

1 **Toward the next CAP reform: determinants of avian communities in hay-meadows reveal current**
2 **policies' inadequacy for biodiversity conservation in grassland**

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

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6 ^a MUSE. Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento, Italy. e-mail:
7 giacomo.assandri@gmail.com. telephone: +39 0461 270432.

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

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

11
12 * Corresponding author

13 **Summary**

14 1. Semi-natural grasslands are among the richest European ecosystems in biodiversity, although they have
15 been severely impacted by farming intensification and land abandonment, both exacerbated by European
16 Union's Common Agricultural Policy (CAP). The last CAP included a 'greening' measure dedicated to
17 grassland conservation, presumed to be beneficial for biodiversity; however, scientific evidence about its
18 effectiveness is still very scarce. In the Alps, hay-meadows underwent dramatic management changes in
19 the recent decades; here, we used a comprehensive community ecology approach to highlight how the
20 multi-scale and interacting effects of such changes are impacting on birds, with the aim of providing
21 knowledge to support improvements to the CAP.

22 2. Birds were surveyed at 63 landscape units in NE Italy, equally subdivided into areas dominated by i)
23 extensive or ii) intensive hay-meadows and iii) areas formerly dominated by meadows but partially
24 converted into other agricultural land-use. This environmental gradient mirrors in space the temporal
25 gradient of the agricultural changes occurred in recent decades in the Alps.

26 Community composition, species richness and the number of meadow specialist species were analysed
27 according to environmental predictors (i.e. landscape, meadow management, and topography), and to
28 spatial factors, aiming at disentangling the exclusive and joint fraction of variation explained by each of
29 them.

30 3. Meadow conversion, allowed by the CAP in force, created a shift in community composition toward
31 assemblages dominated by generalist species at the expense of meadow specialists.

32 The cover of intensive meadows was negatively correlated with species richness, whereas the number of
33 meadow specialists was negatively correlated with the cover of early mown (i.e. within the third week of
34 June) meadows. Mowing date was in turn related to elevation, with meadows at higher elevations mown
35 later in the season, and to meadow intensification (the use of external inputs determines an increase in the
36 number of cuts per year).

37 4. *Policy implications.* Our study confirms the concerns about effectiveness of the CAP grassland measure in
38 conserving biodiversity. We suggest rethinking the CAP environmental prescriptions to account for the

39 importance of Alpine meadow management in determining biodiversity patterns. Finally, market-based
40 conservation strategies are discussed as complementary approaches for preserving grassland biodiversity.

41

42 **Keywords** - avian assemblages, Alps, Pillar One, CAP greening, manure, meadow specialist, mowing.

43 Introduction

44

45 The support towards agriculture provided by the Common Agricultural Policy (CAP) is the most expensive
46 part of the European Union's budget (40% of the total EU expenses; European Commission 2013). CAP has
47 been widely acknowledged as the major driver of agricultural intensification and abandonment in Europe
48 (at least from the Seventies onward), with strong negative impacts on biodiversity (Bignal 1998; Renwick et
49 al. 2013).

50 These effects led to a 2013 CAP reform (in force until 2020), that was announced to be "greener" with 30%
51 of direct payments to farmers dependent on "greening measures" aimed at halting biodiversity loss. One
52 such measure was targeted at counteracting permanent grassland reduction (Pe'er et al. 2014).

53 Most European grasslands are semi-natural habitats characterized by native plants, but they were created
54 to sustain livestock through maintenance by mowing and/or grazing. Semi-natural grasslands are among
55 the most iconic and biodiversity-rich European landscapes (Pykälä 2000; Veen et al. 2009), covering c.8% of
56 the continent and 35% of the utilized agricultural areas (Smit et al. 2008).

57 Permanent grassland has decreased in the EU by 6.4% between 1993 and 2011, and by 11.8% in countries
58 that joined the EU by 2004 (Pe'er et al. 2014), due to conversion to other land-use or abandonment
59 (MacDonald et al. 2000; Laiolo et al. 2004). In several regions, remaining grasslands have been strongly
60 intensified (Humbert et al. 2016). These two opposite processes have been worsened by the CAP (Donald et
61 al. 2002; Souchère et al. 2003) and have had major negative impacts on grassland biodiversity (Vickery et
62 al. 2001; Monteiro et al. 2011).

63 The last CAP greening measure dedicated to permanent grassland (enacted in 2013) is unlikely to have
64 widespread positive effects on grassland biodiversity because: i) it allows a further 5% reduction in
65 grassland extent at a national/regional scale by 2020, an amount higher than the current loss rate in several
66 regions; ii) it has an obligation to maintain the overall grassland area, but not the individual parcels,
67 allowing farmers to plough, reseed and relocate them, iii) it does not distinguish among grassland
68 typologies, so that grasslands of any natural value contribute the same to the overall grassland quota; iv)

69 further degradation by management intensification is allowed due to the lack of targeted environmental
70 prescriptions (Pe'er et al. 2014, 2017; Dicks et al. 2014).

71 Scientific evidence of the measure's effectiveness is still very scarce, given the short period of
72 implementation, and its impacts on biodiversity can only be estimated (Pe'er et al. 2017). Notwithstanding
73 this, discussion on the next reform of the CAP has advanced (European Commission 2017), and appropriate
74 evaluations on grassland measures are urgently required to halt biodiversity loss and to address
75 management strategies and policy for this ecosystem, which is pivotal for biodiversity conservation in
76 Europe.

77 Hay-meadows represent the most emblematic and biodiversity-rich traditional agroecosystem in the Alpine
78 region (Kampmann et al. 2008; Agnoletti 2013) and represent an urgent conservation issue due to the
79 ongoing deep changes in traditional farming (Fischer et al. 2008; Henle et al. 2008). They are permanent
80 semi-natural grasslands, maintained by mowing and only occasionally grazed. Their widespread occurrence
81 in the Alps is related to an extensive form of livestock farming, in which cattle (mainly cows) spend the
82 summer in mountain pastures and the other seasons in stables, fed with the fodder obtained from
83 meadows (Marini et al. 2011; Monteiro et al. 2011).

84 From the second half of the 20th Century, and more markedly in the last c.40 years, the dairy sector in the
85 Alps underwent deep changes, with a concentration of livestock in a few, much larger farms. These farms
86 are highly specialized and breed larger and more productive cows (e.g. Holstein Friesian), largely fed with
87 concentrated cereal feedstuff. This results in a reduction of summer grazing in upland pastures and in a
88 higher production of organic fertilizer, often deposited on meadows as liquid manure (Marini et al. 2011;
89 Graf et al. 2014). Simultaneously, marginal, less productive grasslands were abandoned or converted into
90 more profitable cropland (Zimmermann et al. 2010; Monteiro et al. 2011). This transformation of the dairy
91 sector in the Alps was due to several reasons (i.e. social and cultural changes, local investments in
92 mountain development, technological innovation and policy), although the CAP played a crucial role in
93 sustaining this process (Marini *et al.* 2011; Tappeiner *et al.* 2003). Those agricultural changes impacted (and
94 are still heavily impacting) plant communities (Marini et al. 2008b; Niedrist et al. 2009; Pierik et al. 2017)
95 and invertebrate assemblages (Marini et al. 2008a; Andrey et al. 2014). However, it is uncertain how they

96 are affecting the upper level of food webs. Although several bird species are sensitive to meadow
97 management (Britschgi et al. 2006; Sergio et al. 2009), and especially to mowing (Broyer 2009; Pedrini et al.
98 2012; Strebel et al. 2015), to the best of our knowledge, studies on the multi-faceted effects of modern
99 hay-meadow management on avian communities had never been performed in the Alps.
100 Here we investigate the effects of recent grassland transformation on hay-meadow bird communities,
101 considering broad- (e.g. landscape) and fine-scale (e.g. management) drivers in the Alps. We aimed at
102 disentangling the role in structuring avian assemblages of: i) meadow conversion into more productive
103 crops; ii) landscape-scale intensification, and iii) in-field meadow intensification (increase of external inputs
104 and changes in mowing regimes).
105 Our ultimate goal is to identify best options for biodiversity conservation in this iconic agroecosystem and
106 to provide recommendations for improving the forthcoming CAP reform.

107

108 **Materials and methods**

109

110 ***Study area, design and bird surveys***

111 The study was conducted in the Trento province (NE Italy; 45.67-46.51° N; 10.51-11.96° E; Fig. 1a). Here,
112 anthropogenic grasslands are scattered above 250m and are more widespread between 800–2,000m asl.
113 Permanent hay-meadows cover roughly 200 km², representing 3.3% of the province surface and 14.8% of
114 the Utilised Agricultural Area (ISTAT, 2010).
115 In 2010, 54927 Livestock Units occurred in Trentino, distributed over c.1400 farms (La Notte et al. 2015).
116 From 1990 to 2010, the overall surface of hay-meadows in this region almost halved (Provincia Autonoma
117 di Trento 2017), leading to a considerable increase in stocking rate (Scotton et al. 2012). Rural
118 abandonment was lower than in other Alpine areas, partly due to specific incentives in the framework of
119 the Rural Development Programs, and meadow reduction was primarily due to conversion into other crops
120 (Streifeneder et al. 2007; Marini et al. 2011).

