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Abstract

Bird survival in winter relies on the availability of key population resources such as food, shelter and resting sites. In annual crops, intensive crop management has been shown to affect bird communities through a reduction in winter resources, but much less is known about perennial crops. In this study, we performed bird surveys in 30 orchards for two years to investigate how abundance, species richness and evenness in wintering bird communities were affected by the availability of unharvested fruits in pome fruit orchards and of fruiting ivy in surrounding hedgerows. We further investigated how these resources depend on orchard management. We observed 41 bird species overall, among which 13 were of conservation concern. Bird abundance was mainly driven by the number of unharvested fruits and to a lesser extent by the number of ivy bearing trees. Bird species richness was primarily driven by the number of ivy bearing trees. This result was consistent with analyses at the species level, indicating that the occurrence of seven species (*Sylvia atricapilla*, *Parus caeruleus*, *Parus major*, *Erithacus rubecula*, *Turdus iliacus*, *Turdus merula*, and *Turdus philomelos*) was significantly dependent on the number of ivy-bearing trees. Interestingly, compared to organic orchards, non-organic (conventional and integrated) orchards had significantly more unharvested apples because of the absence of prophylactic measures against pests, thus providing wintering birds with more available resources. Our study supports the conservation value of commercial pome fruit orchards for Palearctic bird species overwintering in Southern Europe.

Key words: Species richness, Bird community, Winter resource, Mediterranean, Hedgerow, Ivy

Introduction

Responses to increasing modern food demands across continents have involved drastic changes in land use through unprecedented conversions of natural ecosystems to simplified and intensively managed ones (Tscharntke et al. 2005). Agricultural intensification processes include a wide variety of components, e.g., increased mechanisation and chemical use, increased areas of monoculture, changes in areas of crop types, changes to sowing and harvesting practices, and suppression of non-farmed habitats such as hedgerows (see Stoate et al. 2001; Vickery et al. 2001; Robinson and Sutherland 2002; Newton 2004). Such processes are major drivers of global biodiversity losses across agricultural landscapes (Matson et al. 1997; Tilman et al. 2001; Tscharntke et al. 2005), and the compatibility of agricultural land use and conservation has been traditionally questioned. In response, the development and implementation of agri-environmental schemes aim at counteracting the environmental impacts of modern agriculture on biodiversity (Stoate et al. 2009), as well as considering the potential for agricultural management to promote biodiversity and ecosystem functions through enhanced biomass productivity (Tscharnkte et al. 2005).

Among the animal groups displaying landscape-wide biodiversity losses, populations of many farmland bird species have severely declined across Europe due to post-war agricultural intensification (Donald et al. 2001; Benton et al. 2003; Geiger et al. 2010; EBCC 2016). Links between agricultural intensification and avian biodiversity loss have also been reported at a global scale, with severe population declines in Africa (Söderström et al. 2003) and North America (Brennan and Kuvlesky 2005). Over several decades, modernisation of agriculture has led to drastic reductions in foraging resources in arable landscapes, which has strongly affected populations of seed-specialist farmland birds (Siriwardena et al. 2007). A large body of the literature has investigated bird responses to agricultural management in annual crops such as cereals and vegetables (e.g., Ponce et al. 2014; Navedo et al. 2015). Perennial crops such as fruit orchards have been much less of a focus (Bruggisser et al. 2010; Rey 2011; Katayama 2016). This is critical information that is lacking because crop management practices and habitat structures that strongly differentiate annual crop systems from perennial ones might influence bird responses to agri-environmental schemes (Bruggisser et al. 2010).

In this study, we aimed to fill these gaps by highlighting the capacity of fruit orchards to be used as habitat for farmland bird communities specifically during their wintering period. Avian communities and bird species requirements for feeding and habitat change throughout the year in agricultural landscapes as in any other environment, and evaluations of the role of agri-environmental schemes as food and habitat provision sites outside of the reproduction period have been increasingly needed (Marfil-Daza et al. 2013; Ponce et al. 2014; Redhead et al. 2018). The quality of winter habitats can affect bird lifetime reproductive success through influences on departure date from winter quarters and on condition during migration (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004; Smith and Moore 2005). As perennial crops, fruit orchards constitute highly stable and predictable habitats for bird communities (Brown and Welker 1992), and their ability to provide quality resources and resting sites for birds is likely to vary with their size, plant diversity, surrounding land cover and management practices (Mangan et al. 2017). Orchards constitute intensively managed agroecosystems maximizing fruit production and subsequently affecting bird populations depending on the amount of chemicals sprayed for crop protection (Bishop et al. 2000; Bouvier et al. 2005; Genghini et al. 2006; Bouvier et al. 2011). The influence of orchard management on farmland bird diversity at both local and landscape scales has been recognized during the reproductive season (Bouvier et al 2011; Belfrage et al. 2005), but their potential for bird conservation during winter is still poorly described globally (but see Myczko et al. 2013 in apple orchards of Central Europe). Fruit production seasons display sharp contrasts with winter seasons, during which anthropogenic disturbance becomes almost non-existent, making orchards substantially beneficial for wintering farmland birds. Fruits can be left in orchards after harvest, the absence of chemical treatments favours survival and overwintering for many insect prey species (Skórka et al. 2006; Tryjanowski et al. 2011), and the occurrence of winter fruiting in the surrounding vegetation in orchard hedgerows can provide a high energy content food resource to many farmland birds (Metcalfe 2005).

Here, we present the first study specifically investigating the response of wintering bird communities to winter resource availability in pome fruit orchards of Southern Europe. This study was conducted in southeastern France, which is at the crossroads of numerous migratory routes of Paleoarctic birds (Berthold 2001). The region includes natural landscapes (e.g., grasslands and wetlands) of international importance that have long been the subject of wildlife protection measures and that face conservation and economic development issues (Beltrame et al. 2013). Pome fruit orchards currently cover an area of approximately 10,000 ha in this region, which corresponds to a quarter of the agricultural area dedicated to these fruits in France, the fourth largest apple producing country in Europe (Agreste 2014; Agreste 2019). However, the ability of such cultivated areas to provide refuge for migratory birds during winter, i.e., outside periods of high anthropogenic activities, has been largely understudied to date. We assessed various parameters of bird abundance and diversity in a network of thirty pome fruit orchards located in an area of key importance for overwintering Palearctic species (Berthold 2001). We tested how they were affected by the quantity of unharvested fruits and wild berries in hedgerows and how different orchard management strategies can influence the availability of these resources for overwintering birds.

Materials and methods

Study sites

Fieldwork was carried out in 30 commercial pome fruit orchards (15 apple and 15 pear) located in a 50 km^2 pome fruit production area (‘Basse vallée de la Durance’, central point: WGS84: 43°8’ N, 3°9’ E) of southeastern France (Fig. 1). This area is a flat agricultural plain ranging from 40 to 60 m a.s.l. characterized by a dense network of ditches and hedgerows and by diverse farming systems. Fruit orchards are the dominant crop in a crop mosaic that also contains vineyards, vegetables, and cereal crops. Pome fruits, i.e., apple and pears together, represent 87% of all fruit production in the study area. The studied orchards had an average area of 1.22 ± 0.14 ha, a plantation density of approximately 1500 trees/ha distributed along an average of 15.5 ± 1.5 rows and a grassy ground cover. The orchards had the following types of management: conventional, integrated pest management (IPM) or organic management (10 orchards each). Disease and pest control treatment strategies in this study area correspond to those described by Bouvier et al. (2005, 2011, 2016). Treatments are carried out from March to October. Conventional orchards were managed with an average of 26.2 and 23.0 treatments in 2009 and 2010, respectively. Treatments included chemical fungicides (13.1 and 13.7 in 2009 and 2010, respectively) and broad-spectrum chemical insecticides (12.5 and 9.3 in 2009 and 2010, respectively). IPM orchards were managed with chemical fungicides, insecticides and herbicides similar to those used in conventional orchards. The use of male mating disruption against the main Lepidopteran pest in these orchards resulted in chemical insecticide input reductions of 1.3 treatments in 2009 and 1.4 in 2010. The average number of annual treatments in the organic orchards was 29.7 and 27.0 in 2009 and 2010, respectively. These treatments included two mineral fungicides, copper and sulfur (2.5 and 8.1 in 2009 and 2010, respectively), a selective viral insecticide against codling moths (7.2 and 7.1 in 2009 and 2010, respectively) and mating disruption. All orchards were bordered by hedgerows (mainly poplar or cypress) for protection against the prevailing winds. Except for treatment strategies, orchards were chosen for their similarity in structure and in local environmental features that might influence bird communities.

