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**Ski-piste revegetation promotes partial bird community recovery in the
European Alps**

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Abstract

Capsule Restoration of grasslands on ski-pistes caused a recovery in the bird community, but not to the extent that it was equivalent to a natural Alpine grassland community.

Aim To test whether revegetation of ski-pistes in open habitat areas results in bird community recovery.

Methods The bird communities in two ski resorts in the Italian Maritime Alps were surveyed using a standardized area count method in three different plot types: non-restored ski-pistes (newly constructed), restored ski-pistes and control plots in grassland far from ski-pistes.

Results In 49 independent plots, 32 species were recorded. Species richness and abundance of birds were significantly higher on restored than on non-restored ski-pistes, independently of the species group considered and the analyses carried out. Bird community parameters of restored ski-pistes were still lower than those of natural grassland, as shown by results of typical grassland species.

Conclusion Our results suggest that an apparently successful restoration of ski-pistes may be not enough to promote a *complete* recovery of bird communities. The complete recovery of local bird communities may be promoted only if an integral recovery of the *original* vegetal communities is achieved. We suggest the best conservation option is to adopt techniques to maintain as far as possible original grassland if construction of new ski-pistes is unavoidable.

55 **Introduction**

56 Over the last century, the European Alps have been subject to an increasing anthropogenic impact
57 due to the building of ski-pistes and the development of winter tourism facilities (Simons 1988;
58 Mackenzie 1989, Pechlaner & Tschurtschenthaler 2003). The skiing industry is of major economic
59 importance in the alpine region, and it has recently experienced a period of great expansion (Koenig
60 & Abegg et al. 1997; Elsasser and Messerli 2001; Wipf et al. 2005). Several thousands of
61 kilometers of ski-pistes are used for downhill skiing (Rolando et al. 2007), and in the Swiss Alps
62 alone about 220 km² are directly affected by ski-pistes (Amacher-Hoppler and Schoch 2008).
63 The main impact of ski-pistes is on vegetation and soils, since the natural vegetation and most of the
64 upper soil horizons are removed during the construction process (machine grading, used to smooth
65 out underlying rock and soil), to provide suitable slopes for skiers and to enhance the use of
66 artificial snow (Mosimann 1985; Wipf et al. 2005; Isselin-Nondedeu & Bédécarrats 2007; Delarze
67 and Gonseth 2008). Moreover, the use of snow-grooming vehicles in the preparation of pistes
68 causes changes in the underlying soil structure and vegetation (Cernusca et al. 1990; Rixen et al.
69 2004). Finally, summer management at regular intervals, involving cutting of shrubs and machine-
70 grading, produces further damage to vegetation (Bayfield 1996; Titus & Tsuyuzaki 1999). The
71 recovery of vegetation may be successful below the treeline, whereas it is extremely difficult above
72 the treeline, because of the scarcity of soil and the peculiar traits of high altitude plant species (very
73 low growth rates, low seed production and the insufficient agents of seed dispersal; Urbanska and
74 Fattorini 2000).
75 In addition to the apparent negative effects on soils and vegetation, the impacts of winter recreation
76 are most often negative for fauna. Results from meta-analyses have shown that richness, abundance
77 and diversity of fauna were lower in areas affected by winter recreation when compared to
78 undisturbed areas (Sato et al. 2013). Several studies have shown negative effects of ski-pistes on

animals, i.e. birds (Laiolo & Rolando 2005; Rolando et al. 2007, Patthey et al. 2008, Caprio et al. 2011), small mammals (Hadley & Wilson 2004; Sanecki et al. 2006; Negro et al. 2009, Rolando et al. 2013), reptiles (Sato et al. 2014a,b) and invertebrates (Negro et al. 2009, 2010, and 2013, Rolando et al. 2013, Kessler et al. 2012, Kašák et al. 2013).

Below the treeline, ski-pistes through forest may induce habitat fragmentation that limits small mammal movements (Negro et al. 2012), whereas above the treeline they likely do not significantly cause habitat fragmentation, but landscape changes may nevertheless affect bird species richness and distribution (Caprio et al. 2011). The area above the treeline is of particular concern, because climate changes will probably induce operators and stakeholders to shift skiing activities and ski-pistes to higher altitudes (Elsasser and Messerli 2001; Fukushima et al. 2002; Bicknell and McManus 2006; Scott et al. 2008) where ecosystems are particularly sensitive (Körner 2003).

