Conservation value of pome fruit orchards for overwintering birds in southeastern France

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28 **Abstract**

29 Bird survival in winter relies on the availability of key population resources such as food, shelter

30 and resting sites. In annual crops, intensive crop management has been shown to affect bird

31 communities through a reduction in winter resources, but much less is known about perennial

32 crops. In this study, we performed bird surveys in 30 orchards for two years to investigate how

33 abundance, species richness and evenness in wintering bird communities were affected by the

34 availability of unharvested fruits in pome fruit orchards and of fruiting ivy in surrounding

35 hedgerows. We further investigated how these resources depend on orchard management. We

36 observed 41 bird species overall, among which 13 were of conservation concern. Bird

37 abundance was mainly driven by the number of unharvested fruits and to a lesser extent by the

38 number of ivy bearing trees. Bird species richness was primarily driven by the number of ivy

39 bearing trees. This result was consistent with analyses at the species level, indicating that the

40 occurrence of seven species (*Sylvia atricapilla*, *Parus caeruleus*, *Parus major*, *Erithacus*

41 *rubecula*, *Turdus iliacus*, *Turdus merula*, and *Turdus philomelos*) was significantly dependent

42 on the number of ivy-bearing trees. Interestingly, compared to organic orchards, non-organic

43 (conventional and integrated) orchards had significantly more unharvested apples because of

44 the absence of prophylactic measures against pests, thus providing wintering birds with more

45 available resources. Our study supports the conservation value of commercial pome fruit

46 orchards for Palearctic bird species overwintering in Southern Europe.

47

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

49 Ivy

50

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

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76 fruit orchards have been much less of a focus (Bruggisser et al. 2010; Rey 2011; Katayama

77 2016). This is critical information that is lacking because crop management practices and

78 habitat structures that strongly differentiate annual crop systems from perennial ones might

79 influence bird responses to agri-environmental schemes (Bruggisser et al. 2010).

80   In this study, we aimed to fill these gaps by highlighting the capacity of fruit orchards to be

81 used as habitat for farmland bird communities specifically during their wintering period. Avian

82 communities and bird species requirements for feeding and habitat change throughout the year

83 in agricultural landscapes as in any other environment, and evaluations of the role of agri-

84 environmental schemes as food and habitat provision sites outside of the reproduction period

85 have been increasingly needed (Marfil-Daza et al. 2013; Ponce et al. 2014; Redhead et al. 2018).

86 The quality of winter habitats can affect bird lifetime reproductive success through influences

87 on departure date from winter quarters and on condition during migration (Marra et al. 1998;

88 Bearhop et al. 2004; Norris et al. 2004; Smith and Moore 2005). As perennial crops, fruit

89 orchards constitute highly stable and predictable habitats for bird communities (Brown and

90 Welker 1992), and their ability to provide quality resources and resting sites for birds is likely

91 to vary with their size, plant diversity, surrounding land cover and management practices

92 (Mangan et al. 2017). Orchards constitute intensively managed agroecosystems maximizing

93 fruit production and subsequently affecting bird populations depending on the amount of

94 chemicals sprayed for crop protection (Bishop et al. 2000; Bouvier et al. 2005; Genghini et al.

95 2006; Bouvier et al. 2011). The influence of orchard management on farmland bird diversity at

96 both local and landscape scales has been recognized during the reproductive season (Bouvier

97 et al 2011; Belfrage et al. 2005), but their potential for bird conservation during winter is still

98 poorly described globally (but see Myczko et al. 2013 in apple orchards of Central Europe).

99 Fruit production seasons display sharp contrasts with winter seasons, during which

100 anthropogenic disturbance becomes almost non-existent, making orchards substantially

5

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

125 Fieldwork was carried out in 30 commercial pome fruit orchards (15 apple and 15 pear) located

126 in a 50 km^2 pome fruit production area ('Basse vallée de la Durance', central point: WGS84:

127 43°8' N, 3°9' E) of southeastern France (Fig. 1). This area is a flat agricultural plain ranging

128 from 40 to 60 m a.s.l. characterized by a dense network of ditches and hedgerows and by diverse

129 farming systems. Fruit orchards are the dominant crop in a crop mosaic that also contains

130 vineyards, vegetables, and cereal crops. Pome fruits, i.e., apple and pears together, represent

131 87% of all fruit production in the study area. The studied orchards had an average area of 1.22

132 ± 0.14 ha, a plantation density of approximately 1500 trees/ha distributed along an average of

133 15.5 ± 1.5 rows and a grassy ground cover. The orchards had the following types of

134 management: conventional, integrated pest management (IPM) or organic management (10

135 orchards each). Disease and pest control treatment strategies in this study area correspond to

136 those described by Bouvier et al. (2005, 2011, 2016). Treatments are carried out from March to

137 October. Conventional orchards were managed with an average of 26.2 and 23.0 treatments in

138 2009 and 2010, respectively. Treatments included chemical fungicides (13.1 and 13.7 in 2009

139 and 2010, respectively) and broad-spectrum chemical insecticides (12.5 and 9.3 in 2009 and

