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Ski-pistes can compensate for the climate change-driven loss of bird communities of avalanche tracks in the Alps

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As a consequence of both climate and land-use change, open alpine habitats are shrinking. Snow avalanches are a natural disturbance that create habitat mosaics which host unique bird communities, but their frequency and severity will probably be influenced by climate change. Ski-pistes can be considered the artificial counterpart of avalanches, and have been shown to have generally negative effects on alpine fauna. In this study, we compared the bird assemblages of these two open, linear habitats in the Italian Alps, to determine if ski-pistes could compensate for the potential loss of avalanche tracks and open habitats in the future. In the forest and treeline ecotone zones, there was little difference in abundance and diversity between avalanche tracks, ski-pistes and reference points. However, above the treeline, avalanche tracks supported greater bird diversity and were characterized by high vegetation diversity, whereas ski-pistes harboured less-abundant and less-diverse bird assemblages in a homogeneous habitat with high grass cover. Shrub-related species were negatively affected by the vegetation removal involved in the creation of ski-pistes, but occurred in suitable habitats in the avalanche tracks at lower elevations. Although ski-pistes had the most negative impacts in high-elevation assemblages, they were used by some species of alpine and low-elevation grasslands, showing that pistes could provide suitable habitats below the natural treeline, which may be of benefit to threatened grassland birds. New high-elevation ski facilities should be discouraged and the conservation potential of ski-pistes could be improved with sustainable management practices by including some important habitat elements from avalanche tracks such as small trees and shrubs.

Keywords: alpine birds, alpine grasslands, disturbance, farmland birds, mountain conservation.

INTRODUCTION

Mountain regions are biodiversity hotspots at the global scale (Myers *et al.* 2000); they play a substantial role in the conservation of many taxa (Catalan *et al.* 2017) and have high rates of endemism (Körner *et al.* 2017, Antonelli *et al.* 2018). However, high-elevation habitats in many areas, especially grasslands above the treeline, are under threat as a result of vegetation encroachment caused by abandonment of traditional pastures (Laiolo *et al.* 2004, Lasanta *et al.* 2017) and climate change, both of which favour the colonization of trees and shrubs towards higher elevations, leading to loss of open habitats (Gehrig-Fasel *et al.* 2007, Harsch *et al.* 2009).

One of the main natural disturbances in mountain regions is represented by snow avalanches

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(Bebi *et al.* 2009). They have a primary ecological role in influencing habitat dynamics by creating open habitat in closed and relatively structurally uniform montane forest (Rixen *et al.* 2007). Avalanches create new habitats with dynamic vegetation mosaics that are influenced by avalanche frequency and severity (Erschbamer 1989, Kulakowski *et al.* 2006, Rixen *et al.* 2007). Even though associations between animal communities and avalanches are poorly studied, the effects they have on mountain biodiversity are likely to be important. Studies on mammals, such as Brown Bears *Ursus arctos horribilis* (Mace *et al.* 1996), Caribou *Rangifer tarandus*, Wolverines *Gulo gulo* (Krajick 1998) and Chamois *Rupicapra pyrenaica* (Garcia-Gonzalez & Cuartas 1996), and on birds such as Galliformes (Klaus *et al.* 1985, Lieser 1995), Rock Buntings *Emberiza cia* (Requena *et al.* 2022) and alpine bird assemblages (Alba *et al.* 2023), have shown that avalanches in the Alps have their greatest impact on the montane forest where the semi-open habitats created can act as refugia for a wide range of shrub-nesting and farmland species, which are otherwise threatened by ongoing land use and climatic changes.

Besides natural disturbances such as avalanches, the human footprint plays an important role in influencing mountain ecosystem dynamics. The rapid growth of tourism in the Alps has had negative consequences for birds (Caprio *et al.* 2023) and for wildlife more generally (Ingold *et al.* 1993), as a consequence both of habitat loss and fragmentation caused by an increase in urban and ski-piste extent, and of direct disturbance by humans (Arlettaz *et al.* 2007, Larson *et al.* 2019). In Europe, the area affected by winter tourism is still expanding (UN [United Nations] 2002, Wipf *et al.* 2005), and is moving into currently undisturbed areas at higher elevations as a consequence of climate change (Marty 2013, Caprio *et al.* 2023). The processes involved in the construction and management of ski-pistes can be extremely damaging to the soil (Roux-Fouillet *et al.* 2011), representing a much greater impact compared to natural sources of disturbance (Rixen & Rolando 2013). Machine-grading, artificial snow and the use of chemical products have pronounced effects on soil structure (Bayfield 1996, Burt & Rice 2009) and associated microbial communities (Gros *et al.* 2004). Ski tourism and winter sports in general have been found to be deleterious for a range of animal taxa (Sato *et al.* 2013), including arthropods (Negro *et al.* 2009, 2013a), small mammals (Negro *et al.* 2013b) and birds. For birds, there is evidence of effects on stress levels (Arlettaz *et al.* 2007, Thiel *et al.* 2008, 2011), abundance (Patthey *et al.* 2008), habitat quality (Braunisch *et al.* 2011), mortality rates (Watson & Moss 2004, Buffet & Dumont-Dayot 2013), and species richness and diversity (Laiolo & Rolando 2005, Rolando *et al.* 2007, Caprio *et al.* 2011). However, there is some potential for ski-pistes to be managed in a more environmentally friendly way to minimize impacts (Caprio *et al.* 2023). Where such management practices are applied, restored ski-pistes and natural grasslands become structurally very similar, and species-richness and abundance are higher in restored rather than in unrestored plots (Caprio *et al.* 2016).