121 Birds were surveyed along 63 200m-long linear transects, scattered over nine areas along an altitudinal
122 gradient (310-1565m asl) encompassing the entire belt in which meadows are found in the study area (Fig.
123 1b).

124 Bird surveys and environmental variable collections were performed within a 100m-buffer around the
125 transect; these 7.15-ha Landscape Units (LU) became the sampling units of the study and were selected
126 according to a stratified design: 22 units were dominated by extensive hay-meadows, 20 units by intensive
127 hay-meadows, and 21 by hay-meadows partly converted into other crops.

128 These three grassland typologies (extensive, intensive, converted) approximate well the modifications that
129 occurred in the last decades in hay meadow-dominated landscapes in our study area, and more in general
130 in several areas in the Alps. In other words, we studied the avian communities found at a specific time in
131 multiple sites chosen along a gradient of hay meadow intensification, assuming this one-year 'snapshot' as
132 a proxy of the community changes occurred in the last c.40 years in relation to the widespread changes
133 from extensive to intensive and then converted grassland. This approach, known as space-for-time
134 substitution, is commonly adopted in ecological studies when long-term data are unavailable and assumes
135 that changes in space reflect those in time, i.e. that there are no important interactions with other factors
136 such as climate or period. This is a simplification of the patterns occurring in real systems, but can still
137 prove useful to understand the impacts of environmental changes on biodiversity (Pickett 1989; Bennett et
138 al. 2006). In our study case, we are confident, thanks both to personal experience and botanical surveys,
139 that current grasslands mirror the main characteristics of past grasslands of the same type.

140 We censused birds during three visits in the 2017 breeding season (12-24.05; 13-23.06; 2-12.07), surveying
141 six/seven transects per morning (see Assandri et al. 2017c and SI for further details).

142

143 ***Avian and environmental variables***

144 From bird surveys, we derived three community variables for each LU: community composition, breeding
145 species richness (number of breeding species), and the number of meadow specialist species. Before
146 computing community variables, we removed records related to juveniles, overflying birds, species not
147 breeding in the study area, and species observed only once.

148 Composition assessment was based on the maximum abundance of each species recorded across the three
149 surveys, which were entered into a site (i.e. LU) by species matrix. Late season high counts (i.e. those
150 exceeding of 10 units the mean of the previous session counts in the same LU) of early-breeding species,
151 which display gregarious habits at the end of the breeding seasons (e.g. flocks of finches, sparrows and
152 corvids) were excluded to avoid abundance over-estimation (Jakobsson and Lindborg 2017). We considered
153 as meadow specialists the species which: i) are known to depend on grassland habitats in the study region
154 (Pedrini et al. 2005), and ii) with >50% of their precise locations falling within meadow. Those include *Crex*
155 *crex*, *Coturnix coturnix*, *Saxicola rubetra*, *Anthus trivialis*, *Alauda arvensis*, *Sylvia nisoria*, *Lanius collurio*,
156 *Turdus viscivorus*, *Emberiza citrinella*. *Pica pica* and *Corvus corone*, which are habitat generalists in the
157 region, satisfy only the second condition and thus were discarded.

158 At each LU, we measured three types of environmental variables: landscape, management, topography,
159 and built a set of spatial variables based on LU coordinates.

160 Landscape variables were measured on aerial photographs that had been validated and updated in the
161 field. We calculated the relative cover of meadows, urban areas, woodlands, traditional high-stem
162 orchards, shrublands/fallows (including small wetlands), and converted meadows (former meadows
163 recently converted into other arable crops, intensive orchards, vineyards, or greenhouses). Based on these,
164 we calculated a land-cover H' Shannon diversity index (Laiolo 2005). The length of hedgerows (with and
165 without trees) and tree rows, and the number of isolated trees and shrubs were also assessed.

166 Management variables were evaluated at the parcel scale (i.e. a meadow with a defined plant community,
167 spatial arrangement, and management characteristics; 882 parcels identified); the percentage surface of
168 highly intensive and that of early mown meadows occurring in each LU were used as management
169 predictors. Highly intensive meadows were defined as species-poor meadows, highly fertilized (85-420 kg N
170 ha⁻¹ year⁻¹) and mown 2-3 times/year in contrast with low intensive meadows (species-rich meadows, not
171 fertilized or poorly fertilized (0-150 kg N ha⁻¹ year⁻¹), and subject to only 1 or, rarely, 2 cuts per year).

172 Early mown meadows were defined (in contrast with late mown) as meadows mown before the end of the
173 third week of June (see SI for further details).

174 Topographic variables (mean elevation and slope) were derived from a 1-m resolution digital elevation
175 model.
176 Spatial variables were built by means of Moran's eigenvector maps (MEMs) (Dray et al. 2006), a method
177 that produces flexible spatial predictors starting from sample plot coordinates, and capturing spatial effects
178 at multiple spatial scales that can be used in regression and ordination to account for spatial
179 autocorrelation (Borcard et al. 2011). Further details are available in SI.

180

181 ***Analyses***

182 All the analyses were performed with R version 3.4.1 (R Core Team, 2017). We scrutinized the three groups
183 of environmental predictors to avoid common statistical problems, following Zuur et al. (2010). We left out
184 meadow cover and landcover diversity from subsequent analyses due to high collinearity with converted
185 meadow area, both pairwise (Spearman's Rho: meadow cover=-0.75; $p < 0.001$; landcover diversity=-0.90;
186 $p < 0.001$) and multivariate (GVIF: converted meadow cover=29.91; meadow cover=40.39; landcover
187 diversity=11.83). Elevation and slope showed a low collinearity ($Rho < 0.5$), and both were retained. We
188 applied a log+1 transformation to hedgerows, tree rows, and slope to reduce the weight of outliers. All the
189 explanatory variables were standardized before analysis (Schielzeth 2010; Cade 2015).

190 We separately tested the effect of each group of environmental and spatial (MEM) predictors on the three
191 response variables. Community composition was analysed by means of redundancy analysis (RDA)
192 performed with the package *vegan* (Oksanen et al. 2017). The abundance site-by-species matrix was first
193 Hellinger-transformed to make it appropriate for linear analyses (Legendre and Gallagher 2001). Global
194 significance ($p < 0.05$) was assessed by means of ANOVA-like permutation ($N=999$) tests. Overall, significant
195 RDAs were obtained by using forward selection (performed in *adespatial* package; Dray et al. 2017), which
196 retained significant variables by applying a double-stopping criterion (Blanchet et al. 2008), which reduces
197 type I errors and the overestimation of explained variance.

198 We built Poisson Generalized Linear Models (GLMs) to evaluate predictor effects on species richness and
199 the number of meadow specialists by adopting an information-theoretic approach (Burnham and Anderson
200 2002) and ranking all possible models for each set of explanatory variables separately according to the

201 relative value of Akaike's Information Criterion corrected for small sample size (AICc). The most
202 parsimonious models ($\Delta\text{AICc} \leq 2$) were selected and averaged within each group of predictors weighing by
203 model weights, and obtaining model-averaged coefficients, their relative SEs, and the relative variable
204 importance (Johnson and Omland 2004) for each explanatory variable applying the "zero-method" (*sensu*
205 Grueber et al. 2011). 'Uninformative parameters' (Arnold 2010), i.e. the variables which, when included,
206 determined an increase of the model's AICc value, were discarded (Richards 2008; Richards et al. 2011).
207 The inclusion of more models ($\Delta\text{AICc} \leq 6$) led to substantially similar results. For subsequent variation
208 partitioning (VP) analyses, we retained only the variables with confidence intervals of parameter estimates
209 not encompassing zero.
210 VP was applied to disentangle the unique and joint fraction of variation among the response variables
211 explained by the four sets of predictors. We performed VP on parsimonious models (simplified models
212 resulting from model selection; Peres-Neto and Legendre 2010) (see SI for details).

213

214 **Results**

215 We obtained 3037 bird records referring to 88 species; we removed records related to 13 species observed
216 only overflying LUs, 10 species exclusively migrants and 6 species observed only once (Table S2).
217 The final dataset included 59 species and 2040 individuals (adults). Ten species alone accounted for c.59%
218 of the data (see SI).

219

220 ***Community composition***

221 The community composition was significantly structured by eight environmental variables (Table S3).
222 *Saxicola rubetra*, *Anthus trivialis*, *Emberiza citrinella*, *Coturnix coturnix*, and *Pica pica* were grouped
223 together and were negatively correlated with the cover of converted meadows (and with orchard and
224 hedgerows, which were in turn positively correlated with the agricultural landscapes that were different
225 from meadows). This group of species also included at its margins, *Turdus viscivorus* (positively related to
226 shrubs and woodland) and *Lanius collurio* (Fig. 2a). All these species but the latter were also positively
227 associated with elevation and secondarily, slope and negatively with early mown grassland. Variables

228 indicating low-elevation agroecosystems different from meadows were positively associated with *Chloris*
229 *chloris*, *Serinus serinus*, *Passer montanus*, *Turdus merula*, *Passer italiae* and less strongly with *Linaria*
230 *cannabina*, *Jynx torquilla*, *Picus viridis* (these three favoured by hedgerows) and *Muscicapa striata*, *Turdus*
231 *philomelos*, *Cyanistes caeruleus*, *Sylvia atricapilla*, *Parus major*, *Columba palumbus*, which were related to
232 more forested landscapes. The woodland specialists found within sampled LUs (which are meadow-
233 dominated) were all clearly aligned according to woodland cover, with several also favoured by slope (Fig.
234 2a-c).