The scarcity of vegetation on ski-pistes of high altitude grasslands is likely the most relevant determinant of bird diversity. Sparsely grass-covered ski-pistes are landscape features which lower grassland species richness and probability of occurrence of certain passerine species (Caprio et al. 2011). Moreover, the amount of grass vegetation controls abundance and diversity of ground dwelling arthropods (Negro et al. 2010) that, in turn, may directly affect birds feeding on invertebrates (Rolando et al. 2007). In general, a further problem regards detecting habitat effects at community levels. A completely holistic approach may be unsatisfactory because different species often react differently to the same environmental factors, therefore communities are often split into guilds, which group animals according to their eco-ethological characteristics (Verner, 1984). The response of specialist species (i.e. grassland species) may be therefore different to those species that are more associated with shrubs and forests (Laiolo et al. 2005, Rolando et al. 2007).

In this paper, we tested the hypothesis that revegetation of grassland ski-pistes promotes bird community recovery. We considered ski-pistes located in pastures ranging from about 1500 to 2200 m a.s.l. at two ski resorts in the Maritime Alps (the southernmost part of the Alps). Here, due to the low altitude of several ski-pistes and the influence of the maritime climate, old ski-pistes have been

recolonized by vegetation and are nowadays grass-covered. Other, more recent, ski-pistes have not recovered and appear as strips of bare ground with scarce vegetation. We therefore compared whole bird community and guild diversity in plots located in i) ski-pistes of recent construction with depleted or no vegetation (hereafter *non-restored ski-pistes*), ii) old ski-pistes that were entirely grass-covered, showing a rather natural appearance (hereafter *restored ski-pistes*), and iii) *natural grasslands*. We also investigated bird–habitat relationships, to identify structural components of the habitat (e.g. grass cover, shrub cover, height of vegetation etc.) that control composition and abundance of grassland bird communities.

Materials and methods

Study Area

The study was carried out within the Limone and Limonetto skiing districts in the Vermentina Valley (south western Italian Alps) (44° 11'N 7° 33'E), partly encompassed within a protected area (Site of Community Interest IT1160056 "Alpi Marittime"). Beech *Fagus sylvatica* forests extend all over the area, but large pastures also occur at the same altitude as forests from 1500 m a.s.l. upwards. Pastures are characterized by *Nardus stricta* prairies interspersed with shrub patches represented by juniper *Juniperus communis*, alpen rose *Rhododendron ferrugineum* and, to a lesser extent, bilberry *Vaccinium myrtillus*. They are the outcome of intensive historical pastoral activities that at first removed beech forests and then maintained open habitats. Cattle and sheep, even though pastoralism is declining, are still present in the area.

We considered all the ski-pistes of the study area (a total of 53 kilometers), but sampling was carried out in open habitat only, i.e. where tracks cross open pastures, from about 1500 to 2200 m a.s.l. Restored ski-pistes are 3-10 years old and are still in use but show in most cases a natural appearance, with a rather high grass cover. This depends on land use and climatic peculiarities of

the study area. Because of the long history of pastoralism, open habitats also occur below the tree line that, due to the influence of the sea (the distance between Limone Piemonte and the Ligurian sea is less than 50 kilometers), is set at a rather high altitude (about 1800 m for the beech and 2500 m for the larch *Larix decidua*). Most of the open habitat ski-pistes are therefore below the natural tree line and because of this, their restoration (partly due to natural dynamics and partly due to artificial seeding) is quicker and more successful than that of other alpine localities where open habitat ski-pistes are located above the tree line. Moreover, during construction, original grass and topsoil were not removed everywhere; smooth pastures, in particular, were left untouched. Restored ski-pistes were not machine-graded during summer. Conversely, non-restored ski-pistes are of recent construction (1-2 years) or have experienced recent summer machine grading and appear as strips with bare ground either without grass, or with a very few dispersed grass tufts. In most of the ski-pistes, snowmaking is used to supplement natural snow during the winter season.

