1 Assessing common birds' ecological requirements to address nature conservation in 2 permanent crops: lessons from Italian vineyards.

- 3 4
- 5 Giacomo Assandri^{a,b},*
- ^aUniversity of Pavia, Dept. of Earth and Environmental Sciences, Via Adolfo Ferrata 9, I-27100,
 Pavia, Italy.
- 8 ^bMUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento,
- 9 Italy. *corresponding author
- 10 giacomo.assandri@gmail.com
- 11 * Corresponding author
- 12
- 13 Giuseppe Bogliani^a
- ¹⁴ ^aUniversity of Pavia, Dept. of Earth and Environmental Sciences, Via Adolfo Ferrata 9, I-27100,
- 15 Pavia, Italy.
- 16 giuseppe.bogliani@unipv.it
- 17
- 18 Paolo Pedrini^b
- ¹⁹ ^bMUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento,
- 20 Italy.
- 21 paolo.pedrini@muse.it
- 22
- 23 Mattia Brambilla^{b,c}
- ^bMUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento,
 Italy.
- ²⁶ ^cFondazione Lombardia per l'Ambiente, Settore biodiversità e aree protette, Largo 10 luglio
- 27 1976 1, 20822, Seveso (MB), Italy.
- 28 brambilla.mattia@gmail.com
- 29
- 30
- 31 *Running title:*
- 32 Conservation of common bird species in vineyards.

33 Abstract

Viticulture contributed to shape "cultural landscapes" in several regions over all the continents.
Recent farming intensification is causing landscape homogenization and biodiversity loss in
several of those areas, but knowledge about the impacts on biodiversity in vineyards is still
scarce.

Simplified agro-ecosystems resulting from intensification host mainly generalist and common
species, which still play a key role in ecosystems' regulation and in the provision of ecosystem
services.

41

42 We assessed the abundance of 11 common bird species at 47 linear transects in a vineyard-

43 dominated landscape in Trentino (NE Italy), in both spring and winter, and analysed

44 abundance variation in relation to three independent groups of predictors: landscape,

45 management and topographic-climatic variables.

In the majority of species (7), abundance was primarily or considerably affected by landscape
attributes. However, other 5 species were largely affected by management practices, often
with conspicuous seasonal differences. Overall, landscape and management heterogeneity
positively affected the abundance of 6 species.

50 Vineyard cover (and in particular the new *spalliera* trellising system) was negatively related to 51 the abundance of 6 species, with the strongest impacts in winter. On the contrary, the cover of 52 marginal habitats had major positive effects over 8 species.

53 Hedgerows, tree rows and dry stone walls, as well as traditional *pergola* vineyards and

54 landscape and management heterogeneity should be conserved or restored in viticultural

55 landscapes to promote the abundance of common bird species. This strategy would ensure the

56 maintenance of the ecosystem services they provide, while promoting the general

57 sustainability of the agroecosystem.

58

59 Keywords – abundance; commonness; hedgerows; marginal habitats; dry stone walls;

60 Trentino.

61 **1. Introduction**

Agricultural-driven land-use intensification is the most important cause of the loss of terrestrial
biodiversity at a global scale (Foley et al., 2011) and nowadays the reduction of this trend,
instead of its stabilization, must be the actual goal for conservation (Butchart et al., 2010).

65

Agricultural intensification acts at two distinct but interconnected spatial scales. At the local
(field) scale, it involves the intensification of farming practices (e.g. increasing fertilizer and
pesticide inputs, deep ploughing, massive use of machinery). At the landscape scale,
intensification causes homogenization and fragmentation through e.g. conversion of perennial
grassland-like habitats into arable fields, increasing field size, removal of marginal habitats,
resulting in highly simplified landscapes (Fahrig et al., 2011; Tscharntke et al., 2005).

72 Agri-environmental schemes (AESs) aim to counteract such negative effects of agricultural

intensification on ecosystems, by providing financial incentives to farmers adopting farming
practices with lower environmental impacts (Kleijn et al., 2006).

Landscape structure can explain much of the patterns of biodiversity in complex landscapes (i.e. those with >20% cover of semi-natural habitat, Batáry et al. (2011)), whereas in simpler landscapes management practices could have important effects on biodiversity (Chamberlain et al., 1999; Schmidt et al., 2005). As a consequence, general (and not specifically landscapeoriented) AESs could be poorly effective in complex landscapes, but pivotal in simpler ones (Batáry et al., 2011).

These simplified systems host mainly generalist and common species, defined as 'those that are abundant and widespread' (Gaston, 2010). Despite the low contribution to community richness, common species are exceptionally influential in determining many macroecological patterns and in providing ecosystem services (Gaston, 2011). As an example, birds provide fundamental services and economic benefits to humans, such as seed dispersal, pollination, biocontrol (Sekercioglu et al., 2004; Whelan et al., 2015).

A small proportional reduction in the abundance of a common species can result in the loss ofa large number of individuals, then dramatically impacting on ecosystems.

A lot of natural and anthropogenic factors could suddenly change a common species into a rare or threatened one (Gaston and Fuller, 2008), and today common species actually 'lie at the very heart of the biodiversity crisis' (Gaston, 2011). In Europe, avian abundance and biomass are declining due to depletion of common species (Inger et al., 2014), with farmland birds being amongst the most threatened ones (Donald et al., 2006).

In temperate regions, permanent crops such as vineyards, olive groves and fruit orchards
could host relevant populations of several common bird species (Brambilla et al., 2013; Rey,
2011). These crops are undergoing severe intensification (Caraveli, 2000), but there is limited
knowledge about their impacts on biodiversity, including farmland common bird species
(Balmford et al., 2012).

99 This is particularly concerning because permanent crops have been excluded from the 100 'greening' obligation introduced in the recent Common Agricultural Policy (CAP) 2013 reform, 101 which aim to reduce the impact of EU agriculture. Such an exemption for permanent crops 102 would hinder efforts to conserve biodiversity in these crops, which are often managed as 103 highly intensive monocultures (Pe'er et al., 2014).