140 2010, respectively). IPM orchards were managed with chemical fungicides, insecticides and

141 herbicides similar to those used in conventional orchards. The use of male mating disruption

142 against the main Lepidopteran pest in these orchards resulted in chemical insecticide input

143 reductions of 1.3 treatments in 2009 and 1.4 in 2010. The average number of annual treatments

144 in the organic orchards was 29.7 and 27.0 in 2009 and 2010, respectively. These treatments

145 included two mineral fungicides, copper and sulfur (2.5 and 8.1 in 2009 and 2010, respectively),

146 a selective viral insecticide against codling moths (7.2 and 7.1 in 2009 and 2010, respectively)

147 and mating disruption. All orchards were bordered by hedgerows (mainly poplar or cypress)

148 for protection against the prevailing winds. Except for treatment strategies, orchards were

149 chosen for their similarity in structure and in local environmental features that might influence

150 bird communities.

151

Overwintering bird assemblages

153 Two surveys were carried out in each orchard, one in January 2009 and one in December 2010,

154 in days without heavy rain or wind and between 9.00 am and 2.30 pm to match bird foraging

155 activity (Skorka et al. 2006; Myczko et al. 2013; Assandri et al. 2016). In two instances, two

156 orchards were less than 300 m apart, and we took the precaution of not surveying them on the

157 same day to avoid moving the birds from one orchard to the other. Birds heard and seen within

158 orchards and their surrounding hedgerows were recorded using transect counts along the

159 periphery and the central tree row of each orchard. Because the orchards had a small area and

160 an elongated shape, this made it possible to cover the whole orchard. The length of the transects

161 varied among the orchards with a mean ± se of 711± 21 m (range: [420, 1013]). This value was

162 not correlated with orchard area (Pearson's r= 0.28, P=0.13). The duration of each survey was

163 approximately 20 min per ha. The similar and simple vegetation structure of the orchards, the

164 similar climatic conditions when the surveys were conducted, and the performance of all

165 surveys by the same experienced ornithologist (JCB) to exclude between-observer variation

166 were meant to ensure that bird detectability did not vary among the orchards (Bibby et al. 2000).

167

Food resource availability for overwintering birds in orchards

169 The two main plant resources available for birds in winter are fruits remaining on the ground

170 or in the pome fruit trees after harvest and the wild berries growing in hedgerows (Metcalfe

171 2005). In a preliminary approach, we investigated the floristic composition of the hedgerows in

172 a random sample of 10 out of the 30 orchards to identify the plant species that produce berries

173 during winter in the area. As ivy (*Hedera helix*) was by far the numerically dominant species

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

175   experimental design.

176   Fruits laying on the ground or remaining in the trees were counted on 10 equidistant 5 m x

177   3 m plots aligned along a diagonal of each orchard. Each plot included a 5 m length of one tree

178   row and its adjacent alley. The counts were performed on the same day as the bird counts. The

179   total number of fruits remaining in each orchard was estimated from its fruit counts in the 5 m

180   x 3 m plots and its total area. This defined the *fruit* continuous independent variable for data

181   analysis. The independent binary variable *presence of fruits* was further used to categorize

182   orchards depending on whether fruits were absent (zero) or present (one).

183   We assessed the amount of available ivy berries in the orchard hedgerows by counting the

184   number of trees carrying fruiting ivy in all hedgerows bordering each orchard. This defined the

185   *ivy* independent variable for data analysis.

186

187   **Statistical analyses**

188   *Overwintering bird assemblages*

189   Data were analysed using R.3.5.1 software (R Core team 2018). We used the vegan R

190   package (Oskasnen et al. 2019) to calculate estimates for richness, abundance, and evenness.

191   These calculations were based either on all bird species when describing the data or excluding

192   prey birds when assessing the effect of resources since this guild was not expected to directly

193   benefit from the presence of fruits (Table 1). In three orchards in 2009, there were large flocks

194   of *Sturnus vulgaris* and *Fringilla coelebs*; the presence of these two species was thus recorded,

195   but these three orchards were removed from statistical analyses on abundance as species

196   abundance was only roughly estimated. Correlations between bird abundance and species

197   richness and between evenness and both bird abundance and species richness were first

198   investigated with Spearman correlation tests.

199

200 Low species detectability may result in the underestimation of species richness, as some species

201 may be undetected. We assessed the extent of this underestimation by also calculating the

202 improved Chao1 index of species richness (Chao and Chiu 2016) using the SpadeR R package

203 (Chao et al. 2016) for the whole dataset, as well as independently for orchards with and without

204 remaining fruits and per year. We also calculated the Chao1 index for 57 out of the 60 orchard

205 x year combinations, with the number of detected species being too low for its calculation for

206 three of them. We further calculated the estimated community coverage, i.e., the estimated

207 fraction of the entire population of individuals in the community that belonged to the detected

208 species (SpadeR, Chao et al. 2016).

209

210 *Effect of available resources on bird assemblages*

211 All statistical analyses were performed on the values of species richness and abundance

212 calculated from detected species. The results based on improved Chao1 index estimations of

213 species richness did not differ substantially (Online resource 2).

