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**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

51 **Introduction**

52 Responses to increasing modern food demands across continents have involved drastic changes
53 in land use through unprecedented conversions of natural ecosystems to simplified and
54 intensively managed ones (Tscharntke et al. 2005). Agricultural intensification processes
55 include a wide variety of components, e.g., increased mechanisation and chemical use,
56 increased areas of monoculture, changes in areas of crop types, changes to sowing and
57 harvesting practices, and suppression of non-farmed habitats such as hedgerows (see Stoate et
58 al. 2001; Vickery et al. 2001; Robinson and Sutherland 2002; Newton 2004). Such processes
59 are major drivers of global biodiversity losses across agricultural landscapes (Matson et al.
60 1997; Tilman et al. 2001; Tscharntke et al. 2005), and the compatibility of agricultural land use
61 and conservation has been traditionally questioned. In response, the development and
62 implementation of agri-environmental schemes aim at counteracting the environmental impacts
63 of modern agriculture on biodiversity (Stoate et al. 2009), as well as considering the potential
64 for agricultural management to promote biodiversity and ecosystem functions through
65 enhanced biomass productivity (Tscharntke et al. 2005).

66 Among the animal groups displaying landscape-wide biodiversity losses, populations of
67 many farmland bird species have severely declined across Europe due to post-war agricultural
68 intensification (Donald et al. 2001; Benton et al. 2003; Geiger et al. 2010; EBCC 2016). Links
69 between agricultural intensification and avian biodiversity loss have also been reported at a
70 global scale, with severe population declines in Africa (Söderström et al. 2003) and North
71 America (Brennan and Kuvlesky 2005). Over several decades, modernisation of agriculture has
72 led to drastic reductions in foraging resources in arable landscapes, which has strongly affected
73 populations of seed-specialist farmland birds (Siriwardena et al. 2007). A large body of the
74 literature has investigated bird responses to agricultural management in annual crops such as
75 cereals and vegetables (e.g., Ponce et al. 2014; Navedo et al. 2015). Perennial crops such as

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

101 beneficial for wintering farmland birds. Fruits can be left in orchards after harvest, the absence
102 of chemical treatments favours survival and overwintering for many insect prey species (Skórka
103 et al. 2006; Tryjanowski et al. 2011), and the occurrence of winter fruiting in the surrounding
104 vegetation in orchard hedgerows can provide a high energy content food resource to many
105 farmland birds (Metcalf 2005).

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

122

123 **Materials and methods**

124 **Study sites**

125 Fieldwork was carried out in 30 commercial pome fruit orchards (15 apple and 15 pear) located
126 in a 50 km² 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

152 **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 \pm 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

168 **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 (Metcalf
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 $\log(\text{ivy} + 1)$ as independent variables. Only the
218 interaction of $\log(\text{ivy} + 1)$ 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 $\log(\text{ivy} + 1)$ as independent variables for both types of
221 orchards and including the ‘ $\log(\text{fruits})$ ’ variable for orchards with remaining fruits only. For
222 these orchards, the interaction of $\log(\text{ivy} + 1)$ with $\log(\text{fruits})$ was also included. All quantitative
223 independent variables were scaled. Orchard identity was included as a random effect in all

224 models to account for the fact that the same orchards were surveyed in 2009 and 2010. Variance
225 inflation factors were below 3 for all models, indicating low levels of multicollinearity (Zuur et
226 al. 2010). Model residuals were inspected for dispersion using a quantile-quantile (QQ) plot of
227 standardized residuals and for uniformity and outliers using a plot of residual versus predicted
228 values. Associated statistical tests were also performed with the DHARMA R package (Hartig
229 2019). Following analyses of residuals, abundance values were square root transformed, and a
230 Gaussian link function was chosen.

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

242 Specific associations between the presence of individual bird species and the total number
243 of fruits or of ivy-bearing trees were assessed for frequent species (i.e., species present in at
244 least 10 year x orchard combinations) using generalized mixed linear models using *year*,
245 $\log(\text{fruits} + 1)$ and $\log(\text{ivy} + 1)$ with a binomial distribution of the data. As above, all quantitative
246 independent variables were scaled and orchard identity was included as a random effect, and
247 model residuals were inspected as above. Variance inflation factors were also below 3 for all
248 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 $\Delta AICc < 4$ (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 $\log(\text{ivy} + 1)$ 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 $\log(\text{fruits} + 1)$ 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 \pm se: 2009: 10799 \pm 1000,
276 2010: 2533 \pm 177). The remaining fruit density per orchard was estimated to be 6.7 $10^{-2} \pm 3.9$
277 10^{-2} (mean \pm se), 2.80 \pm 1.39 and 0.56 \pm 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 (\pm
281 se) of 51.75 \pm 10.19 (range [1, 207]) trees and was similar in orchards with and without
282 remaining fruits (mean \pm se: 43.62 \pm 8.34 and 53.57 \pm 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).