104 Vineyards are an example of permanent crops in which management practices have a direct effect on landscape structure and, in turn, on biological communities (Bruggisser, Schmidt-105 106 Entling & Bacher, 2010; Nascimbene et al., 2013). In the past, viticulture had a preeminent role in creating impressive "cultural landscape" (Cohen et al., 2015; Kizos et al., 2012), 107 108 characterised by extensive and traditionally terraced areas (Petit et al., 2012). Nowadays, viticulture intensification is resulting in homogeneous monocultures (Martínez-Casasnovas et 109 110 al., 2010), determining a substantial reduction of natural habitats in the Mediterranean Biome (Viers et al., 2013). In this context, the landscape-mediated effect of viticulture on biodiversity 111 112 is likely to be relevant for conservation (Hilty & Merenlender, 2004; Isaia, Bona & Badino, 2006; Gillespie & Wratten, 2012), but it is far from being fully understood. 113

Within this study, we explored the effect of landscape and management characteristics of vineyards on several common avian species, in an area largely dominated by viticulture. We investigated several landscapes across a gradient of progressive intensification to understand how landscape traits and management factors shape the abundance pattern of common birds. 118 We expected that some common species may be affected by the availability of marginal, 119 natural and semi-natural habitat remnants. This could particularly apply to species which 120 cannot nest on vines, or to species foraging mostly in other habitats, or feeding on resources 121 not available in or below/above vines. Other species may be tied to traditional elements of 122 agricultural landscapes, e.g. hedgerows, dry stone walls, isolated large trees, which provide 123 nest-sites. Also management practices may be expected to affect bird abundance, by e.g. regulating food availability (e.g. via an effect of the intensity of phytosanitary treatment on 124 125 insectivorous species) or detectability (e.g. creating patches of bare ground where prey 126 detection is enhanced, e.g. Schaub et al. (2010)).

127

128 **2. Materials and Methods**

129

130 2.1. Study area

This study was carried out in Trento Province (South-eastern Alps, Northern Italy; Fig. 1a-b), a mostly mountainous area, where vineyards occur in the main valley floors and on the adjacent hilly sides, from 65 to 750 m asl. See Assandri et al. (2016a) for further details.

134

135 2.2. Model species, experimental design and bird counts

136 In this study we considered 11 common and widespread species in Italy (Nardelli et al., 2015). 137 Three species are commonly found in the study area both in the breeding and wintering seasons: blackbird Turdus merula, great tit Parus major and chaffinch Fringilla coelebs. Four 138 139 species are much more frequent in the breeding season: song thrush Turdus philomelos, blackcap Sylvia atricapilla, serin Serinus serinus and greenfinch Carduelis chloris. Four species 140 141 occur exclusively or predominantly in winter: dunnock Prunella modularis, wren Troglodytes troglodytes, Eurasian robin Erithacus rubecula and rock bunting Emberiza cia. 142 We counted these species along forty-seven 200-m long linear transects distributed across the 143 entire area covered by vineyards (Fig. 1c; Assandri et al., 2016) and within a 100-m buffer 144 145 around the transect, thus each census plot covered 7.15 ha. To avoid double counting of the

same individuals, the minimum distance between neighbouring plots was 300 m. Furtherdetails on bird counts are given in supplementary materials.

148

149 2.3. Environmental variables collection

150 Following our previous approach (Assandri et al., 2016a), we measured landscape,

151 management and topographic-climatic variables (Table 1) using the software QGIS (QGIS

152 Development Team, 2016) and through an accurate field validation for some variables.

153 Phytosanitary treatments are quite uniform as they are recommended by a central agricultural

154 institute, but there are differences in the use of synthetic insecticides, fungicides, fertilizers

and herbicides, which are allowed in conventional fields but not in organic ones. We then

156 quantified the amount of vineyards under conventional and organic management for each plot.

157 Certified organic agriculture in our study area is limited (<3% of vineyard area), but a

specifically targeted design allowed us to include a mean (± SD) cover of organic vineyard

159 equal to 13.9% ± 26.7 (range: 0-100 %).

160 We further distinguished vineyards according to two trellising systems occurring in the area: i)

161 pergola, the traditional system (about 80% of vineyards in the Province; Chemolli et al.,

162 2007), consisting of tall (up to >2 m) and spaced vines (up to 5 m between rows), supported

by poles and beams; ii) *spalliera*, the standard global system, with lower vines supported by

164 wires held between poles and with lower spacing (<2 m between rows).

165 Within these two systems, management is substantially the same, but mechanical harvesting 166 and pruning are impeded by the *pergola* structure.

167 Topographic variables (mean elevation and slope) were derived from a 1-m resolution

digital elevation model (DEM). We also calculated mean direct solar radiation for each plot on

169 21th June (for spring analysis) and 1st January (for winter) using r.sun function from software

170 GRASS 7.0.2 (Neteler et al., 2012), taking into account the shadowing effect of the

topography. We derived mean bioclimatic variables (BIO1-annual mean temperature; BIO12-

annual precipitation) from WorldClim (www.worldclim.org, Hijmans, Cameron, Parra, Jones, &

173 Jarvis, 2005) at a 30 arc-second resolution for each plot.

175 2.4. Statistical analyses

- 176 We grouped environmental variables into three categories of predictors: landscape,
- 177 management and topographic-climatic variables (Table 1).
- 178 We considered the cover of vineyard within the management predictors, in order to: i) correct
- 179 for vineyard cover into the plot when evaluating the effect of the management variables, ii)
- 180 reduce collinearity among landscape variables.
- 181 We placed the length of hedgerows and tree rows among management variables, because in 182 our study area their occurrence is fully determined by farmers' choices.
- 183 We applied the protocol for data exploration proposed by Zuur, Ieno, & Elphick (2010) for each
- group of predictors and applied log+1 transformation to apple, wood, urban and young
- 185 plantations to reduce the weight of outliers. Topographic-climatic variables were highly collinear
- and elevation and BIO12 were consequently discarded.
- 187 We ended up with 16 environmental variables belonging to three groups (Table 1). We
- 188 modelled separately their effect on each species/seasons. We used GLMs with a Poisson error
- distribution and a log-link function. Then, to evaluate whether Poisson distribution was
- 190 appropriate for our data, we calculated the dispersion statistic on the residuals and, in case of
- 191 overdispersion (> 1.5), we changed our distribution into a negative binomial one (Zuur et al.,
- 192 2013) implemented with R package MASS (Venables and Ripley, 2002).
- 193 Our dataset showed a strong spatial structure, and spatial autocorrelation could affect the
- results of regression analyses (Beale et al., 2010), so we performed the Moran's I test on
- regressions' Pearson's residuals with R ape package (Paradis et al., 2004). In case of
- 196 significant spatial autocorrelation we ran Poisson GLMMs with the R package glmmADMB
- 197 (Skaug et al., 2015) using the geographical area (a factor with 9 levels grouping neighbouring
- 198 plots, see Fig. 1c) as a random effect. Then we tested again for residuals' spatial
- autocorrelation and in all cases the GLMM procedure allowed us to remove it.
- 200 We worked within an information-theoretic approach (Burnham and Anderson, 2002) and we
- 201 built all possible models for each species/season/predictor group with the *dredge* function in
- the R package 'MuMIn' (Barton, 2015).