214

215 Models

216 The effect of resources on bird abundance was analysed with linear mixed models including

217 *year*, *orchard area*, *presence of fruits* and log(*ivy* +1) as independent variables. Only the

218 interaction of log(*ivy* +1) with the *presence of fruits* was included. This effect was further

219 analysed separately for orchards with and without remaining fruits, i.e., with linear mixed

220 models including *year, orchard area* and log(*ivy* +1) as independent variables for both types of

221 orchards and including the 'log(*fruits*)' variable for orchards with remaining fruits only. For

222 these orchards, the interaction of log(*ivy* +1) with log(*fruits*) was also included. All quantitative

223 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).

249

250 Significance of independent variables

251 A multimodel inference approach was used to assess the significance of independent variables

252 using the MuMIn R package (Barton, 2020). A model selection procedure using the corrected

253 Akaike information criteria (AICc) was performed on the full models containing all

254 independent variables. All models falling within a ΔAICc < 4 (Online resource 3) were then

255 used in a model averaging procedure (Burnham and Anderson, 2002). This allowed the mean

256 coefficient associated with each independent variable to be calculated, along with its confidence

257 interval as well as each variable importance, i.e. the sum of the Akaike weights (Σw) of the

258 models in which it appeared. The latter indicates the probability that the independent variable

259 is a component of the best model (Burnham & Anderson, 2002). An independent variable was

260 considered significant when the 95% confidence interval of its coefficient did not overlap 0.

261

262 *Effect of crop management on available resources*

263 To assess the effects of the crop treatment strategies on the resources available to the birds after

264 harvest, the effects of crop treatment strategy on log(*ivy* +1) were analysed with a linear model

265 including *year* and *crop management* (i.e., organic, IPM or conventional) as independent

266 variables. The effects of the crop management strategies on the log(*fruits*+1) were analysed

267 similarly in apple orchards only as there were no remaining fruits in the pear orchards (see

268 Results). Model residuals were inspected as above. Pairwise comparisons between crop

269 management strategies were carried out using post hoc Tukey tests (package multcomp,

270 Hothorn et al. 2008).

271

272 **Results**

273 **Food resource availability for overwintering birds in orchards**

274   There were remaining fruits in 12 and 9 orchards in 2009 and 2010, respectively. The estimated

275   number of fruits per orchard was higher in 2009 than in 2010 (mean ± se: 2009: 10799±1000,

276   2010: 2533 ± 177). The remaining fruit density per orchard was estimated to be 6.7 10^{-2} ± 3.9

277   10^{-2} (mean±se), 2.80 ± 1.39 and 0.56 ± 0.15 fruits.m^{-2} in the organic, IPM and conventional

278   orchards, respectively. These fruits were only apples, as pears were totally decayed at that time

279   of year. Fruits mostly laid on the ground.

280   Fruiting trees with ivy were observed in 28 out of the 30 orchards with a mean number (±

281   se) of 51.75 ± 10.19 (range [1, 207]) trees and was similar in orchards with and without

282   remaining fruits (mean ± se: 43.62 ± 8.34 and 53.57 ± 10.16 respectively). Of the two orchards

283   without fruiting ivy, one had remaining fruits both years, and the other had no fruits.

284   Considering only orchards with remaining fruits, the number of fruits and the number of trees

285   with fruiting ivy were uncorrelated (2009: Spearman r=0.18, p=0.55; 2010: r=0.27; p=0.47).

286

287   **Overwintering bird assemblages in orchards**

288   We observed 1480 birds (excluding orchards with flocks) and identified 41 bird species overall,

289   31 species during the 21 surveys in the orchards with fruits and 40 species during the 39 surveys

290   in the orchards without fruits (Table 1). Overall, 93% of observed birds were common

291   songbirds, representing a total of 35 species. Among these, 10 were granivores, 7 were

292   insectivores and 18 fed on both arthropods and seeds or fruits during that period of the year

293   (Table 1). The most frequent species were the black cap *Sylvia atricapilla*, the song thrush

294   *Turdus philomelos*, the Great tit *Parus major*, the common chaffinch *Fringilla coelebs*, and the

295   robin *Erithacus rubecula* (Table 1). Thirteen species were of conservation concern, being

296   threatened either in France or with decreasing population trends at the global level (Table 1 and

297   Online Resource 4).

13

298   The estimated coefficient of variation of species discovery probability was high (2.44). The

299   improved Chao1 index was thus chosen to assess species richness because it does not assume

300   similar species discovery (Chao and Chiu, 2016). The Chao1 index of species richness was

301   slightly higher than the total raw number of species (mean [95% confidence interval], 53.9

302   [42.9,125.5]) when considering orchards with fruits (32.4 [31.4, 35.5]) and when considering

303   orchards without fruits (45.2 [41.7, 55.8]). The raw number of species was higher in 2009 than

304   in 2010 (37 and 30, respectively), as was the Chao1 index of species richness (2009: 42.3 [40.1,

305   49.2]; 2010: 31.9 [30.2, 52.1]). Consistent with the low estimated number of undetected species,

306   the coverage estimate for the entire dataset was 0.99.