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 ± 2.7 birds per orchard. Bird abundance per orchard was higher in
309 2009 than in 2010 (32.2 ± 4.2 and 20.3 ± 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 ± 0.4 , and this number was
311 also higher in 2009 than 2010 (8.3 ± 0.7 and 6.6 ± 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 ± 0.01 on average. It was highly negatively correlated with bird abundance
316 ($r=-0.65$, $P=3.15 \cdot 10^{-8}$) 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

324 *Species richness*

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

330

331 *Occurrence of particular songbird species*

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

343

344 **Effect of crop management on available resources**

345 The number of trees with ivy did not depend on crop management strategy ($P=0.18$). In contrast,
346 the number of remaining fruits depended on crop management in apple orchards ($P=2.7 \cdot 10^{-4}$).
347 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, $P = 6.5 \cdot 10^{-4}$) 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

398 presence of fruits positively affected only bird abundance while the number of trees bearing
399 ivy berries positively affected both bird abundance and bird species richness (Table 2, Figs. 2
400 and 4). Further, the number of trees with ivy was also the only independent variable positively
401 affecting Chao1 index estimations of species richness (Online resource 2). This relatively
402 stronger effect of the number of trees with ivy on species richness was consistent with an
403 increase in the occurrence of seven songbird frequent species (*E. rubecula*, *P. caeruleus*, *P.*
404 *major*, *S. atricapilla*, *T. iliacus*, *T. merula* and *T. philomelos*) with the number of ivy bearing
405 trees but not with that of apples (Table 3). A main difference between the effects of apples and
406 ivy may rely on both the direct and indirect attractivity of apples for different diet guilds.
407 Indeed, unharvested fruits may also host specialized arthropod pests (e.g., codling moth, *Cydia*
408 *pomonella*, caterpillars) or fruit-decaying opportunistic species (e.g., *Drosophila* spp.) and thus
409 attract a large range of birds. This has not been formally tested in the present study, but previous
410 studies suggested that insect infestation can enhance the attractiveness of fruits to frugivorous
411 bird species (Valburg 1992); however, some species may also avoid them (Traveset et al. 1995;
412 Dixon et al 1997). In contrast, trees with ivy may have attracted species that preferentially
413 forage in trees as opposed to on the ground or species that rely on ivy berries as a component
414 of their diet. Four out of the seven species that responded positively to the number of trees with
415 ivy are well known to feed on berries during winter (*S. atricapilla*, *T. iliacus*, *T. merula* and *T.*
416 *philomelos*). On the other hand, the significant positive response of *E. rubecula*, *C. caeruleus*
417 and *P. major* that are not known to feed on ivy berries may emphasize the beneficial role of ivy
418 in microhabitat diversity in hedgerows, as interlacing ivy likely increases hedgerow structural
419 complexity. Microhabitat diversity is a good predictor of bird diversity (Regnery et al. 2013).

420 Conversely, bird abundance was positively correlated with the number of available apples,
421 i.e., the larger the number of apples was, the greater the number of birds (Fig. 3). Consistent
422 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

506 **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

522 **References**

- 523 Agreste (2014) Les Dossiers. Ministère de l'Agriculture et de l'Alimentation 22:2-17
- 524 Agreste (2019) Statistique agricole annuelle. Agreste Chiffres et Données 4:5-64
- 525 Andrews J, Rebane M (1994) Farming and wildlife. A practical management Handbook. Sandy,
526 Bedfordshire
- 527 Assandri G, Bogliani G, Pedrini P, Brambilla M (2016) Diversity in the monotony? Habitat
528 traits and management practices shape avian communities in intensive vineyards. Agric
529 Ecosyst Environ 223:250-260
- 530 Barton K (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. [https://CRAN.R-](https://CRAN.R-project.org/package=MuumIn)
531 [project.org/package=MuumIn](https://CRAN.R-project.org/package=MuumIn)
- 532 Batáry P, Matthiesen T, Tschardt T (2010) Landscape-moderated importance of hedges in
533 conserving farmland bird diversity of organic vs. conventional croplands and grasslands.
534 Biol. Conserv. 143:2020-2027. <http://dx.doi.org/10.1016/j.biocon.2010.05.005>
- 535 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using
536 lme4. Journal of Statistical Software, 67, 1-48.
- 537 Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body
538 condition in migrating passerines is influenced by winter habitat. Proc Roy Soc Lond B
539 271:S215-S218
- 540 Belfrage K, BjoÈrklund J, Salomonsson L (2005) the effects of farm size and organic farming
541 on diversity of birds, pollinators, and plants in a Swedish landscape. Ambio 34:582-8
- 542 Beltrame C, Cohen-Shacham E, Trouillet M, Guillet F (2013) Exploring the links between local
543 management and conservation applying the ecosystem services concept: conservation and
544 tourism service in Camargue, France. Int J Biodiv Sci Ecosys Serv Manag 9:166-177
- 545 Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the
546 key? Trends Ecol Evol 18:82-188