Mountain birds, and more generally mountain ecosystems, are also impacted by indirect threats such as climate change that can have negative effects on the populations at a larger scale, but such effects might be more difficult to detect (Alba *et al.* 2022). Change in snow precipitation regimes, which are predicted with climate change (Gobiet *et al.* 2014), will be likely to result in reduced avalanche frequency owing to lower winter precipitation (Gądek *et al.* 2017, Bormann *et al.* 2018), although there is uncertainty about the extent and direction that climate change will have on avalanche frequency (Eckert *et al.* 2010). In a scenario of climate change with an expansion of the forest towards higher elevations and a decrease in avalanche frequency owing to lower snowfall, ski-pistes might become important as pseudo-substitutes for open habitats at middle elevations. In the future, the distributions of both alpine bird species and the areas of ski complexes are predicted to shrink and increase in overlap towards high elevations (Brambilla *et al.* 2016) where ski-pistes have the most negative impacts (Rolando *et al.* 2007). This would be an additional threat to high-elevation bird species which are those that are mostly likely to be affected by climate change (Chamberlain *et al.* 2013). It is therefore important to develop strategies to minimize the impacts of ski-pistes on alpine biodiversity, including improved management.

With ongoing climate and land-use changes in mountain environments, the likelihood that open habitats will continue to decrease in extent is high. Alba *et al.* (2023) reported positive effects of avalanche tracks in maintaining some degree of habitat heterogeneity, but their existence is potentially threatened if climate change results in lower frequency and/or severity of avalanches (Eckert *et al.* 2013). Ski-pistes might play a role in the conservation of open areas, but the extent to which these can compensate for the loss of open natural habitats is largely unknown. Owing to increasing human pressure in mountain habitats, it is critical to integrate anthropic elements and nature for future coexistence. It is thus important to understand if ski-pistes may have a role in creating habitat of value to mountain birds.

The main aim of this work is to understand the extent to which ski-pistes have the potential to act as avalanche-type habitats, benefitting open-habitat species and supporting their expansion to lower elevations. More specifically, combining data on habitats and bird assemblages collected on avalanche tracks, ski-pistes and reference plots (i.e. natural habitats outside avalanche tracks or ski-pistes) during the breeding season in the Italian Alps, we take a largely community-based approach that aims to: (1) compare habitats between the three different plot types; (2) assess how bird abundance and diversity vary among plot types; and more specifically, (3) compare the abundance of individual grassland and ecotone bird species across plot types.

MATERIALS AND METHODS

Study area and survey design

The study took place in the Western Italian Alps in the area between the Lanzo Valleys in the north (45°13′58″N, 7°13′34″E) and the Germanasca Valley in the south (44°52′1″N, 7°2′24″E, Fig. 1), covering elevations between 1393 and 2769 m asl. European Larch *Larix decidua* is the dominant forest tree in the study area, with sparse Norway Spruce *Picea abies*, Swiss Pine *Pinus cembra* and broadleaved trees. In the treeline ecotone, shrubs such as Juniper *Juniperus communis* and Alpenrose *Rhododendron ferrugineum* are found, whilst alpine grasslands and rocky habitats occur above 2300–2400 m asl. Pastures and secondary grasslands are present below the treeline throughout the area, as are avalanche tracks that create semi-open habitats through the montane forest. There are around 400 km of ski-pistes, distributed over 247 individual pistes.

Using Geographic Information Systems (GIS) software, QGIS 3.14.15 ‘Pi’ (QGIS Development Team 2020) and satellite images from Google Earth, we placed survey points in three different locations (hereafter ‘plot types’): 180 on ski-pistes, 130 on avalanche tracks and 130 on reference points for a total of 440 points. Points were placed randomly inside mapped ski-pistes along the elevational gradient. Using an avalanche track shapefile provided by SIVa – Sistema Informativo Valanghe (Arpa Piemonte 2020), available in the Geoportale Piemonte (www.geoportale.piemonte.it) – we created horizontal and vertical transects with the same amount of points on avalanche tracks, and in reference areas outside the track. Points were also defined according to three broadly defined habitat zones (henceforth ‘zones’) along the elevation gradient: mountain forest, $n = 240$; treeline ecotone, $n = 100$; alpine grassland, $n = 100$. These represent zones of different habitat structure along the elevation gradient (as per Chamberlain *et al.* 2023), although owing to local topographic and land-use influences, they show variation in the elevations at which they occur (see Fig. S1a). Points were placed at least 200 m apart in order to avoid overlap, and one visit for each point was carried out either in 2021 or 2022 during the breeding period (i.e. from 15 May to 15 July). See Alba *et al.* (2023) for further details on study design, zone classification and field methods.

Habitat and vegetation

From the centre of each point, we recorded elevation and estimated by eye the percentage cover of habitat variables within a 100-m radius, the latter measured with a laser rangefinder (following Chamberlain *et al.* 2013, Jähnig *et al.* 2018). These were: high canopy (≥4 m height), low canopy (between 4 and 2 m height), shrubs (woody vegetation ≤2 m height), grass (grass patches), rocks (scree included), snow, dead organic material (trunks, branches and twigs) and bare ground (ground with no or scarce vegetation cover or with small-sized gravel). Within a 50-m radius, we also estimated the number of small trees (trees ≤2 m height) and the number of mature trees (≥2 m height, >20 cm trunk diameter at chest height, divided according to species, i.e. *Larix*, *Pinus*, *Picea*, broadleaved). We retrieved elevation (metres) and slope (degrees) for each point using a