Bird and habitat surveys

Field work was carried out in the morning, during the first 4 h after sunrise, in June and July 2011 by EC, who sampled birds using a standardized area count method, surveying birds in circular plots of 50 m radius. Counts lasted 15 min, during the first 10 minutes of which the observer stood still and quiet at the centre of the plot, as in standard point counts. In the last 5 minutes of the count, the observer moved around, to flush secretive and non-singing individuals, and stopped at suitable vantage points to look and listen, recording all birds seen or heard within the plot (Laiolo et al. 2004, Rolando et al. 2007). Each census plot was visited twice (in June and July); the total number of species from the two censuses was used as a measure of species richness, and the higher number of individuals over the two visits was used as a measure of bird species abundance per plot. Three types of plots were defined: plots centered on non-restored ski-pistes (n = 14), on restored ski-pistes (n = 17) and in natural grassland habitats (n = 18). Points were selected on the basis of accessibility,

also avoiding sources of possible disturbance (i.e. close to roads or livestock), or locations where detectability may have been reduced. At the same time, we kept other landscape features as constant as possible (i.e. distance to forest, slope, exposition and altitude).

When possible, sampling was organized in sets of three, the plots of the three types being located in the same skiing district with the same landscape and topography (see above). Ski-piste strips were 65–185 m wide (mean 114.2 ± 38.5 SD); when the strip was narrower than 100 m (restored ski-pistes $n = 2$, non-restored ski-pistes $n = 3$), a variable portion of open habitat at the side of the ski-piste was included in the plot. Plots were set at a minimum distance of 300 m. Avian communities were described in terms of two diversity parameters, species richness (S) and total abundance.

Following Laiolo et al. (2005), species were classified as ecotone/grassland or shrub/woodland according to their ecological preferences.

Altitude and seven habitat cover and structure variables were collected for each plot: percentage of shrub, stone-rock, soil-rubble (i.e. open-ground) and grass (all coverage estimated by eye), Shannon diversity of the vegetation (Shannon Index, $H' = -\sum p_i * \log(p_i)$), where p_i is the relative frequency of species i calculated according the relative frequency of vegetation types (area of grass, juniper, alpen rose and other bushes estimated by eye), mean height of the vertical component of the habitat (mean of 20 measurements of shrub, stone-rock, soil-rubble and grass per plot, shared according to the relative cover percentages and recorded with a wooden dowel subdivided into 1-cm units) and heterogeneity of the vertical component ($CV = SD/mean \times 100$).

percentage of shrub, stone-rock, soil-rubble

Data Analysis

Differences between plot types

a) Habitat

Differences in habitat cover (i.e. shrub, stone-rock, soil-rubble and grass cover) and habitat structure (i.e. H' of vegetation cover, mean height and CV of vertical structure and heterogeneity)

between the three plot types (i.e. non-restored ski-pistes, restored ski-pistes and natural grasslands) were tested by means of one-way analysis of variance ANOVA. To attain the normal distribution, the values of Shannon index were log transformed [$y=\log(x+1)$]. Factor analysis (FA; Gaunch 1984) was chosen to reveal patterns in the data for habitat cover and structure (i.e. the seven variables listed above).

b) Bird communities

Differences in mean bird species richness and total abundance were tested by means of one-way ANOVA. To attain the normal distribution, the values of species richness and total abundance were transformed to square roots [$y=\sqrt{(x+0.5)}$].

Relationships between bird community and habitat

We tested for the effects of habitat cover (percentage of shrub, stone-rock, soil-rubble and grass cover), habitat structure (H' of vegetation cover, mean height and CV of the vertical component of the habitat), plot type (categorical variable defining plots in natural grasslands, in non-restored and restored ski-pistes) and altitude on bird species richness and abundance of individuals using Generalized Linear Models (GLM). To reduce correlation among variables, we first examined all pair-wise correlations to identify strongly correlated pairs ($r > |0.7|$). The result of this preliminary analysis showed that none of the above habitat cover and structure variables were highly collinear. To model the distribution of species richness and abundance of individuals, count (i.e. number of species or individuals) was modeled specifying a Poisson error distribution and a log link function. Full models were subject to a model reduction procedure whereby non-significant terms were sequentially dropped from a model until only significant terms remained. Since initial models of abundance of individuals showed over-dispersion, we used a quasi-Poisson error distribution model.