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

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

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

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

555 Bouvier JC, Toubon JF, Boivin T, Sauphanor B (2005) Effects of apple orchard management
556 strategies on the great tit (*Parus major*) in Southeastern France. Environ Toxicol Chem
557 24:2846-2852

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

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

563 Breeuwer A, Berendse F, Willems F, Foppen R, Teunissen W, Schekkerman H, Goedhart P
564 (2009) Do meadow birds profit from agri-environment schemes in Dutch agricultural
565 landscapes? Biol Conserv 142:2949-2953

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

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

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

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

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

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

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

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

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

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

589 Duckworth JW (1994) Habitat selection by migrant redstarts *Phoenicurus phoenicurus* and
590 whinchats *Saxicola rubetra* in lowland English Farmland. *Ringing and Migration* 15:119-
591 122

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

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

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

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

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

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

606 Hartig F (2019) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
607 Regression Models. R package version 0.2.4. [https://CRAN.R-](https://CRAN.R-project.org/package=DHARMA)
608 [project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA)

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

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

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

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

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

619 Johnson MD, Sherry TW, Holmes RT, Marra PP (2006) Assessing habitat quality for a
620 migratory songbird wintering in natural and agricultural habitats. *Conserv Biol* 20:1433-
621 1444

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

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

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

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

632 MacDonald MA, Maniakowski M, Cobbold G, Grice PV, Anderson GQA (2012) Effects of
633 agri-environment management for stone curlews on other biodiversity. *Biol Conserv*
634 148:134-145

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

637 Marfil-Daza C, Pizarro M, Moreno-Rueda G (2013) Do hot spots of breeding birds serve as
638 surrogate hot spots of wintering birds? An example from central Spain. *Anim Conserv*
639 16:60-68