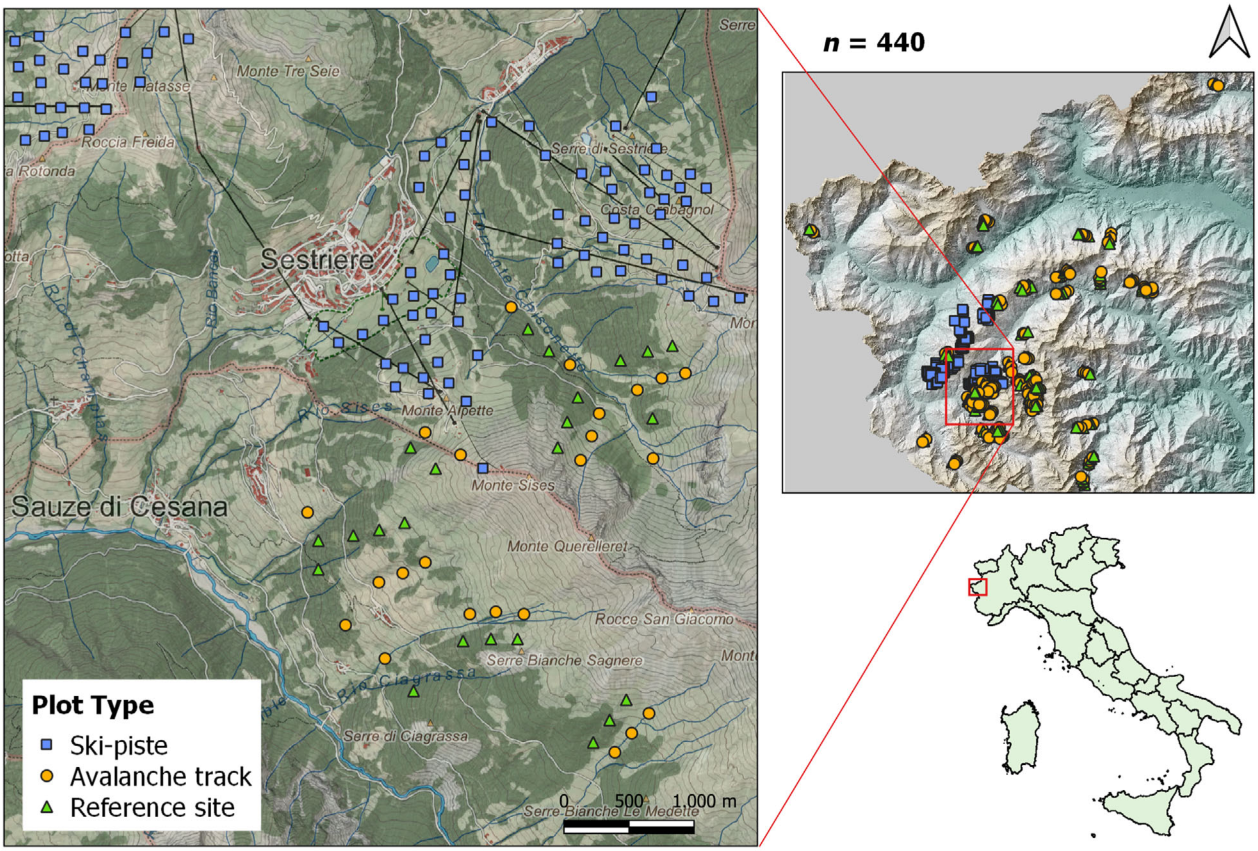

Figure 1. Map of the study area located in northwestern Italy, showing the 440 points investigated in this study. Triangles = reference points, circles = avalanche tracks and squares = ski-pistes.

Digital Terrain Model (DTM) in QGIS 3.14.15 'Pi' (QGIS Development Team 2020).

Bird assemblages

Point counts were carried out using a 10-min count period (Bibby *et al.* 2000), divided into three time-intervals of 3, 2 and 5 min each, which allows detectability to be accounted for even when there is only a single visit per point (Alldredge *et al.* 2007), as in our case. All birds seen or heard within a 100-m radius, and for each individual the time interval in which it was detected, were noted. This method allows detectability to be accounted for using time-removal models (see Statistical analyses) where each individual bird is counted once, so individuals are 'mentally removed' from a closed population of undetected birds by the surveyor. Our goal was to determine which species were using the habitat within a given point-count location. We thus analysed birds that were considered to be actively using the habitat (e.g. foraging, resting, singing), including aerial foragers (e.g. swifts, swallows and martins) and raptors when explicitly seen hunting over the area of the point count. Fly-overs (i.e. species showing no interaction with the point count location) were excluded from our dataset. Surveys were carried out in suitable weather conditions (i.e. good visibility, no rain or strong winds) from 1 to 1.5 h after sunrise until 11:00 AM, when bird activity is highest.

Statistical analyses

Habitat and vegetation

We used the function 'princomp()' and the R package *factoextra* (Kassambara & Mundt 2017) to carry out principal component analyses (PCAs) on habitat and topographic (slope and elevation) variables, first on the general dataset and then one for each zone to visually identify variables mostly associated with each plot type. We classified points by plot type and calculated 99% confidence ellipses to assess overall habitat differences between them. We then carried out Kruskal–Wallis tests to assess significant differences in habitat variables among plot types.

Bird assemblages

Detectability was modelled using time-removal models for each detected bird species using the *detect* package (Sólymos *et al.* 2013) in R software and to correct species abundances (Diefenbach *et al.* 2007). These models were developed with the goal of improving estimates of bird abundance by accounting for the availability bias inherent in point-count data (Sólymos *et al.* 2018). Models were integrated with covariates that could have a potential effect on bird detectability during the breeding season (Sólymos *et al.* 2018) – the day of year (JDAY) and the time of day (TSSR). Time-removal models were fitted with and without covariates, and the best model was selected for each species based on Akaike's information criterion (AIC). It was possible to compute specific detection probabilities only for 25 species for which an abundance threshold was reached ($n > 40$). We used surrogate species detection probabilities based on expert opinion, when possible, for the other species (following Davey *et al.* 2012). When surrogate species could not be identified, the average detection probability of the community (0.59 ± 0.24 sd) was assigned.

To explore spatial patterns of bird assemblages in ski-pistes, avalanche tracks and reference points, we modelled bird abundance and diversity in terms of the true Shannon index (i.e. *exp* (*H′ Shannon Index*)) as response variables with plot type (three levels) and zone (three levels) and their interaction as predictors by fitting a generalized linear model (GLM) with a Poisson distribution and linear model (LM) respectively.