In addition to the full model which tested habitat cover, habitat structure and plot type as covariates, we ran separate models with only habitat cover and structure variables (i.e. percentage of shrub, stone-rock, soil-rubble and grass cover, H' of vegetation cover, mean height and CV of the vertical component of the habitat and relative heterogeneity) or only plot type (i.e. natural grassland, non-restored and restored ski-pistes), to verify through AIC which set of variables carried more information. Generalized linear models were calculated with R 15.0.1 (R Core Team 2014).

Results

We conducted surveys at 49 independent plots ranging in altitude from 1478 m to 2250 m (mean: 1812 ± 161.5 m). 32 species were detected, of which 24 were grassland or ecotone species and eight were shrub or woodland species (see Appendix I). Whinchat *Saxicola rubetra*, water pipit *Anthus spinoletta*, black redstart *Phoenicurus ochruros* and linnet *Linaria cannabina* were the most common species, with frequencies of occurrence (the number of times species were observed within 98 samples) higher than 10%.

Differences between plot types

a) Habitat

Non-restored ski-pistes showed a significantly lower percentage of grass cover and average vertical structure and a higher soil rubble cover than natural grassland and restored ski-pistes. No significant habitat difference between restored ski-pistes and natural grassland was found (Table 1). Shrubs (especially rhododendron) were found in natural grasslands only (an average cover of $4.58 \pm 13.67\%$), because they were removed from ski-pistes during construction.

Factor analysis showed that the first two principal components (PC1, PC2) accounted for 70.06% of the total variation in the habitat structure matrix, with eigenvalues > 1 . The percentage of soil-

228 rubble and the heterogeneity of the vertical component had a negative contribution on PC1
229 (suggesting a gradient of grass cover from bare ground to pastures) and the percentage of rocks and
230 Shannon index of vegetation cover provided the major positive loading on PC2 (suggesting a
231 gradient from grassland-dominated plots to more diversified plots with shrubs and rocks). The
232 relative position of centroids (i.e. the average location of survey plots in ordination space) in the
233 biplot determined by the first two principal components showed that natural grassland and restored
234 ski-pistes were structurally quite similar, and very different from the non-restored ski-piste
235 category, which was identified mainly with soil–rubble cover (Fig. 1).

237 *b) Bird communities*

238 Non-restored ski-pistes, restored ski-pistes and natural grassland plots showed significant
239 differences in terms of species richness and abundance of individuals (Table 1). Plots located in
240 natural grasslands supported the highest bird species richness and abundance, whereas those set in
241 non-restored ski-pistes had the lowest values. However, differences between restored ski-pistes and
242 natural grasslands depended on whether all species or only grassland species were taken into
243 account. When all species were considered, post-hoc tests showed that species richness was not
244 significantly different between plots in natural grasslands and those in restored ski-pistes (even
245 though values were lower in the latter), whilst the abundance of individuals was significantly
246 greater in natural grassland. When only grassland species were considered, pairwise post-hoc tests
247 showed that both ecological parameters (species richness and abundance) were significantly lower
248 on restored ski-pistes than in natural grassland (Table 1, Fig. 2 and Fig. 3).

249 **Relationships between bird community and habitat**

250 Generalized linear models showed that bird community parameters (species richness and
251 abundance) of both non-restored and restored ski-pistes were significantly lower than those of
252 natural grassland (reference category) independently of the community composition (Table 2).

Notably, differences in the abundance of individuals of grassland species of restored ski-pistes and of natural grasslands were highly significantly different ($P < 0.001$), whereas the differences regarding the overall community were less striking ($P < 0.05$).

Bird communities were also influenced by two habitat structure variables, shrub cover and vegetation diversity; grassland species were also positively influenced by altitude. As a rule, community parameters increased with vegetation diversity (3 instances out of 3) and decreased with shrub cover (3 out of 4). In general, separate models with only plot type carried more information than those with only habitat cover and structure variables (Total species richness: plot type only model AIC 233.64, vegetation only model AIC 254.54; Grassland species richness: plot type only model AIC 223.91, vegetation only model AIC 233.66; Abundance of grassland species: plot type only model AIC 325.53, vegetation only model AIC 385.17).