203 We then performed model averaging across models with AICc<2 within each group, obtaining

204 model-averaged coefficients, standard errors and relative variable importance (Johnson and

205 Omland, 2004) for each explanatory variable. We used the full-average option, which is the

206 most suited to determine which predictors have the strongest effect on the response variable

207 (Grueber et al., 2011). We then compared the AICc value of the most supported model

selected for each group to estimate the groups' relative importance.

209 For each species/season/predictor group, model validation and dispersion estimation were

210 performed on single models including all the variables comprised in the most supported (ΔAICc

211 < 2) models. All the analyses were performed with R version 3.2.0 (R Core Team, 2016).</p>

212 **3. Results**

The comparison of the AICc values of the most supported models of each group of predictors (Table 2), allowed an assessment of the relative importance of each group of predictors for each species/seasons. Coherently with the diversity of the birds species here considered, the importance of different types of environmental variables varied among species and seasons. 4 species were mainly affected by landscape variables: blackbird (both seasons), chaffinch and blackcap (spring) and great tit (winter). Dunnock and serin were similarly affected (ΔAICc<2) by landscape and by management, and by landscape and topographic-climatic variables,

220 respectively.

221 The abundance of great tit (spring), chaffinch and rock bunting (winter) mostly varied

according to management variables. Song thrush was affected similarly by management and

topographic-climatic features. Topographic-climatic variables better explained the abundance
patterns of 3 species: greenfinch (spring), robin and wren (winter).

Table 3 summarizes and tables S1, S2, S3 detail the effects of all the 16 environmental variables on the 11 species investigated.

Vineyard cover was the dominant habitat type and had negative effects on the abundance of 6
species; in winter, on robin (Fig. 2b), dunnock, wren and rock bunting and in spring on great
tit and blackcap (Fig. 2a). Only for chaffinch (both seasons) and serin, vineyard cover
promoted abundance.

Wood cover was selected in 10 out of 14 most supported models. In spring it had contrasting effects on species abundance, positive for blackcap, great tit and song thrush, and negative for blackbird, chaffinch, goldfinch and serin. In winter, wood cover effect was positive for dunnock, wren and rock bunting, negative for chaffinch.

The cover of herbaceous crops had a low importance, and its effect was negative for blackbird (both seasons), chaffinch and blackcap (spring), and positive for wren (winter); for great tit, the effect was positive in spring and negative in winter.

The cover of marginal habitats showed positive effects (and a relatively high importance) for 8 species, in particular in winter (e.g. Fig. 2c, e-f). As an example, when marginal habitat cover

is above 15%, the predicted Eurasian robin abundance in winter displays values above the

observed average abundance. Only song thrush was negatively affected by marginal habitats
(spring), whereas a quadratic relationship (positive for intermediate values of habitat cover)
was found for great tit (Fig. 2d).

The cover of intensive apple orchard showed positive effect on the abundance of both thrush species and greenfinch in spring; in winter, blackbird was the only species still positively affected, whereas great tit and chaffinch were negatively associated with apple orchards. Urban cover showed a positive effect on 7 species, and a negative effect on song thrush (spring) and chaffinch and rock bunting (winter).

249 The number of habitat patches had a generally positive (5 species, e.g. Fig. 2j) or quadratic 250 (serin) effect on bird abundance. As an example, when the number of habitat patches is above 251 3 per ha, the predicted great tit abundance in winter displays values above the observed 252 average abundance. Some relevant exceptions occurred (the two thrushes in spring and rock 253 bunting in winter, although for the latter the effect was secondary). The number of vineyard 254 patches affected blackbird abundance (quadratically in winter, negatively in spring), and had a 255 positive effect for great tit (both seasons), chaffinch (both seasons, see Fig. 2k for spring), 256 serin and dunnock, negative for robin.

Hedge and tree rows had positive effects on most species (7) in both seasons (e.g. Fig. 2g),
negative on song thrush (spring) and chaffinch (winter).

As an example, when hedge and tree rows length is above 400 m per plots (56 m/ha), the

260 predicted great tit abundance in spring displays values above the observed average

abundance. The cover of organic vineyards had negative effects on 4 species, and positive only

in the case of greenfinch. The effects were consistent both in spring and winter.

263 The cover of *spalliera* vineyards had negative effect on 6 species and the effects were

264 consistent across seasons. However, song thrush (spring) and rock bunting (winter) were

265 positively affected by them.

The occurrence of dry stone walls along vineyard parcels had negative effects during the breeding period on blackbird, chaffinch and serin and positive on blackcap (Fig. 2h) and great tit. As an example, when more than 60% of vineyards have dry stone walls along at least one of their margins, the predicted blackcap abundance in spring displays values above the

- observed average abundance. In winter the effect was positive for all the 7 species considered(e.g. Fig. 2i).
- 272 The cover of young plantations had negative effects in spring on blackbird and positive on
- 273 great tit, song thrush and chaffinch, negative effects in winter on blackbird, robin and dunnock
- and positive on chaffinch, wren and rock bunting.
- 275 Considering topographic-climatic variables, slope had negative effects in spring (on blackbird,
- chaffinch (Fig. 3b), serin and greenfinch) and positive for great tit and blackcap (Fig. 3c). In
- 277 winter its effect was positive on robin, dunnock, rock bunting, wren and great tit.
- 278 Solar radiation had a lower relative importance than other variables and showed positive
- effects on serin and greenfinch (spring; Fig. 3a) and robin (winter), and negative effects on
- 280 blackbird and chaffinch (spring) and on great tit and dunnock (winter).
- 281 The men annual temperature (BIO1) in spring had positive effect on blackbird, serin and
- greenfinch, negative on song thrush. In winter it had positive effect on the abundance of robin,
- 283 blackbird and great tit.

284 **4. Discussion**

285

286

The species considered in this study are mostly habitat generalists, supposed to have broad ecological requirements, which allow them to dwell in different habitats and to be common also human-shaped habitats such as intensive vineyards. Nevertheless, our results suggested that not all vineyards are equally suitable for those species, and that different landscape and management characteristics definitely affect their abundances.

