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Birds as suppliers of pest control in cider apple orchards: avian biodiversity drivers and insectivory effect

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Highlights

Asturian cider apple orchards harbor species-rich assemblages of insectivorous birds.

Apple tree canopy cover and forest availability drive avian biodiversity in orchards.

Insectivorous birds control arthropod abundance and pest outbreak in apple trees.

Multi-scaled habitat management for promoting apple pest control is suggested.

Abstract

Making farming compatible with biodiversity conservation requires identifying the biodiversity drivers that operate in agricultural landscapes, while also addressing the role of biodiversity in ecosystem services. Such integrative information is, however, rare for specific biodiversity groups and services. Here, we focus on insectivorous birds in cider apple orchards in northern Spain, ascertaining the relationships between landscape- and orchard-scale features and bird biodiversity. We conducted field observations and experiments to estimate the potential of birds for controlling arthropod abundance and pest outbreaks in apple trees. Twenty-nine tree-dwelling, insectivorous bird species were observed during one year, inside and around cider apple orchards, with six abundant species representing a predictable core across sites and seasons. Bird abundance and richness increased with the availability of semi-natural woody habitats (hedgerows, remnant trees, and forest patches) both in the immediate neighborhood of the orchard and in the landscape within a 1-km radius of the orchard. Orchards with higher cover of apple tree canopy also harbored a greater abundance and richness of birds. Apple tree branches that were cage-excluded from birds and manually infested with aphids suffered increased shoot damage and aphid outbreak, compared to those that were aphid-infested but open to birds. Bird exclusion led to increased abundances of pest insects other than aphids, and also of other arthropods considered as natural enemies or mutualists of pests. Arthropod abundance was lower in those orchards showing higher abundances of insectivorous birds during spring and summer. Multi-scaled farming management, involving both within-field practices and regional land use schemes, should be considered in order to promote win-win scenarios in cider apple orchards, whereby species-rich assemblages of insectivorous birds provide effective pest control service.

Key words: arthropods, bird abundance, bird richness, biological control, ecosystem services, forest cover, hedgerows, top-down forces.

1. Introduction

Agriculture intensification is jeopardizing biodiversity worldwide, due to the loss and the alteration of natural habitats (Tscharntke et al. 2005; Newbold et al. 2015). There is, nevertheless, a consensus on the potential compatibility between food security and biodiversity conservation (Fischer et al. 2006; Tscharntke et al. 2012a). In this sense, recent research suggests that some farming schemes can retain habitat conditions that promote biodiversity while still being productive (e.g. Clough et al. 2011; Cunningham et al. 2013). Moreover, local biodiversity may render benefits to crop yield through the provision of ecosystem services like pollination, nutrient cycling or pest control (e.g. Moonen and Barberi 2008; Power 2010). Thus, integrative research on how farming constricts or fosters biodiversity, and on the relationship between biodiversity and ecosystem services, would seem essential for achieving conservation-agriculture win-win solutions (Tscharntke et al. 2012a; Gonthier et al. 2014).

Birds represent a biodiversity group suitable for addressing the farming-conservation dilemma (e.g. Philpott et al. 2008; Rey 2011). Birds worldwide are facing the effects of agricultural intensification (Donald et al. 2001; Bregman et al. 2014), suffering population declines and extinctions that affect both rare and common species (e.g. Phalan et al. 2011; Inger et al. 2015). Specifically, bird biodiversity is sensitive to small-scale habitat alterations that decrease the availability of protection, nesting or roosting sites, or food resources, both within fields (e.g. Castro-Caro et al. 2014; Philpott and Bichier 2012) and in their immediate surroundings (e.g. hedgerows or set-asides; Hiron et al. 2013; Garfinkel and Johnson 2015). In addition, given the potential of birds to spill-over into crop fields from surrounding, sometimes distant, habitat patches (Tscharntke et al. 2008), a significant effect of landscape modifications on bird biodiversity is also to be expected in agroecosystems. For example, bird abundance has been shown to decrease in those crop fields at further distances from semi-natural habitats (Karp et al. 2013) or within landscapes with lower proportions of these habitats (Barbaro et al. 2017). Despite these findings, there is a lack of knowledge on how habitat alteration at multiple scales (from local field to landscape level) affects the different components of bird biodiversity (Fahrig et al. 2011; but see Clough et al. 2009).

Birds, thanks to their usually high functional diversity, are thought to supply generalist services of biological control in tropical and temperate agroecosystems (Whelan et al. 2008;

Sekercioglu 2012), preying upon different types of arthropod pests, from sap feeders and leaf herbivores to frugivores and seed predators (e.g. Kellermann et al. 2008; Maas et al. 2013). The magnitude of this biocontrol service depends, first, on the occurrence of top-down trophic effects by which avian predation would decrease arthropod populations and crop plant damage (Mäntylä et al. 2011). These effects, usually addressed by experiments in which birds are precluded from accessing the arthropod pests naturally occurring on plants, may, however, be hindered due to a suppression of intraguild predation and the concomitant mesopredator release, i.e. the suppression of avian control on arthropods (e.g. spiders) that act as natural enemies of pests as well, hence potentially increasing predation on these pests (Martin et al. 2015; Maas et al. 2016). Second, avian biocontrol potential also relies on the ability of birds to buffer pest outbreaks, by means of numerical or functional responses to population expansive increases in specialist pests (Barbaro et al. 2013; Garfinkel and Johnson 2015). Simulations of pest outbreaks, by the experimental addition of specific insects (e.g. Garfinkel and Johnson 2015), should thus be combined with exclusion experiments that evaluate population changes in the whole arthropod community. What is more, these experimental estimations should be complemented with top-down assessments based on the correlated variability between bird biodiversity and arthropod abundance across observational gradients (Mäntylä et al. 2011; Barbaro et al. 2013).

In this work, we assess the role of birds as natural enemies of arthropod pests in the cider apple orchards of Asturias (N Spain), taking into account the local and landscape determinants of bird biodiversity. The environment-dependent potential of birds as pest predators has been suggested in tropical agroforestry (e.g. Perfecto et al. 2004; Karp et al. 2013), although the existence of such a pattern in temperate woody crops is still unclear, even given that seminal findings on avian biocontrol come from exactly this sort of agroecosystems (e.g. Atlegrim 1989; Mols and Visser 2002). Our study system is suitable for addressing this issue, given that Asturian apple orchards are highly variable in their management regimes and landscape contexts, and the pool of insectivorous birds in the Cantabrian region is among the richest in Europe (Tellería et al. 2008; Santos et al. 2014). Specifically, we seek to answer the following questions: 1) How large and diverse, in terms of abundance, richness and composition, are the assemblages of forest insectivorous birds within the apple orchards and in their immediate surroundings across seasons?; 2) How do bird abundance, richness and species composition relate to landscape structure and orchard features?; and 3) Are birds able to control the abundance of arthropod pests in apple orchards? We then translate the answers of these questions into multi-scaled management guidelines for promoting the ecosystem service by insectivorous birds.

2. Methods

2.1. Study system and sampling spatial design

Apple (*Malus* x *domestica* Borkh.) is the most important fruit crop in Asturias (Dapena et al., 2005). There, almost all apple crops are devoted to cider production, given the long-tradition of cider as a valuable product with a Protected Denomination of Origin status. The majority of cider apple orchards are traditional, with large trees grown on seedling rootstocks, but new orchards are semi-intensive, with trees growing on semi-dwarfing rootstocks. Apple plantations in Asturias are based on local cultivars that are tolerant to common apple diseases (scab, canker and powdery mildew). Among the arthropod pests present (Miñarro et al., 2011), the most prevalent is the codling moth (*Cydia pomonella* L.), which attacks the fruits. Also present are the rosy apple aphid (*Dysaphis plantaginea* Passerini) and the green apple aphid (*Aphis pomi* De Geer), which harm the shoots of young trees, and so may be of particular concern in new orchards. The apple blossom weevil (*Anthonomus pomorum* L.), which attacks blossom, is also a significant pest locally. The cultural tolerance of growers to pests and diseases is high in general, as aesthetical damage is not relevant for cider apples and thus pests are not perceived as severe threats to productivity. Consequently, the use of pesticides is not generalized and, when they are used it is often at low intensity, with spraying mainly done with narrow-spectrum insecticides against the codling moth or the rosy apple aphid and, more occasionally, the apple blossom weevil. The low degree of agricultural intensification in some orchards and in the surrounding landscape (see below) thus allows for a high diversity of arthropods within orchards, including, as well as crop pests, their natural enemies (e.g. spiders, earwigs, hoverfly larvae, predatory beetles) or mutualists (e.g. aphid-tending ants)(Miñarro et al. 2010, 2011).

Asturian cider apple orchards are relatively small (most cover between 0.5 and 4 ha) and are embedded in a highly variegated landscape (Fig. 1; Fig. A1), containing a fine-grained mosaic of orchards, livestock pastures, annual crops (e.g. corn), timber (eucalyptus) plantations, human infrastructures, and semi-natural woody vegetation patches, mostly temperate broad-leaved forest, riverine 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 or small forest patches (Fig. 1; Fig. A1). Hedgerows are very heterogeneous in terms of height, width, number of vegetation strata, plant composition and age (Miñarro and Prida 2013; Fig. A1B-C), and are scarcely managed by farmers, although trimming on the planted side happens occasionally. Apple orchards are frequently adjacent to small patches of semi-natural forests composed by the same coterie of woody species as hedgerows (Fig. A1D). Isolated, remnant trees are also found within and between orchards (Fig. A1E).

In early 2015, we chose 25 orchards for the sampling, located over a 600 km^2 study area in the central part of the cider apple region in Asturias, at altitudes from 10 to 385 m a.s.l. (Fig. 1A-B; see Table A1 for geographical details). Minimum distance between orchards was 1.2 km (Fig. 1B). Due to logistical problems, one of the early sites had to be discarded and replaced for a different orchard of similar characteristics in early spring 2016. Sites were chosen with the aim of representing a gradient of variability in the environmental conditions around orchards, based on preliminary surveys on the structure of surrounding landscapes and the features within orchards. In each orchard, we established a sampling station within the apple tree plantation, 25 m away from orchard edges, and delimited a 50-m radius circular plot around each sampling station (R50 plot, hereafter; Fig 1C).