Discussion

The efforts to restore ski-pistes have changed considerably since the demands for sustainable erosion control arose in the 1970s. Restoration technology has made considerable progress in recent years, and specific revegetation measures are available that make use of local seeds and plants that are adapted to and suited for any elevation. In the long-term, in fact, sufficient protection against erosion can only be guaranteed if stable, enduring and ecologically adapted sub-alpine and alpine plant species become established (Krautzer et al. 2013, Klug et al. 2013, Rixen 2013).

Nevertheless, several thousand kilometers of ski-pistes still require restoration in the European Alps. Above the tree line in particular, vegetation cover on the ski-pistes remains extremely low for long periods after restoration (at least 10-12 years), despite the use of modern techniques such as hydro-seeding (Barni et al. 2007). Worse still, the vegetation cover on high altitude machine-graded pistes may deteriorate over time, illustrating that natural recovery may not occur in these managed alpine habitats (Roux-Fouillet et al. 2011). Only at elevations of several hundred meters below the tree line does re-establishment of vegetation occur rapidly and reliably (Rixen 2013).

278 Despite the amount of research conducted, very little is known about the effect of ski-piste
279 restoration on animal communities. To our knowledge, no study on the effect of restoration on bird
280 communities has been published so far. In this paper, we therefore tested for the first time the
281 hypothesis that revegetation of ski-pistes of open habitat zones goes hand-in-hand with bird
282 community recovery. In terms of habitat structure, restored ski-pistes were in fact not significantly
283 different from natural grassland, thus suggesting that a successful restoration level was achieved.
284 Previous studies carried out on non-restored ski-pistes in open habitat areas have shown that plots
285 located in natural grasslands supported the greatest bird species richness and diversity and the
286 greatest grassland species density, whereas those in ski-pistes had the lowest values; moreover,
287 plots located beside ski-pistes did not support smaller numbers of bird species and diversity than
288 plots in natural areas, but they supported a significantly lower bird density (Rolando et al. 2007).
289 There was no difference in the overall bird community between restored ski-pistes and natural
290 grasslands, but there was a significant difference in grassland specialist species, suggesting that
291 habitat quality for this group in particular is affected by ski-piste type. More broadly, these results
292 show that the guild approach can reveal patterns not evident when considering the community as a
293 whole (Bishop and Mayers 2005, Caprio et al. 2008).

294 The present results suggest that restoration of ski-pistes may partially promote the recovery of local
295 bird communities. Species richness and abundance of birds were in fact significantly higher on
296 restored than on non-restored ski-pistes, independently of the species considered and the analyses
297 carried out. Nevertheless, bird community parameters (especially those of grassland species) of
298 restored ski-pistes were still lower than those of natural grassland, despite the fact that the presence
299 of shrubs (i.e. rhododendrons) in grasslands tended to lower bird diversity. This suggests therefore
300 that an apparently successful restoration of ski-pistes may not be enough to promote a *complete*
301 recovery of bird communities. These results are likely driven by the vegetation of the restored ski-
302 pistes. Several studies have demonstrated that grass cover of ski-pistes is a major determinant of

local animal diversity (Caprio et al. 2011, Negro et al. 2010). However, equal grass cover of restored ski-pistes and natural grassland does not necessarily prove they are ecologically equivalent, because differences may still be great and significant in terms of density of grass species, which remains lower on restored ski-pistes, or in terms of occurrence of alien plant species, which is higher on ski-pistes, especially when hydroseeded (Barni et al. 2007). This means that, even though grass cover is high, the vegetation of restored ski-pistes remains different from that of adjacent pastures and, therefore, poorly attractive to local birds. Previous studies have shown that responses of ground-dwelling arthropods to ski-piste restoration (as a consequence of hydroseeding with commercial mixtures) were contrasting. Restored ski-pistes were colonized by grasshoppers, which were more abundant on ski-pistes than on the adjacent grassland plots, but ski-pistes and adjacent grassland plots were used equally by ground beetles, and ski-pistes were avoided by spiders (Negro et al. 2013). Birds feeding on epigeic invertebrates might be influenced by these changes (e.g. alpine choughs were seen feeding on grasshoppers in ski-restored ski-pistes), but present results suggest that overall attractiveness of restored ski-pistes was lower than that of natural grassland. This study indicates therefore that restoration of ski-pistes of open habitat areas may promote the complete recovery of local bird communities only if an integral recolonisation of the *original* vegetal communities (which is essential to host invertebrates) is achieved. Otherwise, the recovery will be significant (e.g. higher values of bird species richness and abundance than non-restored ski-pistes) but nevertheless, partial (e.g. lower values of species richness and abundance than natural grassland). Considering that thousands of kilometers of ski-pistes have been already constructed in the Alps, and that climate change will probably increase the potential conflict between skiing and high-elevation bird species, the best conservation choice will be that of abstaining from, or at least deferring, the construction of new ski-pistes. If construction of new ski-pistes is unavoidable, it is vitally important that restoration measures follow restoration guidelines that represent today's state-of-the-art (Rixen 2013) and that original grasslands which are compatible with skiing activities are preserved.