292 We showed that the abundance of common avian species inhabiting vineyard agroecosystems 293 depends on a variety of environmental characteristics related to landscape characteristics, 294 management practices and local topographic and climatic variables, with some important 295 seasonal effects. This partially confirms previous findings at the community level in the same 296 area (Assandri et al., 2016a), thus suggesting that common birds could be reliable biological 297 indicators in this environmental system. Biodiversity patterns at the community level were 298 primarily affected by landscape attributes, with management still playing a role and 299 topographic-climatic variables having minor importance (Assandri et al., 2016a). Conversely, 300 individual species abundance could be affected not only by landscape characteristics, but also 301 by climatic-topographic traits and, especially, by management practices, which could have a 302 significant or even predominant effect.

The cover of vineyard had a negative (or irrelevant) effect in determining bird abundances. Only two species, chaffinch and serin, were favoured by this kind of crop, being probably well adapted to it (they are able to nest on vines and forage under them). Both species also showed a positive relationship with the number of vineyard patches, this suggesting that they are favoured by heterogeneity at the field-scale. The largely negative effect of vineyard cover is consistent with the its effect on the richness of the whole avian community in spring (Assandri et al., 2016a).

In our study system, landscape and management heterogeneity in vineyards were positively related with the abundance of most species, with common species mirroring again the pattern reported at the community level (Assandri et al., 2016a). The positive effect of heterogeneity on biodiversity in agricultural systems has been postulated for a long time (Benton et al., 2003; Fischer and Lindenmayer, 2007) and it has been reported also for vineyards (Barbaro et al., 2016; Gaigher and Samways, 2010; Steel et al., 2017; Verhulst et al., 2004). In fact,

317 the presence of habitats different from the vineyard and embedded into the matrix, allowed 318 the occurrence of species less adapted to this kind of habitat, i.e. which are not able to nest or 319 forage on (or under) the crop itself. This is the case of e.g. blackcap, which is favoured by 320 woods, urban areas and hedgerows. Similarly, the greenfinch visits vineyards for feeding, but 321 does not nest into them (Assandri et al., n.d.), and thus was favoured by the occurrence of 322 urban areas (within which it breeds in gardens), hedgerows and apple orchards. Even in apple 323 orchards, where greenfinches regularly nest, their abundance is enhanced by the presence of 324 natural/semi-natural habitats, as for other common species (Brambilla et al., 2015).

In winter, the majority of the species considered occurs in vineyards only if other habitats or structures exist (and accordingly the negative effect of vineyards was particularly evident). Marginal habitats, such as hedgerows, tree rows and small abandoned areas with scattered shrubs, are particularly important for several individual species, as they are for the entire community (Assandri et al., 2016a).

330 There is a general consensus on the importance of hedgerows, which have a key ecological role in a variety of agroecosystems (Baudry et al., 2000), including permanent crops (Castro-331 332 Caro et al., 2015). As a consequence, incentives (provided by e.g. AESs) frequently promote 333 the creation of hedgerow networks. However, the effect of hedgerows on biodiversity is 334 context-dependent. Hedgerow networks (or other forms of tree and shrub restoration) created in areas or ecosystems where they never occurred may cause declines of open-habitat 335 336 specialists (Assandri et al., 2016b; Besnard and Secondi, 2014; Pithon et al., 2016). 337 Conversely, in systems like the one we investigated, where permanent crops occur and hedgerows have a traditional landscape value, such elements must be definitely preserved and 338 339 possibly restored.

340 Dry stone walls, a distinctive and traditional element of several "cultural landscapes" shaped
341 by viticulture (Petit et al., 2012) , hardly had any noticeable effect at the community level

(Assandri et al., 2016a). In the present work we showed that they could be important in determining abundance patterns of common species, probably because they were generally associated with marginal elements, as well as with weeds. This probably also explains the positive effect found in spring on blackcap and great tit abundance. The latter species can also use dry stone walls as nesting site (pers. obs.). In addition, dry stone walls occur on sloping valley sides, and in winter could be associated with a milder micro-climate.

Organic management have no or negative effects (in particular in spring) on the majority of
species. This is a rather unexpected result considering previous findings in a variety of
agricultural systems, e.g. Tuck et al (2014), but it is consistent with other studies in the same
(Assandri et al., 2016a, n.d.) or in other viticultural areas (Brugisser et al., 2010; Rusch et al.,
2015).

353 We believe that the local characteristics and spatial arrangements of organic wine farming play 354 a key role in this sense. In Trentino organic farms cover a small extent and are isolated in a 355 matrix of conventional farms and in an overall complex landscape (sensu Batary et al (2011), in which organic farming is less expected to have positive effects on biodiversity. Moreover, in 356 357 the study area organic farming is quite intensive and phytosanitary treatments are generally more frequent than in conventional farming. Treatments are mostly based on the use of 358 359 copper, sulphur and pyrethrins instead of other synthetic chemicals. Nonetheless, sulphur and 360 copper had been reported to have negative effects on arthropods (Nash et al., 2010). In the study area, the occurrence of two fairly different trellising systems allowed for a 361 comparison of the effect of vineyard structure on species abundance. Spalliera vineyards, 362 363 recently introduced in Trentino viticulture, are subject to an intensive management, with high mechanization levels. This probably led to the negative effect of this trellising system on 364 365 several species here considered. In spring, this effect is due to the fact that the few common species breeding on vines (i.e. blackbird, chaffinch and serin) are favoured by the more 366 complex "tree-like" structure of pergola vineyards, which offer a higher availability of potential 367 breeding sites (Assandri et al., n.d.). In winter, *spalliera* vineyards are a "bare and poor" 368 369 habitat, without any structures apart from poles, wires and single-branch wines. This could 370 explain the general negative effect of this trellising system on most species in this season.

Rock bunting was an exception, as its abundance was promoted by *spalliera* cover. In winter this species exploits areas in proximity of rocky cliffs or dry stone wall-terraced systems, which, due to their harsh topography, are most suitable for *spalliera* vineyards. Moreover, it is the only open-habitat species considered in this study, and the more open appearance of *spalliera* probably better suited its needs.

The climatic-topographic models are generally less supported than the landscape and 376 377 management ones, but for some species these factors could be of high relevance: the 378 abundance of serin and greenfinch, as an example, were affected by both landscape and 379 climatic-topographic variables (both species preferred warm and sunny areas at lower slopes). Song thrush showed important differences when compared with the other species, being 380 381 negatively affected by the cover of marginal habitat, hedgerow length, dry stone walls and by 382 the number of patches, and positively by vineyard cover. We hypothesize that such a distinct 383 pattern was mainly driven by the strong positive preference of this species for apple orchards, 384 which mainly occur in valley floors, in very intensive and simplified agroecosystem. The link 385 with apple orchards was previously demonstrated in Trentino by Brambilla et al. (2013). Song 386 thrush did not avoid intensive vineyards; on the contrary, an apparent process of "spillover" seems to occur in the northern part of the study area, where the species tends to colonize 387 388 vineyards adjacent to apple orchards. This was also indirectly confirmed by the negative effect 389 of temperature (which is higher in the southern part of the study area) on the species 390 abundance.