2.2. Landscape structure and orchard features

Landscape structure was quantifyied by means of a Geographic Information System of the study area (GIS, ArcGIS9.3) based on 1:5000-scale orthophotographs (2014). From there, a layer of cover was carefully digitized in order to include all semi-natural woody vegetation assumed to be suitable habitat for forest insectivorous birds (see below for the definition of this classification). This layer, therefore, included forest patches of variable size, hedgerows, and isolated trees within pastures, but excluded low-height heathland (scrubland) patches. We estimated the availability of semi-natural woody vegetation around each apple orchard, at the large scale, within a circular plot of 1-km radius centered on the sampling station (*prop. woody vegetation R1000*; Figs. 1B, 1D), and at the small scale, within the R50 plot (*prop. woody vegetation R50*, Fig. 1E).

As well as orchard size, measured from GIS, we quantified orchard features related to the structure of apple tree canopy within the plantation, which we assumed potentially affect the foraging behavior of insectivorous birds on apple trees. We estimated the amount of cover by apple tree canopy per orchard as the proportion of *apple canopy cover* in the R50 plot, from a GIS layer representing the projection of apple canopy within the orchards (Fig. 1E). In order to describe the vertical complexity of apple canopy, we randomly selected 25 trees from within a 25-m radius area centered on each sampling station. We held a 5-m long, scaled pole vertically at 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.

2.3. Bird assemblages in apple orchards

We performed bird censuses in order to evaluate the assemblages of birds using apple orchards and the surrounding semi-natural woody vegetation. Each census consisted in a 30-min observation slot, during which all individual birds heard or seen in the R50 plot were counted and identified at the species level, by a single observer working from the sampling station. The identity of the perching habitat was also assessed for most of individual observations, using two categories (surrounding woody vegetation vs. apple tree plantation). When possible, we discarded repeated observations attributable to the same individual birds which had stayed in the plot during a given slot (e.g. individuals that appear intermitently at the same perching site within short time periods). Observations of birds performing high (> 50 m height), non-stopping flights over the sampling station were also discarded. Censuses were performed from 7.30 to 12.30 AM, avoiding days of heavy rain and wind. The order of visitation of the different orchards within each set of censuses varied in order to avoid biases in census timing. Censuses were taken every two weeks during September-December 2015 (Autumn-Winter season) and April-July 2016 (Spring-Summer season), resulting in 18 sets of censuses (9 censuses per season).

From all the bird species detected in censuses, we classified under the category of "forest insectivores" (FI, hereafter) those expected to act as potential predators of apple pest arthropods (Table A2), including all species with a predominantly insectivorous (arthropod) diet (at least for the Spring-Summer season), and frequent tree-dwelling behaviour (e.g. tits *Paridae*, warblers and chiffchaffs *Sylviidae*, thrushes and robins *Turdidae*, treecrepers *Certhidae*, woodpeckers *Picidae*, forest-dwelling small corvids, etc). We excluded from this category tree-dwelling but mostly granivorous birds such as pigeons (*Columbidae*) and most finches (*Fringilidae*), open-habitat corvids, ground-dwelling and aerial insectivores that seldom perch on trees (e.g. wagtails *Motacilla* spp., and swallows *Hirundinidae*, respectively), and open scrubland birds (e.g. chats *Saxicola* spp.). Information on general diet and behavior of species was based on Wilman et al. (2014) and personal observations.

We estimated the abundance and the richness of FI birds per orchard and season (*FI bird abundance R50*, *FI bird richness R50*) as the cumulative number of, respectively, bird individuals and bird species recorded in each R50 plot over the periods of Autumn-Winter and Spring-Summer. In order to assess the abundance of FI birds within the apple habitat (i.e. the apple tree plantation of each orchard, avoiding data of birds using the surrounding woody vegetation), we estimated the proportion of bird observations assigned to "apple tree plantation" perching habitat, as well as the surface area of R50 plot covered by apple tree plantation. We thus calculated, for each orchard, *FI bird abundance in apple habitat* as the product of FI bird abundance R50 by the proportion of birds in apple habitat, divided by the surface area (in hectares) of apple tree plantation in R50. This parameter provided, therefore, a measure of bird density within apple plantations, which was comparable across orchards. Following a similar rationale, we calculated, for each orchard, the *FI bird richness in apple habitat* by dividing the cumulative number of FI bird species observed in apple habitat by the surface area (in hectares) of apple tree plantation in R50. Both FI abundance and richness in apple habitat were estimated for both the Autumn-Winter and the Spring-Summer seasons.

2.4. Bird exclusion experiment

In order to estimate the capability of birds to control arthropod abundance in apple trees, we performed an experiment precluding birds from accessing arthropods living in their branches. As we were especially interested in the potential of birds to constrain pest outbreaks, we complemented this exclusion experiment with a manipulated infestation of rosy apple aphid. On April 15th 2016, before bud burst, we selected 10 apple trees of similar size within a 25-m radius of the sampling station in four of the orchards studied. Then, two large branches of similar length and diameter, but located on opposite sides of the tree at approximately 1.5 m height, were selected per tree. Access to one branch by birds was precluded (excluded treatment) by means of an 80-cm long cylindrical (16-cm radius) cage of 12-mm pore wire mesh, held parallel to the main branch and covered at both ends by 2-mm pore plastic mesh (Fig. A2A). The other branch (open treatment) was left unaltered except from being labeled.

On May 19th 2016, just after bud burst, two gravid females of rosy apple aphid were carefully placed, with the help of a paintbrush, on three separate growing shoots both in the excluded branch and in the open branch of each tree (Fig. A2B-C). The experimental branches were revisited on June 9th 2016, in order to monitor aphid attack by means of counting the number of shoots with extant aphid colonies, the number of shoots with signs of aphid attack but abandoned, the number of shoots attacked by aphids (the sum of abandoned and extant colonies) and the total number of shoots per branch (within the cage in the excluded branch and along an 80-cm stretch starting at the tip for the open branch). Both shoots with aphid colonies and those attacked but abandoned are easily identifiable by visual, non-manipulative inspection: attack leads to typically curled leaves that remain curled even after colony extinction (Fig. A2D). We calculated, for each branch, a *shoot damage rate* as the proportion of shoots attacked by aphids relative to the total number of shoots, and a *shoot colonization rate* as the proportion of shoots harboring extant colonies relative to the number of shoots attacked by aphids.

On June 20-21 2016, we sampled the whole arthropod assemblage on exclusion and control branches using the beating method. Three beats were administered with a stick per branch. A plastic tray (80x50x8 cm) was placed below the branch before beating, and the content of each tray following beating was individually labeled and stored at -20ºC until evaluation. For each beating sample, we estimated the total arthropod biomass using a precision balance with 0.1 mg accuracy. We also counted the abundance (number of individuals) of arthropods per sample, distinguishing the following groups: aphids, apple blossom weevils, natural enemies of pests (e.g. spiders, earwigs, predatory bugs, ladybirds, hoverfly larvae), ants, other herbivores (e.g. Psocoptera), and other insects.

2.5. Arthropod abundance in apple trees

In order to estimate the abundance of the arthropods which could be considered as potential prey for insectivorous birds across all study orchards, in late June 2016 we randomly selected 20 trees within a 25-m radius of the sampling station of each orchard (using different trees to those used for the bird exclusion experiment). We performed beating sampling as described above, on one branch per tree (selected according to the criteria of being >1.5 m long and at a height of >1.5 m). Arthropod samples were treated and classified as above, and weighted for biomass estimation. For each orchard, average (per tree) arthropod biomass was calculated.

2.6. Statistical analysis

In order to evaluate the spatio-temporal variability in the species composition of the assemblages of FI birds, we used nonmetric multidimensional scaling ordination (NMDS; Quinn and Keough 2002), based on a matrix of cumulative abundances per species and orchards in the different seasons (Autumn-Winter and Spring-Summer). Abundance data were fourth-root-transformed to reduce the influence in the ordination of common species relative to rarer ones (one species, *Sylvia communis*, with only one observation in one orchard, was excluded from analysis). Using Bray-Curtis similarity measures, we built a two dimensional (NMDS1 and NMDS2) space to plot the relative position of FI bird species. We performed a further analysis of similarities (ANOSIM) with 999 permutations to compare FI bird assemblages between seasons. NMDS and ANOSIM were performed with, respectively, *metaMDS* and *anosim* functions in the *vegan* package (Oksanen et al. 2015) in R 3.01.2.

We evaluated the role of landscape structure and orchard features for FI bird biodiversity, by means of Generalized Linear Mixed Models (GLMMs; Bolker et al. 2009), considering, as different response variables (Gaussian distribution, identity link), FI bird abundance and richness at R50, FI bird abundance and richness in apple habitat, and NMDS dimensions 1 and 2 scores, all based on data for each orchard and season. We considered, as main predictors, the proportion of woody vegetation at R1000 and R50, apple canopy cover, apple canopy thickness, and orchard size. Predictor variables were standardized prior to the inclusion in the models. All main predictors were included in the full models, but, to avoid model over-parametrization, those terms that were non-significant ($P > 0.05$) were excluded in a backwards stepwise procedure to select the simplest model. All models, nonetheless, included *season* (Autumn-Winter vs Spring-Summer) as a categorical fixed factor, in order to control for the effects of temporal autocorrelation in the data set, as well as *orchard identity* as a random factor given that virtually all orchards were replicated across seasons (Bolker et al. 2009). Analyses were performed with *lmer* function in the *lme4* R package (Zuur et al. 2009).

We analyzed the results of the bird exclusion experiment by means of GLMMs considering different response variables related to pest damage and arthropod abundance. All models included *treatment* (Excluded vs. Open) as a main predictor (fixed factor) and *tree identity* (nested within orchard) and *orchard identity* as random factors. Concerning response variables, models for aphid shoot damage and colonization rates considered a binomial distribution (logit link). The model for arthropod biomass ($\log_{10}$) considered a Gaussian distribution (identity link) and incorporated the number of shoots per branch as covariate predictor. Models for the count-based abundances of different arthropod groups considered Poisson or zero-inflated Poisson distributions (log link). The model for blossom weevil abundance was exclusively based on data from two orchards (as the species was absent from >95% of samples in the other two orchards) and thus orchard identity was considered here as a fixed factor (Bolker et al. 2009). Analyses were performed with functions *lmer* (Gaussian) and *glmer* (binomial and Poisson) in *lme4*, and function *glmmabmd* (zero-inflated Poisson) in *glmmABMD* R-packages (Zuur et al. 2009). In all models, we checked for over-dispersion with *overdisp_fun* R function and, when present, models were corrected by incorporating an observation-level random effect (Harrison 2014).