To detect compositional changes in bird communities within zones between the three plot types that could have been masked by abundance and diversity metrics, and to assess which habitat variables were most closely associated with these changes, we carried out three canonical correspondence analyses (CCAs) using the function 'cca()' from the *vegan* R package (Oksanen *et al.* 2013). CCA is a constrained ordination which combines principles of ordination and regression (Ter Braak 1995, Ter Braak & Smilauer 1998) and is useful to assess how environmental predictors relate to bird species. Before the analysis, we selected the variables that significantly contributed to the variation in species composition by forward selection, using the 'ordistep' function in the *vegan* R package (Oksanen *et al.* 2013). We visually assessed clustering by plot type and species scores in relation to the axes, as well as significance via Monte Carlo bootstrapping tests with 999 permutations for each CCA.

We were particularly interested in the response of the open-habitat bird assemblages to avalanche and ski-piste impacts as they are likely the most vulnerable to climate change in the future (Chamberlain *et al.* 2013). We therefore modelled total abundance (i.e. the sum of all species abundances) and diversity by fitting a GLM and an LM, respectively, using a subset of the previous dataset only containing grassland/ecotone (hereafter GE) species. GE species were classified following Laiolo *et al.* (2004) and Caprio *et al.* (2016) concerning habitat guilds of birds breeding in the Western Alps. The majority of these open and semi-open habitat species are also considered farmland species.

In a final analysis, we modelled species-specific responses of nine GE bird species, because individual species might respond differently to disturbance pressure based on their degree of association with specific open habitats. These species were Whinchat *Saxicola rubetra*, Yellowhammer *Emberiza citrinella*, Rock Bunting, Tree Pipit *Anthus trivialis*, Common Linnet *Linaria cannabina*, Dunnock *Prunella modularis*, Eurasian Skylark *Alauda arvensis*, Northern Wheatear *Oenanthe oenanthe* and Water Pipit *Anthus spinoletta*. We decided to use these species as they had large sample sizes ($n > 60$) and they represented the ecotone/grassland bird community. As above, we fitted Poisson GLMs using abundance as the response variable with plot type, zone and their interaction as predictors.

Initial models for all species and GE species showed evidence of spatial autocorrelation. Therefore, for each GLM and LM we took into account spatial autocorrelation by incorporating a spatially lagged variable as an autocovariate that reflects the influence of neighbouring observation, using the coordinates of each point count with the R package *spdep* (Bivand *et al.* 2015). Model diagnostic plots and goodness-of-fit for GLMs and LMs were evaluated by checking for overdispersion and R-squared, respectively, as well as residual and QQ-norm plots. All models showed an acceptable fit. All analyses were carried out in R software 4.4.2 (R Core Team 2024).

RESULTS

Habitat and vegetation

The PCAs carried out on the general dataset showed a clear distinction between ski-piste points, avalanche track points and reference points (Table S1; Fig. 2a). However, in the PCAs produced for each zone, the similarity between avalanches and reference points increased along the elevation gradient, whilst ski-pistes remained clearly separated (Fig. 2b–d).

Results from Kruskal–Wallis tests highlighted statistically significant differences for the majority of habitat variables (Table S2). In general, ski-pistes were characterized by greater grass and bare ground cover and the absence of woody vegetation. Avalanche tracks were defined by a larger number of small trees, and greater shrub and rock cover. Reference points were mainly characterized by a higher canopy cover. These differences became less clear along the elevational gradient, especially between avalanche tracks and reference points (see Fig. S1 for satellite pictures of an example reference site, avalanche track and ski-piste).

Bird assemblages

Overall, 81 bird species were detected in the study area during the two breeding seasons (see Table S3 for species, abundances and detectability). Of these, 55 were detected in reference points, meaning that avalanches and ski-pistes contribute to overall gamma diversity with 26 species (32% of the total).

Abundance did not vary significantly according to plot type ($\chi^2 = 4.32$, $P = 0.115$), but it showed significant differences between zones ($\chi^2 = 16.33$, $P < 0.001$). There was a significant interaction between the two terms ($\chi^2 = 17.95$, $P = 0.001$). Diversity was significantly different between plot types ($R^2 = 0.18$, $F_{2,430} = 9.16$, $P < 0.001$) and zones ($R^2 = 0.18$, $F_{2,430} = 31.04$, $P < 0.001$) and there was a significant interaction between them ($R^2 = 0.18$, $F_{4,430} = 3.13$, $P = 0.014$). Overall, ski-pistes had lower abundance and diversity in the alpine zone in comparison to avalanche tracks, but not reference points (Fig. 3a; Table S4).

All CCAs were significant ($P < 0.01$), highlighting differences in compositional changes between plot types according to habitat variables in different zones (Table S5; Fig. 4). Differences were more pronounced at lower elevations where species such as Whinchat, Tree Pipit and Rock Sparrow *Petronia petronia* were associated with ski-pistes, which were mainly characterized by grass and bare ground. Rock Bunting, Northern Raven *Corvus corax* and Black Grouse *Lyrurus tetrix* were associated with avalanche tracks with shrubs, rocks and small trees. Reference point assemblages were associated with high canopy and high abundance of trees, with species typical of montane forest such as Common Firecrest *Regulus ignicapilla*, Song Thrush *Turdus philomelos* and Eurasian Bullfinch *Pyrrhula pyrrhula*. Moving to higher elevations, ski-piste assemblages remained separated from the other two plot types that showed a lower degree of clustering. Species such as Alpine Chough *Pyrrhocorax graculus*, Rock Sparrow and White-winged Snowfinch *Montifringilla nivalis* were mainly associated with ski-pistes, these species being able to exploit ski-piste infrastructures as nesting sites.