307   The number of birds per orchard ranged from 2 to 94 (excluding flocks), and there were on

308   average (mean $\pm$ se) 25.9 $\pm$ 2.7 birds per orchard. Bird abundance per orchard was higher in

309   2009 than in 2010 (32.2 $\pm$ 4.2 and 20.3 $\pm$ 3.1, respectively, Table 2). The raw number of species

310   per orchard also varied widely from 1 to 16, with an average of 7.4 $\pm$ 0.4, and this number was

311   also higher in 2009 than 2010 (8.3 $\pm$ 0.7 and 6.6 $\pm$ 0.4, respectively, Table 2). Bird abundance

312   and bird species richness per orchard were highly positively correlated (Spearman r=0.7, P=2.2

313   10^{-9}).

314   The evenness of the observed bird assemblages ranged from 0.25 to 1 (excluding flocks) and

315   was (mean $\pm$ se) 0.82 $\pm$ 0.01 on average. It was highly negatively correlated with bird abundance

316   (r=-0.65, P=3.15 10^{-8}) but not with the observed bird species richness (r=-0.22, P=0.09).

317

318   **Effect of available resources on overwintering bird assemblages**

319   *Abundance*

320   Bird abundance was higher in orchards with fruits. Whatever the orchard type, it increased with

321   an increasing number of trees with fruiting ivy (Table 2, Fig. 2). Bird abundance also increased

322   with the number of remaining fruits in orchards with fruits (Table 2, Fig. 3).

323

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 -

348   6.69, $P<10^{-4}$) or in the conventional (estimate -5.31, $P=6.5 \ 10^{-4}$) orchards, and this value did not

349   differ between the conventional and IPM apple orchards (p=0.605).

350

351   **Discussion**

352   As in other environments, avian species communities and their requirements for feeding and

353   habitat change throughout the year in agricultural landscapes. There is an increasing need to

354   evaluate the role of agri-environmental areas as food and habitat provision sites outside of the

355   breeding season (Marfil-Daza et al. 2013; Ponce et al. 2014; Redhead et al. 2018). Efforts to

356   conserve wintering bird communities in agricultural landscapes rely on improvements in winter

357   habitat by increasing the availability of key resources such as food, shelter and resting sites

358   (Hammers et al. 2015; Redhead et al. 2018). Research on the effectiveness of agri-

359   environmental schemes has usually focused on the responses of a few species (Johnson et al.

360   2006; Ponce 2014; Breeuwer et al. 2009; McHugh et al. 2017), although a large number of

361   species or functional groups may respond (MacDonald et al. 2012; Ponce 2014; Henderson et

362   al. 2000; Navedo et al. 2015; Bouam et al. 2017). Considering the whole bird community as a

363   rule for biodiversity maintenance should thus be a priority (Ponce 2014; Ekroos et al. 2014).

364   Based on a 2-year community study in a local network of commercial pome fruit orchards,

365   we showed that the amount of available fruits during winter, both on the ground or in

366   surrounding vegetation, had a significant influence on the abundance and species richness of

367   wintering bird populations in southeastern France. These orchards hosted no less than 15% of

368   France's wintering avifauna (Issa and Muller 2015), which was predominantly composed of

369   insectivorous and granivorous passerines. Thirteen of the recorded species were of conservation

370   concern as either being threatened in France or having a decreasing population trend at the

371   global level (Online Resource 4). This indicates that such perennial crops favouring the

372   presence of fruits in winter are potentially important and relevant bird wintering areas, similar

373   to other apple orchards in Central Europe (Myczko et al. 2013) or olive groves in southern

374   Spain (Rey 2011). This result is also in line with the provisioning of resources for wintering

375   birds reported from other agricultural landscapes throughout Europe, such as improved

376   grassland fields in Ireland (McMahon et al. 2013), rice fields on the western Iberian Peninsula

377   (Navedo et al. 2015) and farmlands in the Netherlands (Hammers et al. 2015). Although this

378   work was carried out at a local spatial scale, we posit that it sheds important light on the

379   potential for perennial crops to provide sustainable, favourable habitats to overwintering bird

380   populations in France and throughout Europe, where 473,000 ha of apple orchards and 100,000

381   ha of pear orchards represented nearly 44 % of the total fruit cultivated area in 2017 (Eurostat

382   2020. In the context of a large-scale decline in common farmland bird populations in Europe

383   (Donald et al. 2006; EBCC 2016), our study thus supports orchards as one of the key favourable

384   habitats for some Palearctic bird species during their wintering period (Rey 2011; Tryjanowski

385   et al. 2011; Myczko et al. 2013), with potential beneficial effects for subsequent breeding

386   seasons (Siriwardena et al. 2007).

