

1 Giacomo Assandri^{a,b,*}, Giuseppe Bogliani^b, Paolo Pedrini^a, Mattia Brambilla^{a,c}

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3 **Species-specific responses to habitat and livestock management call for carefully targeted conservation**
4 **strategies for declining meadow birds**

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6 ^a MUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento, Italy.

7 ^b University of Pavia, Dept. of Earth and Environmental Sciences, Via Adolfo Ferrata 9, I-27100, Pavia, Italy.

8 ^c Fondazione Lombardia per l'Ambiente, Settore biodiversità e aree protette, Largo 10 luglio 1976 1, I-
9 20822, Seveso (MB), Italy.

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11 * Corresponding author at: MUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-
12 38123, Trento, Italy. e-mail: giacomo.assandri@gmail.com. telephone: +39 0461 270432.

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15 Short title: *Bird decline and conservation in meadowland*

16 **Keywords** - *Anthus trivialis*; grassland; heterogeneity; *Lanius collurio*; mowing; *Saxicola rubetra*.

17

18 **Abstract** – In recent decades, upland hay-meadows underwent large transformations due to the
19 modernization of livestock husbandry system. Such changes impacted on biodiversity, but their
20 consequences on the upper levels of the food web are largely unknown. Grassland specialists could
21 respond differently to landscape structure and management practices, and such potentially different
22 responses should be integrated into conservation and management strategies.

23 The concerning long-term decline of farmland birds is due to multiple factors. To elucidate the effect of
24 meadow characteristics on avian grassland specialists, we considered three declining bird species regularly
25 found in meadowlands.

26 We compared their mean densities at 63 landscape plots in the Italian Alps with that reported from other
27 studies and analysed their environmental preferences in relation to landscape (composition and structural
28 elements), management (meadow fertilization and mowing calendar), topographic (slope and elevation),
29 and spatial predictors. Shedding light on their ecological requirements, we identify possible causes of long-
30 term decline as well as conservation strategies for grassland specialists.

31 Mean territory density of ground-nesting species (whinchat, 0.75 territory/10 ha, and tree pipit, 0.42)
32 resulted lower than most other estimates obtained in the Alps; conversely, the density of the shrub-nesting
33 red-backed shrike (1.97) was comparable to that of many other Alpine areas. Meadow conversion into
34 other crops and the modern livestock husbandry (i.e. first mowing performed before the end of the third
35 week of June, made possible by meadow overfertilization) have likely contributed to regional depletion of
36 whinchat and tree pipit populations, especially below 900-1000 m asl.

37 Heterogeneous landscapes dominated by grassland, with large extents of unimproved meadows, close to
38 meadows interspersed with isolated trees, hedgerows and ecotones, could accommodate the ecological
39 preferences of multiple grassland specialists. As such landscapes have become increasingly rarer, the
40 remaining ones must be preserved via integrated plans for sustainable mountain development.

41 **Introduction**

42 In the last decades, European farmlands experienced a major biodiversity crisis due to agriculture
43 intensification and land conversion or abandonment. This is clearly exemplified by farmland bird
44 populations, which more than halved on the continent since 1980 and are thus considered amongst the
45 most threatened taxa (Gamero et al., 2017; Gregory et al., 2005; Kleijn, Rundlöf, Scheper, Smith, &
46 Tschardtke, 2011).

47 Among farmland systems, permanent grasslands cover about the 8% of European land and 35% of the
48 utilized agricultural areas (Smit, Metzger, & Ewert, 2008). Most of these grasslands are semi-natural
49 habitats, characterized by native plant communities, but managed to sustain livestock, and thus preserved
50 by mowing and grazing. Semi-natural grasslands are considered among the European landscapes richest in
51 biodiversity, and considerably contribute to the High Natural Value Farmland area of the continent (Veen,
52 Jefferson, De Schmidt, & Van Der Straaten, 2009).

53 In recent decades, the cover of permanent grassland dramatically decreased due to abandonment or
54 conversion into other (mostly agricultural and urban) land-uses (Assandri, Bogliani, Pedrini, & Brambilla,
55 2017c; Laiolo, Dondero, & Ciliento, 2004; MacDonald et al., 2000). In parallel, residual grasslands in most
56 regions underwent a strong management intensification (Humbert, Dwyer, Andrey, & Arlettaz, 2016).

57 Abandonment and intensification have been worsened by the European Common Agricultural Policy (CAP;
58 Donald et al., 2002), and both have had major negative impacts on grassland biodiversity (Monteiro, Fava,
59 Hiltbrunner, Della Marianna, & Bocchi, 2011; Vickery et al., 2001). Recent CAP environmental prescriptions
60 (i.e. greening measures included in the pillar I) have been considered unlikely to halt biodiversity loss in
61 grassland (Assandri, Bogliani, Pedrini, & Brambilla, 2019; Pe'er et al., 2014). Similarly, agri-environment
62 schemes, included in the CAP pillar II, although seem to have attenuated the decline of biodiversity in
63 farmland (e.g. contraction of farmland bird populations), did not stop it (Gamero et al., 2017).

64 Hay-meadows, along with pastures, constitute the most iconic and biodiversity-rich traditional
65 agroecosystems in the Alps (Agnoletti, 2013; Kampmann et al., 2008); however, they represent a real
66 conservation challenge, because they are undergoing deep management transformations, due to the
67 modernization of the traditional livestock husbandry, which has guaranteed the existence of grassland

68 ecosystems for millennia (Fischer et al., 2008; Henle et al., 2008). In fact, the widespread occurrence of
69 secondary grasslands in the Alpine region is associated with an extensive form of cattle husbandry, in which
70 cows used to spend 2-3 months in mountain pastures during summer and the other seasons in stables, fed
71 with the fodder retrieved from hay-meadows (Marini, Klimek, & Battisti, 2011; Monteiro et al., 2011). Since
72 the 1950, and more markedly in the last c. 40 years, the dairy sector in the Alps has been subject to huge
73 transformations, with a concentration of cattle in fewer, but larger, farms. These farms are highly
74 specialized and harbour bigger and more productive cows, largely fed with concentrated cereal feedstuff.
75 This change resulted in a reduction of the summer grazing (in particular that of lactating cows) in mountain
76 pastures, and in a much higher production of organic fertilizers, which are disposed on meadows as liquid
77 manure (Faccioni, Sturaro, Ramanzin, & Bernués, 2019; Marini et al., 2011). Concurrently, marginal and less
78 productive grasslands had been abandoned or converted into more profitable crops (Monteiro et al., 2011;
79 Zimmermann, Tasser, Leitinger, & Tappeiner, 2010). This dramatic transformation of the dairy sector in the
80 Alps was driven by multiple factors: social and cultural changes, technological innovation and policies, local
81 investments in mountain development (Marini et al., 2011; Tappeiner, Tappeiner, Hilbert, & Mattanovich,
82 2003).

83 These dramatic transformations impacted – and are still heavily impacting – on plant assemblages (Fischer
84 et al., 2008; Marini, Scotton, et al., 2008; Niedrist et al., 2009) and invertebrates (Andrey, Humbert,
85 Pernollet, & Arlettaz, 2014; Marini, Fontana, Scotton, & Klimek, 2008), and likely also on the upper levels of
86 the food webs (e.g. birds), although the impacts on these trophic level were scarcely addressed by studies
87 in the Alpine region (but see: Assandri et al., 2019; Britschgi, Spaar, & Arlettaz, 2006; Strebel, Jacot, Horch,
88 & Spaar, 2015).