Overwintering bird assemblages

Two surveys were carried out in each orchard, one in January 2009 and one in December 2010, in days without heavy rain or wind and between 9.00 am and 2.30 pm to match bird foraging activity (Skorka et al. 2006; Myczko et al. 2013; Assandri et al. 2016). In two instances, two orchards were less than 300 m apart, and we took the precaution of not surveying them on the same day to avoid moving the birds from one orchard to the other. Birds heard and seen within orchards and their surrounding hedgerows were recorded using transect counts along the periphery and the central tree row of each orchard. Because the orchards had a small area and an elongated shape, this made it possible to cover the whole orchard. The length of the transects varied among the orchards with a mean ± se of 711± 21 m (range: [420, 1013]). This value was not correlated with orchard area (Pearson's r= 0.28, P=0.13). The duration of each survey was approximately 20 min per ha. The similar and simple vegetation structure of the orchards, the similar climatic conditions when the surveys were conducted, and the performance of all surveys by the same experienced ornithologist (JCB) to exclude between-observer variation were meant to ensure that bird detectability did not vary among the orchards (Bibby et al. 2000).

Food resource availability for overwintering birds in orchards

The two main plant resources available for birds in winter are fruits remaining on the ground or in the pome fruit trees after harvest and the wild berries growing in hedgerows (Metcalfe 2005). In a preliminary approach, we investigated the floristic composition of the hedgerows in a random sample of 10 out of the 30 orchards to identify the plant species that produce berries during winter in the area. As ivy (*Hedera helix*) was by far the numerically dominant species

(Online Resource 1), we further focused on the abundance of this species throughout our experimental design.

Fruits laying on the ground or remaining in the trees were counted on 10 equidistant 5 m x 3 m plots aligned along a diagonal of each orchard. Each plot included a 5 m length of one tree row and its adjacent alley. The counts were performed on the same day as the bird counts. The total number of fruits remaining in each orchard was estimated from its fruit counts in the 5 m x 3 m plots and its total area. This defined the *fruit* continuous independent variable for data analysis. The independent binary variable *presence of fruits* was further used to categorize orchards depending on whether fruits were absent (zero) or present (one).

We assessed the amount of available ivy berries in the orchard hedgerows by counting the number of trees carrying fruiting ivy in all hedgerows bordering each orchard. This defined the *ivy* independent variable for data analysis.

Statistical analyses

Overwintering bird assemblages

Data were analysed using R.3.5.1 software (R Core team 2018). We used the vegan R package (Oskasnen et al. 2019) to calculate estimates for richness, abundance, and evenness. These calculations were based either on all bird species when describing the data or excluding prey birds when assessing the effect of resources since this guild was not expected to directly benefit from the presence of fruits (Table 1). In three orchards in 2009, there were large flocks of *Sturnus vulgaris* and *Fringilla coelebs*; the presence of these two species was thus recorded, but these three orchards were removed from statistical analyses on abundance as species abundance was only roughly estimated. Correlations between bird abundance and species richness and between evenness and both bird abundance and species richness were first investigated with Spearman correlation tests.

Low species detectability may result in the underestimation of species richness, as some species may be undetected. We assessed the extent of this underestimation by also calculating the improved Chao1 index of species richness (Chao and Chiu 2016) using the SpadeR R package (Chao et al. 2016) for the whole dataset, as well as independently for orchards with and without remaining fruits and per year. We also calculated the Chao1 index for 57 out of the 60 orchard x year combinations, with the number of detected species being too low for its calculation for three of them. We further calculated the estimated community coverage, i.e., the estimated fraction of the entire population of individuals in the community that belonged to the detected species (SpadeR, Chao et al. 2016).

Effect of available resources on bird assemblages

All statistical analyses were performed on the values of species richness and abundance calculated from detected species. The results based on improved Chao1 index estimations of species richness did not differ substantially (Online resource 2).

Models

The effect of resources on bird abundance was analysed with linear mixed models including *year*, *orchard area*, *presence of fruits* and log(*ivy* +1) as independent variables. Only the interaction of log(*ivy* +1) with the *presence of fruits* was included. This effect was further analysed separately for orchards with and without remaining fruits, i.e., with linear mixed models including *year*, *orchard area* and log(*ivy* +1) as independent variables for both types of orchards and including the 'log(*fruits*)' variable for orchards with remaining fruits only. For these orchards, the interaction of log(*ivy* +1) with log(*fruits*) was also included. All quantitative independent variables were scaled. Orchard identity was included as a random effect in all models to account for the fact that the same orchards were surveyed in 2009 and 2010. Variance inflation factors were below 3 for all models, indicating low levels of multicollinearity (Zuur et al. 2010). Model residuals were inspected for dispersion using a quantile-quantile (QQ) plot of standardized residuals and for uniformity and outliers using a plot of residual versus predicted values. Associated statistical tests were also performed with the DHARMa R package (Hartig 2019). Following analyses of residuals, abundance values were square root transformed, and a Gaussian link function was chosen.

The effect of resource abundance on species richness was analysed with generalized linear mixed models including *year, orchard area, presence of fruits* and log(*ivy* +1) as independent variables assuming a Poisson distribution of the data (log link function). As for abundance, only the interaction of log(*ivy* +1) with the *presence of fruits* was included. The species richness was further analysed separately for orchards with and without remaining fruits. GLMMs included *year, orchard area* and log(*ivy* +1) as independent variables for both types of orchards and included the 'log(*fruits*)' variable for orchards with remaining fruits only. For these orchards, the interaction of log(*ivy* +1) with log(*fruits*) was also included. All quantitative independent variables were scaled. Orchard identity was included as a random effect in all models. Variance inflation factors were below 3 for all models. Model residuals were inspected as above using QQ plots and residuals versus predicted plots and tests for dispersion, uniformity and outliers.

Specific associations between the presence of individual bird species and the total number of fruits or of ivy-bearing trees were assessed for frequent species (i.e., species present in at least 10 year x orchard combinations) using generalized mixed linear models using *year,* log(*fruits* +1) and log(*ivy* +1) with a binomial distribution of the data. As above, all quantitative independent variables were scaled and orchard identity was included as a random effect, and model residuals were inspected as above. Variance inflation factors were also below 3 for all models (Zuur et al. 2010).

Significance of independent variables

A multimodel inference approach was used to assess the significance of independent variables using the MuMIn R package (Barton, 2020). A model selection procedure using the corrected Akaike information criteria (AICc) was performed on the full models containing all independent variables. All models falling within a ΔAICc < 4 (Online resource 3) were then used in a model averaging procedure (Burnham and Anderson, 2002). This allowed the mean coefficient associated with each independent variable to be calculated, along with its confidence interval as well as each variable importance, i.e. the sum of the Akaike weights (Σw) of the models in which it appeared. The latter indicates the probability that the independent variable is a component of the best model (Burnham & Anderson, 2002). An independent variable was considered significant when the 95% confidence interval of its coefficient did not overlap 0.

Effect of crop management on available resources

To assess the effects of the crop treatment strategies on the resources available to the birds after harvest, the effects of crop treatment strategy on log(*ivy* +1) were analysed with a linear model including *year* and *crop management* (i.e., organic, IPM or conventional) as independent variables. The effects of the crop management strategies on the log(*fruits*+1) were analysed similarly in apple orchards only as there were no remaining fruits in the pear orchards (see Results). Model residuals were inspected as above. Pairwise comparisons between crop management strategies were carried out using post hoc Tukey tests (package multcomp, Hothorn et al. 2008).

Results

Food resource availability for overwintering birds in orchards

There were remaining fruits in 12 and 9 orchards in 2009 and 2010, respectively. The estimated number of fruits per orchard was higher in 2009 than in 2010 (mean ± se: 2009: 10799±1000, 2010: 2533 ± 177). The remaining fruit density per orchard was estimated to be 6.7 10^{-2} ± 3.9 10^{-2} (mean±se), 2.80 ± 1.39 and 0.56 ± 0.15 fruits.m^{-2} in the organic, IPM and conventional orchards, respectively. These fruits were only apples, as pears were totally decayed at that time of year. Fruits mostly laid on the ground.

Fruiting trees with ivy were observed in 28 out of the 30 orchards with a mean number (± se) of 51.75 ± 10.19 (range [1, 207]) trees and was similar in orchards with and without remaining fruits (mean ± se: 43.62 ± 8.34 and 53.57 ± 10.16 respectively). Of the two orchards without fruiting ivy, one had remaining fruits both years, and the other had no fruits. Considering only orchards with remaining fruits, the number of fruits and the number of trees with fruiting ivy were uncorrelated (2009: Spearman r=0.18, p=0.55; 2010: r=0.27; p=0.47).