387

388   **Factors affecting bird species richness and abundance in pome fruit orchards**

389   The availability of food resources is a key factor determining the selection of wintering sites by

390   birds (Robinson and Sutherland 1999). One central finding of this study is that the presence of

391   apples left on the ground after harvest and ivy berries in the surrounding hedgerows

392   significantly influenced the use of cultivated area by wintering bird populations in southern

393   France. Although orchards can also be used by birds for resources other than fruits or as a

394   resting area, we suggest that there might be some complementarity between apples and ivy

395   berries as food resources. In comparison to the number of apples, the number of trees bearing

396   ivy berries in the surrounding windbreak hedgerows appeared to affect bird species richness

397   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

423 trend that birds forage preferentially on a food source when it is abundant (Ricklefs and Miller

424 2005). In winter, the gregarious behaviour of particular species (e.g., Turdidae and Fringillidae

425 species) can lead to large flocks of birds (>100 individuals) in a single site. Behavioural

426 aggregation provides them with greater protection from predators and allows them to feed

427 longer during the shorter days of the winter period (Pulliam 1973; Treisman 1975). We

428 observed such flocks of *S. vulgaris* or *F. coelebs* in three orchards in 2009 and excluded these

429 from our analyses as birds were difficult to estimate numerically, but importantly, flocks

430 predominantly occurred in orchards in which apples were highly abundant on the ground (2 out

431 of 3 orchards). Interestingly, the number of trees with ivy was also positively associated with

432 bird abundance in orchards with remaining fruits on the ground (Fig. 2). This may have resulted

433 from an increase in the number of species that responded to the complementarity of these

434 resources, as discussed above.

435   Overall, our results suggest that the presence of hedgerows is likely favourable to the bird

436 communities that use pome fruit orchards during winter. Hedgerows have been acknowledged

437 for their positive influence on local bird abundance and species richness in agricultural

438 landscapes, meadows, and wheat and alfalfa fields (Hinsley and Bellamy 2000; Batáry et al.

439 2010; Kross et al. 2016). In addition, a multi-species composition of vegetal hedgerows can

440 provide short-range shelter to many species, including those that do not forage on berries, which

441 may facilitate resource exploitation in areas that might otherwise be too risky to use (Suhonen

442 1993; Andrews and Rebane 1994). In southern France, hedgerows are mostly planted as a

443 barrier against strong prevailing winds, but a trend in orchard farming consists of removing

444 hedgerows and taking advantage of the wind-breaking efficiency of insect pest exclusion nets

445 that cover trees (Middleton and McWaters 2002; Iglesias and Alegre 2006). Our results,

446 however, showed the likely important role of hedgerows when vegetally diversified in

447 overwintering bird conservation. Additionally, fruits on the ground are food sources that cannot

448 be replenished during winter because they are gradually depleted through bird consumption,

449 decomposition and incorporation into the soil. The presence of hedgerows with tree species that

450 produce berries all winter may provide some bird species with an additional sustainable food

451 supply. In terms of bird population conservation, we suggest that management

452 recommendations include the maintenance of hedgerows concomitantly with the use of insect

453 pest exclusion nets. In addition to maintaining a diversity of hedgerow structures (i.e., in

454 density, width and height) that are generally attractive for numerous bird species (Duckworth

455 1994), diversifying hedgerow composition with different plant species fruiting in winter and

456 reducing hedgerow pruning intensity may also strengthen sustainability in fruit provision to

457 overwintering birds (Hinsley and Bellamy 2000). Given the importance of landscape

458 composition for overwintering birds (Geiger et al. 2010), the maintenance of hedgerow

459 diversity should also be managed at the landscape scale based on good coordination between

460 farmers. Although landscape management is frequently advocated as part of biodiversity

461 conservation, it causes specific challenges in agricultural landscapes due to the spatial scale

462 mismatch between ecological processes and agricultural farm management, and to the strong

463 economic constraints that farmers are facing (Pelosi et al. 2010; Kremen and Merenlender

464 2018). Its implementation is still rare (but see, e.g., Bretagnolle et al 2011). In the study area,

465 collective management could be supported by current French incentives for groups of farmers

466 that want to act collectively to increase the durability of their farming systems (GIEE :

467 Groupements d'intérêt économique et environnemental).

468 Notably, the present study did not consider the presence of seeds from the herbaceous

469 stratum, which were also likely abundant on the ground. Herbaceous seeds may constitute an

470 additional attractive food for birds in orchards (Myczko et al. 2013) and farmlands (Wilson et

471 al. 1999; Newton 2004; Stoate et al. 2009). However, as all orchards were grassed, a common

472   practice in the study area to facilitate the use of agricultural machinery, this is unlikely to affect

473   our conclusions.

474

475   **Effects of farming practices on fruit resource availability**

476   In agroecosystems, the resources available for birds are often dependent on farmers' practices.

477   The number of surrounding trees with ivy around orchards varied among orchards but did not

478   depend on the orchard management strategy. This lack of correlation to management strategy

479   may be explained by the orchards' past history. All plots were initially planted similarly and

480   were managed as conventional orchards, and some of them were later converted to IPM and

481   organic farming without changes in their surrounding environment. In contrast, the quantity of

482   apples left on the ground strongly depended on the type of orchard management. Myczko et al.