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

703 Suhonen J (1993) Predation risk influences the use of foraging sites by tits. *Ecology* 74:1197-
704 1203

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

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

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

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

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

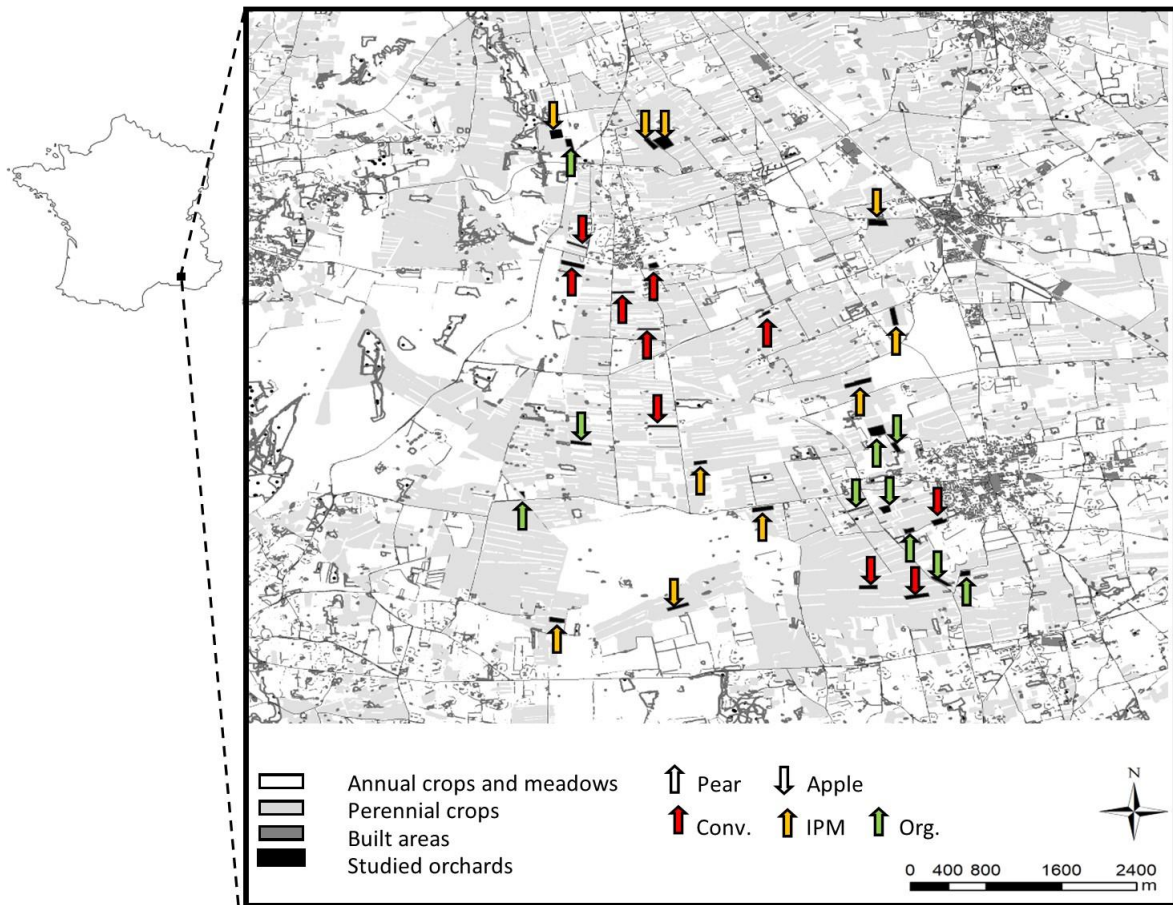
718 Valburg LK (1992) Eating infested fruits: interactions in a plant disperser-pest triad. *Oikos*
719 65:25-28

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

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

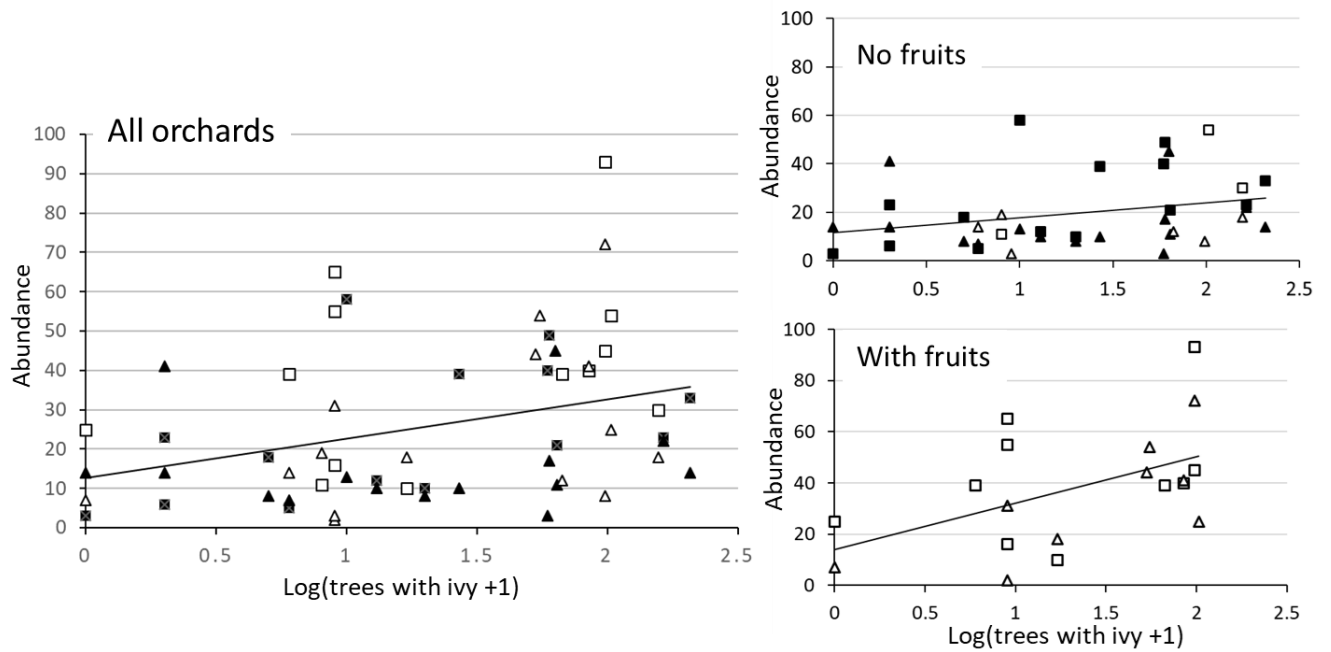
726 Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common
727 statistical problems. *Methods Ecol Evol* 1: 3-14