89 Recent evidence suggests that intensification is rapidly affecting upland areas (e.g. in the Alps), which once
90 were considered as ‘farmland biodiversity hotspots’; therefore, their potential to act as refuges to
91 counteract farmland biodiversity crisis is vanishing (Archaux, 2007; Korner, Graf, & Jenni, 2017; Schmid,
92 Kestenholz, Knaus, Rey, & Sattler, 2018). An assessment of the effects of intensification on animal
93 biodiversity in these areas is therefore definitely needed (Strebel et al., 2015), and although scientific

94 evidence on this topic is now starting to accumulate, negative trends of mountain grassland bird species is
95 becoming more negative years by years (Lehikoinen et al., 2018).

96 Species taxonomically or functionally (i.e. belonging to the same guild or functional group) related could
97 contrastingly respond to landscape composition and configurations, and to agricultural pressure (Fourcade,
98 Besnard, & Secondi, 2017). Different grassland bird species, as an example, respond in different ways to
99 forest edges or hedgerows (Besnard & Secondi, 2014), being positively or negatively associated with them
100 in grassland-dominated landscapes. Such specific responses contribute to the dilution of the potential
101 effectiveness of specific conservation measures (e.g. agri-environment schemes; Besnard & Secondi, 2014;
102 Broyer, Curtet, & Chazal, 2014).

103 When addressing conservation of species sharing similar ecological preferences over a broad scale,
104 designing multi-species conservation strategies could thus be pivotal to correctly address the different
105 ecological preferences shown by different species at a finer scale. This requires the correct identification of
106 i) shared patterns (and potential conflicts) of habitat use, ii) response to landscape composition and
107 configuration and, perhaps even most relevant, iii) response to agricultural management.

108 To further develop this idea and suggest best management and conservation options for grassland
109 specialists, we considered three declining open-habitat bird species (tree pipit *Anthus trivialis*, whinchat
110 *Saxicola rubetra*, and red-backed shrike *Lanius collurio*) which are commonly found in landscapes
111 dominated by hay meadows in the Alps. We aimed (i) to evaluate their densities in this habitat, comparing
112 our results with similar results in other Alpine areas, (ii) to understand their environmental preferences
113 (related to landscape, topography and meadow management), (iii) to disentangle the putative
114 anthropogenic drivers responsible for their long-term decline, and (iv) to identify the practical implications,
115 in terms of landscape and management, for the conservation of these grassland specialists, which inhabit
116 the same environments but potentially have different fine-scale habitat requirements.

117

118 **Materials and methods**

119

120 ***Model species***

121 The three species considered by this study are regularly found (c.f. Assandri et al., 2019; Marti, 2014;
122 Strebel et al., 2015) in Alpine meadows.
123 In Europe, tree pipit underwent a 55% decline in the period 1980-2016. Similarly, the species is declining in
124 Italy and is regarded to have an “inadequate” (*sensu* Brambilla, Gustin, & Celada, 2013) conservation
125 status. Whinchat underwent a 86% decline in Europe in the period 1980-2016; in Italy it is declining and in a
126 “bad” conservation status. Red-backed shrike experienced a long-term trend of 34% in Europe in the period
127 1980-2016; it declined in Italy too, where it also has a “bad” conservation status. Data source:
128 <https://pecbms.info/trends-and-indicators/species-trends/> (European trends); Peronace et al. (2012), Rete
129 Rurale Nazionale & LIPU (2015), and Gustin, Brambilla, & Celada (2016) (conservation status in Italy).

130

131 ***Study area***

132 The study was performed in Trento province (NE Italy; approximatively: 45.67-46.51° N; 10.51-11.96° E).
133 Comprised within a wide elevation belt (65-3764 m asl), the province territory is mainly mountainous, with
134 only the 8.5% laying below 500 m, and 19.9% above 2000 m. Secondary grasslands (i.e. hay-meadows and
135 pastures) occur, interspersed with woodland, crops and urban areas, above 250 m and more commonly
136 between 800 and 2,000 m. Among these, hay-meadows cover roughly 200 km² (3.3% of the province
137 surface; 14.8% of the Utilised Agricultural Area; ISTAT, 2010) and are mostly found below 1600 m.
138 From 1990 to 2010, the overall surface of hay-meadows in Trentino almost halved (Provincia Autonoma di
139 Trento, 2017), while the number of livestock units slightly increased (at least between 2000-2010)
140 determining a considerable increase in stocking rate (La Notte et al., 2015; Scotton, Pecile, & Franchi,
141 2012). At low elevation (<1500 m asl) rural abandonment was lower than in other areas in the Alps, and in
142 recent years the changes in meadow cover were mainly due to the conversion into other crops, mostly
143 orchards and vineyards (Marini et al., 2011; Streifeneder, Tappeiner, Ruffini, Tappeiner, & Hoffmann,
144 2007). In 2010, 54927 Livestock Units were censused in the province, allotted over c.1400 farms (La Notte
145 et al., 2015).

146

147 ***Study design***

148 The three model species were surveyed along 63, 200m-long, linear transects, scattered over nine areas
149 representative of the meadow-dominated landscapes of Trentino, between 310 and 1565m asl. Average
150 distance among transect centroids was 41019 m (SD=20274 m; range=428-90416 m). Bird survey and
151 collection of environmental variables were performed within a 100 m-buffer from the transect (surface:
152 7.15 ha), as done in other studies conducted in agricultural landscapes (Assandri, Bogliani, Pedrini, &
153 Brambilla, 2016, 2017a; Brambilla, Ilahiane, Assandri, Ronchi, & Bogliani, 2017; Ribic, Guzy, & Sample,
154 2009). These 7.15-ha landscape plots (LP) became the sampling units of the study and were selected
155 according to a stratified design: 21 in meadow landscapes, which recently were partly converted into other
156 agricultural land-use (maize, fruit orchards, vineyards, horticultural crops, and greenhouses); 20 units in
157 intensive hay-meadows (for details on meadow intensification, see under the “Environmental predictors”
158 paragraph); finally, 22 units were dominated by extensive hay-meadows. Converted hay-meadows were
159 easily identified by examining recent aerial photographs. These three categories (extensive, intensive, and
160 converted) can represent quite well the management trajectories occurred in the last decades in grassland-
161 dominated landscapes in our study area (as well as several other areas in the Alps). In other words, we
162 studied the three target species in a specific time and in multiple sites chosen along a gradient of hay
163 meadow intensification; such an intensification gradient in meadow management mirrors the widespread
164 transformations, from extensive to intensive and then converted meadowland, occurred in the last c. 40
165 years. Therefore, we can take the variation in species occurrence/abundance along this gradient as a proxy
166 of the occurrence/abundance changes occurred in recent decades because of meadow intensification and
167 conversion. . This approach is known as “space-for-time substitution”, and it is a common routine in
168 ecological studies when long-term data are unavailable. It assumes that changes in space reflect those in
169 time: this is of course a simplification of the real patterns, but can help understand the impacts of
170 environmental changes on biodiversity (Pickett, 1989).