483   (2013) found that abandoned or traditionally managed apple orchards increased food and shelter

484   opportunities to birds than intensively managed ones in Poland. In contrast, we found that

485   available apples in winter were significantly more abundant in both conventional and IPM

486   orchards than in organic orchards, which resulted from a substantial divergence in the

487   management of unharvested apples during winter. Post-harvest apple grinding is a prophylactic

488   method for controlling insect pests in organic orchards, where spring pest control strategies are

489   generally less effective in maintaining insect populations at low risk levels than those used in

490   conventional or IPM orchards. Apple grinding aims to kill insect larvae that develop in apples

491   after they have fallen to the ground, thereby reducing the size of overwintering pest populations.

492   Conversely, higher pesticide pressure in both conventional and IPM orchards during the apple-

493   growing season causes growers to neglect overwintering insect populations that may have

494   escaped treatments and to not manage uncollected fruits. The positive impact of this latter

495   practice on overwintering bird abundance in conventional and IPM orchards occurred in

496   contrast to the adverse effects of phytosanitary treatments (in particular synthetic insecticides)

497   on the reproductive success of passerines and on bird abundance and species richness reported

498   during the breeding season (Bouvier et al. 2005; Bouvier et al. 2011; Katayama 2016; Kajtoch

499   2017). Our results thus suggest that how agricultural management strategies affect bird

500   communities in orchards may change over the course of a year, supporting the claim that

501   environmental impacts of farming practices should be considered not only at the seasonal scale

502   but also at the annual scale. Further work on the impacts of annual farming practices on

503   overwintering insect communities might complement approaches that enable orchards to

504   provide wintering birds with resources.

505

Conclusion

507   This study highlighted that pome fruit orchards likely serve as habitats for overwintering birds

508   due to the presence of unharvested fruits and hedgerows with ivy. Modifications of agricultural

509   practices at local and regional scales can improve the suitability of agroecosystems to a greater

510   number of bird species by incorporating vegetation elements that favour bird species less

511   adapted to croplands (Benton et al. 2003). This scenario is still poorly documented in pome

512   fruit landscapes (Garcia et al. 2018), and our work provides additional support for the potential

513   benefit of hedges in orchards for wintering bird populations.

514   Finally, our results also emphasized the positive effect that the presence of apples had on bird

515   abundance during winter, which suggests that late season practices allowing the persistence of

516   non-harvested fruits in orchards may be beneficial to overwintering bird populations. In the

517   context where leaving unharvested fruits on the ground occurs with the cost of an increased risk

518   for pests in organic orchards, supporting growers with effective pest management tools that are

519   alternatives to pesticides (e.g., pest exclusion nets) could be a means of increasing the surface

520   area favourable to wintering birds in agricultural landscapes.

521

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Fig. 1 Colour for online version
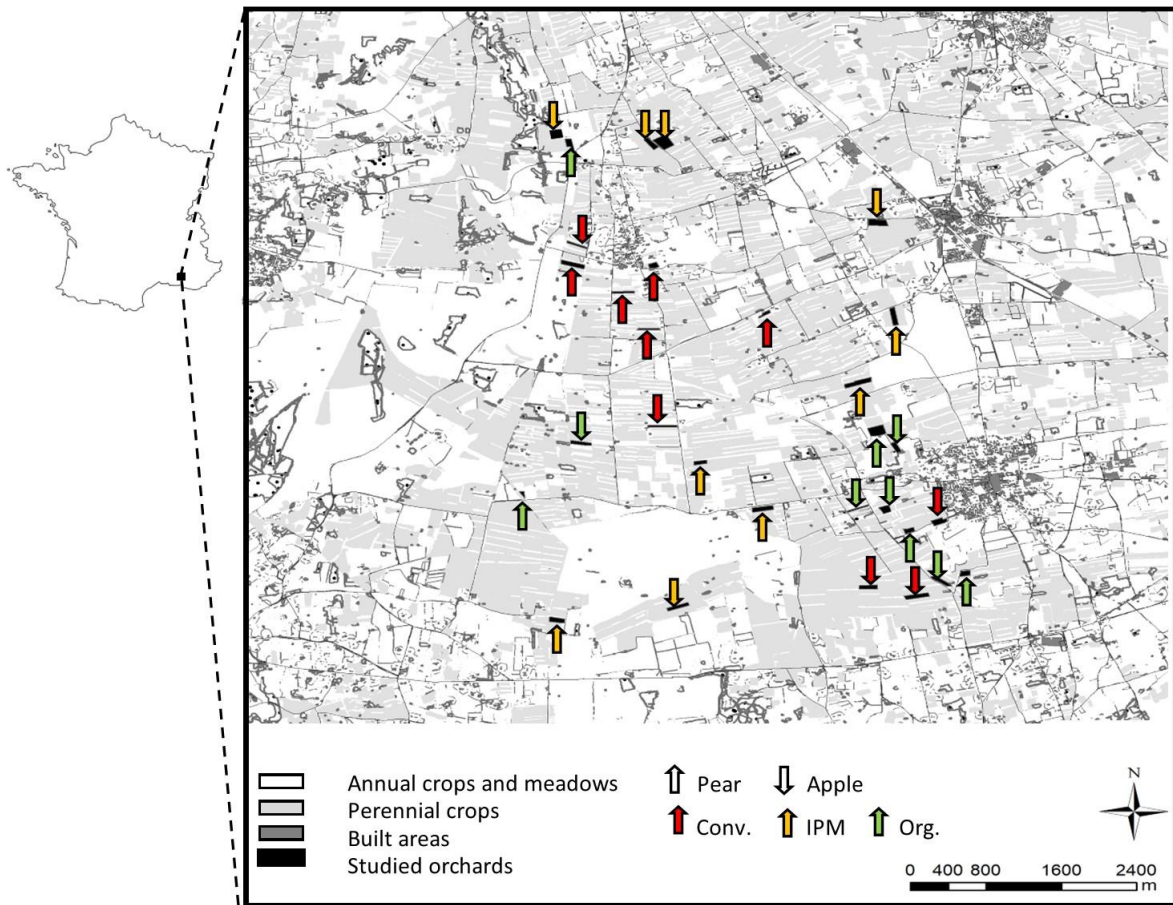
730
Figure 1: Map of the study area. Arrows point to the 30 sampled orchards. The orientation of