391

392 5. Conclusions

Previous studies on biodiversity in vineyards were carried out at the community level (Bruggisser et al., 2010; Nascimbene et al., 2016; Pithon et al., 2016; Steel et al., 2017) or investigated the species-specific requirements of individual taxa of conservation concern (Arlettaz et al., 2012; Isenmann and Debout, 2000). Hence, this study is virtually the first attempt to investigate the basic ecological requirements of several common bird species in vineyards and to derive conservation implications from those results. Initiatives to promote the environmental quality of the wider landscape matrix are fundamental to maintain naturally common species and the invaluable ecosystem services they provide (Kleijn et al., 2006). Protected areascan support only a limited amount of the populations of common species (Gaston and Fuller, 2008), and this implies that farmers have a great responsibility in conserving common bird species in agricultural ecosystems (Guillem and Barnes, 2013).

Unfortunately, the recent CAP reform does not help conserve biodiversity in vineyards and other perennial crops (Pe'er et al., 2014). Recent 'spot' initiatives oriented towards a more sustainable viticulture (e.g., Sigwalt *et al.*, 2012) are too week or interest too limited areas to produce substantial effects at a broader level, and consequently should be strengthened (Viers et al., 2013). At the same time, policy-makers should promote the environmental quality through well designed and scientifically sounding AESs, which should compensate for the lack of 'green' prescription in the European regulation.

In our study system, some key features appear of critical importance when considering at the same time both the different environmental factors and the relative effect on common species (this study) and on avian communities (Assandri et al., 2016a). The conservation or restoration of marginal habitats and hedgerows or tree rows, the maintenance of other traditional elements such as dry stone walls and *pergola* vineyards, and the increase of heterogeneity at both the landscape and the field scale should be the focus of conservation initiatives targeted at biodiversity conservation in vineyards.

If a synergy among farmers, policy-makers and conservationists working on viticultural
systems will be achieved, broad positive effects on common bird species, and possibly on wider
biodiversity, have to be expected.

422

423 Acknowledgements

We are grateful to CTT (Fondazione Edmund Mach) for kind cooperation, in particular: F.
Ghidoni, F. Penner, M. Venturelli, M. Bottura. F. Bigaran (PAT) provided data on organic
farming. L. Ilahiane helped with fieldwork. A. Iemma and F. Ficetola helped with technical
issues and statistics. A. Galimberti provided useful advice.

- 429 References
- Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nusslé, S., Abadi, F., Braunisch, V., Schaub,
 M., 2012. New vineyard cultivation practices create patchy ground vegetation, favouring
 Woodlarks. J. Ornithol. 153, 229–238. doi:10.1007/s10336-011-0737-7
- Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2016a. Diversity in the monotony? Habitat
 traits and management practices shape avian communities in intensive vineyards. Agric.
 Ecosyst. Environ. 223, 250–260. doi:10.1016/j.agee.2016.03.014
- Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2016b. Land-use and bird occurence at
 the urban margin in the Italian Alps: implication for planning and conservation. North
 West. J. Zool. in press, e161601.
- Assandri, G., Giacomazzo, M., Brambilla, M., Griggio, M., Pedrini, P., n.d. Nest density, nestsite selection, and breeding success of birds in vineyards: Management implication for
 conservation in a highly intensive farming system. Biol. Conserv.
 doi:http://dx.doi.org/10.1016/j.biocon.2016.11.020
- Balmford, A., Green, R.E., Phalan, B., 2012. What conservationists need to know about farming. Proc. R. Soc. B Biol. Sci. 279, 2714–2724. doi:10.1098/rspb.2012.0515
- Barbaro, L., Rusch, A., Muiruri, E.W., Gravellier, B., Thiery, D., Castagneyrol, B., 2016. Avian
 pest control in vineyards is driven by interactions between bird functional diversity and
 landscape heterogeneity. J. Appl. Ecol. doi:10.1111/1365-2664.12740
- Barton, C., 2015. MuMIn: Multi-Model Inference. R package version 1.13.4.
- Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity
 effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci.
 278, 1894–1902. doi:10.1098/rspb.2010.1923
- Baudry, J., Bunce, R.G., Burel, F., 2000. Hedgerows: An international perspective on their
 origin, function and management. J. Environ. Manage. 60, 7–22.
 doi:10.1006/jema.2000.0358
- Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J., Elston, D.A., 2010. Regression analysis
 of spatial data. Ecol. Lett. 13, 246–64. doi:10.1111/j.1461-0248.2009.01422.x
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity
 the key? Trends Ecol. Evol. 18, 182–188. doi:10.1016/S0169-5347(03)00011-9
- Besnard, A.G., Secondi, J., 2014. Hedgerows diminish the value of meadows for grassland
 birds: Potential conflicts for agri-environment schemes. Agric. Ecosyst. Environ. 189, 21–
 27. doi:10.1016/j.agee.2014.03.014
- Brambilla, M., Assandri, G., Martino, G., Bogliani, G., Pedrini, P., 2015. The importance of
 residual habitats and crop management for the conservation of birds breeding in intensive
 orchards. Ecol. Res. 30, 597–604. doi:10.1007/s11284-015-1260-8
- Brambilla, M., Martino, G., Pedrini, P., 2013. Changes in Song thrush Turdus philomelos
 density and habitat association in apple orchards during the breeding season. Ardeola 60,
 73–83.
- Bruggisser, O.T., Schmidt-Entling, M.H., Bacher, S., 2010. Effects of vineyard management on
 biodiversity at three trophic levels. Biol. Conserv. 143, 1521–1528.
 doi:10.1016/j.biocon.2010.03.034
- 471 Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical 472 Information-Theoretic Approach. Springer Science & Business Media.
- Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A.,
 Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson,
 Chenery, A.M., Ceirke, J., Devideen, N.C., Dentener, F., Fester, M., Celli, A., Celleway,
- J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway,
 J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington,
- 477 F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Hernández Morcillo, M., Oldfield,
- T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-
- 479 Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010.
- 480 Global biodiversity: indicators of recent declines. Science 328, 1164–8.
 481 doi:10.1126/science.1187512
- 482 Caprio, E., Nervo, B., Isaia, M., Allegro, G., Rolando, A., 2015. Organic versus conventional 483 systems in viticulture: Comparative effects on spiders and carabids in vineyards and