171

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173

Bird surveys

174 We carried out three visits during the 2017 breeding season (12-24.05; 13-23.06; 2-12.07) to survey birds at
175 each LP. Six to seven transects were surveyed per day, from dawn to a maximum of five hours after it
176 (5.30/6.00–10.30/11.00 a.m.), when bird activity is highest. Surveys were conducted by the same author
177 (GA), walking at a slow pace along transects and avoiding precipitations and strong winds. We changed the
178 census order across transects from one visit to the following one, to ensure variability in the census time
179 within the morning.

180 We mapped all the first contacts with every bird inside the 100-m buffer on updated aerial photographs
181 (scale 1:2500). Such a method is considered quite reliable and precise, because it forces the observer to pay
182 attention to the exact location of each individual, reducing the risk of double counts of the same birds and
183 easily avoiding those outside the plot. This is particularly true for visible species, as the ones here
184 investigated, which usually stand on exposed song-posts during the breeding season. From these counts we
185 obtained the number of territories per each LP, for each model species, based on reproductive and
186 territorial behaviour, interactions between individuals and simultaneous contacts (Assandri et al., 2018;
187 Broyer, Curtet, & Boissenin, 2012). We adopted a conservative approach, counting two (or more) territories
188 coexisting in the same LP only when we got simultaneous contacts with individuals performing territorial
189 behaviour in different sites. We calculated the average breeding density (number of territories/10 ha) of
190 each species within the sampled LPs, as overall value as well as after the exclusion from the computation of
191 the LPs with converted meadows. The LPs dominated by converted meadows indeed are likely to
192 represent, almost invariably, sites with strongly reduced suitability for all the target species.

193

194 ***Environmental predictors***

195 At each LP we recorded environmental variables belonging to three different sets: landscape (landcover
196 and structural characteristics), meadow management, and topography (Table 1). Landscape variables were
197 measured on aerial photographs validated and updated in the field. We calculated the relative cover of six
198 habitat categories: meadows, woodlands, urban areas, shrubland/fallows, traditional high-stem orchards,
199 and converted meadows (i.e. former meadows recently converted into other agricultural land-use, such as
200 arable crops, vineyards, intensive orchards, and greenhouses). Additionally, landscape structural elements

201 (i.e. length of hedgerows -with and without trees- and tree rows, number of isolated trees and shrubs)
202 were assessed.

203 Management variables were measured at the parcel scale (i.e. a meadow with a defined spatial
204 arrangement, plant community, and management characteristics). Overall, we distinguished 882 meadow
205 parcels. The intensification level of meadow management was assessed by a two-step procedure. First, we
206 attributed each parcel to one of the 16 meadow plant communities found in the study area (Provincia
207 Autonoma di Trento - Servizio Sviluppo sostenibile e aree protette, 2015; based on data 2013-2015). The
208 plant community is determined by the combined effects of local environment and meadow management,
209 thus could be considered as a good proxy of management intensity at the local scale (Scotton et al., 2012).
210 Second, we attributed the typologies to one of two categories: low intensification and high intensification.
211 Meadows under high intensification are species-poor meadows, highly fertilized ($85\text{-}420\text{ kg N ha}^{-1}\text{ year}^{-1}$),
212 mown 2-3 times/year. Low-intensive meadows are (plant) species-rich meadows, no or poorly fertilized (0-
213 $150\text{ kg N ha}^{-1}\text{ year}^{-1}$), subject to only 1 or, rarely, 2 cuts per year (Assandri et al., 2019; Scotton et al., 2012).
214 Additionally, at each LP we visually evaluated the grass height three times (coinciding with bird surveys) to
215 assess the mowing chronology during the bird breeding period. Each parcel was thus attributed to one of
216 the following two categories: early mown or late mown meadows, according to mowing taking place before
217 (one or two times) or after the end of the third week of June. Finally, the percentage surface of high-
218 intensive and that of early mown meadows occurring in each LP (referred to the overall meadow cover)
219 were chosen to be used as management predictors in the analyses and that of low-intensive and late mown
220 discarded (as complementary and perfectly collinear with the other two).

221 Topographic variables (i.e. mean slope and mean elevation) were derived for each LP from a 1-m resolution
222 digital elevation model.

223

224 ***Spatial predictors***

225 We accounted for possible spatial autocorrelation by mean of a fourth category of predictors (i.e. Moran's
226 eigenvector maps - MEMs; Dray, Legendre, & Peres-Neto, 2006). MEMs are flexible predictors, capturing

227 spatial effects at multiple spatial scales, which are used in regression models to account for spatial
228 autocorrelation (Borcard, Gillet, & Legendre, 2011).

229 To build MEMs we used the data-driven approach proposed by Dray et al. (2006) and adopted by Borcard
230 et al. (2011), proceeding as follow: i) we built a connectivity matrix based on centroid coordinates of each
231 LP using Delaunay triangulation to define neighbouring locations (e.g. Sattler et al., 2010); ii) we weighted
232 the connectivity matrix by means of this function based on the Euclidean distance among the sites: $f=1-$
233 $(d/d_{max})^\alpha$, where d is a distance value, d_{max} is the maximum value in the distance matrix, and α is set to
234 vary from 2 to 10; iii) we calculated Moran's eigenvectors and eigenvalues by means of the function `test.W`
235 in the R package *adespatial* (Dray et al., 2017), which also test different values of the f parameters and
236 return the most supported ones (with the lowest AICc).

237 In the subsequent analyses we included as spatial predictors (MEMs) the eigenvectors with positive
238 eigenvalues (representing positive spatial autocorrelation) selected according to the best model identified
239 by the `test.W`.

240

241 ***Statistical analyses***

242 We separately tested the effect of each group of environmental and spatial (MEMs) variables on the
243 number of territories of the three model species in each LP by means of Generalized Linear Models (GLMs).
244 This approach was adopted because information embedded in different sets of variables partially
245 overlapped (for similar approaches see Coudrain et al. (2010); Assandri et al. (2017b)). We used Poisson
246 error distribution for the red-backed shrike and the whinchat (which have number of territories/LP ranging
247 from zero to five) and a Bernoulli error distribution (with data converted in 0-1) for the tree pipit, as its
248 territory count could be easily approximated to simple presence-absence (only five LPs included two
249 territories, no LPs more than two).

250 We left out from the landscape analysis meadow cover due to high multi-collinearity (GVIF = 40.39). All the
251 explanatory variables were standardized before analyses. Poisson final model residuals meet the
252 assumption of overdispersion parameter ≈ 1 (Zuur, Hilbe, & Ieno, 2013).

253 For model selection, we adopted an information-theoretic approach (Burnham & Anderson, 2002) using
254 the *dredge* function in the R package MuMIn (Barton, 2015) to build all the possible models for each set of
255 explanatory variables separately. Models were ranked based on the relative value of Akaike's Information
256 Criterion corrected for small sample size (AICc) and the most parsimonious models ($\Delta AICc \leq 2$) were
257 selected. We then carried out model averaging, considering these most supported models within each
258 group of predictors, obtaining model-averaged coefficients, their relative SEs, and the relative variable
259 importance (Johnson & Omland, 2004) for each explanatory variable applying the "zero method" (*sensu*
260 Grueber et al., 2011). In this process, 'uninformative parameters' (Arnold, 2010), i.e. the variables included
261 only in models comprising more parsimonious nested models, were discarded (Richards, 2008; Richards,
262 Whittingham, & Stephens, 2011).