We searched for observational evidence of a bird-mediated top-down effect on arthropod abundance by checking negative relationships between the total biomass of arthropods per site, as estimated from the beating samples (log-transformed) and the abundance of FI birds during Spring-Summer (in the R50 plot and in apple habitat). A visual inspection of per-site values of these variables in bivariate plots suggested the occurrence of an analytical outlier (Quinn and Keough 2002), with extremely low values of arthropod abundance and bird abundance. Thus, we first estimated the relationships between arthropod biomass and FI bird abundances, for the whole dataset, with non-parametric Spearman's rank correlation coefficients. Second, we fitted linear simple regression models with arthropod biomass (log-transformed, response variable) and the abundances of FI birds at R50 and in apple habitat (predictors) after the exclusion of the outlier, following a Cook's distance criterion (with a threshold value of $D_i > 4/N$; Quinn and Keough 2002). Throughout the text, mean values are shown ± sd.

3. Results

3.1. Bird assemblages in apple orchards

A total of 4934 birds, belonging to 53 species, were observed in bird censuses in R50 plots. Of these, 80.7% of observations belonged to some of the 29 (54.7%) species classified as FI, including robins, tits, warblers, wrens, thrushes, woodpeckers, flycatchers (Table A2). Among these FI birds, from 3771 observations where habitat was assigned, 52.9% corresponded to apple habitat (i.e. inside the apple tree plantations). Twenty-two species (75.9%) were common to apple habitat and the semi-natural woody vegetation around orchards, whereas three species were exclusively observed in apple habitat and four only in woody vegetation. As regards seasons, 24 FI species were detected in Autumn-Winter and 23 in Spring-Summer, with 18 (62%) species being common to both seasons. The abundance as well as the richness of FI birds per R50 plot slightly changed across seasons, with, on average, 85.4 ± 4.4 birds from 13.8 ± 0.42 species in Autumn-Winter, and 73.2 ± 3.42 birds from 12.4 ± 0.39 species in Spring-Summer (Wilcoxon's paired test: $|z| > 80.5$, $P < 0.0001$; for both variables). FI species accounted for a similar proportion of abundance, from that of all bird species per R50 plot, in Autumn-Winter (0.84 ± 0.04) and in Spring-Summer (0.80 ± 0.03; $|z| = 49.0$, $P = 0.166$). However, the proportion of the richness accounted by FI species, from that of all bird species per R50 plot, decreased from Autumn-Winter (0.80 ± 0.02) to Spring-Summer (0.72 ± 0.02; $|z| = 105.0$, $P = 0.0011$). There was also a seasonal difference in the percentage of observations of

FI species recorded in apple habitat (Autumn-Winter: 56.8%, Spring-Summer: 49.3%; Likelihood Ratio Chi-square = 22.12; *P* < 0.0001).

The NMDS analysis (stress = 0.23) suggested some variability in the composition of the FI bird assemblages across sites and seasons. The values of NMDS dimensions evidenced a stronger spatio-temporal segregation across sites and seasons for scarce species than for abundant species, as judged from the differences in the relative positions (peripheral vs central) of bird species in the bi-dimensional NMDS space (Fig. 2). The composition of the bird assemblages differed significantly between seasons (ANOSIM; global *R* = 0.44, *P* = 0.001).

3.2. Role of landscape and orchard features for bird biodiversity

The sampling stations selected presented a wide gradients of variability in the proportion of semi-natural woody vegetation around apple orchards, both at the large-scale of the 1000-m radius plot (*mean* = 0.22 ± 0.02, *min-max* = 0.06-0.41) and at the small-scale of the 50-m radius plot (*mean* = 0.16 ± 0.02, *min-max* = 0.00-0.39), though these gradients were not correlated across scales (Pearson's correlation: *r* = 0.22, *P* = 0.29, *N* = 26). Orchards also varied greatly in terms of their interior structure, as judged by the proportion of cover by apple tree canopy in R50 (*mean* = 0.29 ± 0.02, *min-max* = 0.15-0.48), and apple canopy thickness (*mean* = 17.4 ± 1.3, *min-max* = 6.5-29.0), although these variables were found to be positively correlated *(r* = 0.42, *P* = 0.04, *N* = 26). No relationship was found between the proportion of semi-natural woody vegetation at the different scales and the proportion of apple tree cover in R50 (*r* < 0.11, *P* > 0.57, *N* = 26; for both cases).

Both the proportion of semi-natural woody vegetation around apple orchards and the apple canopy cover within orchards were significant predictors in the GLMM of the abundance of FI birds in R50: more birds being detected across the whole year in those plots with more surrounding hedgerows, forest and remnant trees Table 1; Fig.3A), but also in those showing a denser canopy by apple trees (Table 1). The proportion of woody vegetation also positively predicted the number of FI bird species in R50 (Table 1; Fig. 3B). The statistical effects of landscape and orchard features also emerged when the abundance and the richness of FI birds in apple habitat (i.e. within apple plantations) were considered in GLMM. Namely, the abundance of FI birds in apple habitat increased in orchards located in landscapes with a higher proportion of semi-natural woody habitats within a 1000-m radius (Table 1) and, especially, for those with a denser canopy from apple trees (Table 1; Fig. 3C). Similar positive effects of woody vegetation in R1000 and apple canopy cover were observed for the richness of FI birds in apple habitat, in this case with these two predictors having almost equivalent effects (Table 1; Fig. 3D). The composition of bird assemblages (NMDS dimensions 1 and 2) was neither related to landscape structure nor to orchard features in GLMM (Table A3).

3.3. Arthropod control by birds in apple orchards

The bird exclusion and aphid infestation experiment demonstrated significant effects of avian presence on pest damage to apple trees and the occurrence of arthropods (Tables 2-3; Fig. 4). Aphid damage to apple shoots differed significantly for excluded branches compared to open branches (Table 2, Fig. 4A). Namely, excluded branches showed a higher proportion of shoots being damaged by aphids (shoot damage rate) as well as a higher proportion of aphid damaged shoots bearing colonies (shoot colonization rate) than open branches. Bird presence also significantly decreased the total biomass of arthropods, and excluded branches contained 7.7 times more biomass than open branches, even after controlling for the effect of the number of shoots per branch (Table 3, Fig. 4B). From this total biomass, aphids accounted for 61.1% on excluded, but only for 0.98% on open branches. In terms of the abundance of the various groups of arthropods, bird exclusion led to increased numbers of apple pests such as aphids and blossom weevils, but also of their mutualists (ants) and natural enemies (Table 3, Fig. 4C). No differences between excluded and open branches were found in the abundances of other herbivores or insects (Table 3, Fig. 4C).

Beating sampling across 25 sites showed a diverse assemblage of insects and spiders living on apple branches during summer. Herbivorous insects, including aphids, other pests (blossom weevils, folivorous caterpillars, etc) and other herbivores (other types of weevils, stink bugs, etc.) accounted for 31.9% of captured individuals, whereas natural enemies (spiders, earwigs, predatory bugs and ladybirds, and hoverfly larvae) accounted for 17.8%. A large percentage of sampled arthropods (41.1%) were classified as other insects (mostly Psocoptera). The total biomass of arthropods per site, estimated from beating samples, was negatively correlated with the abundance of FI birds during Spring-Summer, both in the R50 plot

(Spearman's rank correlation coefficient: ρ = -0.41, P = 0.04, N = 25) and in apple habitat (ρ = -0.44, P = 0.03, N = 25). Linear regression models also showed significant negative relationships between bird abundance (predictors) and arthropod biomass (response), for the abundance of FI birds both in R50 ($F_{1,22}$ = 10.9, P = 0.003, N = 24; Fig. 5) and in apple habitat ($F_{1,22}$ = 8.6, P = 0.007; N = 24; Fig. 5). Both regression models were fitted after controlling for the effect of one outlier sampling unit (FI bird abundance R50: Cox's Distance, D = 1.12; FI bird abundance apple habitat: Cox's Distance, D = 0.20; threshold D-value = 0.16, in both cases; Fig. 5).

4. Discussion

The present work identifies the habitat features affecting the biodiversity of tree-dwelling insectivorous birds in apple orchards while simultaneously evidencing the potential of birds to supply a pest control service. By covering a large gradient of environmental variability we detected positive effects of tree cover on bird abundance and richness at different scales, from apple orchards and their fringes to the surrounding landscapes. Moreover, by combining the experimental exclusion of birds with regional-scale observations our study suggests that birds have a high capability for controlling the abundance of arthropods and pest outbreaks in apple trees. Results on bird assemblage composition, the determinants of bird abundance and richness, and avian predatory activity are discussed in order to develop management guidelines for the preservation of bird biodiversity and its insectivore role in apple orchards.

4.1. Bird assemblages in apple orchards

A large number of bird individuals and species, classifiable as tree-dwelling and known to feed mostly on invertebrates, were found in Asturian cider apple orchards and their immediate surroundings (for other apple orchards under environmental-friendly management in Europe, see Bouvier et al. 2011; Myczko et al. 2013). Such a high local richness is not surprising given the expectedly large bird species pool of the Cantabrian region, which renders the low-altitude farmlands from northern Spain a passerine hotspot (Tellería et al. 2008; Santos et al. 2014). This biogeographical location also explains the seasonal differences in abundance and richness, a result of the arrival of wintering effectives and species (Santos et al. 2014).

In terms of composition, the bird assemblages in cider apple orchards were characterized by a fairly predictable (across sites and seasons) small core of abundant species. Namely, six species (European robin, common blackbird, Eurasian blackcap, Eurasian wren, great tit and Eurasian blue tit) accounted for ca. 70% of observations and were each present in >94% of sites. There was also a large group of rarer seasonal species, only present during breeding (e.g. red-backed shrike) or wintering season (e.g. European pied flycatcher), which underpinned the temporal changes of bird community composition (Fig. 2). In addition, the whole pool of species represents a wide gradient of morphological and behavioral variability (e.g. body mass ranges from the 6-g common firecrest to the 176-g Eurasian green woodpecker; from Dunning 2008), suggesting a high functional diversity of pest predators. For example, small-sized foliage gleaners (e.g. firecrests, chiffchaffs, tits) are known to actively forage on aphids and leaf caterpillars (Glen et al. 1981; Mols and Visser 2002), branch gleaners (e.g. larger tits, robins) may feed on dispersing caterpillars and apple blossom weevils (Solomon et al. 1976; Wearing 1975), and trunk, bark and ground gleaners (e.g. treecreepers, woodpeckers, thrushes) may actively forage on codling moth cocoons (Solomon and Glen 1979). A large part of this functional diversity is expected to be maintained across seasons, and even across sites within the core of commoner species (Fig. 2). Answering whether the magnitudes of taxonomic and functional diversities of these forest insectivores do relate positively with the strength of pest control goes, however, beyond the scope of the present work (but see Barbaro et al. 2017).