235 Ten MEMs were retained in the parsimonious spatial RDA (Table S3).

236 RDAs had an overall low explanatory power (Fig. 4), as is commonly found in ecological studies (Borcard et
237 al. 2011).

238

239 ***Species richness and meadow specialist species***

240 The most supported models on the effect of environmental and spatial predictors on species richness and
241 the number of meadow specialists are summarized in Tables S4 and S6.

242 Species richness was positively affected by woodland cover, the length of woody hedgerows and tree rows,
243 and slope, and negatively by the cover of highly intensive meadows and elevation (Fig. 3a-f). The positive
244 effects of urban cover and hedgerow length were weaker, since their estimates had confidence intervals
245 encompassing zero. Two MEMs were retained after model selection, but only MEM12 had confidence
246 intervals not encompassing zero (Table S5).

247 The number of meadow specialists was negatively affected by the cover of converted meadows and of
248 early mown meadows, plus the length of tree rows and orchard cover (although the latter had confidence
249 intervals encompassing zero), positively by elevation plus the number of shrubs (although its confidence
250 intervals encompassed zero) (Fig. 3g-i). Nine MEMs were retained after model selection, but only MEM3
251 and MEM9 had confidence intervals for the estimate not encompassing zero (Table S7).

252

253 ***Variation partitioning***

254 Variation partitioning highlighted a complex contribution of different sets of predictors in explaining
255 variation in the response variables; shared fractions were often conspicuous, indicating that multiple
256 factors co-explain the observed patterns (Fig. 4). For community composition and the number of meadow
257 specialists, the intersection of all four components was particularly relevant.
258 For community composition, the spatial component had the main role in explaining the observed variation,
259 and 41% of this component was unique (i.e. not joint), followed by landscape and topography components,
260 which were for three quarters interrelated to other components. Management (cover of early mown
261 meadows) explained a reduced quota of variation and was always interrelated with other components.
262 For species richness, variation was mainly explained by landscape (35% uniquely) and topography
263 components (mostly jointly with landscape), whereas management (cover of highly intensive meadows)
264 and spatial components had a limited explanatory power.
265 Vice-versa, the number of meadow specialists was mainly jointly explained by management (cover of early
266 mown meadows) and topography (elevation); about half of the variation explained jointly by management
267 and topography was also explained by the landscape component (cover of converted meadows). The
268 contribution of the spatial component was mostly interrelated with that of other components.

269

270 **Discussion**

271 We used a broad and comprehensive community ecology approach to show the impacts of the multi-scale
272 and interacting trajectories of Alpine grassland changes on birds, which here occupy the highest levels of
273 the trophic web. Mountains have been reported to act as refuges for lowland farmland species, which
274 strongly declined at lower elevations in response to agricultural mechanisation and intensification (Schmid
275 et al. 1998). A study in the French Alps showed that this is still true for farmland generalists, but that
276 farmland specialists (which match quite well with our meadow specialists) also declined at elevations
277 higher than 1000 m (Archaux 2007). Coherent patterns had been reported from the Swiss Alps (Korner et
278 al. 2017) and suggest that recent agricultural transformations are also impacting these species in mountain
279 'refuges', which are rapidly losing their conservation potential for farmland birds.

280 These negative transformations are at least partly linked with the European CAP. The greening measure
281 specifically included in the current CAP for permanent grassland, aimed at halting grassland biodiversity
282 loss, is unlikely to invert this negative trend (Pe'er et al. 2014). One of the main shortcomings of this
283 measure is that it allows a further 5% grassland reduction at national and regional scales. Our study
284 highlighted that one of the major causes of grassland reduction in the Alps, the conversion of hay-meadows
285 into other crops, does not drive an increase on overall avian biodiversity (species richness) in a meadow
286 dominated landscape. Such an increase in species richness could have been expected, because different
287 crops co-occurring at a landscape scale could increase overall landscape heterogeneity, which is widely
288 recognised to be positively correlated with the diversity of many taxa (Benton et al. 2003; Fahrig et al.
289 2015). Results showed that meadow conversion caused a shift in the community composition towards
290 assemblages dominated by generalist species, especially Turdidae and Fringillidae, which are known to
291 adapt to intensive permanent monocultures (i.e. apple orchards and vineyards; Brambilla et al. 2015;
292 Assandri et al. 2017a), which usually replace semi-natural grassland in the Alps. These changes occurred at
293 the expense of the meadow specialists, which disappear with the increase of these crops. The conversion of
294 hay-meadows into other crops thus has a clear negative effect on meadow specialists, which are mostly
295 decreasing species at the European level.

296 The cover of highly intensive meadows was negatively correlated with overall species richness. This pattern
297 could be due both to the fact that intensive meadows tend to occur in more agriculturally intensive
298 landscapes (which in most cases host a lower biodiversity than extensive ones; e.g. Verhulst *et al.* 2004),
299 and to a negative effect of meadow intensification *per se* on bird assemblages, via an effect on generalist
300 species too. These latter species, which are not obligate meadow-dwellers (e.g. doves, woodpeckers,
301 raptors, wagtails, corvids, thrushes, finches, starlings, and sparrows), often use meadows for feeding.
302 This negative effect did not emerge for the community composition and meadow specialists, mainly
303 affected by the mowing regime. Early mown meadows (i.e. those mown within the third week of June) have
304 considerably fewer meadow specialists than meadows mown later. The impact of (intensive) hay making on
305 birds determines high rates of nest destruction and nestling mortality (Schekkerman et al. 2009;
306 Buckingham et al. 2015), finally resulting in lowering reproductive success (Müller et al. 2005; Broyer 2009),

307 modifying behaviour (Grüebler et al. 2015) and even mating systems, sexual selection, and consequently,
308 evolutionary processes (Perlut et al. 2008), turning once favourable habitats into ecological traps (Broyer et
309 al. 2012). Also in our study area, modern hay-making is resulting in a drastic decline (sometimes eventually
310 leading to local extinction) of once very common meadow birds breeding on the ground (e.g. *Coturnix*
311 *coturnix*, *Crex crex*, *Alauda arvensis*, *Anthus trivialis*, *Saxicola rubetra*, and *Emberiza citrinella*; Pedrini et al.
312 2005, Brambilla and Pedrini 2013; this study).

313 The date of mowing, as shown by variation partitioning (Figure 4c), is strictly related to elevation, with
314 meadows at higher elevations mown later in the season (see also Fig. S3). This is mirrored by the positive
315 effect of elevation on meadow specialists, opposite to the effect on species richness in our study area and,
316 in general, in mountain ranges worldwide (Nogués-Bravo et al. 2008; McCain and Grytnes 2010). This
317 confirms the key importance of meadow management and its interaction with seasonal progression (which
318 is delayed at higher elevation) for grassland birds in areas with elevation gradients (Brambilla and Rubolini
319 2009; Brambilla and Pedrini 2011).

320 Recent intensification in meadow management also determines an earlier mowing, since the two are
321 intimately connected in a cyclic positive feedback: the use of external inputs (water/fertilizer
322 supplementation) allows advanced mowing (and then increased number of cuts/year) and to sustain a
323 larger number of (more productive) cattle, which produce more manure that is usually deposited on
324 meadows, further increasing their productivity (Scotton et al. 2014). In-field meadow intensification thus
325 also negatively affects meadow specialists. It also promotes new vegetation types dominated by a few
326 species to the point that, after some years, only a few nitrophilous species of low forage value occur, and
327 the semi-natural meadows have to be ploughed and re-sown with industrial seed mixtures (Marini et al.
328 2008b; Andrey et al. 2014; Humbert et al. 2016). This is also a widespread practice in our study areas,
329 where 9% of meadows are reseeded, and 10% were dominated by weeds (e.g. Apiaceae), i.e. those near to
330 being ploughed and reseeded (see SI). This causes a shift from a long-established ecosystem dominated by
331 autochthonous plants and harbouring structured animal communities (Humbert et al. 2009), into a new,
332 artificial and temporary one, with few (and often allochthonous) species. However, according to the current
333 grassland CAP measure, these degraded meadows, as well as the intensively managed ones, contribute the

334 same as the biodiversity-rich, permanent and unimproved grassland in reaching the grassland quota
335 needed to access the greening requirement under the CAP (Pe'er et al. 2014).