263 Spatial predictors were included in the analyses only when at least one of the other three groups of
264 parsimonious models presented significant spatial autocorrelation in the Pearson's residuals, assessed by
265 means of Moran's I test (run with R *ape* package; Paradis, Claude, & Strimmer, 2004).

266 We finally applied variation partitioning to disentangle the independent and joint fraction of variation of
267 the response variables explained by different sets of predictors (Legendre, Legendre, Legendre, &
268 Legendre, 2012). We performed VP on parsimonious models (i.e. simplified models resulting from model
269 selection) (Peres-Neto and Legendre, 2010), using likelihood ratio-adjusted pseudo- R^2 as the goodness-of fit
270 measure of variation explained (Coyle & Hurlbert, 2016; Nagelkerke, 1991). All the analyses were
271 performed with R version 3.4.1 (R Core Team, 2017).

272

273 **Results**

274 Analyses were based on the following number of territories: 19 for tree pipit (range: 0 to 2 per LP; density:
275 0.42 territory/10 ha - 0.57 territory/10 ha excluding LPs with converted meadow cover); 89 for red-backed
276 shrike (range: 0-5; density: 1.97 territory/10 ha - 2.35 territory/10 ha excluding LPs with converted meadow
277 cover); 34 for whinchat (range: 0-5; density: 0.75 territory/10 ha - 1 territory/10 ha excluding LPs with
278 converted meadow cover), of which 4 were defended only in May and then deserted and were thus
279 discarded from territory count for subsequent analyses.

280 Most parsimonious models ($\Delta AICc \leq 2$) on the effect of environmental and spatial predictors on the number
281 of territories/occurrences for the three species are summarized in Tables S1, S2, S3.

282 Tree pipit occurrence was positively related with the number of isolated trees and elevation (Fig. 1a), and
283 negatively with the cover of early mown meadow (Fig. 1b). The negative associations of tree row and
284 hedgerows without trees length and of orchard, urban, woodland and converted meadows cover were less
285 supported: although such variables were selected in the set of most supported models, their estimates had
286 confidence intervals encompassing zero (Table 2).

287 The number of whinchat territories was negatively associated with woodland cover and with the cover of
288 early mown meadows (Fig. 1c), with the number of isolated trees, and with the length of hedgerows
289 without trees, and positively with elevation (Fig. 1d). The negative association with converted meadows
290 cover was less supported; although this variable was selected in the set of most supported models, its
291 estimates had confidence intervals encompassing zero (Table 3).

292 For red-backed shrike, the number of territories was positively related with the length of hedgerows
293 without trees (Fig. 1e) and with the number of shrubs (Fig. 1f). The negative associations with the
294 converted meadows, and the positive ones with the shrubland/fallow covers and slope, were less
295 supported (selected in the set of most supported models, but with estimates with confidence intervals
296 encompassing zero; Table 4).

297 For tree pipit occurrence, all sets of environmental predictors had a high explanatory power, with just
298 20.28% of variation unexplained. The variation partitioning showed that all the three sets had a comparable
299 importance in explaining the variation; however, landscape and management (only early mown meadow
300 cover in this case) ones had fraction uniquely explained (17.34% and 9.60% respectively), whereas
301 topography (only elevation here) had not. The structured (shared) portions of variation explained by more
302 than a set of predictors were conspicuous, specifically the component shared among all the three sets,
303 suggesting a complex association of the species to the environmental factors investigated (Fig. 2a). For
304 whinchat abundance, management and topographic components (also in this case, only early mown
305 meadow cover and elevation, respectively) mostly explained variation shared with the landscape and the
306 spatial component, which conversely also explained unique fractions of variation (16.46% and 12.42%,

307 respectively). The fraction jointly explained by all the four sets was conspicuous (20.9%). Overall, the four
308 sets of predictors explained an important quota of variation (84.56%) (Fig. 2b).
309 For red-backed shrike abundance, the total variation explained was lower (41.25%) than for the other
310 species, with a relevant contribution of landscape and, to a lesser extent, spatial component. Topography,
311 which in this case was represented only by slope, explained only a modest 5%, mostly shared with the
312 other components. The fraction structured among all the three sets was low (3.55%) (Fig. 5c). Notably, the
313 best management model for this species was the null model, thus this set was not included in the variation
314 partitioning, being irrelevant to explain variation pattern.

315

316 **Discussion**

317

318 The estimates of territory density obtained from this study, when compared to other studies performed in
319 the Alps (Table 5), suggest a dramatic status for the whinchat and the tree pipit in the study region.
320 Although caution is necessary when comparing bird densities obtained from different studies, which are
321 likely to have been carried out with different methods, in different habitats, and during different periods,
322 such a comparison may be useful for a first appraisal of the species' status in the study area. The mean
323 whinchat density of 1 territory/10 ha (obtained excluding all LPs with some converted meadows, which are
324 completely avoided by the species) is lower when compared with the majority of other density estimates
325 obtained in the Italian, Swiss and French Alps. Similarly, the mean density of tree pipit, equal to 0.57
326 territory/10 ha (obtained excluding all LPs with some converted meadow), is comparable with the lowest
327 densities observed at other Alpine study areas in Italy, Germany, and Switzerland (Table 5). Conversely, the
328 red backed shrike density of 2.35 territory/10 ha (or 1.97 territory/10 ha including all LPs with some
329 converted meadows) appears to be in line with the densities recorded in other Alpine contexts in Italy and
330 Switzerland, although definitely lower than the higher densities found in optimal sites (B(Table 5).
331 Meadow conversion into other crops is a driver of habitat loss and fragmentation, which have a recognized
332 negative effect on biodiversity (Fahrig, 2003; Fischer & Lindenmayer, 2007). In this study, territory densities
333 for all the three species were definitely higher when excluding the landscape plots with converted

334 meadows, with the extreme example of the whinchat, which was completely absent from partly converted
335 landscapes. The cover of converted meadow was always included with a negative effect in the set of the
336 most supported models, and this is in accordance with similar results on the whole avian community of hay
337 meadows in the region, supporting the evidence that partial conversion of meadows into other crops
338 determined the reduction, and finally the disappearance, of grassland specialists from the community
339 (Assandri et al., 2019).