4.2. Landscape and local drivers of bird biodiversity

Both the abundance and the richness of forest insectivores in Asturian cider apple orchards covaried with habitat structural features related to the availability of tree and woody cover at different spatial scales (for tropical agroforestry systems, see Clough et al. 2009; Philpott and Bichier 2012; Karp et al. 2013). The composition of bird assemblages did not relate, however, with none of the studied habitat features. At the fine-scale of orchards and their immediate surroundings, woody vegetation cover around orchards promoted bird abundance and richness in and around apple orchards. Trees and shrubby hedgerows, together with remnant non-apple trees within orchards, represented woody microhabitats intensely used by birds, probably resulting from the fact that they provide nesting sites, shelter against predators, and complementary feeding resources (Hinsley and Bellamy 2000; Otieno et al. 2011). For example, big oaks and chestnuts, frequent at orchard edges and even as remnant trees (Fig. A1D), may facilitate cavity-nesters (e.g. tits, treecreepers and woodpeckers; Mols and Visser 2007), whereas fleshy-fruited plant dominated hedgerows (Fig. A1C) may provide food to winter frugivores (e.g. chiffchaffs, blackcaps, robins and thrushes; Hernández 2007). Beyond these effects of non-productive woody vegetation, the apple tree canopy in itself largely promoted forest insectivores to actually use the productive habitat. In this sense, bird entry into orchards was favored by the existence of wider, more continuous tree cover, rather than by the occurrence of larger canopy volumes in individual trees (as no effect of canopy thickness was found). Thus, bird abundance and richness within apple orchards seem to be affected by the maintenance of a higher degree of connectivity to ensure safe foraging, rather than by the availability of foraging resources per se (see also Henry et al. 2007).

Fine-scaled effects of habitat features on bird biodiversity occurred simultaneously with, and independently of, the large-scale environmental context (see also Myczko et al. 2013). Namely, the apple orchards located in landscapes with a higher proportion of semi-natural woody vegetation (including forest patches and hedgerows) were visited by more individuals from more bird species than those in intensively managed and open landscapes. This pattern suggests the significant role of semi-natural woody habitats as sources for the spillover of bird individuals and species (Tscharntke et al. 2008; Blitzer et al. 2012), even over long distances (Bianchi et al. 2010; Railsback and Johnson 2014). In contrast, the large-scale availability of woody vegetation showed no effect on bird abundance or richness, when these were estimated by accounting for observations both in the apple orchard habitat and in the surrounding woody vegetation. This lack of effect may be related to the constraints of our approach for detecting non-linear biodiversity-habitat relationships (e.g. Tscharntke et al. 2008). In fact, a post-hoc analysis, considering annual cumulative values of bird abundance and richness in R50 plots evidenced positive responses to woody vegetation cover in orchards occupying the low-to-medium range of the landscape gradient, but a lack of effects in those above a threshold proportion of 0.25-0.30 of woody vegetation cover (Fig. A3). Thus, bird assemblages in forest-rich landscapes would be less predictable from large-scale features, but would remain controlled by local features (see also Castro-Caro et al. 2014). As suggested for other agroecosystems, there seems to be a trade-off between local and landscape-scale habitat structures when driving bird biodiversity patterns (Tscharntke et al. 2012b). In sum, the large-scale availability of semi-natural woody habitats, such as forest and hedgerows, promoted the biodiversity of forest insectivorous birds within cider apple orchards and in their immediate surroundings, especially across landscape gradients characterized by a high degree of land use.

4.3. Arthropod control by birds in apple orchards

Our results suggest the strong potential of insectivorous birds for limiting arthropod and pest-insect populations in cider apple orchards. Namely, bird exclusion from apple branches led to 1) increased abundances across most arthropod types, 2) population outbreak (as judged by the 400-fold differences in abundance between treatments; Fig. 4C) of the introduced aphid pest, and 3) enhanced levels of crop plant damage. Interestingly, these experimental data agreed with the negative, observational relationship between avian and arthropod abundances across the study region. This relationship became stronger when we excluded the one orchard that was hardly visited by birds (probably due to its low apple canopy cover) but showed low abundance of arthropods (probably derived from a higher level of pesticide application against aphids and weevils; see also Markó et al. 2017). From this observational pattern, we infer that higher densities of insectivorous birds would be able to impose stronger predation pressure and hence to reduce the abundance of arthropods in apple trees through the spring season (Maas et al. 2016). Thus, our complementary and integrative findings would reinforce the previous research interpreting the biocontrol capacity of insectivorous birds (reviewed in Mäntylä et al. 2011; Maas et al. 2016; see also Peisley et al. 2016 for apple).

The exclusion experiment also enabled us to interpret top-down forces exerted by predatory birds. In the presence of birds, we found decreased abundance of the herbivorous insects representing the major apple pests (aphids and apple blossom weevil) but also of other arthropods known to be their natural enemies (spiders, earwigs, ladybirds) or mutualists (ants; Miñarro et al. 2010, 2011). The decrease in these arthropods was probably due to bird generalist predation (e.g. Martin et al. 2013; Maas et al. 2016). Nevertheless, we cannot exclude some kind of resource-tracking process, by which the number of predatory and mutualistic arthropods would rise as a response to the higher abundances of pest insects in excluded branches, especially in the case of aphid-tending ants (Miñarro et al. 2010). In any case, even considering some intraguild predation, the global effects of bird predation suggested no significant constraints on pest control due to mesopredator release (an increase in the abundance of mesopredatory arthropods, due to bird exclusion, would also lead to high levels of predation on pest insects, with potentially no final differences between experimental treatments, Martin et al. 2013; 2015; Maas et al. 2016). Thus, our results indicating the strong effect of bird exclusion on natural enemies and pests abundances highlight the importance of birds, compared to other natural enemies, as suppliers of pest biocontrol (Miñarro et al. 2005; Dib et al. 2010). Further research, by means of selective exclusion experiments (e.g. Martin et al. 2013), is required to assess the actual relative role of birds and arthropods as common predators of apple pests as well as the true magnitude of intraguild predation.

Although we found evidences that insectivorous birds actively decreased pest pressure in cider apple orchards, further research would be needed to relate pest control with changes in apple yield. In this sense, previous research has shown the harmful effects on apple crop yield of rosy apple aphid (Dib et al. 2010), apple blossom weevil (Markó et al. 2017) and codling moth (Peisley et al. 2016). We thus assume that bird-caused arthropod limitation will be beneficial for cider apple farming in Asturias. Moreover, the potential for an avian ecosystem disservice associated with fruit damage (by typically frugivorous and pulp-picking species such as blackcaps, tits, and finches) seems very low in cider apple orchards. The early apple harvest (beginning of October) and the availability of more profitable fruiting resources around apple orchards from late summer, could explain the extremely low frequency of apple pecking observed in the field (authors’ obs. pers.). Therefore, a positive balance between pest control service and the eventual fruit damage disservice is strongly suggested (Peisley et al. 2016).

5. Concluding remarks and recommendations for management

We found that, on the one hand, species-rich bird assemblages are possible within apple orchards, under specific levels of habitat availability driven by regional land-use and farming management. On the other, by controlling arthropod pressure and pest outbreaks on apple trees, birds would be rendering benefits for apple crop yield. Within the context of a severe decline in common bird species (Inger et al. 2015) and the need for alternative farming schemes (e.g. high-quality local yield) in order to avoid rural abandonment in Europe (Renting et al. 2003), we present the case of Asturian cider apple orchards as a temperate, wildlife-friendly agroecosystem where both biodiversity conservation and farming goals may be compatible.

Once an insectivore effect of wild birds in cider apple orchards is proven, our results lead to specific recommendations for the promotion of this ecosystem service. Specifically, we found complementary, multi-scaled effects of both crop-productive and non-productive habitat structure in bird biodiversity. Thus, at the level of individual orchards, owners should be encouraged to maintain apple canopy cover by preserving large trees, by avoiding excessive pruning to clear inter-row spaces as well as spatially aggregated removal of old trees (so as to avoid large, long-lasting cover gaps within plantations). Also, they should be encouraged to maintain tall, complex and diverse woody hedgerows as orchard borders (Miñarro and Prida 2013). These local, owner-dependent measures should be combined with landscape-level management, driven or at least informed by municipalities and local government, in order to promote a fine-scaled mosaic of semi-natural woody habitats around apple orchards. These measures could include the avoidance of further forest habitat loss (e.g. through fire control measures) as well as the potential recovery of abandoned land by secondary succession (i.e. rewilding, Navarro and Pereira 2012).

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Author contributions

Author sequence reflects decreasing order of contribution. DG and MM designed the study. DG, RMS and MM collected the data. DG analyzed the data and wrote the manuscript. MM and RMS revised the manuscript.

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Table 1. Results of Generalized Linear Mixed Models evaluating the effects of landscape structure, orchard features and sampling season (Autumn-Winter vs Spring-Summer) on the abundance and the richness of forest insectivorous birds, both in the R50 plot and in apple habitat. The variance (± SD) estimate for orchard identity, considered as a random factor, is also shown.