329 We wish to stress that successful restoration of ski-pistes will not solve eventual problems
330 connected with snow cover management. Snow cover of ski-pistes is very different from that of
331 natural grassland because of the use of artificial snow produced by snow-making facilities and/or
332 the snow compression caused by skiers and heavy machinery. In both cases, the main effect is that
333 of postponing the time of melt-out (Rixen 2013). This causes a delay in vegetative growth and
334 flowering, which has been demonstrated to affect alpine butterfly communities (Rolando et al.
335 2012). Hence, it cannot be excluded that, all other things being equal, this phenological delay may
336 also affect bird communities, irrespective of the restoration status of the ski-pistes. Even nature-
337 friendly management does not necessarily guarantee animal conservation. In ski-pistes of an alpine
338 open habitat zone whose vegetation cover never experienced any disturbance, a noticeable decline
339 in the abundance of most epigeic beetle species in patches with artificially increased accumulation
340 of snow was found (Kašák et al. 2013).

341 Much published research (as here) is based on models that take into account habitat and vegetation
342 cover (Caprio et al. 2001, Chamberlain et al. 2013). This kind of approach is adequate in depicting
343 and identifying major responses and processes, but much effort should also be made in order to
344 better understand underlying mechanisms, including fine-scale studies of the relationship between
345 birds, vegetation, snow cover and invertebrate availability. This in-depth analysis is needed to drive
346 management interventions to improve habitat conditions in alpine areas which are also already
347 threatened by climate change (Chamberlain et al. 2013). This suggests that, in addition to research
348 on the effects of ski-restoration, more studies on the effect of winter snow on birds and invertebrate
349 communities of ski-pistes are desirable. For example, species such as Alpine Chough, Red-billed
350 Chough and Snowfinch are dependent on invertebrates during the spring and summer, whose
351 availability is likely to be affected by vegetation structure and snow cover. The effect of snow melt
352 (including artificial snow) on plant and invertebrate phenology, both on and off pistes, and

353 consequently feeding ecology of high altitude grassland birds, should be a priority research topic in
354 this field.

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496 Appendix I. List of the bird species recorded in the 49 plots. Frequency of occurrence is the number
 497 of plots in which a certain species was observed/ the total number of plots per each plot type.
 498 Values in brackets indicate the total number of individuals recorded. Guild classification was
 499 according to Laiolo et al. 2004 (GE: grassland and ecotone species; SW: shrub and woodland
 500 species)