336 Previous studies highlighted that steepness better predicts the occurrence of meadows with high diversity
337 of plants (Marini et al. 2008b) and invertebrates (Marini et al. 2011) than elevation. This occurs because
338 steeper slopes prevent meadow intensification (e.g. irrigation and fertilization are difficult to achieve);
339 additionally, the more extreme microclimates of these grasslands are disadvantageous to more competitive
340 plant species while favouring less competitive ones, allowing them to co-exist and to increase diversity
341 (Marini et al. 2008b). Comparably, in our study areas, less intensified meadows and richer plant
342 communities are found on steeper slopes (Fig. 5). However, slope has a positive effect on overall species
343 richness, but not on meadow specialists. The community composition analysis indeed suggests that the
344 positive effect of slope on species richness is most likely related to the fact that the steepest slopes are
345 associated with abandoned areas invaded by shrubs and first-stage successional woods and this, in a
346 landscape dominated by meadows, allows some species (e.g. *Prunella modularis*, *Troglodytes troglodytes*,
347 *Phylloscopus collybita*, *Erithacus rubecula*) to occur, increasing the overall species number (Laiolo et al.
348 2004). This is also confirmed by the observed positive effect of woodland cover (and also of hedgerow and
349 tree row length) on overall species richness.

350 Landscape linear elements, such as hedgerows and tree rows, often favours birds in agroecosystems
351 (Baudry et al. 2000; Hinsley and Bellamy 2000); however, hedgerow networks (or other forms of tree and
352 shrub restoration) may negatively affect grassland specialists, via habitat fragmentation for open-habitat
353 species (Besnard and Secondi 2014; Assandri et al. 2017b). In our study, tree rows do not have any effect
354 on meadow specialists, whereas woody hedgerows have a negative (non-significant) effect. Conversely,
355 isolated shrubs are positively related with most of these species, whereas (shrubby) hedgerows are
356 positively related with species found in mixed farmland (e.g. *Picus viridis*, *Jynx torquilla*, *Sturnus vulgaris*,
357 *Passer italiae*) and locally with two species commonly found in grassland, *Lanius collurio* and *Sylvia nisoria*.

358 In areas in which meadows were converted to other crops, the maintenance or creation of hedgerows with
359 shrubs could sustain richer avian communities and declining farmland species, whereas in grassland-

360 dominated areas, where hedgerows are not part of the traditional landscape, their creation is not
361 recommended.

362

363 **Conclusion**

364 With the next CAP reform expected soon, recommendations for major amendments to current measures
365 are particularly timely and are required to reverse the negative trend of farmland species and, in particular,
366 of avian grassland specialists, which still do not show any recovery (Inger et al. 2014; Gamero et al. 2017).

367 If the conservation of grassland biodiversity is a priority for the European Union, the CAP greening measure
368 referring to permanent grassland must be rethought. Our study confirms the concerns about its low
369 expected effectiveness for biodiversity conservation for birds (Pe'er et al. 2014). The further 5% grassland
370 reduction at the national and regional scale means -in most cases- further conversion to other crops, with
371 potentially severe consequences for biodiversity. Additionally, the lack of distinction between intensive,
372 low-natural value grasslands and traditional, high-natural value grasslands, could lead to further
373 biodiversity losses, since vast extents of permanent grassland could be transformed into non-permanent
374 grassland regulated by ploughing and reseeded, which are allowed by the measure. If the 5% threshold had
375 to be maintained, it would be essential to avoid the conversion of unimproved/low-intensive meadows.

376 This implies that further efforts and resources should be allocated to map unimproved meadows and to
377 design high tier agri-environment schemes to compensate farmers for the income loss due to, e.g., mowing
378 being delayed after the third week of June.

379 This considered, agri-environmental schemes specifically thought to halt the decline of grassland birds and
380 to maintain grassland surface resulted in mixed effects (Broyer et al. 2014; Batáry et al. 2015; Darnhofer *et*
381 *al.* 2017); thus complementary strategies are desirable to address this conservation issue from a different
382 perspective.

383 In the U.S.A., sustainable market-based conservation models were suggested as the best opportunity to
384 conserve grassland bird populations. These models assume that consumers will pay more for a product if its
385 sustainability, healthiness, and quality are evident (Perlut 2014). In an Alpine perspective, these models
386 could take the form of self-sustaining dairy micro-economies, based on the promotion of the local specific

387 characteristics (“buy local”), which can enhance product quality, while promoting the maintenance of
388 traditional landscapes, which in turn favour tourism and other recreational activities (Lindemann-Matthies
389 et al. 2010; Assandri et al. 2018), and, hopefully, grassland biodiversity. These initiatives should be
390 recognised, sustained (by e.g. dedicated measures in the framework of Rural Development Programmes)
391 and controlled by public authorities and guaranteed by means of dedicated quality brand and certification
392 for the producers, highlighting the support to biodiversity and mountain traditional agriculture given by a
393 product, which in turn justifies its higher cost.

394 Meadow management, although mediated by the topographic, landscape and spatial context, played a
395 fundamental role in allowing meadow specialists to persist in grassland landscapes, thus conservation
396 strategies for grassland should necessarily include well-focused management prescriptions and should be
397 shared and discussed with farmers and other stakeholders in order to develop sustainable and effective
398 solutions.

399

400 **Authors’ contributions**

401 GA, MB, and PP conceived the idea; GA carried out fieldwork and led the analyses, helped by MB; PP
402 acquired funding; GA and MB wrote a first draft of the paper; GB supervised the research development; all
403 authors contributed critically to the drafts.

404

405 **Data accessibility**

406 Data available from the Figshare repository [http://dx.doi.org/ 10.6084/m9.figshare.7296905](http://dx.doi.org/10.6084/m9.figshare.7296905) (Assandri et al.
407 2019).

408

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416

417 **References**

- 418 Agnoletti M (2013) Italian Historical Rural Landscapes. Springer
- 419 Andrey A, Humbert J-Y, Pernollet C, Arlettaz R (2014) Experimental evidence for the immediate impact of
420 fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. *Ecol*
421 *Evol* 4:2610–2623. doi: 10.1002/ece3.1118
- 422 Archaux F (2007) Are mountains refuges for farmland bird species? A case study in the northern French
423 Alps. *Bird Study* 54:73–79. doi: 10.1080/00063650709461458
- 424 Arnold TW (2010) Uninformative parameters and model selection using Akaike’s information criterion. *J*
425 *Wildl Manage* 74:1175–1178. doi: 10.2193/2009-367
- 426 Assandri G, Bogliani G, Pedrini P, Brambilla M (2017a) Assessing common birds’ ecological requirements to
427 address nature conservation in permanent crops: Lessons from Italian vineyards. *J Environ Manage*
428 191:145–154. doi: 10.1016/j.jenvman.2016.12.071
- 429 Assandri G, Bogliani G, Pedrini P, Brambilla M (2017b) Land-use and bird occurrence at the urban margins in
430 the Italian Alps: Implications for planning and conservation. *North West J Zool* 13:77–84.
- 431 Assandri, G., Bogliani, G., Pedrini, P. & Brambilla, M. (2017c) Insectivorous birds as “non-traditional”
432 flagship species in vineyards: Applying a neglected conservation paradigm to agricultural systems.
433 *Ecological Indicators* 80, 275–285.
- 434 Assandri G, Bogliani G, Pedrini P, Brambilla M (2018) Beautiful agricultural landscapes promote cultural
435 ecosystem services and biodiversity conservation. *Agric Ecosyst Environ* 256:200–210. doi:
436 10.1016/j.agee.2018.01.012
- 437 Batáry P, Dicks L V., Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in conservation
438 and environmental management. *Conserv Biol* 29:1006–1016. doi: 10.1111/cobi.12536
- 439 Baudry J, Bunce RG., Burel F (2000) Hedgerows: An international perspective on their origin, function and
440 management. *J Environ Manage* 60:7–22. doi: 10.1006/jema.2000.0358
- 441 Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: Implications for nature conservation
442 in agricultural environments. *Biol Conserv* 133:250–264. doi: 10.1016/j.biocon.2006.06.008
- 443 Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends*
444 *Ecol Evol* 18:182–188. doi: 10.1016/S0169-5347(03)00011-9
- 445 Besnard AG, Secondi J (2014) Hedgerows diminish the value of meadows for grassland birds: Potential
446 conflicts for agri-environment schemes. *Agric Ecosyst Environ* 189:21–27. doi:
447 10.1016/j.agee.2014.03.014
- 448 Bignal, E. (1998) Using an ecological understanding of farmland to reconcile nature conservation
449 requirements, EU agriculture policy and world trade agreements. *Journal of Applied Ecology* 35, 949–
450 954.
- 451 Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecology* 89:2623–
452 2632. doi: 10.1890/07-0986.1
- 453 Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer New York, New York, NY
- 454 Brambilla M, Assandri G, Martino G, et al (2015) The importance of residual habitats and crop management
455 for the conservation of birds breeding in intensive orchards. *Ecol Res* 30:597–604. doi:
456 10.1007/s11284-015-1260-8
- 457 Brambilla M, Pedrini P (2013) The introduction of subsidies for grassland conservation in the Italian Alps
458 coincided with population decline in a threatened grassland species, the Corncrake *Crex crex*. *Bird*
459 *Study* 60:404–408.
- 460 Brambilla M, Pedrini P (2011) Intra-seasonal changes in local pattern of Corncrake *Crex crex* occurrence
461 require adaptive conservation strategies in Alpine meadows. *Bird Conserv Int* 21:388–393.
- 462 Brambilla M, Rubolini D (2009) Intra-seasonal changes in distribution and habitat associations of a multi-
463 brooded bird species: implications for conservation planning. *Anim Conserv* 12:71–77. doi:
464 10.1111/j.1469-1795.2008.00226.x