- 484 adjacent forests. Agric. Syst. 136, 61-69. doi:10.1016/j.agsy.2015.02.009 485 Caraveli, H., 2000. A comparative analysis on intensification and extensification in mediterranean agriculture: dilemmas for LFAs policy. J. Rural Stud. 16, 231-242. 486 doi:10.1016/S0743-0167(99)00050-9 487 Castro-Caro, J.C., Barrio, I.C., Tortosa, F.S., 2015. Effects of hedges and herbaceous cover on 488 passerine communities in Mediterranean olive groves. Acta Ornithol. 50, 180-192. 489 490 doi:10.3161/00016454AO2015.50.2.006 Chamberlain, D.E., Wilson, J.D., Fuller, R.J., 1999. A comparison of bird populations on organic 491 492 and conventional farm systems in southern Britain. Biol. Conserv. 88, 307–320. 493 doi:10.1016/S0006-3207(98)00124-4 Chemolli, M., Rizzo, M., Bona, E., Tonon, C., 2007. Vigneti e aziende viticole. Terra Trent. 4, 494 495 12-18. 496 Cohen, M., Bilodeau, C., Alexandre, F., Godron, M., Andrieu, J., Grésillon, E., Garlatti, F., Morganti, A., 2015. What is the plant biodiversity in a cultural landscape? A comparative, 497 498 multi-scale and interdisciplinary study in olive groves and vineyards (Mediterranean
- 498 multi-scale and interdisciplinary study in olive groves and vineyards (Mediterranean
 499 France). Agric. Ecosyst. Environ. 212, 175–186. doi:10.1016/j.agee.2015.06.023
 500 Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of
- continent-wide impacts of agricultural intensification on European farmland birds, 1990–
 2000. Agric. Ecosyst. Environ. 116, 189–196. doi:10.1016/j.agee.2006.02.007
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena,
 G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in
 agricultural landscapes. Ecol. Lett. 14, 101–112. doi:10.1111/j.1461-0248.2010.01559.x
- 506 Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a 507 synthesis. Glob. Ecol. Biogeogr. 16, 265–280. doi:10.1111/j.1466-8238.2007.00287.x
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller,
 N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill,
 J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks,
 D.P.M., 2011. Solutions for a cultivated planet. Nature 478, 337–42.
- 512 doi:10.1038/nature10452
- Gaigher, R., Samways, M.J., 2010. Surface-active arthropods in organic vineyards, integrated
 vineyards and natural habitat in the Cape Floristic Region. J. Insect Conserv. 14, 595–
 605. doi:10.1007/s10841-010-9286-2
- 516 Gaston, K.J., 2011. Common Ecology. Bioscience 61, 354–362. doi:10.1525/bio.2011.61.5.4
- 517 Gaston, K.J., 2010. Valuing common species. Science 327, 154–155.
- 518 doi:10.1126/science.1182818
- Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology.
 Trends Ecol. Evol. 23, 14–19. doi:10.1016/j.tree.2007.11.001
- Gillespie, M., Wratten, S.D., 2012. The importance of viticultural landscape features and
 ecosystem service enhancement for native butterflies in New Zealand vineyards. J. Insect
 Conserv. 16, 13–23. doi:10.1007/s10841-011-9390-y
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in
 ecology and evolution: Challenges and solutions. J. Evol. Biol. 24, 699–711.
 doi:10.1111/j.1420-9101.2010.02210.x
- 527 Guillem, E.E., Barnes, A., 2013. Farmer perceptions of bird conservation and farming 528 management at a catchment level. Land use policy 31, 565–575. 529 doi:10.1016/j.landusepol.2012.09.002
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution
 interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
 doi:10.1002/joc.1276
- Hilty, J. a., Merenlender, A.M., 2004. Use of Riparian Corridors and Vineyards by Mammalian
 Predators in Northern California. Conserv. Biol. 18, 126–135. doi:10.1111/j.1523 1739.2004.00225.x
- Inger, R., Gregory, R.D., Duffy, J.P., Stott, I., Voříšek, P., Gaston, K.J., 2014. Common
 European birds are declining rapidly while less abundant species' numbers are rising. Ecol.
 Lett. 18, 28–36. doi:10.1111/ele.12387
- Isaia, M., Bona, F., Badino, G., 2006. Influence of Landscape Diversity and Agricultural
 Practices on Spider Assemblage in Italian Vineyards of Langa Astigiana (Northwest Italy).
 Environ. Entomol. 35, 297–307. doi:10.1603/0046-225X-35.2.297

