of fruit plantations (probably representing habitat homogenization and a saturation effect; Samnegård et al., 2019), negatively affected wild bee abundance.

We also found clear effects of local-scale orchard features on pollinator biodiversity. Specifically, greater magnitudes of bloom in apple trees attracted more wild pollinator and wild bee species (see also Westphal et al., 2003; Holzschuh et al., 2013). However, in terms of the flower availability in the ground cover, our results contrast with studies suggesting positive effects of this feature on crop pollinators (e.g. Alomar et al., 2018; for other apple orchards see also Campbell et al., 2017; Samnegård et al., 2019). The lack of ground cover effect shown here may be due to the high contrast represented by the mass flowering of apple and the disperse flowering of ground cover in Asturian orchards, with apple monopolizing generalist pollinators and making them indifferent to other floral resources (Holzschuh et al., 2011; Joshi et al., 2016).

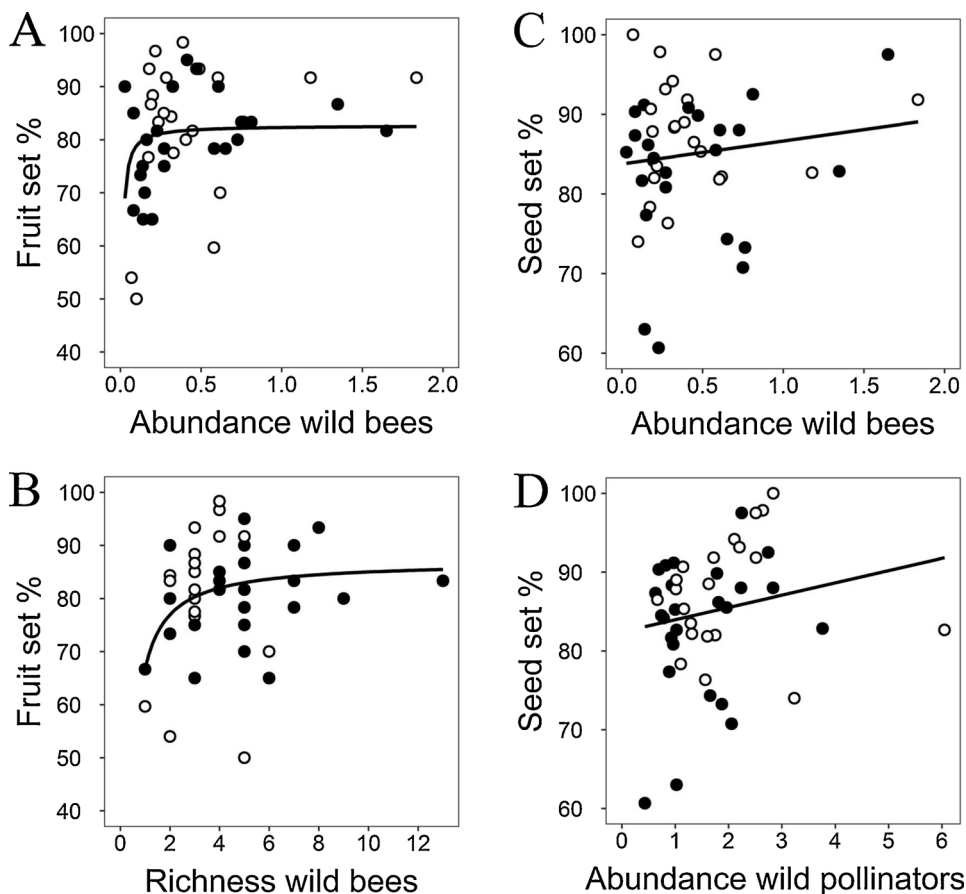


Fig. 5. Examples of significant effects predicted by Generalized Linear Mixed Models of pollinator insect biodiversity on pollination in terms of: (A) abundance and (B) richness of wild bees on fruit set; (C) abundance of wild bees and (D) abundance of wild pollinators on seed set. Fruit/seed set (represented in percentages) were estimated as the quotient between the value of fruit/seed set in open-pollination treatment and those in the hand-pollination treatment. Dots indicate different orchards, with different colors for years, 2015 (black) and 2016 (white). Non-linear trends are fitted for fruit set combinations and linear trends for seed set combinations are shown.

4.2. Effects of animal biodiversity on insectivory and pollination

Our study shows birds and insects to be effective providers of respectively, insectivory and pollination in cider apple orchards. More importantly, by addressing these ecological functions across orchards, we evidence positive effects of abundance and species richness of both animal groups on the magnitude of their respective functions. We found, therefore, functional consequences of biodiversity across groups of organisms co-occurring in a given agroecosystem.