FI bird abundance R50				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R50	8.39 ± 2.90	22.08	2.89	0.009
Apple canopy cover	7.37 ± 2.88	22.52	2.55	0.018
Season	6.40 ± 1.61	23.09	3.97	0.001
Orchard (random factor)	141.86 ± 11.91			
FI bird richness R50				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R50	0.81 ± 0.31	20.00	2.59	0.017
Season	0.64 ± 0.22	20.67	2.95	0.008
Orchard (random factor)	1.25 ± 1.12			
FI bird abundance in apple habitat				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R1000	9.82 ± 2.36	21.13	4.17	0.0004
Apple canopy cover	20.46 ± 2.37	21.81	8.63	<0.0001
Season	11.32 ± 2.94	24.09	3.85	0.0008
Orchard (random factor)	83.44 ± 35.90			
FI bird richness in apple habitat				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R1000	2.28 ± 0.83	22.34	2.74	0.012
Apple canopy cover	2.17 ± 0.82	22.78	2.64	0.015
Season	0.30 ± 0.40	23.37	0.75	0.46
Orchard (random factor)	13.06 ± 3.61			

Table 2. Generalized Linear Mixed Models evaluating the effects of experimental bird exclusion on aphid damage in apple trees. Models included treatment (Open vs. Excluded) as a main predictor (fixed factor) and tree identity (nested within orchard) and orchard identity as random factors (variance estimates are given). Response variables were fitted by considering a binomial error distribution (logit link) and a correction for over-dispersion.

Shoot damage rate				
Treatment (Excluded)			Random factor	Variance Est. ± SD
Estimate ± SE	z	P	Tree [Orchard]	0.01 ± 0.04
1.51 ± 0.18	8.03	<0.0001	Orchard	0.15 ± 0.39
			Observation	0.39 ± 0.62

Shoot colonization rate				
Treatment (Excluded)			Random factor	Variance Est. ± SD
Estimate ± SE	z	P	Tree [Orchard]	0.01 ± 0.05
1.19 ± 0.39	3.01	0.0022	Orchard	0.07 ± 0.08
			Observation	1.62 ± 1.27

Table 3. Generalized Linear Mixed Models evaluating the effects of experimental bird exclusion on arthropod abundance. Models included treatment (Open vs. Excluded) as a main predictor (fixed factor) and tree identity (nested within orchard) and orchard identity as random factors (variance estimates are given). In parentheses, details on the family of error distribution and link function used, and whether correction for over-dispersion was applied are given. The model for arthropod biomass incorporated the number of shoots per branch as covariate predictor. The model for blossom weevil abundance considered orchard identity as a fixed factor, as it was based on data from only two orchards.

Insect biomass ($\log_{10}$) (Gaussian, identity)

	Estimate ± SE	t	P	Random factor	Variance Est. ± SD
Treatment (Excluded)	0.71 ± 0.11	6.05	<0.0001	Tree [Orchard]	0.01 ± 0.05
Number of shoots	0.01 ± 0.02	0.38	0.72	Orchard	0.04 ± 0.21

Aphid abundance (Poisson, log, correction for over-dispersion)

	Estimate ± SE	z	P	Random factors	Variance Est. ± SD
Treatment (Excluded)	5.63 ± 0.86	6.55	<0.0001	Tree [Orchard]	0.01 ± 0.03
				Orchard	1.39 ± 1.18
				Observation	7.74 ± 2.78

Blossom weevil abundance (Zero-inflated Poisson, log)

	Estimate ± SE	z	P	Random factor	Variance Est. ± SD
Treatment (Excluded)	1.72 ± 0.67	2.57	0.010	Tree [Orchard]	0.02± 0.04
Orchard (Masaveu)	0.85 0.54	1.57	0.12		

Natural enemies abundance (Poisson, log)

	Estimate ± SE	t	P	Random factors	Variance Est. ± SD
Treatment (Excluded)	0.59 ± 0.14	4.03	<0.0001	Tree [Orchard]	0.26 ± 0.51
				Orchard	0.07 ± 0.27

Ants (Poisson, log)

	Estimate ± SE	t	P	Random factors	Variance Est. ± SD
Treatment (Excluded)	2.16 ± 0.53	4.11	<0.0001	Tree [Orchard]	1.50 ± 3.87
				Orchard	0.03 ± 0.05

Other herbivores (Zero-inflated Poisson, log)

	Estimate ± SE	t	P	Random factors	Variance Est. ± SD
Treatment (Excluded)	-0.41 ± 0.28	-1.45	0.15	Tree [Orchard]	0.97 ± 0.98
				Orchard	0.08 ± 0.11

Other insects (Poisson, log)

Treatment (Excluded)	Estimate ± SE	t	P	Random factors	Variance Est. ± SD
	0.59 ± 0.37	1.53	0.11	Tree [Orchard]	0.27 ± 0.52
				Orchard	0.21 ± 0.46

Figure captions

Figure 1. Schematic representation of study sites and spatial design, depicting (A) the region of study (Asturias province in dark grey within the Iberian peninsula); (B) the study sites, highlighting the landscape-scale gradient of cover of woody vegetation (dark gray patches) around each site (1000-m radius plots); (C) an example of the 50-m radius plot (white circle) around one sampling station (white dot); (D) an example of cover of woody vegetation (pale yellow patches) in the 1000-m radius plot (white circle) around the same sampling station; (E) the cover of woody vegetation (pale yellow patches) and apple tree canopy (brown patches) in the 50-m radius plot (white circle) around the same sampling station.

Figure 2. Results of Non-Metric Multidimensional Scaling (NMDS) Analysis. Scores from NMDS dimensions 1 and 2 are combined to represent the position of the different bird species (dots), with acronyms of scientific names being used for identification (e.g. Eri rub: *Erithacus rubecula*). Dot size represents bird specific relative abundance (proportion of observations accounted by a given species relative to all observations across seasons and orchards). The six most abundant species are represented in a comparative size scale (artwork by Daniel García).

Figure 3. Examples of significant effects of landscape structure and orchard features on the abundance and richness of FI birds in the R50 plot and in apple habitat. Dots indicate different orchards, with different colors for Autumn-Winter (white) and Spring-Summer (black) seasons. Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

Figure 4. Results of field experiment comparing the proportion of shoots damaged or colonized by aphids (A), the total biomass of arthropods (B) and the total number of individuals of different arthropod groups (C) between apple tree branches either open to or excluded from birds. Boxplots (A-B) indicate 25-75% quartiles, median (thick horizontal bar), 5-95% centiles (whiskers) and extreme values of individual branches, whereas bars (C) represent the cumulative number of insects in all branches. Differences in abundance between treatments after Generalized Linear Mixed Models are shown (*: $P < 0.05$; n.s.: $P > 0.05$). The drawing shows a firecrest *Regulus ignicapilla* (artwork by Daniel García).

Figure 5. Relationhips between the abundance of FI birds in Spring-Summer at R50 plots and in apple habitat and the biomass (log) of arthropods in beating samples, for different orchards (dots). Linear fits predicted by Linear Regression Models are shown. The white dot represents an analytical outlier excluded from linear fit.

Figure 1.

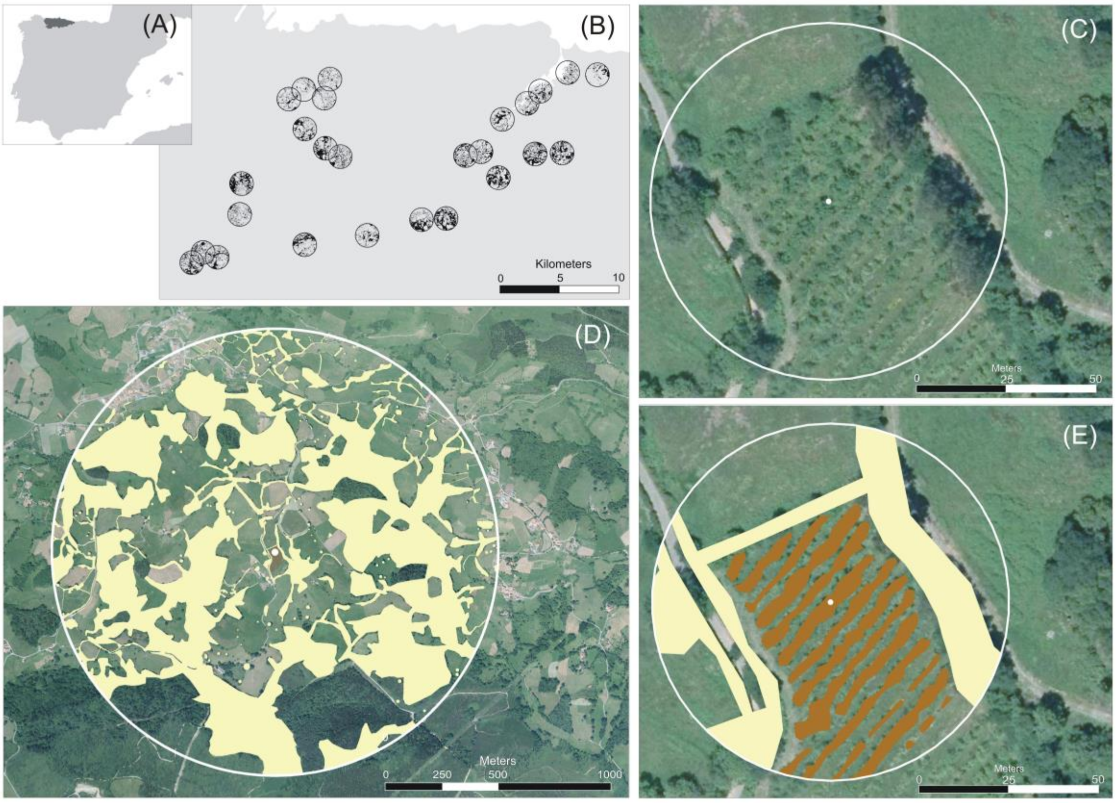

(A)
(B)
Kilometers
0
5
10
(C)
Meters
0
25
50
(D)
Meters
0
250
500
1000
(E)
Meters
0
25
50

Figure 2.