465 Britschgi A, Spaar R, Arlettaz R (2006) Impact of grassland farming intensification on the breeding ecology
466 of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine
467 meadowland management. *Biol Conserv* 130:193–205. doi: 10.1016/j.biocon.2005.12.013

468 Broyer J (2009) Whinchat *Saxicola rubetra* reproductive success according to hay cutting schedule and
469 meadow passerine density in alluvial and upland meadows in France. *J Nat Conserv* 17:160–167. doi:
470 10.1016/j.jnc.2009.02.004

471 Broyer J, Curtet L, Boissenin M (2012) Does breeding success lead meadow passerines to select late mown
472 fields? *J Ornithol* 153:817–823. doi: 10.1007/s10336-011-0799-6

473 Broyer J, Curtet L, Chazal R (2014) How to improve agri-environment schemes to achieve meadow bird
474 conservation in Europe? A case study in the Saône valley, France. *J Ornithol* 155:145–155. doi:
475 10.1007/s10336-013-0996-6

476 Buckingham DL, Giovannini P, Peach WJ (2015) Manipulating grass silage management to boost
477 reproductive output of a ground-nesting farmland bird. *Agric Ecosyst Environ* 208:21–28. doi:
478 10.1016/j.agee.2015.04.018

479 Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-*
480 *Theoretic Approach*. Springer Science & Business Media

481 Cade BS (2015) Model averaging and muddled multimodel inferences. *Ecology* 96:2370–2382. doi:
482 10.1890/14-1639.1

483 Darnhofer, I., Schermer, M., Steinbacher, M., Gabille, M. & Daugstadd, K. (2017) Preserving permanent
484 mountain grasslands in Western Europe: Why are promising approaches not implemented more
485 widely? *Land Use Policy* 68, 306–315.

486 Dicks L V., Hodge I, Randall NP, et al (2014) A Transparent Process for “Evidence-Informed” Policy Making.
487 *Conserv Lett* 7:119–125. doi: 10.1111/conl.12046

488 Donald PF, Pisano G, Rayment MD, Pain DJ (2002) The Common Agricultural Policy, EU enlargement and the
489 conservation of Europe’s farmland birds. *Agric Ecosyst Environ* 89:167–182. doi: 10.1016/S0167-
490 8809(01)00244-4

491 Dray S, Blanchet, Guillaume Borcard D, Clappe S, et al (2017) *adespatial: Multivariate Multiscale Spatial*
492 *Analysis*. R package version 0.0-9.

493 Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal
494 coordinate analysis of neighbour matrices (PCNM). *Ecol Modell* 196:483–493. doi:
495 10.1016/J.ECOLMODEL.2006.02.015

496 European Commission (2013) *Overview of CAP Reform 2014-2020*. *Agric Policy Perspect Briefs* 5:1–10.

497 European Commission (2017) *The future of food and farming*. Communication from the Commission to the
498 European Parliament, the Council, the European Economic and Social committee and the committee of
499 the Regions

500 Fahrig L, Girard J, Duro D, et al (2015) Farmlands with smaller crop fields have higher within-field
501 biodiversity. *Agric Ecosyst Environ* 200:219–234. doi: 10.1016/j.agee.2014.11.018

502 Fischer M, Rudmann-Maurer K, Weyand A, Stöcklin J (2008) Agricultural land use and biodiversity in the
503 Alps: How Cultural Tradition and Socioeconomically Motivated Change are Shaping Grassland
504 Biodiversity in the Swiss Alps. *Mt Res Dev* 28:148–155. doi: 10.1659/mrd.0964

505 Gamero A, Brotons L, Brunner A, et al (2017) Tracking Progress Toward EU Biodiversity Strategy Targets: EU
506 Policy Effects in Preserving its Common Farmland Birds. *Conserv Lett* 10:395–402. doi:
507 10.1111/conl.12292

508 Graf R, Muller M, Jenny M, Jeny L (2014) 20% loss of unimproved farmland in 22 years in the Engadin, Swiss
509 Alps. *Agric Ecosyst Environ* 185:48–58. doi: 10.1016/J.AGEE.2013.12.009

510 Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution:
511 Challenges and solutions. *J Evol Biol* 24:699–711. doi: 10.1111/j.1420-9101.2010.02210.x

512 Gruebler MU, Schuler H, Spaar R, Naef-Daenzer B (2015) Behavioural response to anthropogenic habitat
513 disturbance: Indirect impact of harvesting on whinchat populations in Switzerland. *Biol Conserv*
514 186:52–59. doi: 10.1016/j.biocon.2015.02.031

515 Henle K, Alard D, Clitherow J, et al (2008) Identifying and managing the conflicts between agriculture and
516 biodiversity conservation in Europe—A review. *Agric Ecosyst Environ* 124:60–71. doi:
517 10.1016/j.agee.2007.09.005

518 Hinsley S., Bellamy P. (2000) The influence of hedge structure, management and landscape context on the
519 value of hedgerows to birds: A review. *J Environ Manage* 60:33–49. doi: 10.1006/jema.2000.0360
520 Humbert J-Y, Dwyer JM, Andrey A, Arlettaz R (2016) Impacts of nitrogen addition on plant biodiversity in
521 mountain grasslands depend on dose, application duration and climate: a systematic review. *Glob*
522 *Chang Biol* 22:110–120. doi: 10.1111/gcb.12986
523 Humbert J-Y, Ghazoul J, Walter T (2009) Meadow harvesting techniques and their impacts on field fauna.
524 *Agric Ecosyst Environ* 130:1–8. doi: 10.1016/J.AGEE.2008.11.014
525 Inger R, Gregory RD, Duffy JP, et al (2014) Common European birds are declining rapidly while less
526 abundant species' numbers are rising. *Ecol Lett* 18:28–36. doi: 10.1111/ele.12387
527 ISTAT (2010) Caratteristiche strutturali delle aziende agricole. 6° Censimento Generale dell'Agricoltura. 24
528 ottobre 2010. Roma
529 Jakobsson S, Lindborg R (2017) The importance of trees for woody pasture bird diversity and effects of the
530 European Union's tree density policy. *J Appl Ecol* 54:1638–1647. doi: 10.1111/1365-2664.12871
531 Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108. doi:
532 10.1016/j.tree.2003.10.013
533 Kampmann D, Herzog F, Jeanneret P, et al (2008) Mountain grassland biodiversity: Impact of site conditions
534 versus management type. *J Nat Conserv* 16:12–25. doi: 10.1016/J.JNC.2007.04.002
535 Korner P, Graf R, Jenni L (2017) Large changes in the avifauna in an extant hotspot of farmland biodiversity
536 in the Alps. *Bird Conserv Int* 1–15. doi: 10.1017/S0959270916000502
537 La Notte A, Marongiu S, Masiero M, et al (2015) Livestock and Ecosystem Services: An Exploratory
538 Approach to Assess Agri-Environment-Climate Payments of RDP in Trentino. *Land* 4:688–710. doi:
539 10.3390/land4030688
540 Laiolo P (2005) Spatial and seasonal patterns of bird communities in Italian agroecosystems. *Conserv Biol*
541 19:1547–1556. doi: 10.1111/j.1523-1739.2005.00207.x
542 Laiolo P, Dondero F, Ciliento E (2004) Consequences of pastoral abandonment for the structure and
543 diversity of the alpine avifauna. *J Appl Ecol* 41:294–304.
544 Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data.
545 *Oecologia* 129:271–280. doi: 10.1007/s004420100716
546 Lindemann-Matthies P, Briegel R, Schüpbach B, Junge X (2010) Aesthetic preference for a Swiss alpine
547 landscape: The impact of different agricultural land-use with different biodiversity. *Landsc Urban Plan*
548 98:99–109. doi: 10.1016/j.landurbplan.2010.07.015
549 MacDonald D, Crabtree J, Wiesinger G, et al (2000) Agricultural abandonment in mountain areas of Europe:
550 Environmental consequences and policy response. *J Environ Manage* 59:47–69. doi:
551 10.1006/jema.1999.0335
552 Marini L, Fontana P, Scotton M, Klimek S (2008a) Vascular plant and Orthoptera diversity in relation to
553 grassland management and landscape composition in the European Alps. *J Appl Ecol* 45:361–370. doi:
554 10.1111/j.1365-2664.2007.01402.x
555 Marini L, Klimek S, Battisti A (2011) Mitigating the impacts of the decline of traditional farming on mountain
556 landscapes and biodiversity: a case study in the European Alps. *Environ Sci Policy* 14:258–267.
557 Marini L, Scotton M, Klimek S, Pecile A (2008b) Patterns of plant species richness in Alpine hay meadows:
558 Local vs. landscape controls. *Basic Appl Ecol* 9:365–372. doi: 10.1016/j.baae.2007.06.011
559 McCain CM, Grytnes J-A (2010) Elevational Gradients in Species Richness. In: *Encyclopedia of Life Sciences*.
560 John Wiley & Sons, Ltd, Chichester, UK,
561 Monteiro AT, Fava F, Hiltbrunner E, et al (2011) Assessment of land cover changes and spatial drivers
562 behind loss of permanent meadows in the lowlands of Italian Alps. *Landsc Urban Plan* 100:287–294.
563 doi: 10.1016/j.landurbplan.2010.12.015
564 Müller M, Spaar R, Schifferli L, Jenni L (2005) Effects of changes in farming of subalpine meadows on a
565 grassland bird, the whinchat (*Saxicola rubetra*). *J Ornithol* 146:14–23. doi: 10.1007/s10336-004-0059-
566 0
567 Niedrist G, Tasser E, Lüth C, et al (2009) Plant diversity declines with recent land use changes in European
568 Alps. *Plant Ecol* 202:195–210. doi: 10.1007/s11258-008-9487-x
569 Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational
570 species richness gradients. *Nature* 453:216–219. doi: 10.1038/nature06812