Our results suggest the strong ability of insectivorous birds to reduce arthropod load on cider apple trees. Namely, excluding birds from branches led to an almost four-fold increase in arthropod biomass, a considerably higher figure than applying this condition to other woody crops such as coffee (Karp and Daily, 2014) or cacao (Maas et al., 2013). The positive effects of bird biodiversity on insectivory may emerge from sampling (or dominance) effects, with richer orchards incorporating abundant and highly effective insectivores (e.g. tits; Mols and Visser, 2002), and from functional complementarity, with richer orchards including a birds with a greater variety of traits and behaviors (i.e. flycatchers, foliage gleaners, bark gleaners; García et al., 2018) which would lead to additive predatory effects across bird species.

As in the case of insectivorous birds, we found evidence of a positive –B-EF link between wild insects and pollination in cider apple orchards, especially when focusing on wild bees. Namely, abundance and richness of wild bees impacted positively on fruit set (see also Mallinger and Gratton, 2015; Martins et al., 2015). The relationship between fruit set and wild bee abundance and richness showed a nonlinear, saturating pattern, suggesting a dominant effect of abundant species at low richness levels but redundancy at higher richness levels, when maximum fruit set levels are attained (Winfree, 2013). These positive patterns on fruit set were, however, somehow diluted when all wild pollinators were considered. This may be due to the greater pollination effectiveness of

wild bees compared to other groups (Martins et al., 2015), facilitating that they would better reflect dominance or complementarity effects across their biodiversity gradients (Fontaine et al., 2005; Földesi et al., 2016). In other words, some inefficient non-bee pollinators could have almost null effects on fruit set: having these species or individuals in the pollinator assemblage would not necessarily mean significant improvement in pollination function, even at low richness levels (Schwartz et al., 2000). Concerning seed set, although wild pollinator abundance positively affected this pollination parameter, our study shows a surprisingly negative effect of wild pollinator richness (but see, for example, Martins et al., 2015; Campbell et al., 2017). Such negative effects of richness could emerge from interspecific competition, as the incorporation of some species may trigger negative interactions that reduce the global effectiveness of the pollinator set (Valido et al., 2014; Agüero et al., 2018).

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 production, in order to explicitly quantify animal services in terms of the balance between costs and benefits (Peisley et al., 2015). Nevertheless, our results suggest that win-win solutions for biodiversity conservation and sustainable agricultural production are possible in cider apple crop.

The present results suggest co-occurring agricultural benefits of two different biodiversity groups, opening the door to simultaneous management. This is a challenging task, as even single biodiversity groups, such as vertebrate pest enemies, require integrative and multi-scaled management plans to be implemented (Lindell et al., 2018). Nevertheless, here we have identified several, albeit none of which were clearly common, environmental drivers of bird and insect assemblages. This hinders the identification of simple strategies for the simultaneous improvement of pest predation and pollination. In other words, different measures at landscape and orchard scales are needed in order to enhance simultaneously the biodiversity of birds and that of insects. At the landscape scale, maintaining semi-natural woody habitats (i.e. shrubs, hedgerows, mixed forests), by conserving extant patches (i.e. avoiding losses due to land consolidation programs) or even allowing rewilding (i.e. ecological succession in abandoned fields towards shrubland and secondary forest), but also allowing some eucalyptus plantations, would enhance wild pollinators. At least moderate levels of landscape-scale forest cover also seem to be beneficial to bird biodiversity, which also benefits from woody hedgerows and small forest patches in orchard boundaries (García et al., 2018). These large-scale and out-of-orchard features may not be open to management by apple farmers, and thus should be considered in land management plans that also involve municipal and regional public administrations. At the orchard scale, maintaining wide apple canopy cover would promote insectivorous birds. This measure may indirectly ensure wider flowering canopies and therefore the bloom that fosters the biodiversity of pollinators. However, bloom promotion may be in conflict with the interest of stabilizing yield across years (Asturian apple varieties show bi-annual masting, a production problem generally treated with chemicals and pruning). The trade-off between bloom and masting control, mediated by apple canopy cover, needs further study to assess management thresholds. Finally, even with no evidence of any direct effect on apple pollination, we would still encourage farmers to maintain well-developed and diverse ground covers in order to promote indirect benefits, such as the provision of habitat for other natural enemies of apple pests (e.g. hoverflies or parasitoid wasps; Rosa García and Miñarro, 2014), as well food and shelter resources outside of the apple blossom season for apple pollinators.

Author contributions

DG and MM designed the study. All authors collected the data. RMS performed the analysis with input from DG. RMS drafted the manuscript and all authors contributed to interpretation and writing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Carlos Guardado, Alejandro Núñez, David Luna, Rocío Peña, and José A. Molina for technical support, Ronnie Lendrum for linguistic advice, and all orchard owners for permissions and logistical facilities to work on their properties. Two anonymous referees provided valuable comments on an earlier version of the manuscript. Funding was provided by an FPI-INIA fellowship to RMS (CPD2015-0059), and MinEco/FEDER grants INIA-RTA2013-00139-C03-01 and RTA2017-00051-C02-01 to MM, and PCIN2014-145-C02-02 (BiodivERSA-FACCE2014-74) and CGL2015-68963-C2-2-R to DG. Funding sources had no involvement in study design, collection, analysis or interpretation of data, the writing of the report or decision to submit the article for publication.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.106918>.

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