- Isenmann, P., Debout, G., 2000. Vineyards harbour a relict population of Lesser Grey Shrike
 (Lanius minor) in Mediterranean France. J. für Ornithol. 141, 435–440.
 doi:10.1046/j.1439-0361.2000.00038.x
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol.
 19, 101–108. doi:10.1016/j.tree.2003.10.013
- Kizos, T., Plieninger, T., Harald, S., Petit, C., 2012. HNV permanent crops: olives, oaks, vines,
 fruit and nut trees, in: Oppermann, R., Beafoy, G., Gwyn, J. (Eds.), High Nature Value
 Farming in Europe 35 European Countries, Experiences and Perspectives. Verlag
 Regionalkultur, pp. 70–84.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D.,
 Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., SteffanDewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity
 benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243–257.
 doi:10.1111/j.1461-0248.2005.00869.x
- Martínez-Casasnovas, J.A., Ramos, M.C., Cots-Folch, R., 2010. Influence of the EU CAP on
 terrain morphology and vineyard cultivation in the Priorat region of NE Spain. Land use
 policy 27, 11–21. doi:10.1016/j.landusepol.2008.01.009
- Nardelli, R., Andreotti, A., Bianchi, E., Brambilla, M., Brecciaroli, B., Celada, C., Dupré, E.,
 Gustin, M., Longoni, V., Pirrello, S., Spina, F., Volponi, S., Serra, L., 2015. Rapporto
 sull'applicazione della Direttiva 147/2009/CE in Italia: dimensione, distribuzione e trend
 delle popolazioni di uccelli (2008-2012)., Serie Rapp. ed. ISPRA.
- Nascimbene, J., Marini, L., Ivan, D., Zottini, M., 2013. Management intensity and topography
 determined plant diversity in vineyards. PLoS One 8, e76167.
 doi:10.1371/journal.pone.0076167
- Nascimbene, J., Marini, L., Paoletti, M.G., 2012. Organic farming benefits local plant diversity
 in vineyard farms located in intensive agricultural landscapes. Environ. Manage. 49,
 1054–60. doi:10.1007/s00267-012-9834-5
- Nascimbene, J., Zottini, M., Ivan, D., Casagrande, V., Marini, L., 2016. Do vineyards in
 contrasting landscapes contribute to conserve plant species of dry calcareous grasslands?
 Sci. Total Environ. 545–546, 244–9. doi:10.1016/j.scitotenv.2015.12.051
- Nash, M.A., Hoffmann, A.A., Thomson, L.J., 2010. Identifying signature of chemical
 applications on indigenous and invasive nontarget arthropod communities in vineyards.
 Ecol. Appl. 20, 1693–1703. doi:10.1890/09-1065.1
- 575 Neteler, M., Bowman, M.H., Landa, M., Metz, M., 2012. GRASS GIS: A multi-purpose open 576 source GIS. Environ. Model. Softw. 31, 124–130. doi:10.1016/j.envsoft.2011.11.014
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: Analyses of Phylogenetics and Evolution in R
 language. Bioinformatics 20, 289–290. doi:10.1093/bioinformatics/btg412
- Pe'er, G., Dicks, L. V, Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich,
 M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns,
 T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F., Scott, A. V, 2014. EU
 agricultural reform fails on biodiversity. Science (80-.). 344, 1090–1092.
- 583 Petit, Č., Konold, W., Höchtl, F., 2012. Historic terraced vineyards: impressive witnesses of 584 vernacular architecture. Landsc. Hist. 33, 5–28. doi:10.1080/01433768.2012.671029
- Pithon, J.A., Beaujouan, V., Daniel, H., Pain, G., Vallet, J., 2016. Are vineyards important
 habitats for birds at local or landscape scales? Basic Appl. Ecol. 17, 240–251.
 doi:10.1016/j.baae.2015.12.004
- 588 QGIS Development Team, 2016. QGIS Geographic Information System. Open Source 589 Geospatial Foundation Project.
- 590 R Core Team, 2016. R: A language and environment for statistical computing.
- Rey, P.J., 2011. Preserving frugivorous birds in agro-ecosystems: Lessons from Spanish olive
 orchards. J. Appl. Ecol. 48, 228–237. doi:10.1111/j.1365-2664.2010.01902.x
- Rusch, A., Delbac, L., Muneret, L., Thiéry, D., 2015. Organic farming and host density affect
 parasitism rates of tortricid moths in vineyards. Agric. Ecosyst. Environ. 214, 46–53.
 doi:10.1016/j.agee.2015.08.019
- 596 Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S.,
- Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of bare ground as a staple
 commodity for declining ground-foraging insectivorous farmland birds. PLoS One 5,
 e13115. doi:10.1371/journal.pone.0013115

- Schmidt, M.H., Roschewitz, I., Thies, C., Tscharntke, T., 2005. Differential effects of landscape
 and management on diversity and density of ground-dwelling farmland spiders. J. Appl.
 Ecol. 42, 281–287. doi:10.1111/j.1365-2664.2005.01014.x
- 603 Sekercioglu, C.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. 604 Proc. Natl. Acad. Sci. 101, 18042–18047. doi:10.1073/pnas.0408049101
- Sigwalt, A., Pain, G., Pancher, A., Vincent, A., 2012. Collective Innovation Boosts Biodiversity
 in French Vineyards. J. Sustain. Agric. 36, 337–352. doi:10.1080/10440046.2011.654008
- Skaug, H., Fournier, D., Bolker, B.M., Magnusson, A., Nielsen, A., 2015. Generalized Linear
 Mixed Models using "AD Model Builder."
- Steel, Z.L., Steel, A.E., Williams, J.N., Viers, J.H., Marquet, P.A., Barbosa, O., 2017. Patterns
 of bird diversity and habitat use in mixed vineyard-matorral landscapes of Central Chile.
 Ecol. Indic. 73, 345–357. doi:10.1016/j.ecolind.2016.09.039
- Tscharntke, T., Klein, A.-M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape
 perspectives on agricultural intensification and biodiversity ecosystem service
 management. Ecol. Lett. 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. a., Bengtsson, J., 2014. Land-use
 intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis.
 J. Appl. Ecol. 51, 746–755. doi:10.1111/1365-2664.12219
- Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Fourth edition. Springer,
 New York.
- Verhulst, J., Báldi, A., Kleijn, D., 2004. Relationship between land-use intensity and species
 richness and abundance of birds in Hungary. Agric. Ecosyst. Environ. 104, 465–473.
 doi:10.1016/j.agee.2004.01.043
- Viers, J.H., Williams, J.N., Nicholas, K. a., Barbosa, O., Kotzé, I., Spence, L., Webb, L.B.,
 Merenlender, A., Reynolds, M., 2013. Vinecology: pairing wine with nature. Conserv. Lett.
 6, 287–299. doi:10.1111/conl.12011
- Whelan, C.J., Şekercioğlu, Ç.H., Wenny, D.G., 2015. Why birds matter: from economic
 ornithology to ecosystem services. J. Ornithol. 156, 227–238. doi:10.1007/s10336-0151229-y
- Zuur, A., Hilbe, J.M., Ieno, E.N., 2013. A Beginner's Guide to GLM and GLMM with R: A
 Frequentist and Bayesian Perspective for Ecologists. Highland Statistic.
- Zuur, A., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
 statistical problems. Methods Ecol. Evol. 1, 3–14. doi:10.1111/j.2041-210X.2009.00001.x

634 *Figure captions*

635

Fig. 1. Study area. A: Localization of Trento Province in Northern Italy. B: Vineyard cover in
Trento Province (in violet). C: position of the 47 study plots in Trento Province viticultural
district with the nine geographical areas used as levels in the GLMMs' random effect. Legend of
Figure 1c: 1) Piana Rotaliana; 2) colline di Lavis-San Michele; 3) Val di Cembra; 4) colline di
Trento; 5) Alta Vallagarina; 6) Mori; 7) Bassa Vallagarina; 8) Benaco; 9) Valle dei Laghi.