340 Considering meadow management, whinchat abundance and tree pipit occurrence were negatively
341 associated with the cover of early mown (cut before the third week of June) meadow. For the whinchat, the
342 negative association with earlier mowing, which determines high levels of nest loss or direct impact on
343 female and nestling survival, was widely recognized as a major driver of decline in a number of studies
344 (Britschgi et al., 2006; Broyer, 2009; Gruebler et al., 2008; Gruebler, Schuler, Spaar, & Naef-Daenzer, 2015;
345 Müller, Spaar, Schifferli, & Jenni, 2005). On the other side, for tree pipit this represents a new finding. The
346 density of both species was positively associated with elevation; this was expected because at higher
347 elevation meadows are mown later in the season, allowing grass-nesting species to complete their breeding
348 cycle (Assandri et al., 2019; Brambilla & Pedrini, 2011). In the study area, whinchat was not found below
349 930 m asl, and tree pipit below 1050 m. These lower elevation bounds depict a very different situation from
350 the one found less than 30 years ago (1986-1995), when both species regularly bred below 1000 m and
351 occasionally even below 500 m (Pedrini, Caldonazzi, & Zanghellini, 2005). Our results suggest that the
352 recent dairy sector transformations, and the associated modifications of meadow mowing calendar, have
353 likely turned once favourable habitats for whinchat and tree pipit (and likely also for other species with
354 similar ecological requirements) into unfavourable ones, probably wiping out entire local populations of
355 these once common grassland species. Similar results were reported from other studies. In Switzerland,
356 Germany, Austria, and France, whinchat almost disappeared from lowland (Müller et al., 2005). Broyer
357 (2009) set at 1200 m the upper elevation limit of the negative influence of mowing on the whinchat in
358 France, considering the meadow located in the elevation interval of 1000-1200 m asl as a possible sink for
359 the species. The same author suggested that the period in which the 80% of the juvenile are fledged in the
360 belt of 1200-2000 is between July 10-20, whereas Müller *et al.* (2005) for Engadine suggested that the 75%

361 of juvenile have fledged by the 30 June - 4 July at 1160 m. Tome and Denac (2012) found that, 22 days after
362 hatching, 80% of the nestlings are safely fledged and are able to fly away from mowing machines; on this
363 basis, Strebel et al. (2015), in a study conducted in Valais (1350-1550 m), suggest that 80% of the nestlings
364 are safely fledged by 6 July. Similarly, tree pipit disappeared from elevation below 1000 m in several Swiss
365 cantons since the second half of the '60, in particular from meadows, possibly due to modification in
366 mowing regimes and overfertilization, although clear evidence of the mechanism(s) underlying this process
367 lacks (Glutz von Blotzheim, 2000; Marti, 2004, 2014).

368 The overall low densities recorded also above 1000 m in our study could confirm concerns that farmland
369 "Alpine refuges" are no longer acting as true refuges for farmland birds (Archaux, 2007; Korner et al., 2017).
370 In-field meadow intensification level (based on meadow typology and hence on liquid manure disposed on
371 meadows) for all the species was never selected in the most supported models, possibly suggesting that
372 this variable is less relevant than others, and in particular than mowing regime, in determining patterns of
373 occurrence and abundance of the target species. However, overfertilization and mowing chronology are
374 strictly related in a positive feed-back, as the use of high amount of fertilizers allow to increase meadow
375 productivity and also to anticipate mowing, increasing the number of cuts per year, sustaining large
376 number of (more productive) cows, which in turn produce more manure that is disposed on meadows,
377 further increasing their productivity (Assandri et al., 2019; Scotton, Sicher, & Kasal, 2014). Considering two
378 studies conducted in the Swiss Alps on whinchat, Britschgi et al. (2006) suggested that the species is
379 negatively affected by the joint effect of mowing and arthropod reduction due to meadow intensification;
380 Strebel et al. (2015) did not find such an effect, suggesting that, in an early stage of intensification, early
381 mowing is the most relevant threat to the species. For tree pipit, Glutz von Blotzheim (2000) suggested that
382 overfertilization was the cause of the disappearance of the species from hay-meadows in Central
383 Switzerland; however, Marti (2004) found that below 840 m the species disappeared also from unimproved
384 meadows.

385 Isolated trees are recognised keystone structures in a wide range of landscapes worldwide (Manning,
386 Fischer, & Lindenmayer, 2006; Prevedello, Almeida-Gomes, & Lindenmayer, 2017) and their importance for
387 birds in grassland landscape is well known (Jakobsson & Lindborg, 2017). Number of isolated trees is the

388 only landscape predictor showing a significantly positive association with tree pipit occurrence in our study
389 area. Tree pipit is an ecotone species (Laiolo, 2004) commonly found in semi-open and open landscapes, if
390 enough song posts (e.g. isolated trees) are available (Moga, Hartel, & Öllerer, 2009; Schwarz et al., 2018).
391 This explains the importance of these landscape structural elements for the species, contrasting with the
392 landscape-scale preference of whinchat, which, being mostly an open-habitat specialist, was negatively
393 associated with isolated trees, hedgerows, and woodland cover. Conversely, the red-backed shrike was
394 positively associated with the extension of hedgerows without trees and isolated shrubs (also see
395 Brambilla, Rubolini, & Guidali, 2007; Brambilla et al., 2009; Morelli, 2012). Hedgerows with trees (and tree
396 rows) were not selected in the most parsimonious models for the species, suggesting that their periodic
397 management, to avoid tree species to take over, could benefit the species.

398 Variation partitioning showed that patterns of tree pipit and whinchat occurrence/abundance are likely
399 mediated by joint influence of multiple predictors. Landscape and management predictors explain the
400 higher amount of variation (in the case of whinchat, along with spatial patterns). However, most of
401 'landscape' best predictors (i.e. number of isolated trees, hedgerow length) are influenced by the
402 agricultural management. The same applies to red-backed shrike, which abundance, in contrast, is not
403 influenced by in-field meadow management practices (fertilization, mowing), at least at the working scale
404 we considered. This species is the only one, out of the three here considered, listed in the Annex I of the EU
405 Birds Directive 2009/147/EC (i.e. a species for which Member States are obliged to implement special
406 conservation measures); however, in the Alpine meadows investigated in this study, it has a less worrying
407 status than the other two species, although being negatively associated with meadow conversion and
408 landscape simplification.

409

410 **Conclusions**

411 Even if this study confirms the importance of in-field meadow management (and specifically of time of
412 mowing) for ground-nesting grassland species (i.e. whinchat and tree pipit), it also highlights several
413 contrasts in species-specific ecological preferences in three species generally considered as open-habitat
414 dwellers, making the challenge of grassland bird conservation even more challenging. Specifically, in Alpine

415 meadow-dominated landscapes, the whinchat emerged as a ‘pure grassland-dweller’, negatively associated
416 with any element breaking grassland continuity, trees and hedgerows included. In contrast, trees and
417 hedgerows are structural elements essential for tree pipit and red-backed shrike, respectively. From a
418 conservation and landscape planning perspective, this pattern highlights the importance of maintaining
419 landscape scale heterogeneity to conserve multiple species also in upland hay meadows, which are now
420 facing the negative impacts of intensification experienced by lowland in the past decades (Graf, Muller,
421 Jenny, & Jeny, 2014). This could be achieved by boosting the maintenance of areas of pure unimproved
422 meadows next to meadows interspersed with isolated trees, hedgerows, and ecotone areas.

423 Preserving the heterogeneity of traditional landscapes in the Alps, and in upland areas in general, and then
424 the associated high level of biodiversity, could be easier than elsewhere because mountains are generally
425 complex in their geography and topography, favouring natural heterogeneity of environmental gradients,
426 climate, and, consequently, of management practices too. However, targeted plans for sustainable
427 mountain development are urgently needed. They should integrate EU policies (e.g. “green” options
428 included in CAP “Pillar 1” and Rural Development Plans), self-sustaining micro-economies based on high-
429 quality dairy products, and sustainable recreational and tourist activities. Biodiversity should be the target
430 of these plans, and several virtuous experiences suggest that it is possible. In the Netherlands, Birdlife has
431 started working with dairy producers in order to conserve the endangered black-tailed godwit (*Limosa*
432 *limosa*), a meadow-nesting bird species, iconic of the Dutch farmland. There, biodiversity-rich farms are
433 paid off by biodiversity-friendly dairy product profits, agri-environment schemes and ecotourism. Dairy
434 producers and farmers are starting to be convinced that biodiversity should be at the heart of their
435 sustainability programs, and this can also be a successful part of their business model (Gerritsen, 2018).
436 This success feeds the hope for other contexts, including the currently vanishing Alpine meadow birds.