Overwintering bird assemblages in orchards

We observed 1480 birds (excluding orchards with flocks) and identified 41 bird species overall, 31 species during the 21 surveys in the orchards with fruits and 40 species during the 39 surveys in the orchards without fruits (Table 1). Overall, 93% of observed birds were common songbirds, representing a total of 35 species. Among these, 10 were granivores, 7 were insectivores and 18 fed on both arthropods and seeds or fruits during that period of the year (Table 1). The most frequent species were the black cap *Sylvia atricapilla*, the song thrush *Turdus philomelos*, the Great tit *Parus major*, the common chaffinch *Fringilla coelebs*, and the robin *Erithacus rubecula* (Table 1). Thirteen species were of conservation concern, being threatened either in France or with decreasing population trends at the global level (Table 1 and Online Resource 4).

The estimated coefficient of variation of species discovery probability was high (2.44). The improved Chao1 index was thus chosen to assess species richness because it does not assume similar species discovery (Chao and Chiu, 2016). The Chao1 index of species richness was slightly higher than the total raw number of species (mean [95% confidence interval], 53.9 [42.9,125.5]) when considering orchards with fruits (32.4 [31.4, 35.5]) and when considering orchards without fruits (45.2 [41.7, 55.8]). The raw number of species was higher in 2009 than in 2010 (37 and 30, respectively), as was the Chao1 index of species richness (2009: 42.3 [40.1, 49.2]; 2010: 31.9 [30.2, 52.1]). Consistent with the low estimated number of undetected species, the coverage estimate for the entire dataset was 0.99.

The number of birds per orchard ranged from 2 to 94 (excluding flocks), and there were on average (mean ± se) 25.9 ± 2.7 birds per orchard. Bird abundance per orchard was higher in 2009 than in 2010 (32.2 ± 4.2 and 20.3 ± 3.1, respectively, Table 2). The raw number of species per orchard also varied widely from 1 to 16, with an average of 7.4 ± 0.4, and this number was also higher in 2009 than 2010 (8.3 ± 0.7 and 6.6 ± 0.4, respectively, Table 2). Bird abundance and bird species richness per orchard were highly positively correlated (Spearman r=0.7, P=2.2 10^{-9}).

The evenness of the observed bird assemblages ranged from 0.25 to 1 (excluding flocks) and was (mean ± se) 0.82 ± 0.01 on average. It was highly negatively correlated with bird abundance (r=-0.65, P=3.15 10^{-8}) but not with the observed bird species richness (r=-0.22, P=0.09).

Effect of available resources on overwintering bird assemblages

Abundance

Bird abundance was higher in orchards with fruits. Whatever the orchard type, it increased with an increasing number of trees with fruiting ivy (Table 2, Fig. 2). Bird abundance also increased with the number of remaining fruits in orchards with fruits (Table 2, Fig. 3).

Species richness

Bird species richness did not differ between orchards with or without remaining fruits, and it increased significantly with the number of trees with fruiting ivy in the hedgerows (Table 2, Fig. 4). Bird species richness also increased significantly with the amount of fruits in orchards with remaining fruits and with the number of trees with fruiting ivy in orchards without fruits (Table 2, Fig. 4).

Occurrence of particular songbird species

The 17 most frequent species (i.e., occurring in more than 10 year x orchard combinations) were *Carduelis carduelis*, *Carduelis chloris*, *Corvus corone*, *Erithacus rubecula*, *Fringilla coelebs*, *Garrulus glandarius*, *Parus caeruleus*, *Parus major*, *Phoenicurus ochruros*, *Pica pica*, *Picus viridis*, *Prunella modularis*, *Sylvia atricapilla*, *Sylvia melanocephala*, *Turdus iliacus*, *Turdus merula* and *Turdus philomelos* (Table 1). Analyses were carried out on all these species except *P. ochruros* and *S. melanocephala* due to incorrect model residuals in these two cases. The occurrence of seven songbird species (*S. atricapilla*, *P. caeruleus*, *P. major*, *E. rubecula*, *T. iliacus*, *T. merula* and *T. philomelos*) was significantly positively associated with the number of ivy-bearing trees (Table 3). These species were also those with the highest difference in occurrence between the 12 surveys in orchards with the most ivy bearing trees and the 12 surveys in orchards with least ivy bearing trees (Table 1).

Effect of crop management on available resources

The number of trees with ivy did not depend on crop management strategy (P=0.18). In contrast, the number of remaining fruits depended on crop management in apple orchards (P=2.7 10^{-4}). The number of remaining fruits was lower in the organic orchards than in the IPM (estimate -

6.69, $P<10^{-4}$) or in the conventional (estimate -5.31, $P=6.5\ 10^{-4}$) orchards, and this value did not differ between the conventional and IPM apple orchards (p=0.605).

Discussion

As in other environments, avian species communities and their requirements for feeding and habitat change throughout the year in agricultural landscapes. There is an increasing need to evaluate the role of agri-environmental areas as food and habitat provision sites outside of the breeding season (Marfil-Daza et al. 2013; Ponce et al. 2014; Redhead et al. 2018). Efforts to conserve wintering bird communities in agricultural landscapes rely on improvements in winter habitat by increasing the availability of key resources such as food, shelter and resting sites (Hammers et al. 2015; Redhead et al. 2018). Research on the effectiveness of agri-environmental schemes has usually focused on the responses of a few species (Johnson et al. 2006; Ponce 2014; Breeuwer et al. 2009; McHugh et al. 2017), although a large number of species or functional groups may respond (MacDonald et al. 2012; Ponce 2014; Henderson et al. 2000; Navedo et al. 2015; Bouam et al. 2017). Considering the whole bird community as a rule for biodiversity maintenance should thus be a priority (Ponce 2014; Ekroos et al. 2014).

Based on a 2-year community study in a local network of commercial pome fruit orchards, we showed that the amount of available fruits during winter, both on the ground or in surrounding vegetation, had a significant influence on the abundance and species richness of wintering bird populations in southeastern France. These orchards hosted no less than 15% of France's wintering avifauna (Issa and Muller 2015), which was predominantly composed of insectivorous and granivorous passerines. Thirteen of the recorded species were of conservation concern as either being threatened in France or having a decreasing population trend at the global level (Online Resource 4). This indicates that such perennial crops favouring the presence of fruits in winter are potentially important and relevant bird wintering areas, similar to other apple orchards in Central Europe (Myczko et al. 2013) or olive groves in southern Spain (Rey 2011). This result is also in line with the provisioning of resources for wintering birds reported from other agricultural landscapes throughout Europe, such as improved grassland fields in Ireland (McMahon et al. 2013), rice fields on the western Iberian Peninsula (Navedo et al. 2015) and farmlands in the Netherlands (Hammers et al. 2015). Although this work was carried out at a local spatial scale, we posit that it sheds important light on the potential for perennial crops to provide sustainable, favourable habitats to overwintering bird populations in France and throughout Europe, where 473,000 ha of apple orchards and 100,000 ha of pear orchards represented nearly 44 % of the total fruit cultivated area in 2017 (Eurostat 2020. In the context of a large-scale decline in common farmland bird populations in Europe (Donald et al. 2006; EBCC 2016), our study thus supports orchards as one of the key favourable habitats for some Palearctic bird species during their wintering period (Rey 2011; Tryjanowski et al. 2011; Myczko et al. 2013), with potential beneficial effects for subsequent breeding seasons (Siriwardena et al. 2007).

Factors affecting bird species richness and abundance in pome fruit orchards

The availability of food resources is a key factor determining the selection of wintering sites by birds (Robinson and Sutherland 1999). One central finding of this study is that the presence of apples left on the ground after harvest and ivy berries in the surrounding hedgerows significantly influenced the use of cultivated area by wintering bird populations in southern France. Although orchards can also be used by birds for resources other than fruits or as a resting area, we suggest that there might be some complementarity between apples and ivy berries as food resources. In comparison to the number of apples, the number of trees bearing ivy berries in the surrounding windbreak hedgerows appeared to affect bird species richness more. Indeed, when the full set of orchards (i.e. with and without fruits) was considered, the presence of fruits positively affected only bird abundance while the number of trees bearing ivy berries positively affected both bird abundance and bird species richness (Table 2, Figs. 2 and 4). Further, the number of trees with ivy was also the only independent variable positively affecting Chao1 index estimations of species richness (Online resource 2). This relatively stronger effect of the number of trees with ivy on species richness was consistent with an increase in the occurrence of seven songbird frequent species (*E. rubecula*, *P. caeruleus*, *P. major*, *S. atricapilla*, *T. iliacus, T. merula* and *T. philomelos*) with the number of ivy bearing trees but not with that of apples (Table 3). A main difference between the effects of apples and ivy may rely on both the direct and indirect attractivity of apples for different diet guilds. Indeed, unharvested fruits may also host specialized arthropod pests (e.g., codling moth, *Cydia pomonella*, caterpillars) or fruit-decaying opportunistic species (e.g., *Drosophila* spp.) and thus attract a large range of birds. This has not been formally tested in the present study, but previous studies suggested that insect infestation can enhance the attractiveness of fruits to frugivorous bird species (Valburg 1992); however, some species may also avoid them (Traveset et al. 1995; Dixon et al 1997). In contrast, trees with ivy may have attracted species that preferentially forage in trees as opposed to on the ground or species that rely on ivy berries as a component of their diet. Four out of the seven species that responded positively to the number of trees with ivy are well known to feed on berries during winter (*S. atricapilla*, *T. iliacus, T. merula* and *T. philomelos*). On the other hand, the significant positive response of *E. rubecula*, *C. caeruleus* and *P. major* that are not known to feed on ivy berries may emphasize the beneficial role of ivy in microhabitat diversity in hedgerows, as interlacing ivy likely increases hedgerow structural complexity. Microhabitat diversity is a good predictor of bird diversity (Regnery et al. 2013).