Common name	Scientific name	Natural grassland	Non-restored ski-pistes	Restored ski-pistes	Guild
Common quail	<i>Coturnix coturnix</i>	6.12 (3)	0.00 (0)	0.00 (0)	GE
Cuckoo	<i>Cuculus canorus</i>	2.04 (1)	0.00 (0)	0.00 (0)	GE
Great spotted woodpecker	<i>Dendrocopos major</i>	2.04 (1)	0.00 (0)	0.00 (0)	SW
Red-backed Shrike	<i>Lanius collurio</i>	12.24 (6)	4.08 (2)	0.00 (0)	GE
Black Grouse	<i>Tetrao tetrix</i>	4.08 (2)	0.00 (0)	2.04 (1)	GE
Alpine chough	<i>Pyrrhocorax graculus</i>	0.00 (0)	0.00 (0)	51.02 (25)	GE
Jay	<i>Garrulus glandarius</i>	6.12 (3)	0.00 (0)	0.00 (0)	SW
Coal Tit	<i>Parus ater</i>	4.08 (2)	0.00 (0)	2.04 (1)	SW
Skylark	<i>Alauda arvensis</i>	10.20 (15)	0.00 (0)	4.08 (6)	GE
Garden Warbler	<i>Sylvia borin</i>	14.29 (7)	0.00 (0)	0.00 (0)	SW
Lesser Whitethroat	<i>Sylvia corruca</i>	36.73 (18)	6.12 (3)	10.20 (5)	SW
Ring ouzel	<i>Turdus torquatus</i>	18.37 (9)	0.00 (0)	2.04 (1)	GE
Blackbird	<i>Turdus merula</i>	2.04 (1)	0.00 (0)	0.00 (0)	SW
Fieldfare	<i>Turdus pilaris</i>	2.04 (1)	0.00 (0)	0.00 (0)	GE
Mistle thrush	<i>Turdus viscivorus</i>	2.04 (1)	0.00 (0)	2.04 (1)	GE
Black Redstart	<i>Phoenicurus ochruros</i>	36.73 (18)	24.49 (12)	53.06 (26)	GE
Winchat	<i>Saxicola rubetra</i>	65.31 (32)	57.14 (28)	24.49 (12)	GE
Rock-Thrush	<i>Monticola saxatilis</i>	20.41 (10)	0.00 (0)	6.12 (3)	GE
Wheatear	<i>Oenanthe oenanthe</i>	20.41 (10)	14.29 (7)	12.24 (6)	GE
Alpine accentor	<i>Prunella collaris</i>	4.08 (2)	0.00 (0)	12.24 (6)	GE
Dunnock	<i>Prunella modularis</i>	26.53 (13)	0.00 (0)	8.16 (4)	GE

White Wagtail	<i>Motacilla alba</i>	8.16 (4)	6.12 (3)	6.12 (3)	GE
Tree pipit	<i>Anthus trivialis</i>	44.90 (22)	6.12 (3)	24.49 (12)	GE
Water pipit	<i>Anthus spinoletta</i>	59.18 (29)	36.73 (18)	30.61 (15)	GE
Snowfinch	<i>Montifringilla nivalis</i>	14.29 (7)	0.00 (0)	0.00 (0)	GE
Chaffinch	<i>Fringilla coelebs</i>	20.41 (10)	8.16 (4)	0.00 (0)	SW
Bullfinch	<i>Pyrrhula pyrrhula</i>	4.08 (2)	0.00 (0)	4.08 (2)	SW
Linnet	<i>Linaria cannabina</i>	83.67 (41)	8.16 (4)	20.41 (10)	GE
Goldfinch	<i>Carduelis carduelis</i>	0.00 (0)	2.04 (1)	0.00 (0)	GE
Yellowhammer	<i>Emberiza citrinella</i>	18.37 (9)	2.04 (1)	14.29 (7)	GE
Rock bunting	<i>Emberiza cia</i>	4.08 (2)	0.00 (0)	0.00 (0)	GE
Ortolan bunting	<i>Emberiza hortulana</i>	2.04 (1)	0.00 (0)	0.00 (0)	GE

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Table 1. Mean $\pm$ SD habitat cover and structure variables, bird species richness and abundance of individuals in natural grasslands, non-restored and restored ski-pistes. Inter-plot differences were tested with a one-way ANOVA. LSD post-hoc tests were used for pairwise comparisons of means. *P < 0.05; **P < 0.01; ***P < 0.001; NS Not Significant.