642 Fig. 2. Graphical representation of the effect of several landscape and management predictors on species abundance as predicted by the averaged models. Other predictors included in the 643 models are kept constant at their mean value. Dashed lines represent the 95% confidence 644 645 intervals of the mean. a) vineyard cover effect on blackcap abundance (spring); b) vineyard 646 cover effect on Eurasian robin abundance (winter); c) marginal habitat cover effect on great tit 647 abundance (spring); d) marginal habitat cover effect on great tit abundance (winter); e) 648 marginal habitat cover on Eurasian robin abundance (winter); f) marginal habitat cover on 649 dunnock abundance (winter); g) hedgerow length effect on great tit abundance (spring); h) 650 vineyard with dry stone walls effect on blackcap abundance (spring); i) vineyard with dry stone 651 walls effect on Eurasian robin abundance (winter); j) number of patches effect on great tit 652 abundance (winter); k) number of vineyard patches effect on chaffinch abundance (spring).

653

661

664

Figure 3. Graphical representation of the effect of several topographic-climatic predictors on species abundance as predicted by the averaged models. Other predictors included in the models are kept constant at their mean value. Dashed lines represent the 95% confidence intervals of the mean. a) solar radiance effect on greenfinch abundance (spring); b) slope effect on chaffinch abundance (spring); c) slope effect on blackcap abundance (spring).

660 Table captions

Table 1. List of variables used in the analysis. Variables were measured in a GIS environment and then checked/validated in the field at the end of the breeding season.

Table 2. Type of model and relative AICc of the best model for each combination of groups of predictors and species/seasons. Type of model - GLM p: generalized linear model with a

- 667 poisson error distribution; GLM nb: generalized linear model with a negative binomial error 668 distribution; GLMM p: generalized linear mixed model with a poisson error distribution. The 669 most supported winter topographic-climatic model for the chaffinch was the null model.
- Table 3. Synthetic representation of the effect of the environmental variables on
- 671 species'abundance. Legend: +: linear positive effect; -: linear negative effect; q: quadratic
- effect (positive for intermediate values, negative for low and high values). For more details on
- 673 models output see tables S1, S2, S3 in supplementary materials online.

674 Table 1

Acronym	Description	Mean ± SD							
Landscape variables									
Woods	% cover of woodlands (large majority of broadleaved woodlands)	6.2 ± 8.9 %							
Crops	% cover of croplands (mainly small fields and vegetable gardens; contain also extirpated wood crops)	2.3 ± 5.7 %							
Marginal	% cover of marginal habitats (field margins, hedgerows and tree rows, abandoned areas with scattered shrubs, roads)	14.2 ± 6.1 %							
Apple	% cover of intensive apple orchards	4.6 ± 9.4 %							
Urban	% cover of urban areas	2.7 ± 4.3 %							
Patches	Number of patches totally or partially overlapping with the plot	29 ± 11							
Management variables									
Vineyards	% cover of vineyards	64.0 ± 18.7 %							
Hedgerows	Length of hedgerows and tree rows in the plot defined as is Assandri <i>et al.</i> (2016)	318.0 ± 285.7 m							
Organic	% of organic vineyards into the plot (the remaining part is conventional)	13.9 ± 26.7 %							
Spalliera	% of <i>spalliera</i> vineyards into the plot (the remaining part is <i>pergola</i> vineyards)	18.3 ± 29.7 %							
Wall	% of vineyard into the plot with dry stone wall along at least one of their sides	46.9 ± 40.5 %							
Vineyard patches	Number of vineyard patches totally or partially overlapping with the plot	20 ± 9							
Young plantations	% of <i>young</i> vineyard plantation (<15 years) into the plot	30.2 ± 21.1 %							
	Topographic-climatic variables								
Slope		8.9 ± 7.8 °							
Solar radiance	Mean solar radiance on 1^{st} January and 21^{th} June	$1774 \pm 460 \text{ W/m}^2;$ 8610 ± 240 W/m ²							
BIO1	Mean annual temperature derived from Hijmans et al., 2005	11.6 ± 1.5 °C							

	Landscape model		Management m	odel	Topographic-climatic model			
	Type of model	AICc	Type of model	AICc	Type of model	AICc		
Blackbird spring	GLM nb	243.29	GLM nb	249.64	GLM nb	250.21		
Blackbird winter	GLM nb	251.22	GLM nb	262.13	GLM nb	263.29		
Great tit spring	GLM p	139.41	GLM p	135.54	GLM p	141.43		
Great tit winter	GLM p	186.16	GLM p	191.50	GLM p	200.05		
Chaffinh spring	GLM p	194.67	GLM p	197.03	GLM p	201.60		
Chaffinch winter	GLM nb	421.02	GLM nb	418.59	GLM nb			
Song thrush spring	GLMM p	148.69	GLMM p	132.66	GLMM p	132.64		
Blackcap spring	GLM p	136.45	GLM p	151.92	GLM p	143.29		
Serin spring	GLM p	178.80	GLM p	181.19	GLM p	177.79		
Greenfinch spring	GLM nb	145.82	GLM nb	145.82	GLM nb	142.65		
Eurasian robin winter	GLM p	188.51	GLM p	196.06	GLM p	186.18		
Dunnock winter	GLMM p	151.39	GLMM p	150.52	GLMM p	152.85		
Wren winter	GLMM p	147.28	GLMM p	144.17	GLMM p	139.37		
Rock bunting	GLM nb	224.94	GLM nb	220.26	GLMM p	225.63		

	Blackbird spring	Blackbird winter	Great tit spring	Great tit winter	Chaffinch spring	Chaffinch winter	Song thrush spring	Blackcap spring	Serin spring	Greenfinch spring	Eurasian robin winter	Dunnock winter	Wren winter	Rock bunting winter
Woods	-		+		-	-	+	+	-	-		+	+	+
Crops	-	-	+	-	-			-					+	
Marginal		+	+	q			-	+	+		+	+	+	+
Apple	+	+		-		-	+			+				
Urban	+	+		+		-	-	+	+	+	+	+		-
Patches	-		+	+	+	+	-		q		+	+	+	-
Vineyards			-		+	+		-	+		-	-	-	-
Hedgerows	+	+	+	+		-	-	+	+	+	+	+		
Organic	-	-	-	-				-	-	+				
Spalliera	-	-			-	-	+		-	-	-	-		+
Wall	-	+	+	+	-	+		+	-		+	+	+	+
Young plantations	-	+	+		+	+	+				-	-	+	+
Vineyard patches	-	q	+	+	+	+			+		-	+		
Slope	-		+	+	+	-		+	-	-	+	+	+	+
Solar radiance	-			-	-	-			+	+	+	-		
BIO1	+	+		+	+		-		+	+	+			

Table 3