Conversely, bird abundance was positively correlated with the number of available apples, i.e., the larger the number of apples was, the greater the number of birds (Fig. 3). Consistent with the results of Myczko et al. (2013) in Polish apple orchards, our study confirms the general trend that birds forage preferentially on a food source when it is abundant (Ricklefs and Miller 2005). In winter, the gregarious behaviour of particular species (e.g., Turdidae and Fringillidae species) can lead to large flocks of birds (>100 individuals) in a single site. Behavioural aggregation provides them with greater protection from predators and allows them to feed longer during the shorter days of the winter period (Pulliam 1973; Treisman 1975). We observed such flocks of *S. vulgaris* or *F. coelebs* in three orchards in 2009 and excluded these from our analyses as birds were difficult to estimate numerically, but importantly, flocks predominantly occurred in orchards in which apples were highly abundant on the ground (2 out of 3 orchards). Interestingly, the number of trees with ivy was also positively associated with bird abundance in orchards with remaining fruits on the ground (Fig. 2). This may have resulted from an increase in the number of species that responded to the complementarity of these resources, as discussed above.

Overall, our results suggest that the presence of hedgerows is likely favourable to the bird communities that use pome fruit orchards during winter. Hedgerows have been acknowledged for their positive influence on local bird abundance and species richness in agricultural landscapes, meadows, and wheat and alfalfa fields (Hinsley and Bellamy 2000; Batáry et al. 2010; Kross et al. 2016). In addition, a multi-species composition of vegetal hedgerows can provide short-range shelter to many species, including those that do not forage on berries, which may facilitate resource exploitation in areas that might otherwise be too risky to use (Suhonen 1993; Andrews and Rebane 1994). In southern France, hedgerows are mostly planted as a barrier against strong prevailing winds, but a trend in orchard farming consists of removing hedgerows and taking advantage of the wind-breaking efficiency of insect pest exclusion nets that cover trees (Middleton and McWaters 2002; Iglesias and Alegre 2006). Our results, however, showed the likely important role of hedgerows when vegetally diversified in overwintering bird conservation. Additionally, fruits on the ground are food sources that cannot be replenished during winter because they are gradually depleted through bird consumption, decomposition and incorporation into the soil. The presence of hedgerows with tree species that produce berries all winter may provide some bird species with an additional sustainable food supply. In terms of bird population conservation, we suggest that management recommendations include the maintenance of hedgerows concomitantly with the use of insect pest exclusion nets. In addition to maintaining a diversity of hedgerow structures (i.e., in density, width and height) that are generally attractive for numerous bird species (Duckworth 1994), diversifying hedgerow composition with different plant species fruiting in winter and reducing hedgerow pruning intensity may also strengthen sustainability in fruit provision to overwintering birds (Hinsley and Bellamy 2000). Given the importance of landscape composition for overwintering birds (Geiger et al. 2010), the maintenance of hedgerow diversity should also be managed at the landscape scale based on good coordination between farmers. Although landscape management is frequently advocated as part of biodiversity conservation, it causes specific challenges in agricultural landscapes due to the spatial scale mismatch between ecological processes and agricultural farm management, and to the strong economic constraints that farmers are facing (Pelosi et al. 2010; Kremen and Merenlender 2018). Its implementation is still rare (but see, e.g., Bretagnolle et al 2011). In the study area, collective management could be supported by current French incentives for groups of farmers that want to act collectively to increase the durability of their farming systems (GIEE : Groupements d’intérêt économique et environnemental).

Notably, the present study did not consider the presence of seeds from the herbaceous stratum, which were also likely abundant on the ground. Herbaceous seeds may constitute an additional attractive food for birds in orchards (Myczko et al. 2013) and farmlands (Wilson et al. 1999; Newton 2004; Stoate et al. 2009). However, as all orchards were grassed, a common practice in the study area to facilitate the use of agricultural machinery, this is unlikely to affect our conclusions.

Effects of farming practices on fruit resource availability

In agroecosystems, the resources available for birds are often dependent on farmers' practices. The number of surrounding trees with ivy around orchards varied among orchards but did not depend on the orchard management strategy. This lack of correlation to management strategy may be explained by the orchards' past history. All plots were initially planted similarly and were managed as conventional orchards, and some of them were later converted to IPM and organic farming without changes in their surrounding environment. In contrast, the quantity of apples left on the ground strongly depended on the type of orchard management. Myczko et al. (2013) found that abandoned or traditionally managed apple orchards increased food and shelter opportunities to birds than intensively managed ones in Poland. In contrast, we found that available apples in winter were significantly more abundant in both conventional and IPM orchards than in organic orchards, which resulted from a substantial divergence in the management of unharvested apples during winter. Post-harvest apple grinding is a prophylactic method for controlling insect pests in organic orchards, where spring pest control strategies are generally less effective in maintaining insect populations at low risk levels than those used in conventional or IPM orchards. Apple grinding aims to kill insect larvae that develop in apples after they have fallen to the ground, thereby reducing the size of overwintering pest populations. Conversely, higher pesticide pressure in both conventional and IPM orchards during the apple-growing season causes growers to neglect overwintering insect populations that may have escaped treatments and to not manage uncollected fruits. The positive impact of this latter practice on overwintering bird abundance in conventional and IPM orchards occurred in contrast to the adverse effects of phytosanitary treatments (in particular synthetic insecticides) on the reproductive success of passerines and on bird abundance and species richness reported during the breeding season (Bouvier et al. 2005; Bouvier et al. 2011; Katayama 2016; Kajtoch 2017). Our results thus suggest that how agricultural management strategies affect bird communities in orchards may change over the course of a year, supporting the claim that environmental impacts of farming practices should be considered not only at the seasonal scale but also at the annual scale. Further work on the impacts of annual farming practices on overwintering insect communities might complement approaches that enable orchards to provide wintering birds with resources.

Conclusion

This study highlighted that pome fruit orchards likely serve as habitats for overwintering birds due to the presence of unharvested fruits and hedgerows with ivy. Modifications of agricultural practices at local and regional scales can improve the suitability of agroecosystems to a greater number of bird species by incorporating vegetation elements that favour bird species less adapted to croplands (Benton et al. 2003). This scenario is still poorly documented in pome fruit landscapes (Garcia et al. 2018), and our work provides additional support for the potential benefit of hedges in orchards for wintering bird populations.

Finally, our results also emphasized the positive effect that the presence of apples had on bird abundance during winter, which suggests that late season practices allowing the persistence of non-harvested fruits in orchards may be beneficial to overwintering bird populations. In the context where leaving unharvested fruits on the ground occurs with the cost of an increased risk for pests in organic orchards, supporting growers with effective pest management tools that are alternatives to pesticides (e.g., pest exclusion nets) could be a means of increasing the surface area favourable to wintering birds in agricultural landscapes.

References

Agreste (2014) Les Dossiers. Ministère de l'Agriculture et de l'Alimentation 22:2-17

Agreste (2019) Statistique agricole annuelle. Agreste Chiffres et Données 4:5-64

Andrews J, Rebane M (1994) Farming and wildlife. A pratical management Handbook. Sandy, Bedfordshire

Assandri G, Bogliani G, Pedrini P, Brambilla M (2016) Diversity in the monotony? Habitat traits and management practices shape avian communities in intensive vineyards. Agric Ecosyst Environ 223:250-260

Barton K (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Batáry P, Matthiesen T, Tscharntke T (2010) Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. Biol. Conserv. 143:2020-2027. http://dx.doi.org/10.1016/j.biocon.2010.05.005

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67, 1-48.

Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proc Roy Soc Lond B 271:S215-S218

Belfrage K, BjoÈrklund J, Salomonsson L (2005) the effects of farm size and organic farming on diversity of birds, pollinators, and plants in a Swedish landscape. Ambio 34:582-8

Beltrame C, Cohen-Shacham E, Trouillet M, Guillet F (2013) Exploring the links between local management and conservation applying the ecosystem services concept: conservation and tourism service in Camargue, France. Int J Biodiv Sci Ecosys Serv Manag 9:166-177

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:82-188

Berthold P (2001) Bird Migration: A General Survey. Oxford University Press, Oxford

Bibby C, Burgess N, Hill D, Mustoe S (2000) Bird census techniques. Academic Press, London.