	(1) Natural Grassland	(2) Non-restored ski-pistes	(3) Restored ski- pistes	Interplot differences	Significant pairwise comparison at P < 0.05
Habitat					
Grass cover (%)	71.39 $\pm$ 20.17	22.21 $\pm$ 25.54	65.71 $\pm$ 24.30	F _{2,46} = 22.49 ***	(1) vs (2) (2) vs (3)
Soil rubble cover (%)	1.67 $\pm$ 7.071	39.85 $\pm$ 38.39	2.32 $\pm$ 4.21	F _{2,46} = 14.88 ***	(1) vs (2) (2) vs (3)
Stone-rock cover (%)	17.92 $\pm$ 15.22	26.47 $\pm$ 34.99	26.96 $\pm$ 23.21	F _{2,46} = 0.66 NS	
Shannon habitat	0.59 $\pm$ 0.21	0.53 $\pm$ 0.36	0.57 $\pm$ 0.27	F _{2,46} = 0.87 NS	
Mean vertical structure	17.92 $\pm$ 14.88	3.94 $\pm$ 3.41	15.04 $\pm$ 10.02	F _{2,46} = 8.15 ***	(1) vs (2) (2) vs (3)
CV vertical structure	1.06 $\pm$ 0.35	1.44 $\pm$ 0.90	1.09 $\pm$ 0.32	F _{2,46} = 2.074 NS	
Overall community					
Species richness	6.28 $\pm$ 3.16	2.65 $\pm$ 1.87	4.71 $\pm$ 2.97	F _{2,46} = 7.81 ***	(1) vs (2) (2) vs (3)
Abundance of individuals	16.11 $\pm$ 8.81	5.18 $\pm$ 3.83	10.57 $\pm$ 9.25	F _{2,46} = 9.02 ***	(1) vs (2) (1) vs (3)
Grassland guild					
Species richness	5.72 $\pm$ 2.89	2.59 $\pm$ 1.70	4.43 $\pm$ 2.79	F _{2,46} = 8.41 ***	(1) vs (2) (1) vs (3) (2) vs (3)
Abundance of individuals	14.94 $\pm$ 8.43	4.94 $\pm$ 3.27	10.21 $\pm$ 9.17	F _{2,46} = 6.87 ***	(1) vs (2) (1) vs (3) (2) vs (3)

Table 2. GLM of bird species richness and abundance of individuals of the overall community, and of species richness and abundance of individuals of grassland species in relation to non-restored ski-pistes, restored ski-pistes and natural grasslands (reference level), habitat parameters and altitude.
*P < 0.05; **P < 0.01; ***P < 0.001; NS Not Significant.

Overall Community			
Species richness			
	Estimate	Std. Error	P
Intercept	1.488	0.189	***
Non-restored ski-piste	-0.903	0.178	***
Restored ski-piste	-0.333	0.157	*
Shannon index of vegetation cover	0.673	0.258	**
Shrubs cover	0.21	0.096	*
Abundance of individuals			
	Estimate	Std. Error	P
Intercept	2.3009	0.2584	***
Non-restored ski-piste	-1.1874	0.2517	***
Restored ski-piste	-0.4754	0.2095	*
Shannon index of vegetation cover	0.8965	0.3542	*
Shrubs cover	-0.278	0.1237	*

Grassland species guild			
Species Richness			
	Estimate	Std. Error	P
Intercept	-0.316	0.743	0.67
Non-restored ski run	-0.828	0.180	***
Restored ski run	-0.301	0.164	*
Shannon index of vegetation cover	0.655	0.295	*
Altitude	0.001	0.000	*
Shrubs cover	-0.225	0.088	*
Abundance of individuals			
	Estimate	Std. Error	P
Intercept	0.703	0.461	0.12
Non-restored ski run	-1.138	0.126	***
Restored ski run	-0.400	0.105	***
Altitude	0.001	0.000	***
Shrubs cover	-0.229	0.050	***

536 Fig. 1. Biplot of a principal component analysis (PC1 vs. PC2) where both environmental
 537 descriptors and survey plots are plotted together. As a matter of clarity, to avoid plotting too many
 538 confounding points (i.e. 49 survey plots plus seven descriptors), the distribution of survey plots for
 539 each plot type is synthetically represented by centroids (i.e. the weighted mean of survey plots).
 540 Soil, percentage of soil–rubble cover; Rock, percentage of stone–rock cover; Shrub, percentage of
 541 shrub cover; Grass, percentage of grass cover; H'hab, Shannon diversity of the habitat; CV Height,
 542 heterogeneity of the vertical component; Height, mean height of the vertical component. Dots
 543 indicate environmental descriptors (habitat structure variables), squares indicate centroids of survey
 544 plots.

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548 Fig. 2. Average value of species richness of grassland species per point count in natural grasslands,
549 non-restored ski-pistes and restored ski-pistes. Bars are standard errors.

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554 Fig. 3. Average value of number of individuals of grassland species per point count in natural
555 grasslands, non-restored ski-pistes and restored ski-pistes. Bars are standard errors.

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