GE species abundance and diversity differed significantly according to plot type ($\chi^2 = 73.70$, $P < 0.001$; $\chi^2 = 43.01$, $P < 0.001$ (respectively)) and zone ($\chi^2 = 75.46$, $P < 0.001$; $\chi^2 = 65.69$, $P < 0.001$), and there was an interaction between them ($\chi^2 = 59.53$, $P < 0.001$; $\chi^2 = 98.09$, $P < 0.001$). Abundance and diversity were lower in reference points in the montane forest zone and diversity was lower on ski-pistes in the alpine zone. Abundance and diversity of the two open habitats (ski-pistes and avalanche tracks) were higher than reference points in the ecotone treeline and montane forest zones (Fig. 3b; Table S4).

Species-specific responses were reported for the nine GE species according to plot type and zone (Fig. 5; Table S6). In the montane forest, Whinchat, Tree Pipit and Yellowhammer were abundant in ski-pistes and avalanche tracks, whilst Rock Bunting was strongly associated with avalanche tracks. In the treeline ecotone, Whinchat, Common Linnet and Dunnock showed positive associations with avalanches, whilst species typical of alpine grasslands such as Eurasian Skylark and Water Pipit were more abundant in ski-pistes. In

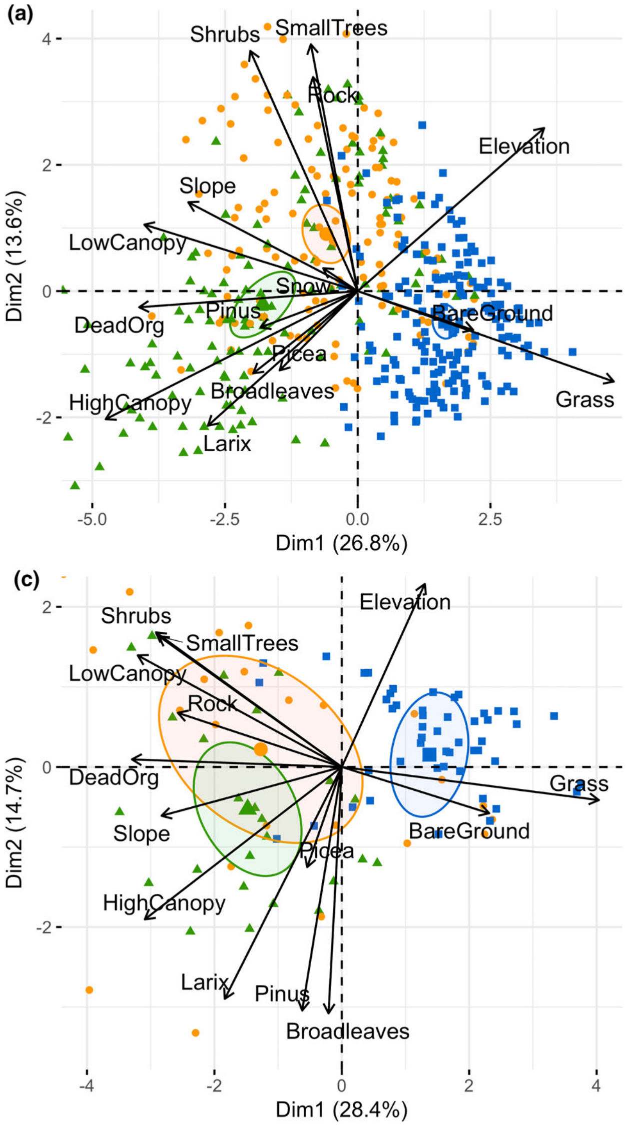

Figure 2. Biplots of the PCAs performed on the general dataset (a), and on the montane forest (b), treeline ecotone (c) and alpine grassland (d) datasets. Arrows represent continuous environmental variables. 99% confidence ellipses are shown for each plot type. Triangles = reference points, circles = avalanche tracks and squares = ski-pistes. Full results and details on habitat-variable names are given in Table S1.

the alpine grasslands, species linked to habitat mosaics such as Tree Pipit, Rock Bunting, Common Linnet, Whinchat and Dunnock were less abundant on ski-pistes.

DISCUSSION

In this study, we analysed the effects of two different sources of disturbance that have a strong influence in shaping mountain landscapes and, as a consequence, biodiversity. Avalanche tracks hosted relatively high levels of bird abundance and diversity, and were characterized by high vegetation diversity with an elevated cover of rocks, shrubs and small trees. Ski-pistes harboured lower levels of bird diversity and abundance in comparison to avalanche tracks, especially in the alpine grassland zone, and had high grass and bare ground cover. However, it is interesting to note how some species such as Skylark, Water Pipit, Northern