Bishop C, Collins B, Mineau P, Burgess N, Read W, Risley C (2000) Reproduction of cavity-nesting birds in pesticide-sprayed apple orchards in southern Ontario, Canada, 1988-1994. Environ Toxicol Chem 19:588-599

Bouam I, Si Bachir A, Katayama N (2017) Variation in Bird Assemblages along an Agricultural Intensification McHugh Gradient: A case study of olive orchards in North-Eastern Algeria. Ornithol Sci 16:147-157

Bouvier JC, Toubon JF, Boivin T, Sauphanor B (2005) Effects of apple orchard management strategies on the great tit (*Parus major*) in Southeastern France. Environ Toxicol Chem 24:2846-2852

Bouvier JC, Ricci B, Agerberg J, Lavigne C (2011) Apple orchard pest control strategies affect bird communities in Southeastern France. Environ Toxicol Chem 30:212-9

Bouvier JC, Boivin T, Charmantier A, Lambrechts M, Lavigne C (2016) More daughters in a less favourable world: Breeding in intensively-managed orchards affects tertiary sex-ratio in the great tit. Basic Appl Ecol 17:638-647

Breeuwer A, Berendse F, Willems F, Foppen R, Teunissen W, Schekkerman H, Goedhart P (2009) Do meadow birds profit from agri-environment schemes in Dutchagricultural landscapes? Biol Conserv 142:2949-2953

Brennan LA, Kuvlesky WP (2005) North American grassland bird: an unfolding conservation crisis. J Wildl Manage 69:1-13

Bretagnolle V, Villers A, Denonfoux L, Cornulier T, Inchausti P, Badenhausser I (2011) Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. Ibis 153:4-13

Brown MW, Welker WV (1992) Development of the phytophagous arthropod community on apple as affected by orchard management. Environ Entomol 21:485-492

Bruggisser OT, Schmidt-Entling M, Bacher S (2010) Effects of vineyard management on biodiversity at three trophic levels. Biol Conserv 143:1521-1528

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Chao A, Chiu CH (2016) Species richness: estimation and comparison. Wiley StatsRef: Statistics Reference Online:1-26

Chao A, Ma KH, Hsieh TC, Chiu CH (2016) SpadeR: Species-Richness Prediction and Diversity Estimation with R. R package version 0.1.1. https://CRAN.R-project.org/package=SpadeR

Dixon MD, Johnson WC, Adkisson CS (1997) Effects of weevil larvae on acorn use by blue jays. Oecologia 111:201-208

Donald RF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe’s farmland bird populations. Proc R Soc Lond B 268:25-29

Donald PE, Sanderson FJ, Burfield IJ, van Bommel FPJ (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1900-2000. Agric Ecosyst Environ 116:189-196

Duckworth JW (1994) Habitat selection by migrant redstarts *Phoenicurus phoenicurus* and whinchats *Saxicola rubetra* in lowland English Farmland. Ringing and Migration 15:119-122

EBCC (2016) European wild bird indicators, 2016 update. Pan-European Common Bird Monitoring Scheme (PECBMS), http://www.ebcc.info/pecbm.html

Ekroos J, Olsson O, Rundlöf M, Wätzold F, Smith HG (2014) Optimizing agri-environment schemes for biodiversity, ecosystem services or both? Biol Conserv 172: 65-71

Garcia D, Minarro M, Martinez-Sastre R (2018) Birds as suppliers of pest control in cider apple orchards: Avian biodiversity drivers and insectivory. Agric Ecosyst Environ 254: 233-243

Geiger F, de Snoo GR, Berendse F et al. (2010) Landscape composition influences farm management effects on farmland birds in winter: A pan-European approach. Agric Ecosyst Environ 139:571-577

Genghini M, Gellini S, Gustin M (2006) Organic and integrated agriculture: the effects on bird communities in orchards farms in northern Italy. Biodiv Conserv 15:3077-3094

Hammers M, Müskens GJDM, van Kats RJM , Teunissen WA, Kleijn D (2015) Ecological contrasts drive responses of wintering farmland birds to conservation management. Ecography 38:813-821

Hartig F (2019) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.4. https://CRAN.R-project.org/package=DHARMa

Henderson IG, Cooper J, Fuller RJ, Vickery J (2000) The relative abundance of birds on set-aside and neighbouring fields in summer. J Appl Ecol 37:335-347

Hinsley SA, Bellamy PE (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. J Environ Manag 60:33-49

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biometrical J 50:346-363

Iglesias I, Alegre S (2006) The effect of anti-hail nets on fruit protection, radiation, temperature, quality and profitability of Mondial Gala apples. J Appl Horti 8:91-100

Issa N, Muller Y (2015) Atlas des oiseaux de France métropolitaine. Nidification et présence hivernale. Delachaux et Niestlé, Paris.

Johnson MD, Sherry TW, Holmes RT, Marra PP (2006) Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conserv Biol 20:1433-1444

Kajtoch L (2017) The importance of traditional orchards for breeding birds: the preliminary study on Central European example. Acta Oecol 78:53-60

Katayama N (2016) Bird diversity and abundance in organic and conventional apple orchards in northern Japan. Scientific Reports 6: 34210/DOI: 10.1038/srep34210

Kremen C, Merenlender AM (2018) Landscapes that work for biodiversity and people. Science 362: eaau6020.

Kross SM, Kelsey TR, McColl CJ, Townsend JM (2016) Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agric. Ecosyst. Environ. 225:140-149. http://dx.doi.org/10.1016/j.agee.2016.03.043

MacDonald MA, Maniakowski M, Cobbold G, Grice PV, Anderson GQA (2012) Effects of agri-environment management for stone curlews on other biodiversity. Biol Conserv 148:134-145

Mangan AM, Pejchar L, Werner SJ (2017) Bird use of organic apple orchards: Frugivory, pest control and implications for production. PLoS ONE 12:e0183405.

Marfil-Daza C, Pizarro M, Moreno-Rueda G (2013) Do hot spots of breeding birds serve as surrogate hot spots of wintering birds? An example from central Spain. Anim Conserv 16:60-68

Marra PP, Hobson KA, Holmes RT (1998) Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. Science 282:1884-1886

Matson PA, Parton WJ, Power AG Swift MJ (1997) Agricultural intensification and ecosystem properties. Science 277:504-509

McHugh NM, Prior M, Grice PV, Leather SR, Holland JM (2017) Agri-environmental measures and the breeding ecology of a declining farmland bird. Biol Conserv 212:230-239

McMahon BJ, Carnus T, Whelan J (2013) A comparison of winter bird communities in agricultural grassland and cereal habitats in Ireland: implications for Common Agricultural Policy reform. Bird Study 60:176-184

Metcalfe DJ (2005) Hedera helix L. J Ecol 93:632-648

Middleton S, McWaters A (2002) Hail netting of apple orchards Australian experience. Compact Fruit Tree 35:51-55

Myczko L, Rosin ZM, Skorka P, Wylegala P, Tobolka M, Fliszkiewiecz M, Mizera T, Tryjanowski P (2013) Effects of management intensity and orchard features on bird communities in winter. Ecol Res 28:503-5012

Navedo JG, Hahn S, Parejo M, Abad-Gómez JM, Gutiérrez JS, Villegas A, Sánchez-Guzmán JM, Masero JA (2015) Unravelling trophic subsidies of agroecosystems for biodiversity conservation: Food consumption and nutrient recycling by waterbirds in Mediterranean ricefields. Sci Total Environ 511:288-297

Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579-600

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc Roy Soc Lond B 271:59-64

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, R. B. O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Eduard Szoecs E, Wagner H (2019). vegan: Community Ecology Package. R package version 2.5-5. https://CRAN.R-project.org/package=vegan

Pelosi C, Goulard M, Balent G (2010) The spatial scale mismatch between ecological processes and agricultural management: Do difficulties come from underlying theoretical frameworks? Agric Ecosyst Environ 139:455-462

Ponce C, Bravo C, Alonso JC (2014) Effects of agri-environmental schemes on farmland birds: do food availability measurements improve patterns obtained from simple habitat models? Ecol Evol 4:2834-2847

Pulliam HR (1973) On the advantages of flocking. J Theor Biol 38:419-422

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Redhead JW, Hinsley SA, Beckmann BC, Broughton RK, Pywell RF (2018) Effects of agri-environmental habitat provision on winter and breeding season abundance of farmland birds. Agric Ecosyst Environ 251:114-123

Regnery B, Couvet D, Kubarek L, Julien JF, Kerbiriou C (2013) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol Indic 34:221-230

Rey PJ (2011) Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards. J Appl Ecol 48:228-237

Ricklefs RE, Miller GL (2005) Ecologie. De Boeck Université, Bruxelles

Robinson RA, Sutherland WJ (1999) The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. Ecography, 22:447-454

Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. J Appl Ecol 39:157-176

Siriwardena GM, Stevens DK, Anderson GQA, Vickery JA, Calbrade NA, Dodds S (2007) The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. J Appl Ecol 44:920-932

Skorka P, Babiarz T, Skorka J, Wojcik JD (2006) Winter territoriality and fruit defence by the fieldfare (Turdus pilaris). J ornithol 147:371-375

Smith RJ, Moore FR (2005) Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav Ecol Sociobiol 57:231-239

Söderström B, Kiema S, Reid RS (2003) Intensified agricultural land-use and bird conservation in Burkina Faso. Agric Ecosyst Environ 99:113-124

Stoate C, Boatman ND, Borralho RJ, Carvalho CR, de Snoo GR, Eden P (2001) Ecological impacts of arable intensification in Europe. J Environ Manage 63:337-365

Stoate C, Báldi A, Beja P, Boatman ND, Herzon I, Van Doorn A, de Snoo GR, Rakosy L, Ramwell C (2009) Ecological impacts of early 21st century agricultural change in Europe-a review. J Environ Manage 91:22-46

Suhonen J (1993) Predation risk influences the use of foraging sites by tits. Ecology 74:1197-1203

Tilman D, Fargione J, Wolff B et al. (2001) Forecasting agriculturally driven global environmental change. Science 292:281-284

Traveset A, Willson MF, Gaither JC Jr (1995) Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. Oikos 73:381-386

Treisman M (1975) Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. Anim Behav 23:801-825

Tryjanowski P, Hartel T, Baldi A, Szymanski P, Tobolka M, HERZON I, Golawski A, Konvicka M, Hromada M, Jerzak L, Kujawa K, Lenda M, Orlowski G, Panek M, Skorka P, Sparks TH, Tworek S, Wuczynski A, Żmihorski M (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. Acta Ornithol 46:1-12

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol Letters 8:857-874

Valburg LK (1992) Eating infested fruits: interactions in a plant disperser-pest triad. Oikos 65:25-28

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J Appl Ecol 38:647-664

Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agric Ecosyst Environ 75:13-30

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1: 3-14

Fig. 1 Colour for online version

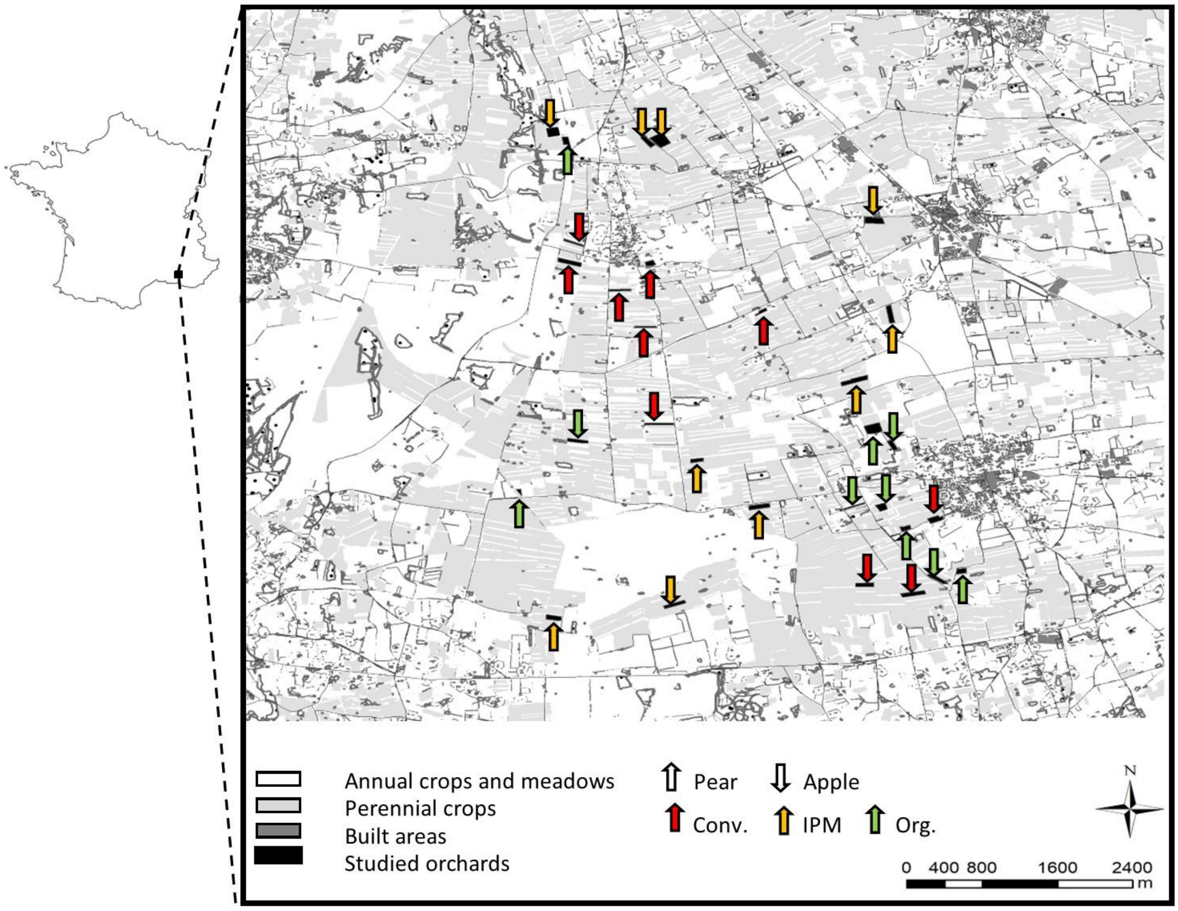

Figure 1: Map of the study area. Arrows point to the 30 sampled orchards. The orientation of the arrows differentiates pear and apple orchards, the colour of the arrow indicates the management strategy (Org.: Organic, IPM : Integrated pest management, Conv.: Conventional).

Fig. 2

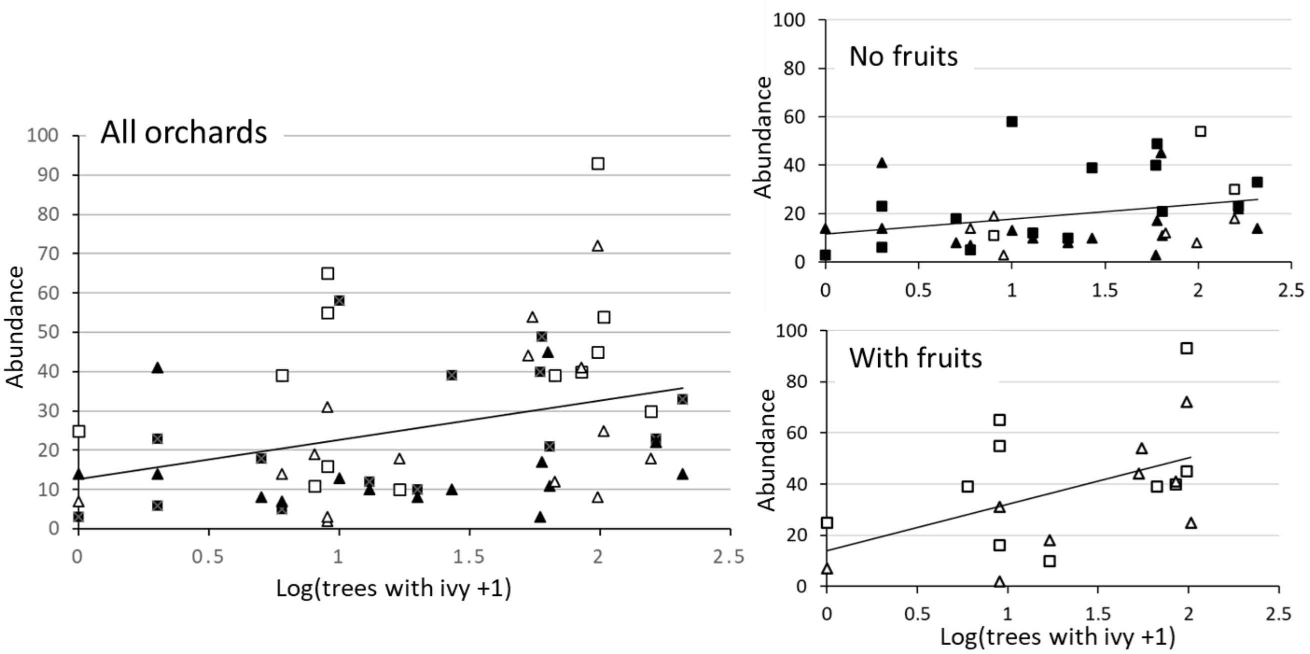

Figure 2: Observed bird abundance as a function of the log-transformed number of ivy bearing trees in hedgerows considering either all orchards or considering separately orchards with and without remaining fruits on the ground. Abundance was assessed in 2009 and 2010 in pome fruit orchards in southeastern France. Filled symbols: pear orchards; open symbols: apple orchards; Squares 2009; triangles 2010.