571 Oksanen J, Guillaume Blanchet F, Friendly M, et al (2017) vegan: Community Ecology Package. R package
572 version 2.4-4.

573 Pe'er G, Dicks L V., Visconti P, et al (2014) EU agricultural reform fails on biodiversity. *Science* (80-)
574 344:1090–1092.

575 Pe'er G, Lakne S, Müller R, et al (2017) Is the CAP fit for purpose? An evidence-based fitness check
576 assessment. Halle-Jena-Leipzig

577 Pedrini P, Caldonazzi M, Zanghellini S (eds) (2005) Atlante degli Uccelli nidificanti e svernanti in provincia di
578 Trento. Museo Tridentino di Scienze Naturali, Trento

579 Pedrini P, Rizzolli F, Rossi F, Brambilla M (2012) Population trend and breeding density of corncrake *Crex*
580 *crex* (Aves : Rallidae) in the Alps: monitoring and conservation implications of a 15-year survey in
581 Trentino , Italy. *Ital J Zool* 79:377–384.

582 Peres-Neto PR, Legendre P (2010) Estimating and controlling for spatial structure in the study of ecological
583 communities. *Glob Ecol Biogeogr* 19:174–184. doi: 10.1111/j.1466-8238.2009.00506.x

584 Perlut NG (2014) Grassland birds and dairy farms in the northeastern United States. *Wildl Soc Bull* 38:574–
585 579. doi: 10.1002/wsb.415

586 Perlut NG, Freeman-Gallant CR, Strong AM, et al (2008) Agricultural management affects evolutionary
587 processes in a migratory songbird. *Mol Ecol* 17:1248–1255. doi: 10.1111/j.1365-294X.2008.03695.x

588 Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed)
589 Long-term studies in ecology. Approaches and alternatives. Springer-Verlag, New York, pp 110–135

590 Pierik ME, Gusmeroli F, Marianna G Della, et al (2017) Meadows species composition, biodiversity and
591 forage value in an Alpine district: Relationships with environmental and dairy farm management
592 variables. *Agric Ecosyst Environ* 244:14–21. doi: 10.1016/j.agee.2017.04.012

593 Provincia Autonoma di Trento (2017) Italy - Rural Development Programme (Regional) - Trento. 2014-2020.
594 Version 2.1.

595 Pykälä J (2000) Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry.
596 *Conserv Biol* 14:705–712. doi: 10.1046/j.1523-1739.2000.99119.x

597 Renwick A, Jansson T, Verburg PH, et al (2013) Policy reform and agricultural land abandonment in the EU.
598 *Land use policy* 30:446–457. doi: 10.1016/J.LANDUSEPOL.2012.04.005

599 Richards SA (2008) Dealing with overdispersed count data in applied ecology. *J Appl Ecol* 45:218–227. doi:
600 10.1111/j.1365-2664.2007.01377.x

601 Richards SA, Whittingham MJ, Stephens PA (2011) Model selection and model averaging in behavioural
602 ecology: The utility of the IT-AIC framework. *Behav Ecol Sociobiol* 65:77–89. doi: 10.1007/s00265-010-
603 1035-8

604 Schekkerman H, Teunissen W, Oosterveld E (2009) Mortality of Black-tailed Godwit *Limosa limosa* and
605 Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: Influence of predation and agriculture. *J*
606 *Ornithol* 150:133–145. doi: 10.1007/s10336-008-0328-4

607 Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol*
608 *Evol* 1:103–113. doi: 10.1111/j.2041-210X.2010.00012.x

609 Schmid H, Luder R, Naef-Daenzer B, et al (1998) Atlas des oiseaux nicheurs de Suisse et au Liechtenstein en
610 1993-1996. Station Ornithologique Suisse, Sempach, Switzerland

611 Scotton M, Pecile A, Franchi R (2012) I tipi di prato permanente in Trentino.

612 Scotton M, Sicher L, Kasal A (2014) Semi-natural grasslands of the Non Valley (Eastern Italian Alps):
613 Agronomic and environmental value of traditional and new Alpine hay-meadow types. *Agric Ecosyst*
614 *Environ* 197:243–254. doi: 10.1016/j.agee.2014.08.003

615 Sergio F, Marchesi L, Pedrini P (2009) Conservation of Scops Owl *Otus scops* in the Alps: relationships with
616 grassland management, predation risk and wider biodiversity. *Ibis (Lond 1859)* 151:40–50.

617 Smit HJ, Metzger MJ, Ewert F (2008) Spatial distribution of grassland productivity and land use in Europe.
618 *Agric Syst* 98:208–219. doi: 10.1016/J.AGSY.2008.07.004

619 Souchère, V., King, C., Dubreuil, N., Véronique, L.-M., Le Bissonais, Y. & Chalot, M. (2003) Grassland and
620 crop trends: role of the European Union Common Agricultural Policy and consequences for runoff and
621 soil erosion. *Environmental Science & Policy* 6, 7–16.

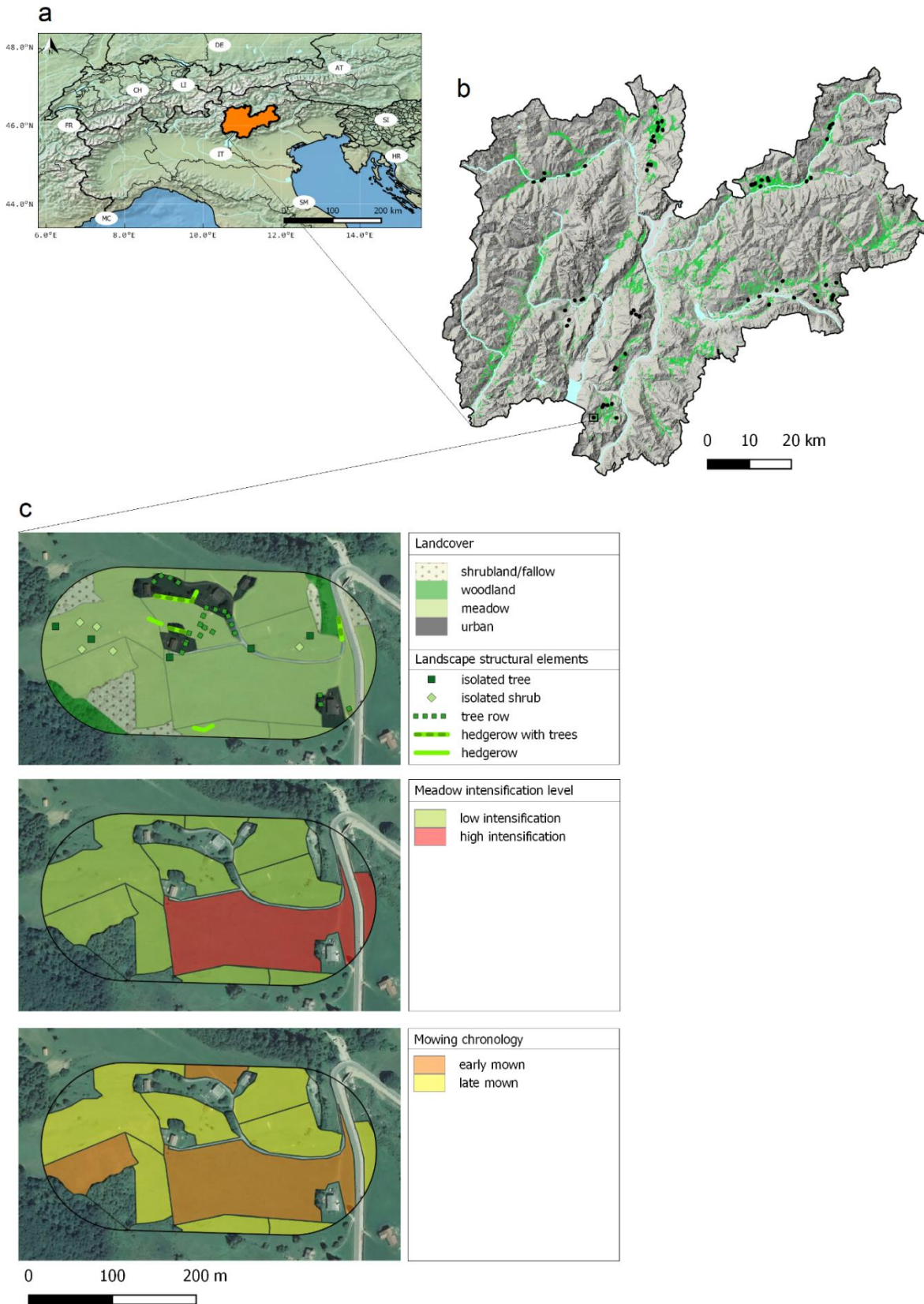
622 Strebel G, Jacot A, Horch P, Spaar R (2015) Effects of grassland intensification on Whinchats *Saxicola*
623 *rubetra* and implications for conservation in upland habitats. *Ibis (Lond 1859)* 157:250–259. doi:

624 10.1111/ibi.12250
625 Streifeneder T, Tappeiner U, Ruffini F V, et al (2007) Selected aspects of agro-structural change within the
626 Alps a comparison of harmonised agro-structural indicators on a municipal level. *Rev Geogr Alpine-*
627 *journal Alp Res* 95:41–52. doi: 10.4000/rga.295
628 Tappeiner, U., Tappeiner, G., Hilbert, A. & Mattanovich, E. (2003) *The EU Agricultural Policy and the*
629 *Environment: Evaluation of the Alpine Region*. Blackwell, Berlin.
630 Veen P, Jefferson R, De Schmidt J, Van Der Straaten J (2009) Grassland in Europe of High Nature Value.
631 KNNV Publishing, Zeist, the Netherlands
632 Verhulst, J., Báldi, A. & Kleijn, D. (2004) Relationship between land-use intensity and species richness and
633 abundance of birds in Hungary. *Agriculture, Ecosystems & Environment* 104, 465–473.
634 Vickery JA, Tallowin JR, Feber RE, et al (2001) The management of lowland neutral grasslands in Britain:
635 effects of agricultural practices on birds and their food resources. *J Appl Ecol* 38:647–664. doi:
636 10.1046/j.1365-2664.2001.00626.x
637 Zimmermann P, Tasser E, Leitinger G, Tappeiner U (2010) Effects of land-use and land-cover pattern on
638 landscape-scale biodiversity in the European Alps. *Agric Ecosyst Environ* 139:13–22. doi:
639 10.1016/j.agee.2010.06.010
640 Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems.
641 *Methods Ecol Evol* 1:3–14. doi: 10.1111/j.2041-210X.2009.00001.x
642
643

644 **Figures**

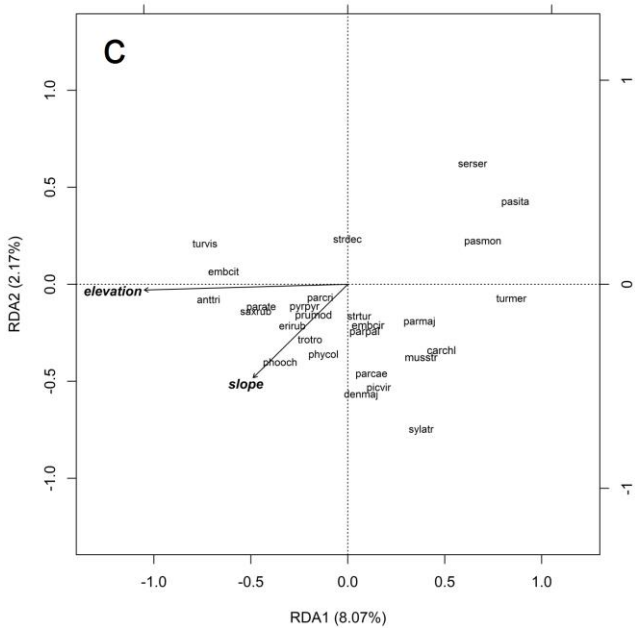
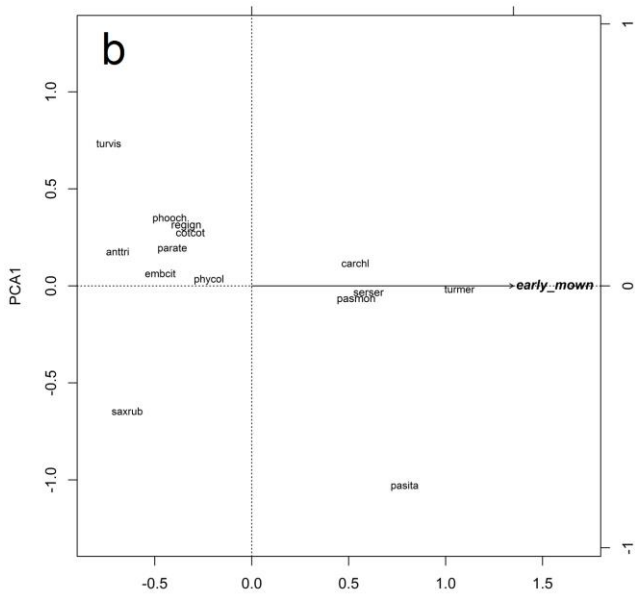
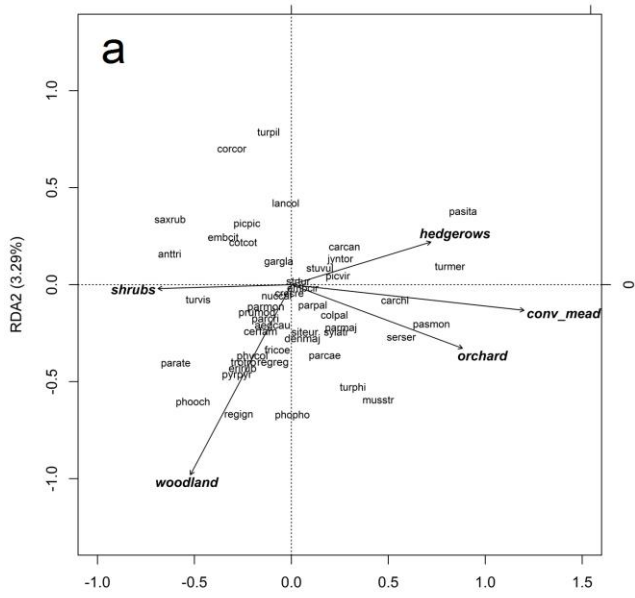
645

646 **Fig. 1.** Study area. (a) Location of the study area in the Alpine region (Trentino in orange). (b) The 63
647 landscape units investigated are shown in black and hay-meadow cover is in green. (c) Detail on one
648 landscape unit showing the field mapping of the landscape and management variables. Base maps: Natural
649 Earth; Ortofoto 2011 ©AGEA – Agenzia per le Erogazioni in Agricoltura, Roma.