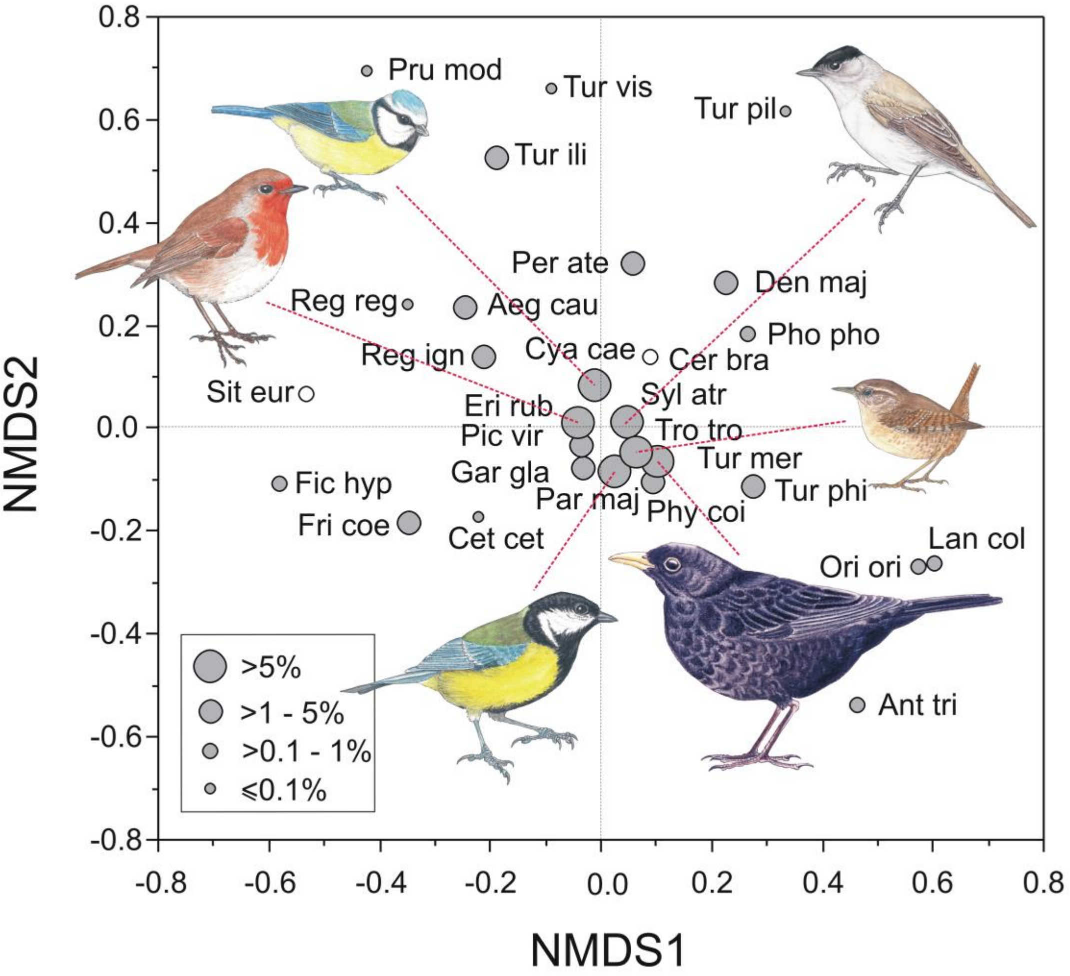

0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
NMDS2
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
NMDS1
Pru mod
Tur vis
Tur pil
Tur ili
Per ate
Den maj
Reg reg
Aeg cau
Pho pho
Reg ign
Cya cae
Cer bra
Sit eur
Eri rub
Syl atr
Pic vir
Tro tro
Tur mer
Gar gla
Tur phi
Fic hyp
Par maj
Phy coi
Fri coe
Cet cet
Lan col
Ori ori
Ant tri
>5%
>1 - 5%
>0.1 - 1%
≤0.1%

Figure 3.

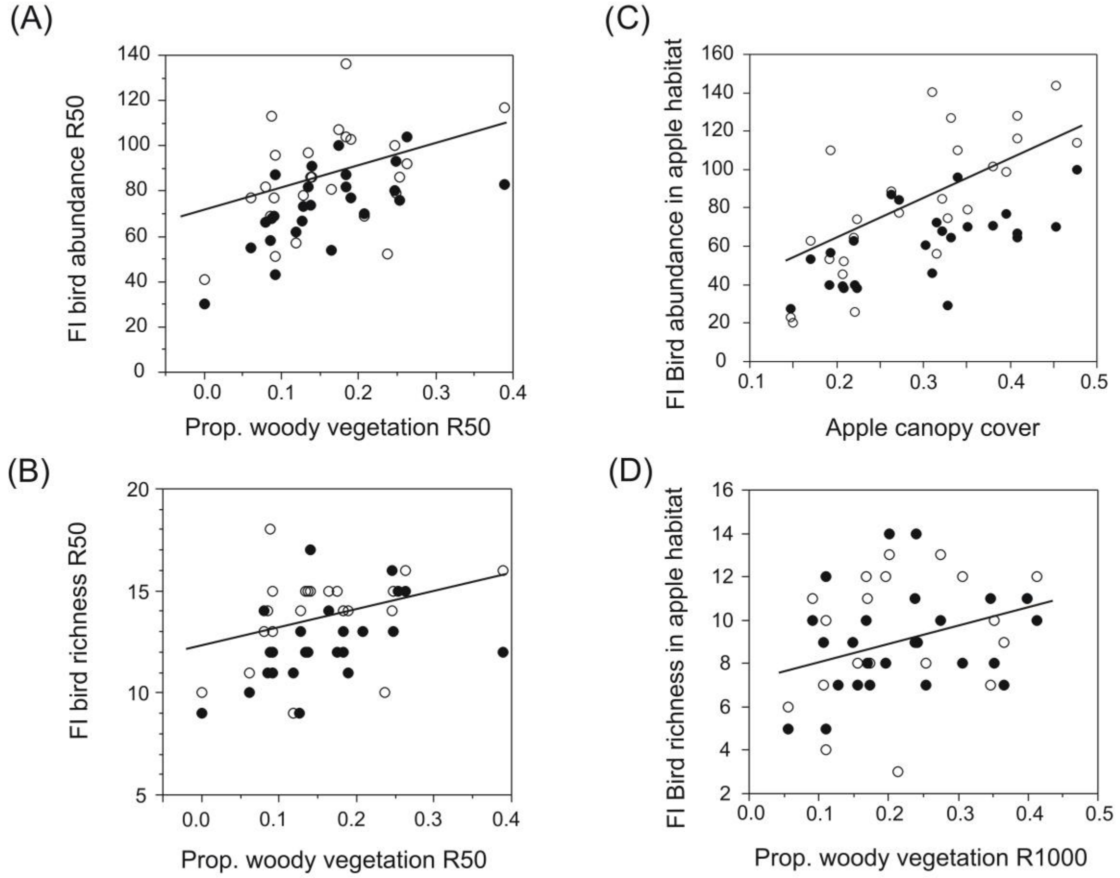

(A)
FI bird abundance R50
140
120
100
80
60
40
20
0
0.0
0.1
0.2
0.3
0.4
Prop. woody vegetation R50
(B)
FI bird richness R50
20
15
10
5
0.0
0.1
0.2
0.3
0.4
Prop. woody vegetation R50
(C)
FI Bird abundance in apple habitat
160
140
120
100
80
60
40
20
0
0.1
0.2
0.3
0.4
0.5
Apple canopy cover
(D)
FI Bird richness in apple habitat
16
14
12
10
8
6
4
2
0.0
0.1
0.2
0.3
0.4
0.5
Prop. woody vegetation R1000

Figure 4.

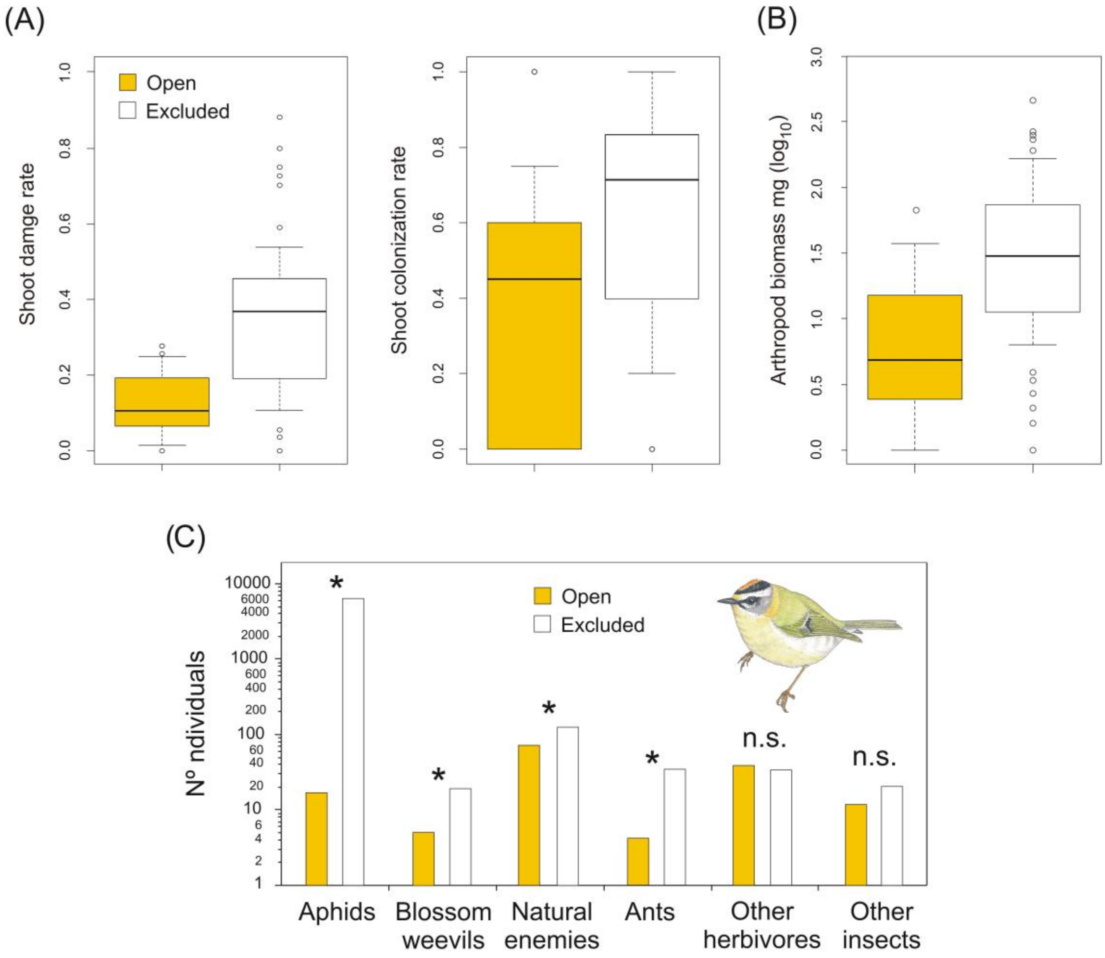
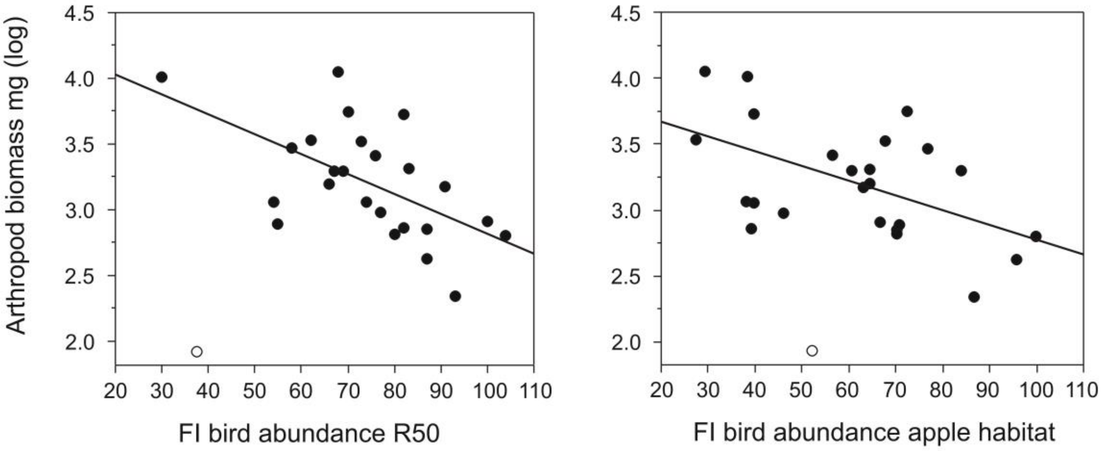