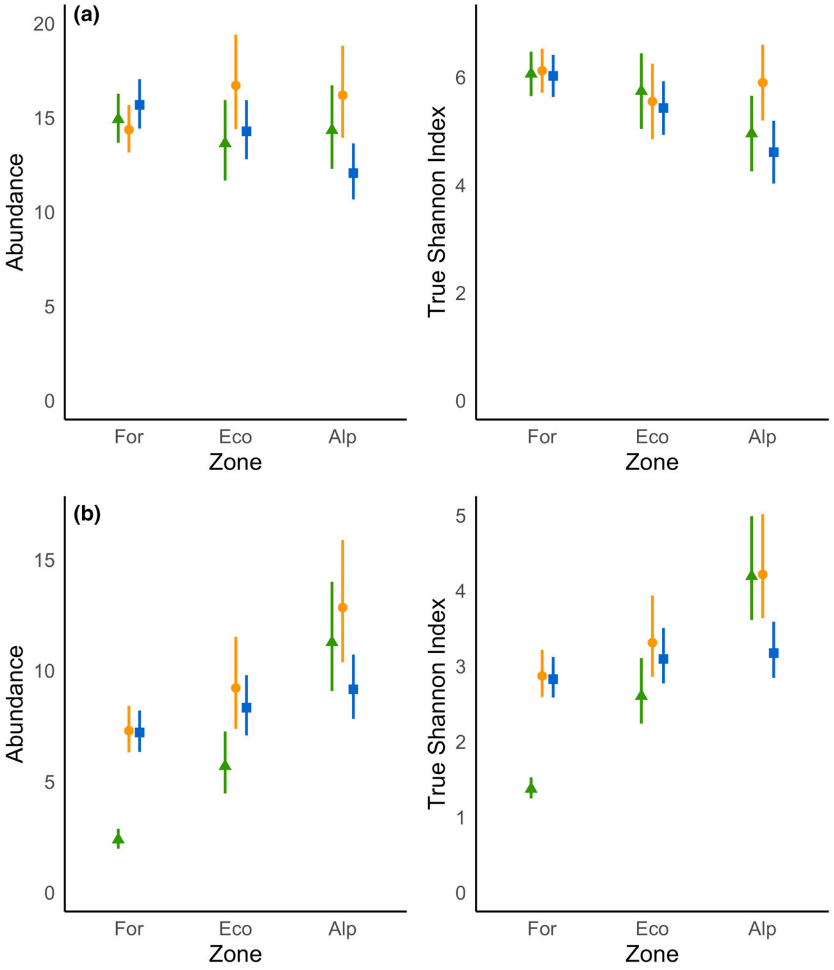

Figure 3. Differences in abundance (mean birds per point ±95% CIs) and diversity (i.e. true Shannon index per point) according to plot type and zone for the entire bird assemblage (a) and for the grassland/ecotone bird assemblage (b). Triangles = reference points, circles = avalanche tracks and squares = ski-pistes. For = montane forest, Eco = the treeline ecotone and Alp = the alpine grassland zone. Full results are given in Table S4.

Wheatear, Whinchat and Tree Pipit showed high abundances in ski-pistes. For the former three species, ski-pistes thus represented the creation of suitable habitat below the treeline at elevations where the species would not usually occur under natural conditions (Fig. S1b). On the contrary, species tied to shrubby and habitat mosaic areas were negatively affected by ski-pistes, but found suitable habitat in avalanche tracks, especially in the montane forest and treeline ecotone zones.

The habitat differences seemed to have the greatest impact in open habitats, with most negative effects of ski-pistes at higher elevations. Both on the bird community as a whole and when focusing on grassland species, abundance and diversity were notably lower than on avalanche tracks and, to a lesser extent, reference points. This is probably because the open areas provided by ski-pistes in the forest are used by a range of species. Previous studies carried out in grasslands in the same area (Rolando *et al.* 2007, Caprio *et al.* 2011) found negative effects of ski-pistes on bird species, supporting our findings. Conversely to our results, Laiolo and Rolando (2005) found negative effects of ski-pistes on the bird community in the forest zone. The differences between studies may arise because Laiolo and Rolando (2005) were focused specifically on edge habitat and at generally lower elevations (1100–2200 m asl) than our study site. Each of