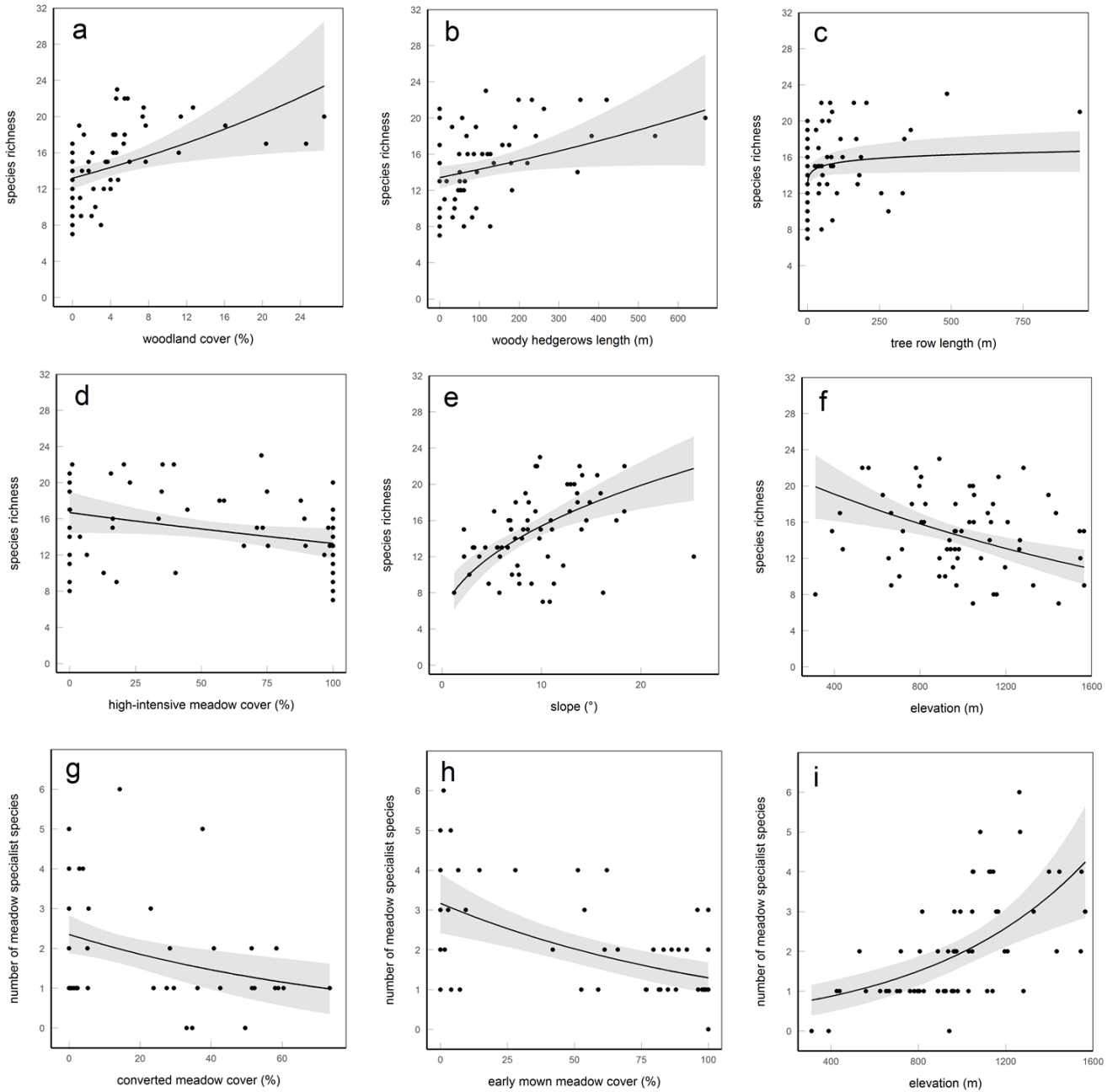


650

651 **Fig. 2.** Distance biplots of the effects of environmental predictors (a. landscape; b. management; c.
652 topographic) on avian community composition according to parsimonious RDA analysis. Selected variables
653 are represented by arrows. Species are abbreviated with 6 letters (initials of genus and species; see Table
654 S2). Only species with goodness-of-fit > 0.10 are shown. Angles between species and predictors reflect their
655 correlation (angle<90°: positive correlation; angle>90° negative correlation; angle=90°: no correlation).
656 Values in parentheses give the percentage of total variance explained by each canonical axis. N=63.

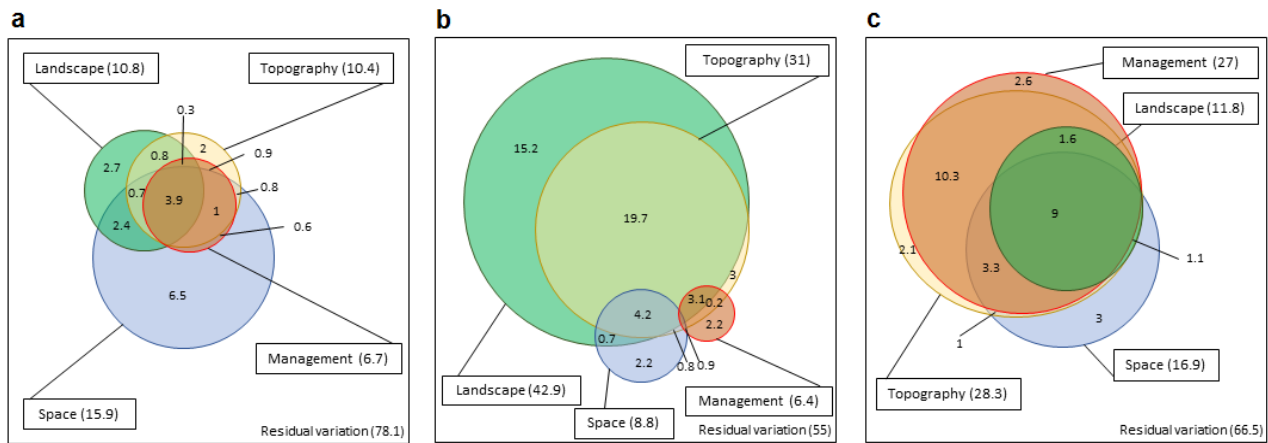


658 **Fig. 3.** Graphical representation of the effect of environmental predictor on species richness (a-f) and
 659 number of meadow specialists (g-i) as predicted by averaged models. Only variables for which confidence
 660 intervals of estimates did not include zero are shown. Other predictors included in the models are kept
 661 constant at their mean value. Variables in subfigures c and e were log+1 transformed for the analyses
 662 (untransformed values are displayed to facilitate understanding). 95% C.I. of the mean are shown in grey.
 663 N=63.
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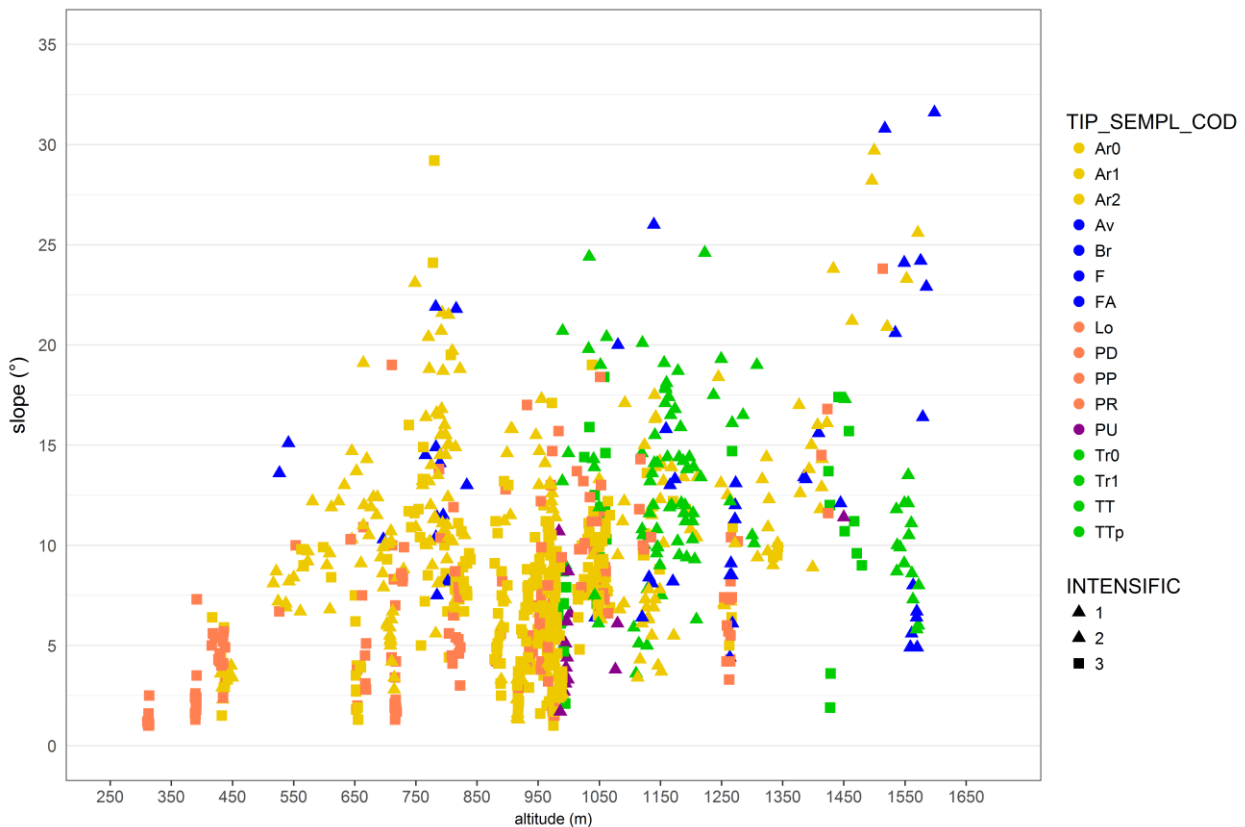
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668 **Fig. 4.** Venn diagrams for variation partitioning showing the percentage contribution of landscape, management, topography, and spatial components in explaining a) community composition, b) species richness, and c) the number of meadow specialists in the 63 landscape units. Circle areas is roughly proportional to the percentage of variation explained. Areas within overlapping circles indicate approximate percent variation shared by different components. Numbers in brackets inside component labels refer to the percentage of overall variation explained by a component (including shared quotas). Values < 0 not shown.



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Fig. 5. Joint effect of slope and elevation on meadow typology and intensification level. Each point refers to a meadow parcel (N=882). The 16 meadow typologies found in the study area are grouped (by colours) in 5 categories: yellow: *Arrhenateretum* meadows; blue: meadow rich of species typical of non-fertilized soils (dominated by *Bromus*, *Festuca*, *Avenula*, *Agrostis*); orange: highly fertilized, disturbed, and reseeded meadows; violet: wet meadows; green: *Trisetetum* meadows. The meadow intensification level is shown by symbols (see SI for further details).



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