(A)
Open
Excluded
Shoot damge rate
0.0
0.2
0.4
0.6
0.8
1.0
Shoot colonization rate
0.0
0.2
0.4
0.6
0.8
1.0
(B)
Arthropod biomass mg (log_{10})
0.0
0.5
1.0
1.5
2.0
2.5
3.0
(C)
Nº ndividuals
10000
6000
4000
2000
1000
600
400
200
100
60
40
20
10
6
4
2
1
Open
Excluded
*
*
*
*
n.s.
n.s.
Aphids
Blossom weevils
Natural enemies
Ants
Other herbivores
Other insects

Figure 5.


Arthropod biomass mg (log)
4.5
4.0
3.5
3.0
2.5
2.0
20 30 40 50 60 70 80 90 100 110
FI bird abundance R50
4.5
4.0
3.5
3.0
2.5
2.0
20 30 40 50 60 70 80 90 100 110
FI bird abundance apple habitat

Birds as suppliers of pest control in cider apple orchards: avian biodiversity drivers and insectivory effect.

Daniel García, Marcos Miñarro & Rodrigo Martínez-Sastre

Supplementary material

Figure A1. Examples of the environmental context of cider apple orchards in Asturias (N Spain). At the large scale (A), orchards (an example is delimited by yellow lines) are embedded in a highly variegated landscape, containing a fine-grained mosaic of orchards, livestock pastures, annual crops (e.g. corn), timber (eucalyptus) plantations, human infrastructures, and semi-natural woody vegetation patches, mostly temperate broad-leaved forest (dominated by oak *Quercus robur*, and chestnut *Castanea sativa*), riverine forest (with common alder *Alnus glutinosa*), hedgerows, and heathland patches (with heather *Calluna vulgaris* and *Erica* spp., and common gorse *Ulex europaeus*). At the small scale of immediate neighborhoods (B-E), apple orchards are typically surrounded, total or partially, by natural woody vegetation in the form of hedgerows or small forest patches. Tall hedgerows (B) may harbor trees (*Quercus robur*, *Salix caprea*, *Fraxinus excelsior*, *Populus nigra*, *Laurus nobilis, Alnus glutinosa*), whereas medium-to-low height hedgerows (C) are mostly composed of treelets and shrubs (*Crataegus monogyna*, *Prunus spinosa*, *Corylus avellana*, *Lygustrum vulgaris*, *Rhamnus alaternus*, *Euonymus europaeus*), scrub (*Rubus fruticosus/ulmifolius*, *Rosa* sp.) and vines (*Smilax aspera*, *Hedera helix*). Apple orchards are also frequently adjacent to small patches of semi-natural forests (D) composed of the same coterie of woody species as hedgerows. Isolated, remnant trees (*Quercus robur*, *Populus nigra*) are also found within some orchards (E). White arrows indicate apple tree rows within the orchards. Pictures by Daniel García (B, E) and Marcos Miñarro (C, D)

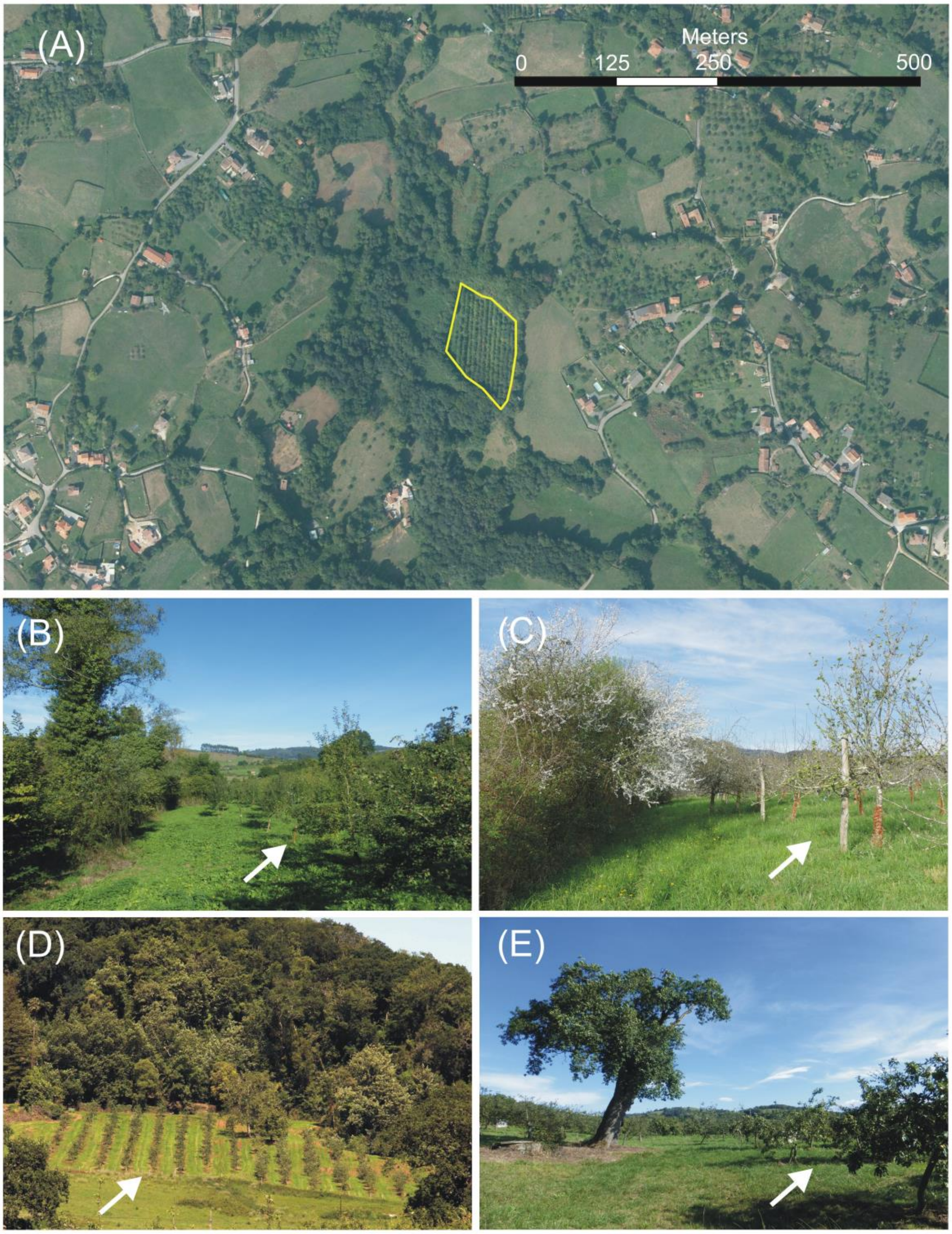

(A)
Meters
0
125
250
500
(B)
(C)
(D)
(E)

Table A1. Spatial information on cider apple orchards selected for sampling. Season of sampling (AW: Autumn-Winter 2016, SS: Spring-Summer 2016) is also indicated.

Site name	Municipality	UTM coordinates (30 T)		Surface (Ha)	Sampling
		North	East		
La Camocha	Gijón	284227.9	4818818.4	1.62	SS
La Quemada	Gijón	285482.5	4819626.5	2.90	AW, SS
Lavandera	Gijón	285573.2	4816297.0	1.58	AW, SS
Caldones	Gijón	287212.6	4818898.7	2.38	AW, SS
Quintana	Gijón	287314.7	4814681.4	0.54	AW, SS
Santurio	Gijón	287688.2	4820503.9	0.64	AW, SS
Valdornón	Gijón	288564.2	4813974.3	4.13	AW
Noreña	Noreña	280089.7	4809113.0	1.84	AW, SS
Masaveu	Sariego	295411.3	4808665.9	20.59	AW, SS
Verdera	Sariego	297484.2	4808767.3	0.81	AW, SS
Tiñana	Siero	276052.0	4805046.9	0.82	AW, SS
Muñiz	Siero	277001.2	4805902.6	1.39	AW, SS
El Obispu	Siero	278198.1	4805499.4	1.80	AW, SS
Pañeda	Siero	280271.3	4811705.8	1.27	AW, SS
La Salve	Siero	285563.8	4806559.4	4.86	AW, SS
Collao	Siero	290833.4	4807344.8	1.57	AW, SS
Camoca	Villaviciosa	299114.7	4814066.1	0.81	AW, SS
Bustariega	Villaviciosa	300418.3	4814382.2	5.36	AW, SS
Poreñu	Villaviciosa	301888.5	4812201.2	6.77	AW, SS
Sorribes	Villaviciosa	302217.5	4817112.4	1.43	AW, SS
El Gaiteru	Villaviciosa	304304.1	4818459.1	6.14	AW, SS
Cayao	Villaviciosa	304979.3	4814202.5	1.71	AW, SS
Tornón	Villaviciosa	305418.0	4819490.4	5.60	AW, SS
Ceyanes	Villaviciosa	307251.9	4814285.2	1.01	AW, SS
La Ría	Villaviciosa	307726.5	4821047.3	3.36	AW, SS
Seloriu	Villaviciosa	310225.9	4820866.2	2.42	AW, SS

Figure A2. Details of the bird exclusion experiment, showing (A) one branch (excluded treatment) where access by birds is precluded by a cylindrical cage of wire mesh and installed before bud burst; (B) a detail of a rosy aphid colony; (C) the procedure for the experimental infestation of apple shoots with rosy aphid females; and (D) a shoot infested with rosy apple aphids showing signs of damage (curled leaves). Pictures by Daniel García (A, C) and Marcos Miñarro (B, D).