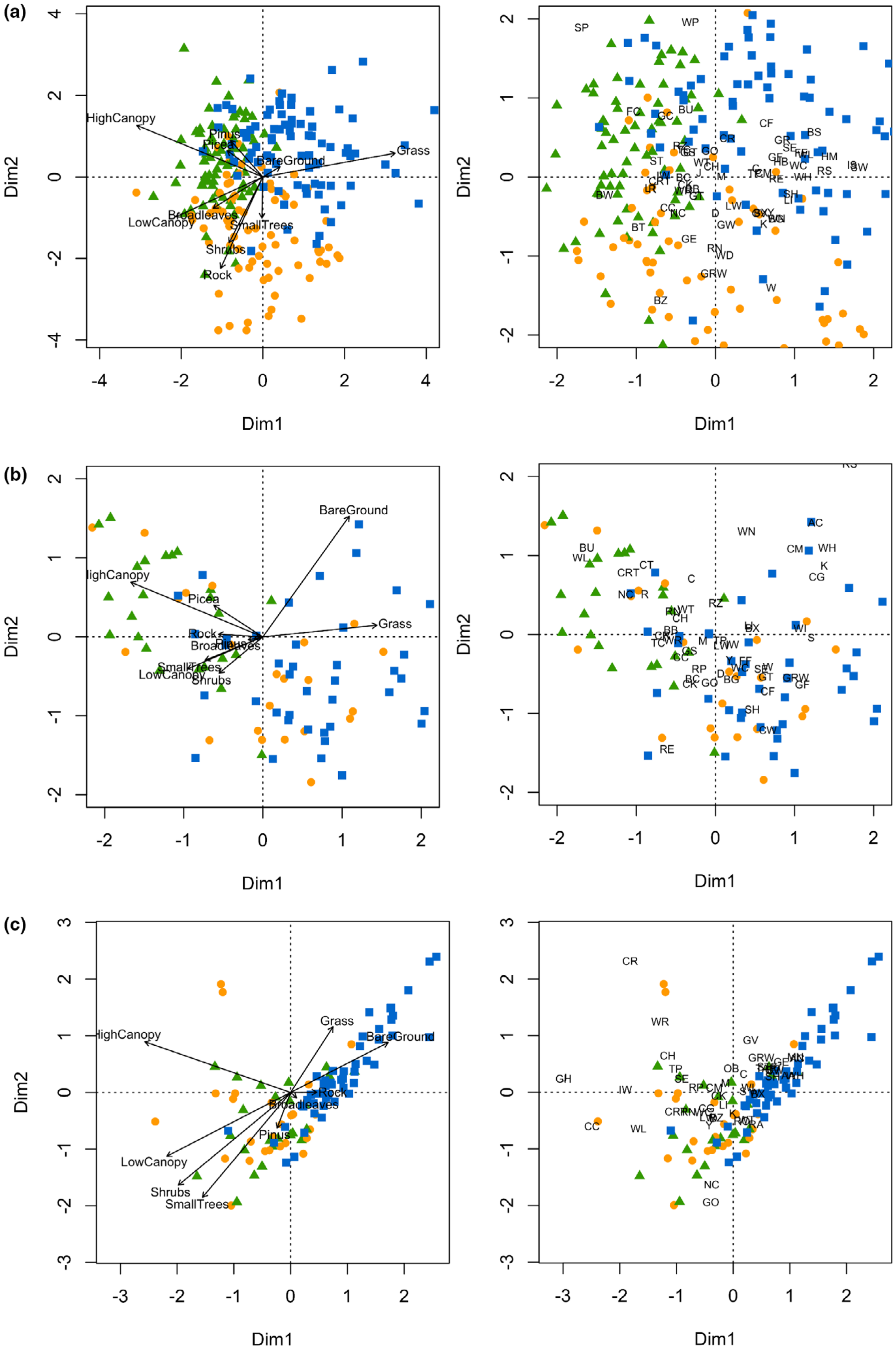

Figure 4. Biplots of the CCAs (left panels = habitat variables, right panels = bird species) performed on the montane forest (a), the treeline ecotone (b) and alpine grassland (c) datasets. Triangles = reference points, circles = avalanche tracks and squares = ski-pistes. See species codes in Table S3 and full results of the CCAs in Table S5.

these previous studies was carried out when the ski-pistes were just created and hence had high bare ground cover (Laiolo & Rolando 2005, Rolando *et al.* 2007). After two decades, re-vegetation and grass cover might have provided a partial restoration of soil on these pistes (Rolando *et al.* 2007, Roux-Fouillet *et al.* 2011), yet similar low levels of bird diversity were recorded in grasslands. Such substantial impacts at high elevations are noteworthy given that the proportion of bird species (and other sensitive taxa) is higher in these fragile habitats (Viterbi *et al.* 2013). Ski-pistes at lower elevations in the montane forest are assumed to have experienced a faster vegetation growth, because the bird assemblages were more diverse in comparison to previous studies where higher bare ground cover and poor vegetation structure were reported (Laiolo & Rolando 2005). No information about the frequency or degree of habitat management (e.g. machine grading, vegetation removal) on ski-pistes was available to include in our analyses, although it would be interesting to test the extent to which different degrees of management influence bird assemblages.

Ski-pistes had the most negative impacts on species related to shrub cover in the alpine zone. This is not surprising as the artificial removal of trees, shrubs, rocks and even the topsoil (Bayfield 1996, Rixen & Rolando 2013) can have negative effects on vegetation dynamics (Barni *et al.* 2007, Roux-Fouillet *et al.* 2011), and consequently on biodiversity, that can last for decades. The abundance of Rock Bunting, Whinchat, Tree Pipit, Dunnock and Common Linnet were significantly lower in ski-pistes in the alpine zone in comparison to avalanche tracks, where a more heterogeneous vegetation was present. Species-specific habitat requirements are not met in these areas, such as the presence of rocks and shrubs for Rock Bunting (Requena *et al.* 2022), low canopy and small trees for Tree Pipit and Whinchat (Fischer *et al.* 2013, Fonderflick *et al.* 2013), shrubs for Dunnock and a high overall habitat complexity for Linnet, and more broadly for all shrub-related species (Caplat & Fonderflick 2009, Jähnig *et al.* 2018) which were more closely associated with avalanche tracks (Fig. 5).

Positive effects of ski-pistes on Whinchat and to a lesser extent on Tree Pipit were evident in the montane forest zone. Whinchats were mostly observed using small larches on the sides of less-heavily-managed pistes (i.e. with more natural elements and higher vegetation structure), whilst Tree Pipit, which needs the presence of both grass and trees (Fonderflick *et al.* 2013), occurred in pistes where there was a marked contrast between forests and open habitats. Grassland specialists such as Eurasian Skylark and Water Pipit also seemingly benefitted from ski-pistes at lower elevations as they allowed these species to expand their range downwards into the treeline ecotone. Other species were even able to exploit ski-piste infrastructures, including Rock Sparrow, White-winged Snowfinch and Alpine Chough, which were observed using buildings and pylons along and close to ski-pistes as nesting sites.

Changes in snow precipitation, and consequently in avalanche frequency and severity, which are forecast in a context of climate change (Beniston *et al.* 2018, Pörtner *et al.* 2019), are expected to have negative consequences for open habitats and their associated biodiversity. Avalanche frequency and severity may decrease as a consequence of lower snow cover (e.g. Gądek *et al.* 2017, Bormann *et al.* 2018), resulting in a process of vegetation encroachment with loss of suitable habitats for semi-open habitat species. However, we should acknowledge that there is no consensus on how climate change will affect avalanches in the future. Indeed, some forecasts predict that avalanche frequency and severity may actually increase as a result of warmer winters (e.g. Ballesteros-Cánovas *et al.* 2018) and higher precipitation in February and March (e.g. Laute & Beylich 2018). In such scenarios, avalanche tracks would play a substantial conservation role as refugia for open habitat species.

Our results have highlighted how avalanche tracks harbour more natural conditions and high levels of biodiversity, when considering both the entire bird community and only GE species, especially at higher elevations. Indeed, the abundance of GE bird species is even greater on avalanche tracks than in undisturbed habitat (Fig. 3b), highlighting their conservation importance for GE bird assemblages (see Alba *et al.* 2023). Whinchat, Tree Pipit, Yellowhammer, Rock Bunting, Common Linnet and Dunnock will be substantially affected if there is a reduction in avalanche frequency in the near future, whether or not open habitats created by avalanches undergo vegetation encroachment. These predictions become even more relevant if we consider a progressive upshift