Fig. 3

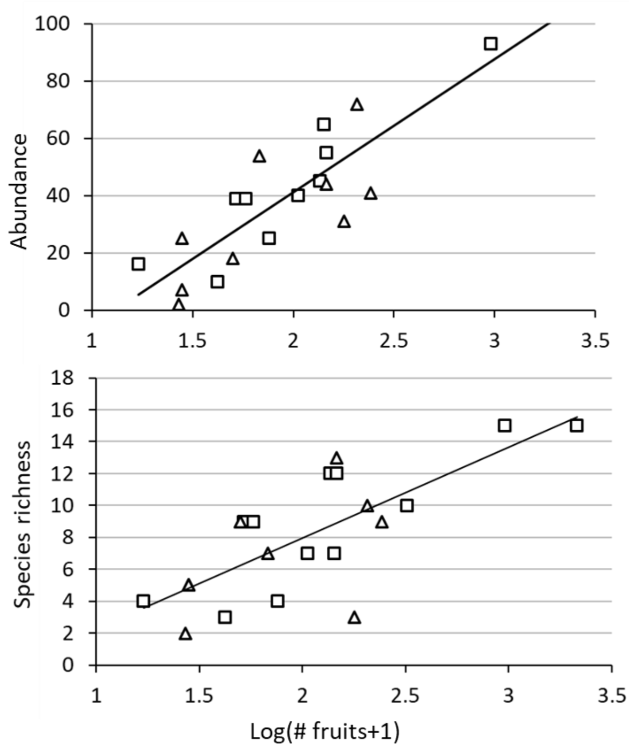

Figure 3: Bird abundance and species richness per orchard as a function of the log-transformed number of remaining fruits per orchard. Abundance and species richness were assessed in 2009 and 2010 in pome fruit orchards in southeastern France. Regression lines are presented for these two significant ($p<0.05$) relationships. Squares 2009; triangles 2010.

Fig. 4

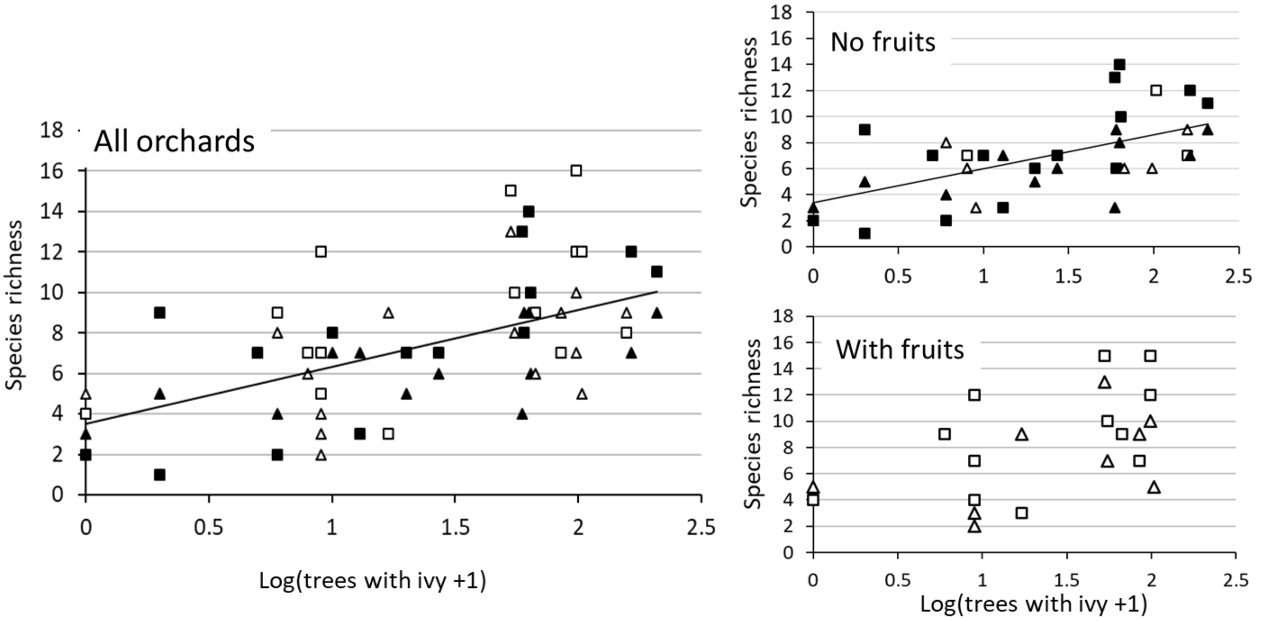

Figure 4: Bird species richness as a function of the log-transformed number of ivy-bearing trees in hedgerows considering either all orchards or considering separately orchards with or without remaining fruits on the ground. Species richness was assessed in 2009 and 2010 in pome fruit orchards in southeastern France. Regression lines are presented for significant ($p<0.05$) relationships. Filled symbols: pear orchards; open symbols: apple orchards; squares 2009; triangles 2010.

Table 1: Frequency of occurrence of bird species in orchards in southeastern France. The table provides the frequency of occurrence of bird species in orchards with and without remaining fruits after harvest in 2009 and 2010, the number of orchards in which they occurred among the 12 orchards with the most (ivy +) or less (ivy -) ivy bearing trees and their overall frequency of occurrence.

		Without fruits		With fruits		Ivy +	Ivy -	Total
Year		2009	2010	2009	2010			
# Orchards		18	21	12	9	12	12	60
Species name	Winter diet							
Aegithalos caudatus	I; Gr	0.06	0.00	0.00	0.00	0	0	0.02
*Anthus pratensis**	I	0.11	0.05	0.17	0.11	2	1	0.10
Buteo buteo	P	0.28	0.19	0.08	0.11	1	2	0.18
*Carduelis cannabina**	Gr	0.00	0.05	0.17	0.00	1	1	0.05
*Carduelis carduelis**	Gr	0.28	0.14	0.50	0.33	3	5	0.28
*Carduelis chloris**	Gr	0.00	0.19	0.25	0.33	3	1	0.17
Certhia brachydactyla	I	0.00	0.19	0.00	0.11	1	0	0.08
Cettia cetti	I	0.00	0.05	0.00	0.00	0	0	0.02
Coccothraustes coccothraustes	Gr	0.06	0.00	0.00	0.00	0	0	0.02
Corvus corone	O	0.28	0.24	0.50	0.56	1	3	0.35
Corvus monedula	O	0.11	0.05	0.00	0.00	0	0	0.05
Dendrocopos major	I; Gr	0.06	0.00	0.00	0.00	1	0	0.02
Emberiza cia	I; Gr	0.06	0.00	0.00	0.00	0	1	0.02
Emberiza cirlus	I; Gr	0.06	0.00	0.33	0.00	2	0	0.08
*Emberiza schoeniclus**	I; Gr	0.17	0.05	0.08	0.11	0	1	0.10
Erithacus rubecula	I; Gr	0.33	0.67	0.50	0.67	7	3	0.53
*Falco tinnunculus**	P	0.06	0.00	0.00	0.00	0	0	0.02
Fringilla coelebs	Gr	0.89	0.81	1.00	0.89	11	11	0.88
*Fringilla montifringilla**	Gr	0.11	0.00	0.33	0.11	0	1	0.12
Garrulus glandarius	O	0.11	0.19	0.58	0.11	4	2	0.23
Motacilla alba	I	0.00	0.00	0.08	0.00	1	0	0.02
Parus caeruleus	I; Gr	0.33	0.24	0.17	0.33	6	1	0.27
Parus major	I; Gr	0.44	0.57	0.58	0.67	9	4	0.55
*Passer montanus**	Gr	0.17	0.05	0.00	0.00	1	1	0.07
*Phasianus colchicus**	Gr	0.06	0.00	0.00	0.00	1	0	0.02
Phoenicurus ochruros	I; Gr	0.17	0.24	0.17	0.11	1	3	0.18
Phylloscopus collybita	I	0.06	0.14	0.08	0.11	1	1	0.10
Pica pica	O	0.56	0.29	0.25	0.33	3	4	0.37
Picus viridis	I	0.17	0.14	0.33	0.00	5	1	0.17
*Prunella modularis**	I; Gr	0.28	0.10	0.08	0.11	1	0	0.15
Regulus ignicapillus	I	0.11	0.00	0.17	0.00	2	2	0.07
*Serinus serinus**	Gr	0.00	0.05	0.08	0.00	1	0	0.03
Streptopelia decaocto	Gr	0.06	0.00	0.08	0.00	1	1	0.03
Sturnus vulgaris	I; Gr	0.17	0.00	0.25	0.00	1	0	0.10
Sylvia atricapilla	I; Gr	0.67	0.52	0.42	0.67	11	3	0.57
Sylvia melanocephala	I; Gr	0.22	0.05	0.00	0.22	4	1	0.12
Troglodytes troglodytes	I; Gr	0.17	0.19	0.00	0.00	2	0	0.12
*Turdus iliacus**	I; Gr	0.11	0.24	0.33	0.22	6	0	0.22
Turdus merula	I; Gr	0.44	0.10	0.50	0.44	8	2	0.33
Turdus philomelos	I; Gr	0.67	0.29	0.75	0.44	10	3	0.52
Turdus pilaris	I; Gr	0.00	0.10	0.25	0.11	3	0	0.10

Gr: granivores, I: insectivores; O: omnivores; P: birds of prey; * bird species of conservation concern.