the arrows differentiates pear and apple orchards, the colour of the arrow indicates the

management strategy (Org.: Organic, IPM : Integrated pest management, Conv.: Conventional).

734

736   Fig. 2
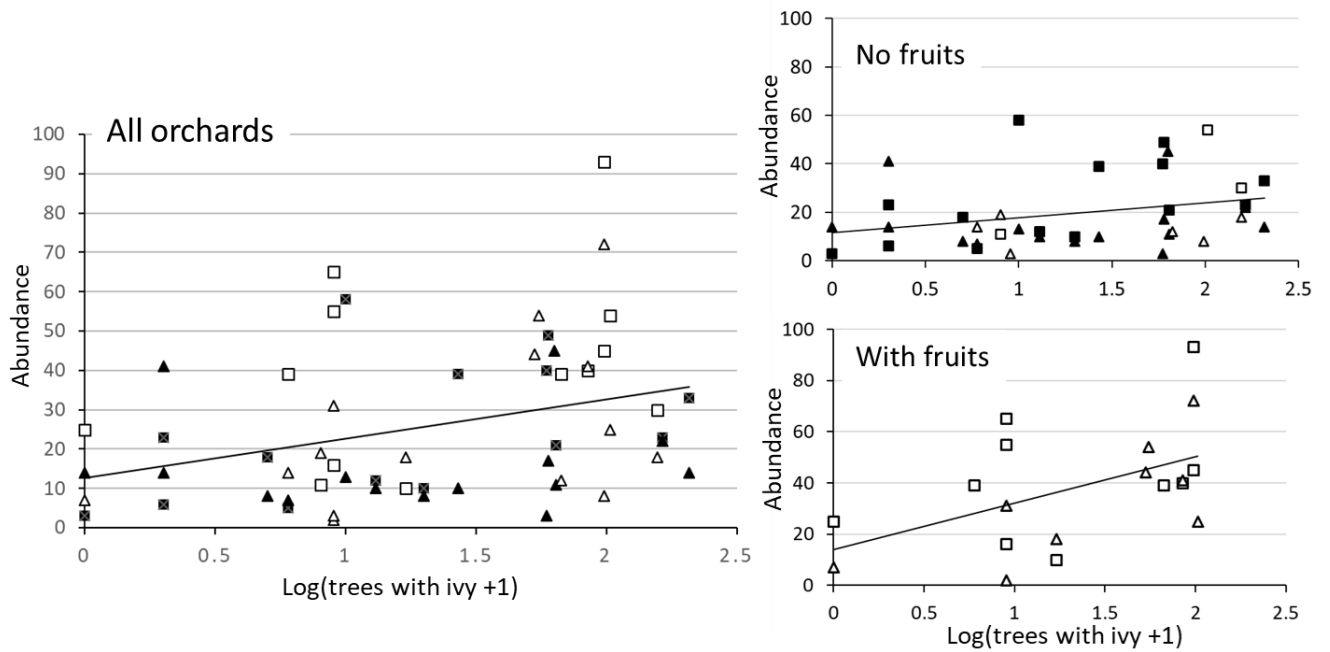
739   **Figure 2**: Observed bird abundance as a function of the log-transformed number of ivy bearing

740   trees in hedgerows considering either all orchards or considering separately orchards with and

741   without remaining fruits on the ground. Abundance was assessed in 2009 and 2010 in pome

742   fruit orchards in southeastern France. Filled symbols: pear orchards; open symbols: apple

743   orchards; Squares 2009; triangles 2010.