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443

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729

730 **Table 1** List of environmental predictors used in the analysis and their mean value and range. N=63
 731

Variable name	Description	Mean value (and range)
<i>Landscape</i>		
woodlands	% cover of woodlands	4.1 (0 - 26.5)
urban	% cover of urban areas	2.2 (0 - 15.5)
shrublands	% cover of shrublands/fallows	2.7 (0 - 14.2)
orchards	% cover of traditional high-stem orchards	1.8 (0 - 12.1)
converted meadows	% cover of former meadows recently converted in other agricultural land-use (i.e. arable crops, vineyards, intensive orchards, and greenhouses)	15.0 (0 - 73.4)
hedgerows with trees	length of hedgerows with trees (m)	107.8 (0 - 668.8)
hedgerows	length of hedgerows without trees (m)	95.4 (0 - 640.5)
tree rows	length of tree rows (m)	90.6 (0 - 947.7)
trees	number of isolated trees	6 (0 - 27)
shrubs	number of isolated shrubs	3 (0 - 14)
<i>Management</i>		
early mown	% of early mown meadows (before the end of the fourth week of June)	56.1 (0 - 100)
high-intensive	% of high-intensive meadows	54.9 (0 - 100)
<i>Topography</i>		
elevation	mean elevation (m)	976 (312 - 1565)
slope	mean slope (°)	9.6 (1.2 - 25.3)

732

733 **Table 2** Model averaged standardized parameters (β), standard errors (SE), and relative variable importance of predictors ($\sum w_i$;
734 measured considering the sum of the Akaike weights over the most supported models in which that variable appears) derived from
735 the most supported (based on models with $\Delta AICc < 2$) environmental and spatial models for the occurrence of tree pipit *Anthus*
736 *trivialis*. 95% confidence intervals (C.I.) for the parameter estimates are given; in bold, the parameters in which confidence intervals
737 do not include zero. Covariates are ranked according to cumulative weights. See methods for details. N=63
738

	β	SE	$\sum w_i$	C.I.
Landscape				
intercept	-2.81	0.88	-	-4.59 – -1.04
trees	1.57	0.61	1	0.34 – 2.79
tree rows	-1.43	1.61	0.57	-4.67 – 1.74
orchards	-1.66	1.33	0.81	-4.31 – 0.99
hedgerows	-1.08	1.26	0.61	-3.59 – 1.41
urban	-0.20	0.50	0.23	-1.20 – 0.78
woodland	-0.15	0.40	0.19	-0.94 – 0.63
converted meadows	-0.20	0.51	0.19	-1.21 – 0.80
Management				
intercept	-2.61	0.84	-	-5.01 – -1.37
early mown	-2.34	0.71	1	-4.31 – -1.24
Topography				
intercept	-2.21	0.55	-	-3.49 – -1.27
elevation	2.38	0.65	1	1.29 – 3.94

739

740 **Table 3.** Model averaged standardized parameters (β) standard errors (SE), and relative variable importance of predictors ($\sum w_i$;
741 measured considering the sum of the Akaike weights over the most supported models in which that variable appears) derived from
742 the most supported (based on models with $\Delta AICc < 2$) environmental and spatial models for whichat *Saxicola rubetra* number of
743 territories. 95% confidence intervals (C.I.) for the parameter estimates are given; in bold, the parameters in which confidence
744 intervals do not include zero. Covariates are ranked according to cumulative weights. See methods for details. N=63
745

	β	SE	$\sum w_i$	C.I.
Landscape				
Intercept	-5.67	5.00	-	-22.82 – -2.19
trees	-0.56	0.28	1	-1.18 – -0.07
woodlands	-0.89	0.35	1	-1.68 – -0.29
converted meadows	-6.42	7.33	1	-20.79 – 7.93
hedgerows	-2.24	0.78	1	-4.00 – -0.91
Management				
early mown	-1.30	0.29	1	-1.66 – -0.64
Topography				
elevation	0.64	0.18	1	0.28 – 1.02
Space				
MEM10	-2.00	0.52	1	-3.04 - -0.95
MEM11	0.84	0.37	1	0.09 - 1.59
MEM2	1.17	0.47	0.76	-0.38 – 2.17
MEM20	-0.47	0.23	0.89	-0.95 – 0.10
MEM23	0.88	0.37	1	0.14 – 1.62
MEM24	-0.50	0.28	0.38	-0.79 – 0.40
MEM3	-1.71	0.51	1	-2.75 – -0.75
MEM5	2.40	0.64	1	1.11 – 3.69
MEM9	-1.97	0.64	1	-3.26 – -0.69
MEM19	0.86	0.46	0.57	-0.60 – 1.58
MEM8	-0.93	0.41	0.24	-1.10 – 0.65

746

747 **Table 4.** Model averaged standardized parameters (β), standard errors (SE), and relative variable importance of predictors ($\sum w_i$;
748 measured considering the sum of the Akaike weights over the most supported models in which that variable appears) derived from
749 the most supported (based on models with $\Delta AICc < 2$) environmental and spatial models for red backed shrike *Lanius collurio*
750 number of territories. 95% confidence intervals (C.I.) for the parameter estimates are given; in bold, the parameters in which
751 confidence intervals do not include zero. Covariates are ranked according to cumulative weights. See methods for details. N=63
752

	B	SE	$\sum w_i$	C.I.
Landscape				
intercept	0.24	0.11	-	0.01 – 0.47
shrubs	0.23	0.09	1	0.04 – 0.43
shrublands	0.07	0.11	0.41	-0.14 – 0.29
hedgerows	0.26	0.07	1	0.10 – 0.41
converted meadows	-0.08	0.13	0.37	-0.35 – 0.18
Topography				
intercept	0.35	0.10	-	0.10 - 0.53
slope	0.18	0.10	1	-0.02 – 0.37
Space				
intercept	0.12	0.13	-	-0.14 – 0.39
MEM12	-0.18	0.11	0.87	-0.42 – 0.05
MEM13	0.03	0.08	0.17	-0.12 – 0.19
MEM17	0.17	0.13	0.80	-0.08 – 0.43
MEM2	-0.07	0.11	0.40	-0.29 – 0.14
MEM21	-0.19	0.12	0.86	-0.45 – 0.05
MEM22	-0.16	0.15	0.70	-0.46 – 0.13
MEM23	-0.25	0.11	1	-0.49 – -0.02
MEM5	0.20	0.13	0.87	-0.06 – 0.48
MEM6	-0.30	0.12	1	-0.55 – -0.05
MEM9	-0.32	0.11	1	-0.55 – -0.08

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Table 5. Whinchat, Tree pipit and Red-backed shrike densities at several study areas in the Alps retrieved from literature. Densities from this study are also given for comparison.