728 Fig. 1 Colour for online version
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731 **Figure 1:** Map of the study area. Arrows point to the 30 sampled orchards. The orientation of
732 the arrows differentiates pear and apple orchards, the colour of the arrow indicates the
733 management strategy (Org.: Organic, IPM : Integrated pest management, Conv.: Conventional).
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736 Fig. 2



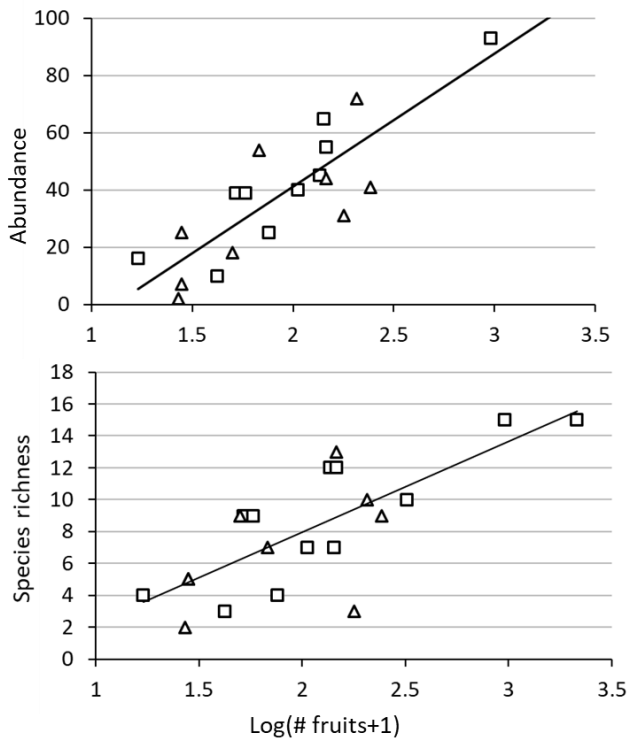
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Figure 2: Observed bird abundance as a function of the log-transformed number of ivy bearing trees in hedgerows considering either all orchards or considering separately orchards with and without remaining fruits on the ground. Abundance was assessed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

746

747 Fig. 3

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

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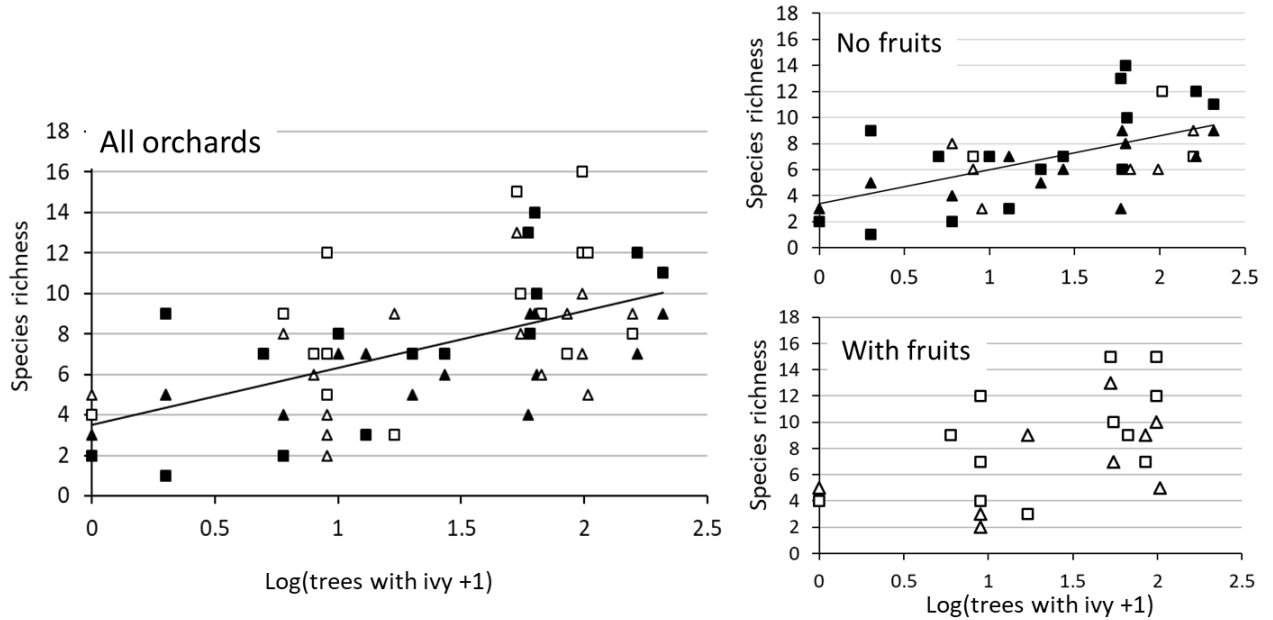
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756 Fig. 4