Table 2: Multimodel analysis of the variation in bird abundance and species richness. Average parameter estimates (± standard error), associated 95% confidence intervals and variable importance (I) are provided for the subset of models with ΔAIC<4 as compared to the best model. '-' indicates that the variable was not retained in the subset of models. '/' indicates that the variable was not included in the analysis. Parameter values for which the confidence intervals does not overlap 0 are in bold.

	All orchards			With fruits			Without fruits		
	Estimate ± se	C95%	I	Estimate ± se	C95%	I	Estimate ± se	C95%	I
Abundance									
Year (2010)	**-0.299 ± 0.1102**	**[-0.515; -0.083]**	1	-0.262 ± 0.141	[-0.539; 0.014]	0.53	**-0.341 ± 0.159**	**[-0.651; -0.030]**	0.85
Transect	-0.010 ± 0.146	[-0.296; 0.277]	0.12	**-**	**-**	**-**	0.159 ± 0.197	[-0.229; 0.546	0.17
Area	0.215 ± 0.114	[-0.008; 0.438]	0.45	-0.101 ± 0.182	[-0.458; 0.256]	0.04	[0.120 ± 0.160	[-0.193; 0.546]	0.12
Log(ivy +1)	**0.323 ± 0.136**	**[0.057; 0.589]**	1	**0.300 ± 0.147**	**[0.012; 0.588]**	0.46	**0.320 ± 0.163**	**[0.001; 0.639]**	0.55
Log(fruits)	/	/	/	**0.758 ± 0.160**	**[0.444; 1.072]**	1	/	/	/
Log(fruits) x Log(ivy+1)	/	/	/	**-**	**-**	**-**	/	/	/
Presence fruits	**0.357 ± 0.116**	**[0.130; 0.583]**	1	/	/	/	/	/	/
Presence fruits x Log(ivy+1)	0.193 ± 0.131	[-0.063; 0.449]	0.46	/	/	/	/	/	/
Richness									
Year (2010)	**-0.034 ± 0.015**	**[-0.063; -0.005]**	0.9	-0.019 ± 0.023	[-0.064; 0.027]	0.13	-0.033 ± 0.021	[-0.074; 0.009]	0.5
Transect	$7.5\ 10^{-5}$ ± 0.018	[-0.034; 0.035]	0.15	0.002 ± 0.023	[-0.042; 0.047]	0.09	-0.010 ± 0.028	[-0.066; 0.045]	0.19
Area	0.006 ± 0.015	[-0.024; 0.035]	0.17	-0.031 ± 0.024	[-0.078; 0.015]	0.26	-0.002 ± 0.022	[-0.045; 0.042]	0.18
Log(ivy +1)	**0.081 ± 0.016**	**[0.049; 0.113]**	1	0.046 ± 0.027	[-0.007; 0.098]	0.56	**0.091 ± 0.023**	**[0.045; 0.137]**	1
Log(fruits)	/	/	/	**0.071 ± 0.024**	**[0.023; 0.118]**	1	/	/	/
Log(fruits) x Log(ivy+1)	/	/	/	$-4.6\ 10^{-4}$ ± 0.028	[-0.055; 0.054]	0.05	/	/	/
Presence fruits	0.019 ± 0.014	[-0.009; 0.048]	0.49	/	/	/	/	/	/
Presence fruits x Log(fruits)	0.007 ± 0.019	[-0.029; 0.044]	0.07	/	/	/	/	/	/

Table 3

Multimodel analysis of the variation in the presence of individual species as a function of study year, transect length, presence of fruits and number of ivy bearing trees. Values provided are average parameter estimates (± standard error), associated 95% confidence intervals and variable importance (I) in the subset of models with ΔAIC<4 as compared to the best model. Values are highlighted in bold when 95% confidence intervals do not overlap value 0.

	Year (2010)		*Transect*		*Fruits*		Log(*ivy*+1)	
	Estimate ± se	C95%	Estimate ± se	C95%	Estimate ± se	C95%	Estimate ± se	C95%
Carduelis carduelis	-1.002 ± 0.710	[-2.426; 0.421]	-0.13 ± 0.878	[-1.888; 1.628]	1.264 ± 0.792	[-0.321; 2.851]	-0.392 ± 0.843	[-2.082; 1.297]
Carduelis chloris	1.595 ± 1.062	[-0.532; 3.722]	-0.086 ± 1.209	[-2.504; 2.332]	1.763 ± 0.964	[-0.168; 3.694]	1.685 ± 1.192	[-0.702; 4.073]
Corvus corone	-0.123 ± 0.653	[-1.432; 1.186]	**2.490 ± 0.853**	**[0.784; 4.197]**	1.185 ± 0.640	[-0.098; 2.468]	-1.207 ± 0.788	[-2.787; 0.373]
Erithacus rubecula	**1.211 ± 0.572**	**[0.064; 2.358]**	-0.526 ± 0.659	[-1.849; 0.795]	0.367 ± 0.575	[-0.786; 1.521]	**1.336 ± 0.631**	**[0.071; 2.601]**
Fringilla coelebs	-1.628 ± 1.410	[-4.453; 1.195]	-1.062 ± 1.465	[-3.994; 1.870]	1.928 ± 1.770	[-1.617; 5.474]	0.976 ± 1.493	[-2.012; 3.965]
Garrulus glandarius	-0.837 ± 0.770	[-2.381; 0.705]	0.274 ± 0.865	[-1.459; 2.007]	1.416 ± 0.762	[-0.110; 2.944]	0.846 ± 0.853	[-0.864; 2.556]
Parus caeruleus	$-3\ 10^{-12}$ ± 0.729	[-1.460; 1.460]	1.024 ± 0.917	[-0.813; 2.863]	-0.329 ± 0.732	[-1.797; 1.138]	**2.587 ± 1.017**	**[0.551; 4.623]**
Parus major	0.478 ± 0.564	[-0.651; 1.609]	-0.505 ± 0.651	[-1.809; 0.798]	0.418 ± 0.567	[-0.717; 1.554]	**1.593 ± 0.638**	**[0.315; 2.871]**
Pica pica	-0.621 ± 0.567	[-1.756; 0.514]	-0.033 ± 0.559	[-1.154; 1.087]	-0.573 ± 0.583	[-1.741; 0.594]	0.123 ± 0.561	[-1.001; 1.248]
Picus viridis	-1.419 ± 1.028	[-3.480; 0.641]	1.602 ± 1.135	[-0.670; 3.875]	0.245 ± 0.944	[-1.646; 2.136]	1.797 ± 1.222	[-0.649; 4.244]
Prunella modularis	-1.166 ± 1.070	[-3.311; 0.978]	0.721 ± 1.048	[-1.377; 2.820]	-1.032 ± 1.146	[-3.328; 1.264]	-0.015 ± 1.043	[-2.105; 2.074]
Sylvia atricapilla	$1\ 10^{-12}$ ± 0.627	[-1.256; 1.256]	-0.352 ± 0.891	[-2.139; 1.434]	-0.430 ± 0.750	[-1.932; 1.072]	**2.493 ± 0.881**	**[0.728; 4.259]**
Turdus iliacus	0.364 ± 0.877	[-1.395; 2.123]	**-3.594 ± 1.580**	**[-6.762; -0.427]**	1.011 ± 0.879	[-0.752; 2.774]	**4.791 ± 1.670**	**[1.443; 8.138]**
Turdus merula	**-1.780 ± 0.775**	**[-3.335; -0.226]**	**-3.687 ± 1.363**	**[-6.418; -0.956]**	1.512 ± 0.796	[-0.083; 3.108]	**4.226 ± 1.366**	**[1.488; 6.963]**
Turdus philomelos	**-2.061 ± 0.702**	**[-3.468; -0.655]**	1.264 ± 0.838	[-0.412; 2.942]	0.501 ± 0.675	[-0.853; 1.855]	**2.113 ± 0.843**	**[0.426; 3.800]**

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