Average number of territories or pairs/10 ha	Study area	Habitat	Year(s)	Reference
Tree pipit (<i>Anthus trivialis</i>)				
0.3-1.3	Orsiera, Torino - ITALY	-	-	(Brichetti & Fracasso, 2007)
0.42	<i>Trentino (plot of converted meadow included) - ITALY</i>	Hay-meadows	2017	<i>present study</i>
0.57	<i>Trentino (plot of converted meadow excluded) - ITALY</i>	Hay-meadows	2017	<i>present study</i>
0.59-1.34	Alpe Veglia e Devero, Ossola - ITALY	-	1996-2001	(Brichetti & Fracasso, 2007)
1.2	Mendrisotto - SWITZERLAND	-	1988	(Brichetti & Fracasso, 2007)
2	Prealps, Brescia - ITALY	-	1983-1984	(Brichetti & Fracasso, 2007)
3.1	Alps, Novara - ITALY	-	1963	(Brichetti & Fracasso, 2007)
1 - 6	Italian central Alps - ITALY	-	'70 - '80	(Brichetti & Fracasso, 2007)
1.32 (0.7 including cultivated control plots)	Bavarian Alps - GERMANY	Pastures	2014	(Schwarz et al., 2018)
1.76 declined to 1.07	Engadine - SWITZERLAND (plot with at least a territory present)	Hay-meadows and pastures	1987-1988 and 2009-2010	(Korner et al., 2017)
2 - 4 declined to 1.5 - 3	Val Camonica, Brescia - ITALY	Open coniferous woodland	'80 and '90	(Brichetti & Fracasso, 2007)
4 / 4.5	Varese mountains - ITALY	Mountain heathland	1986	(Brichetti & Fracasso, 2007)
Whinchat (<i>Saxicola rubetra</i>)				
0.55	Malles, Alto Adige - ITALY	Hay-meadows	2011	(Birrer, Gasser, Hagist, Niederfriniger, & Unterholzner, 2015)
0.75	<i>Trentino (plot of converted meadow included) - ITALY</i>	Hay-meadows	2017	<i>present study</i>
0.75	Alto Adige - ITALY	Wet meadows	1975	(Brichetti & Fracasso, 2008)
1	<i>Trentino (plot of converted meadow excluded) - ITALY</i>	Hay-meadows	2017	<i>present study</i>
1.19	Valsassina, Lecco - ITALY	Hay-meadows and pastures	2010	(Bazzi et al., 2014)
1.8	Cansiglio - ITALY	Hay-meadows	1996	(Brichetti & Fracasso, 2008)
2	Prealps, Brescia - ITALY	-	1986	(Brichetti & Fracasso, 2008)
2.5	Alps, Novara - ITALY	-	1963	(Brichetti & Fracasso, 2008)
2.7	Valsesia, Vercelli - ITALY	Wet pasture	1993	(Brichetti &

				Fracasso, 2008)
3.25	Vanoise - FRANCE	Hay-meadows	2004	(Broyer, 2009)
4	Ecrins - FRANCE	Hay-meadows	2004	(Broyer, 2009)
4.4	Goms Valley, Valais - SWITZERLAND	Hay-meadows	2011-2012	(Strebel et al., 2015)
1.25 -1.5	Varese - ITALY	Mountain heathland	'80	(Brichetti & Fracasso, 2008)
2 - 7	Italian central Alps - ITALY	-	'70 - '80	(Brichetti & Fracasso, 2008)
3 - 4	Lessinia - ITALY	Hay-meadows	1991	(Brichetti & Fracasso, 2008)
5 -6	Valle d'Aosta - ITALY	-	1996	(Brichetti & Fracasso, 2008)
0.4 - 1.26	Ossola, Piemonte - ITALY	Pastures	2000-2002	(Brichetti & Fracasso, 2008)
0.4-1.26	Val Buscagna, Verbania	<i>Nardus</i> grassland	2000 - 2002	(Brichetti & Fracasso, 2008)
0.6-1.2	Mendrisotto - SWITZERLAND	-	'80	(Brichetti & Fracasso, 2008)
2.54 - 1.48	Engadine - SWITZERLAND (plot with at least a territory present)	Hay-meadows and pastures	1987-1988 and 2009-2010	(Korner et al., 2017)
3.9 declined to 0.5	Valcamonica, Brescia - ITALY	Pastures with shrubs	'70 and 2006	(Brichetti & Fracasso, 2008)
4.1 and then stable	Pradellas, Engadine - SWITZERLAND	Hay-Meadows	1988 and 2000-2002	(Müller et al., 2005)
4.16 declined to 2.23	Alpe Devero, Verbania (1997-2002) - ITALY	Hay-meadows	1997 to 2002	(Brichetti & Fracasso, 2008)
8.1 declined to 3.6	Vnà, Engadine - SWITZERLAND	Hay-Meadows	1988 and 2002	(Müller et al., 2005)
Red-backed shrike (<i>Lanius collurio</i>)				
0.14	Alps, Novara - ITALY	-	1963	(Brichetti & Fracasso, 2011)
0.29-1.34 (locally 9-10)	Val d'Ajas - ITALY	-	2007-2008	(Brichetti & Fracasso, 2011)
0.3-0.4	Alpe Devero, Verbania - ITALY	-	2006	(Brichetti & Fracasso, 2011)
0.30 - 0.45	Lecco - ITALY	Hay-meadows and pastures	2010	(Bazzi et al., 2014)
0.46 -2.22	Trentino - ITALY	Hay-meadows and pastures (mainly)	2009-2010	(Ceresa, Bogliani, Pedrini, & Brambilla, 2012)
0.6 - 0.8	Val d'Aosta - ITALY	Hay-meadows and arable land	1978	(Brichetti & Fracasso, 2011)
0.6 - 0.8	Val d'Aosta - ITALY	-	2006	(Brichetti & Fracasso, 2011)
0.95 declined to 0.64	Engadine - SWITZERLAND (plot with at least a territory present)	Hay-meadows and pastures	1987-1988 and 2009-2010	(Korner et al., 2017)
1.1	Prali, Torino - ITALY	Abandoned pastures	2004 - 2005	Assandri G., pers. obs.
1.2	Verona - ITALY	Hay meadows and termophilus woodland	'80	(Brichetti & Fracasso, 2011)
1.8	Monte Guglielmo, Brescia - ITALY	Natural grassland	2004-2008	(Brichetti & Fracasso, 2011)
1.97	Trentino (plot of converted meadow	Hay-meadows	2017	present study

	<i>included) - ITALY</i>			
2.2	Monte Guglielmo, Brescia - ITALY	Natural grassland	2004-2008	(Brichetti & Fracasso, 2011)
2.3	Valsassina, Lecco - ITALY	Hay-meadows and pastures	2008	(Casale & Brambilla, 2009)
2.35	<i>Trentino (plot of converted meadow excluded) - ITALY</i>	<i>Hay-meadows</i>	<i>2017</i>	<i>present study</i>
2.5	Val di Cogne, Aosta - ITALY	-	1996	(Brichetti & Fracasso, 2011)
2.5	Monte Guglielmo, Brescia - ITALY	Hay meadows	2004-2008	(Brichetti & Fracasso, 2011)
3	Prealps, Brescia - ITALY	-	1983-1984	(Brichetti & Fracasso, 2011)
3.7	Pian di Spagna, Como - ITALY	Hay-meadow and arable land	2008	(Casale & Brambilla, 2009)
3.7-5	Valsesia, Vercelli - ITALY	Arable land and natural grassland	1993	(Brichetti & Fracasso, 2011)
4	Altopiano di Cariadeghe, Brescia - ITALY	Hay-meadows	2008	(Casale & Brambilla, 2009)
5.4	Val Taleggio, Bergamo - ITALY	Pastures	2008	(Casale & Brambilla, 2009)
7.1	Peglio, Como - ITALY	Hay-meadows and pastures	2008	(Casale & Brambilla, 2009)
8.1	Rescascia, Como - ITALY	Pastures	2008	(Casale & Brambilla, 2009)
10	Livo, Como - ITALY	Hay-meadows	2008	(Casale & Brambilla, 2009)