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

762 in hedgerows considering either all orchards or considering separately orchards with or without

763 remaining fruits on the ground. Species richness was assessed in 2009 and 2010 in pome fruit

764 orchards in southeastern France. Regression lines are presented for significant ($p < 0.05$)

765 relationships. Filled symbols: pear orchards; open symbols: apple orchards; squares 2009;

766 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.

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

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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 (\pm standard error), associated
774 95% confidence intervals and variable importance (I) are provided for the subset of models with $\Delta AIC < 4$ 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 \pm se	C95%	I	Estimate \pm se	C95%	I	Estimate \pm se	C95%	I
Abundance									
Year (2010)	-0.299 \pm 0.1102	[-0.515; -0.083]	1	-0.262 \pm 0.141	[-0.539; 0.014]	0.53	-0.341 \pm 0.159	[-0.651; -0.030]	0.85
Transect	-0.010 \pm 0.146	[-0.296; 0.277]	0.12	-	-	-	0.159 \pm 0.197	[-0.229; 0.546]	0.17
Area	0.215 \pm 0.114	[-0.008; 0.438]	0.45	-0.101 \pm 0.182	[-0.458; 0.256]	0.04	[0.120 \pm 0.160	[-0.193; 0.546]	0.12
Log(ivy +1)	0.323 \pm 0.136	[0.057; 0.589]	1	0.300 \pm 0.147	[0.012; 0.588]	0.46	0.320 \pm 0.163	[0.001; 0.639]	0.55
Log(fruits)	/	/	/	0.758 \pm 0.160	[0.444; 1.072]	1	/	/	/
Log(fruits) x Log(ivy+1)	/	/	/	-	-	-	/	/	/
Presence fruits	0.357 \pm 0.116	[0.130; 0.583]	1	/	/	/	/	/	/
Presence fruits x Log(ivy+1)	0.193 \pm 0.131	[-0.063; 0.449]	0.46	/	/	/	/	/	/
Richness									
Year (2010)	-0.034 \pm 0.015	[-0.063; -0.005]	0.9	-0.019 \pm 0.023	[-0.064; 0.027]	0.13	-0.033 \pm 0.021	[-0.074; 0.009]	0.5
Transect	7.5 10^{-5} \pm 0.018	[-0.034; 0.035]	0.15	0.002 \pm 0.023	[-0.042; 0.047]	0.09	-0.010 \pm 0.028	[-0.066; 0.045]	0.19
Area	0.006 \pm 0.015	[-0.024; 0.035]	0.17	-0.031 \pm 0.024	[-0.078; 0.015]	0.26	-0.002 \pm 0.022	[-0.045; 0.042]	0.18
Log(ivy +1)	0.081 \pm 0.016	[0.049; 0.113]	1	0.046 \pm 0.027	[-0.007; 0.098]	0.56	0.091 \pm 0.023	[0.045; 0.137]	1
Log(fruits)	/	/	/	0.071 \pm 0.024	[0.023; 0.118]	1	/	/	/
Log(fruits) x Log(ivy+1)	/	/	/	-4.6 10^{-4} \pm 0.028	[-0.055; 0.054]	0.05	/	/	/
Presence fruits	0.019 \pm 0.014	[-0.009; 0.048]	0.49	/	/	/	/	/	/
Presence fruits x Log(fruits)	0.007 \pm 0.019	[-0.029; 0.044]	0.07	/	/	/	/	/	/

778

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 (\pm standard error), associated 95% confidence intervals and
 782 variable importance (I) in the subset of models with $\Delta AIC < 4$ as compared to the best model. Values are highlighted in bold when 95%
 783 confidence intervals do not overlap value 0.

784

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