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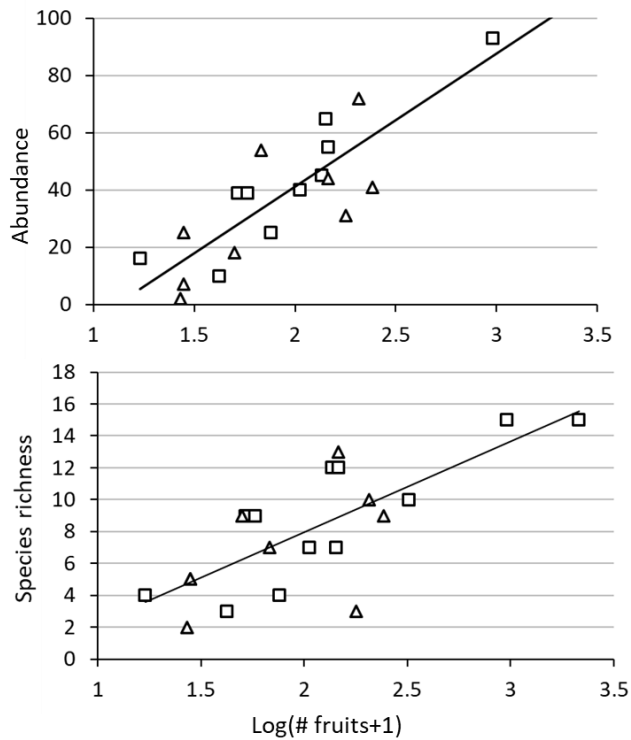
Figure 3: Bird abundance and species richness per orchard as a function of the log-transformed number of remaining fruits per orchard. Abundance and species richness were assessed in 2009 and 2010 in pome fruit orchards in southeastern France. Regression lines are presented for these two significant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

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756 Fig. 4

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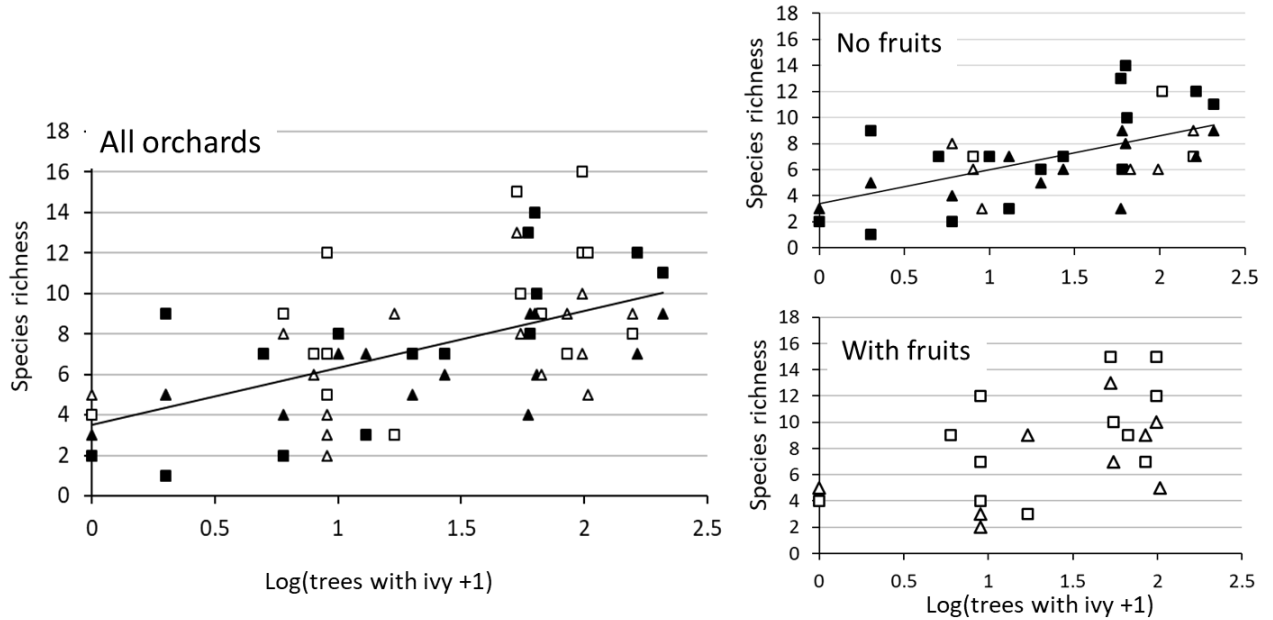
Figure 4: Bird species richness as a function of the log-transformed number of ivy-bearing trees

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.

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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.

773 **Table 2**: Multimodel analysis of the variation in bird abundance and species richness. Average parameter estimates (± standard error), associated

774 95% confidence intervals and variable importance (I) are provided for the subset of models with ΔAIC<4 as compared to the best model. '-'

775 indicates that the variable was not retained in the subset of models. '/' indicates that the variable was not included in the analysis. Parameter

776 values for which the confidence intervals does not overlap 0 are in bold.

777

	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	/	/	/	/	/	/

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779 **Table 3**

780 Multimodel analysis of the variation in the presence of individual species as a function of study year, transect length, presence of fruits and

781 number of ivy bearing trees. Values provided are average parameter estimates (± standard error), associated 95% confidence intervals and

782 variable importance (I) in the subset of models with ΔAIC<4 as compared to the best model. Values are highlighted in bold when 95%

783 confidence intervals do not overlap value 0.

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	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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