758 *Figure captions*

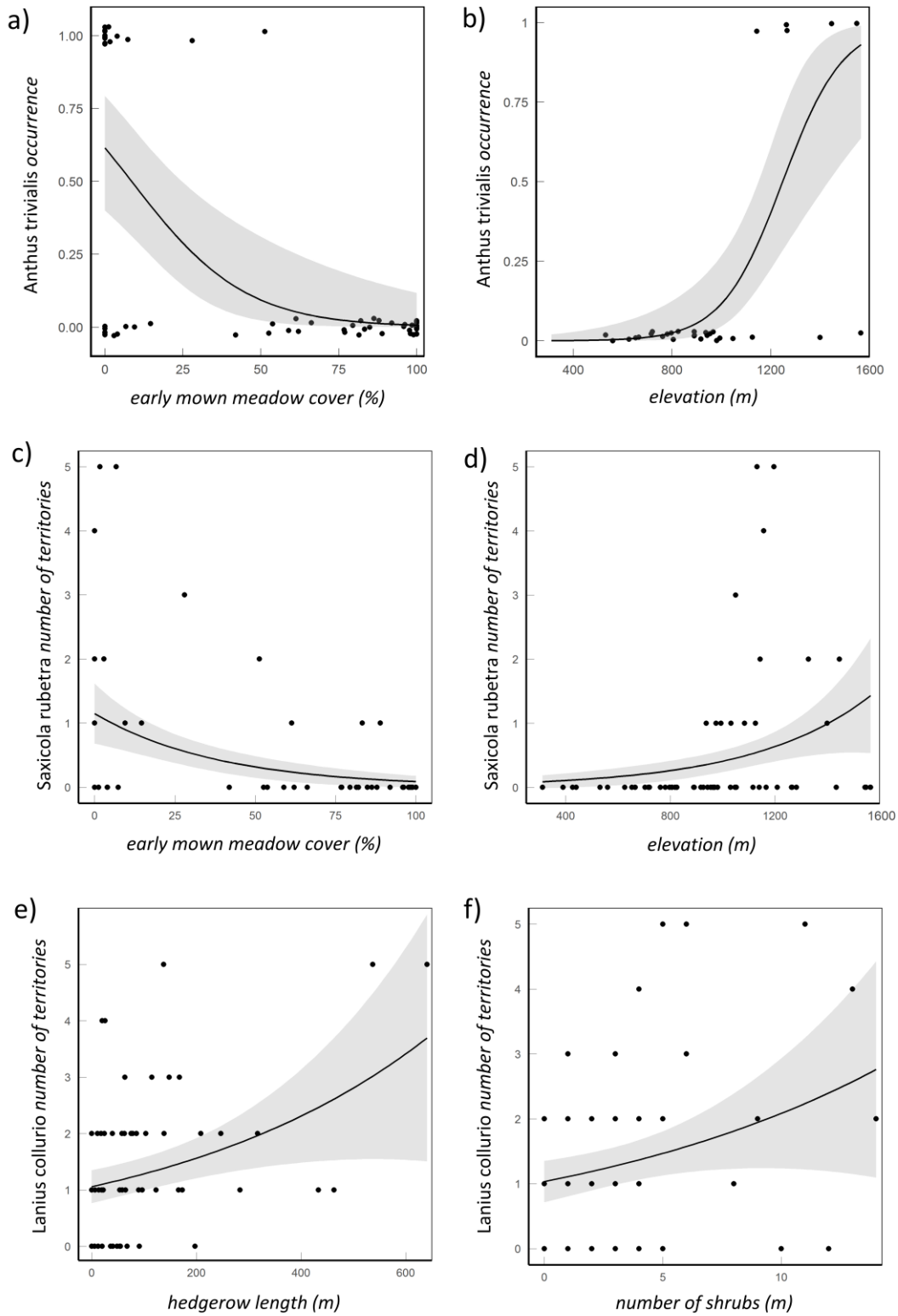
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760 **Figure 1.** Graphical representation of the effect of a selection of environmental predictors on tree pipit
761 *Anthus trivialis* occurrence (a-b), and abundance (number of territories) of whinchat *Saxicola rubetra* (c-d)
762 and red backed shrike *Lanius collurio* (e-f), according to the most supported models. Other predictors
763 included in the models are kept constant at their mean value. Tree pipit overlapping data points are plotted
764 with random jitter to increase readability. 95% C.I. of the mean are shown in grey. N=63.

765

766 **Figure 2.** Venn diagrams for variation partitioning showing the percentage contribution of each group of
767 environmental (i.e. landscape (L), management (M), topography (T)) and spatial predictors (S) in explaining
768 a) tree pipit *Anthus trivialis* probability of occurrence, b) whinchat *Saxicola rubetra*, and c) red-backed
769 shrike *Lanius collurio* abundance (number of territories) in the study area. Areas within overlapping circles
770 indicate percent variation shared by different components.

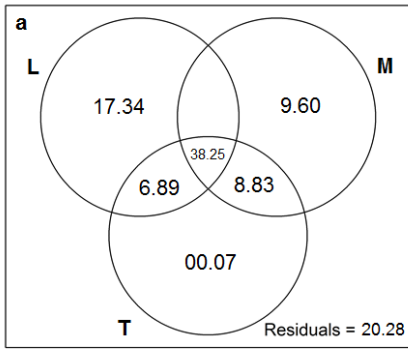
771 *Figure 1*
772



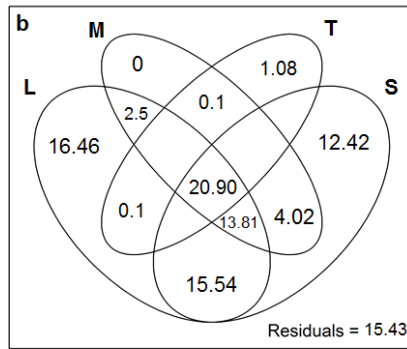
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774 Figure 2

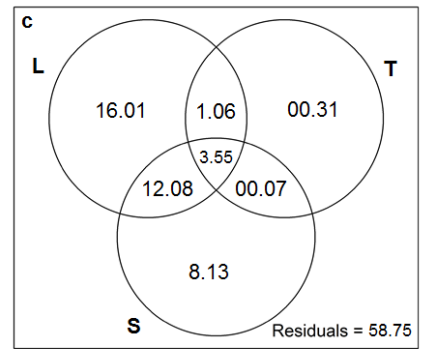
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Values <0 not shown



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