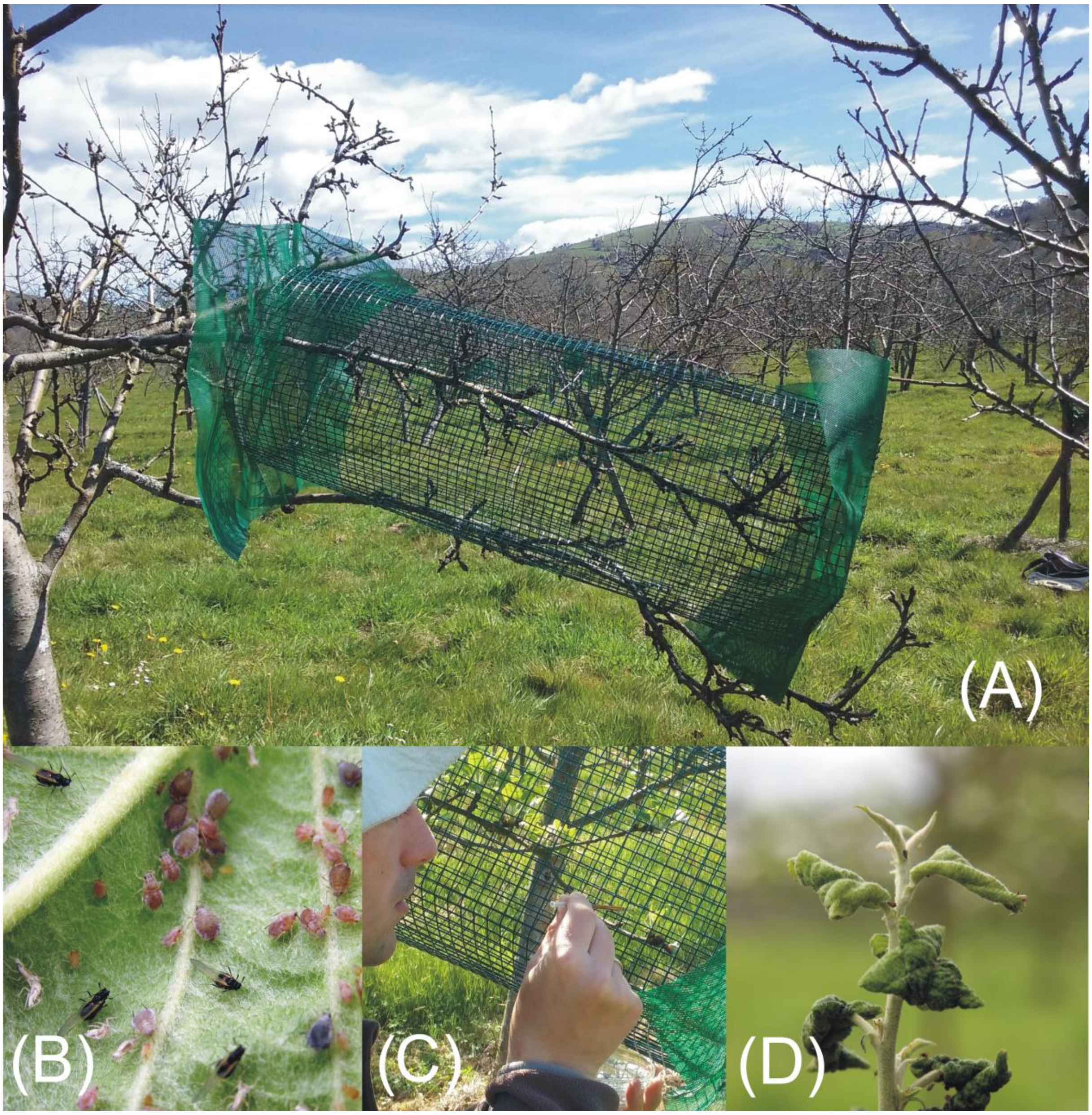


Table A2. List of birds observed in the study, indicating the total number of observations (number of individual birds recorded) in Autumn-Winter 2015 and Spring-Summer 2016 seasons. The classification of the different species as "forest insectivore" or not (-/+) is also shown.

Species name	Common name	Autumn-Winter	Spring-Summer	Forest Insectivore
Acrocephalus schoenobaenus	Sedge warbler	1	0	-
Aegithalos caudatus	Long-tailed tit	107	52	+
Anthus pratensis	Meadow pipit	21	6	-
Anthus trivialis	Tree pipit	0	17	+
Carduelis carduelis	European goldfinch	163	83	-
Carduelis spinus	Eurasian siskin	27	1	-
Certhia brachydactyla	Short-toed treecreeper	10	22	+
Cettia cetti	Cetti's warbler	3	1	+
Chloris chloris	European greenfinch	9	46	-
Cisticola juncidis	Zitting cisticola	0	1	-
Columba palumbus	Common wood pigeon	16	35	-
Corvus corone	Carrion crow	22	7	-
Corvus corax	Common raven	12	1	-
Cyanistes caeruleus	Eurasian blue tit	155	104	+
Dendrocopos major	Great spotted woodpecker	19	28	+
Emberiza cia	Rock bunting	1	1	-
Emberiza citrinella	Yellowhammer	0	1	-
Erithacus rubecula	European robin	604	330	+
Ficedula hypoleuca	European pied flycatcher	37	0	+
Fringilla coelebs	Common chafinch	154	20	+
Garrulus glandarius	Eurasian jay	58	56	+
Lanius collurio	Red-backed shrike	0	3	+
Motacilla alba	White wagtail	2	11	-
Motacilla cinerea	Grey wagtail	1	0	-
Oriolus oriolus	Eurasian golden oriole	0	17	+
Periparus ater	Coal tit	19	26	+
Parus major	Great tit	157	142	+
Passer domesticus	House sparrow	0	52	-
Phoenicurus ochruros	Black redstart	1	0	-
Phoenicurus phoenicurus	Common redstart	0	9	+
Phylloscopus collybita/ibericus	Common/Iberian chiffchaff	51	90	+
Pica pica	Eurasian magpie	57	47	-
Picus viridis	Green woodpecker	44	35	+
Prunella modularis	Dunnock	2	0	+
Pyrrhula pyrrhula	Eurasian bullfinch	19	59	-
Regulus ignicapilla	Common firecrest	84	24	+
Regulus regulus	Goldcrest	3	0	+
Saxicola rubetra	Whinchat	0	2	-
Saxicola torquatus	African stonechat	3	2	-
Serinus serinus	European serin	33	83	-
Sitta europaea	Eurasian nuthatch	6	0	+

Table A2 (cont.)

Species name	Common name	Autumn-Winter	Spring-Summer	Forest Insectivore
Sturnus unicolor	Spotless starling	18	10	-
Sturnus vulgaris	Common starling	79	15	-
Sylvia atricapilla	Eurasian blackcap	191	210	+
Sylvia communis	Common whitethroat	0	1	+
Sylvia undata	Dartford warbler	4	1	-
Troglodytes troglodytes	Eurasian wren	107	204	+
Turdus iliacus	Redwing	64	0	+
Turdus merula	Common blackbird	233	341	+
Turdus philomelos	Song thrush	36	98	+
Turdus pilaris	Fieldfare	3	0	+
Turdus viscivorus	Mistle thrush	3	1	+

Table A3. Results of Generalized Linear Mixed Models evaluating the effects of landscape structure, orchard features and sampling season (Autumn-Winter vs Spring-Summer) on the composition of the assemblages of forest insectivorous birds (as depicted by dimensions of NMDS analysis) in the R50 plot. The variance estimate for orchard identity, considered as a random factor, is also shown.

NMDS1				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R1000	0.002 ± 0.02	19.43	0.16	0.876
Prop. woody vegetation R50	-0.01 ± 0.02	19.95	-0.42	0.678
Apple canopy cover	0.02 ± 0.02	20.75	1.12	0.274
Apple canopy thickness	-0.02 ± 0.02	19.84	-0.99	0.333
Orchard size	-0.012 ± 0.02	19.23	-0.69	0.498
Season	-0.15 ± 0.02	25.16	-8.00	<0.0001
Random factor	Variance Estimate ± SD			
Orchard	0.02 ± 0.05			

NMDS2				
Predictors	Estimate ± SE	Denominator df	t	P
Prop. woody vegetation R1000	0.03 ± 0.03	18.10	1.31	0.207
Prop. woody vegetation R50	0.03 ± 0.03	28.56	0.97	0.345
Apple canopy cover	0.04 ± 0.03	19.28	1.53	0.143
Apple canopy thickness	0.01 ± 0.03	18.47	0.39	0.700
Orchard size	0.02 ± 0.03	17.93	0.75	0.463
Season	0.02 ± 0.02	22.72	1.22	0.234
Random factor	Variance Estimate ± SD			
Orchard	0.39 ± 0.02			

Figure A3. Results of piecewise regression models relating the proportion of woody vegetation cover in a 1000-m radius (R1000) around apple orchards with the abundance and the richness of forest insectivorous birds in the 50-m radius (R50) sampling plot. Bird abundance and richness values account for the cumulative number of individuals and species across seasons (Autumn-Winter and Spring-Summer). Only apple orchards sampled across both seasons were included (N = 24). Slopes (±SE), their t-values and their significance levels (*: *P* ≤ 0.05; n.s.: *P* > 0.05) are shown for broken-line relationships (initial guess for breakpoint was provided at psi = 0.28). Analyses were carried out using the R package *segmented* (version 1.4; Muggeo, VMR, 2008. segmented: an R Package to Fit Regression Models with Broken-Line Relationships. R News, 8/1, 20-25).