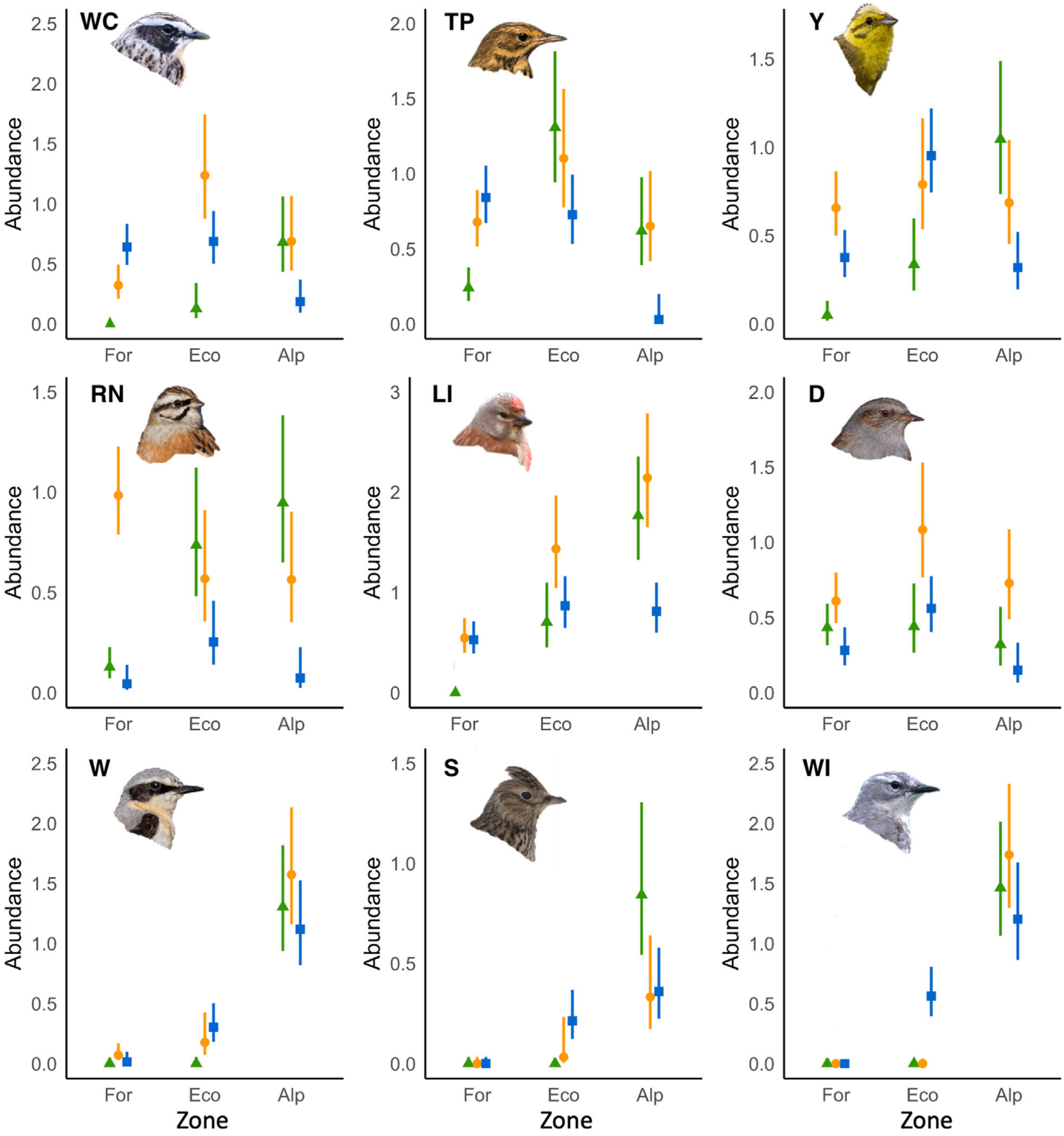

Figure 5. Relationships between abundance (mean birds per point ±95% CIs) and the interaction between plot type and zone for the nine selected grassland/ecotone species (from top left Whinchat, Tree Pipit, Yellowhammer, Rock Bunting, Common Linnet, Dunnock, Northern Wheatear, Eurasian Skylark, Water Pipit). Triangles = reference points, circles = avalanche tracks and squares = ski-pistes. For = montane forest, Eco = the treeline ecotone and Alp = the alpine grassland zone. Full results are given in Table S6.

of the forest at the expense of the treeline ecotone, where these species are also found. Furthermore, this shift in the treeline poses a major risk to species which are exclusively found at higher elevations, such as Northern Wheatear, Eurasian Skylark and Water Pipit. The role of mountain ecosystems in the conservation of biodiversity, which has become increasingly important especially for open habitat taxa, might be jeopardized by these environmental changes.

CONCLUSIONS

This study is the first to compare the effects of natural (i.e. avalanche tracks) and artificial (i.e. ski-pistes) sources of disturbance on mountain bird assemblages. Although ski-pistes generally harbour low levels of biodiversity, we argue that they have the potential to provide suitable habitats for mountain biodiversity and become refugia for open habitat species, in a context of climate and land-use changes. Because our results are based on a large sample of points scattered over a wide area, we are confident that these findings are generally applicable to the management of ski-pistes in other mountain areas. Birds are considered good indicators of ecosystem health (Montevecchi 1993, Bibby 1999, Gregory *et al.* 2003), so these findings should also provide useful insights for other taxa associated with these habitats.

We know from recent studies (Requena *et al.* 2022, Alba *et al.* 2023) that certain elements characteristic of avalanche tracks, such as small trees, shrubs and small rocks, are likely to increase their bird diversity. Our results align with these studies and we suggest that these key habitats should be retained during the construction of ski-pistes, or implemented during post-construction management, also including other beneficial management interventions for ski-pistes such as vegetation patches (see 'safety islands' in Urbanska 1997) to lower the negative impact of pistes and make them more biodiversity-friendly. Maintaining a more natural ski-piste edge (see Fig. S1c) and re-seeding newly constructed pistes might also potentially have positive effects on bird communities, without any repercussions on piste functionality (Caprio *et al.* 2023). This is important, especially at higher elevations, where the bird community is impacted the most.

Even with improved management, it is unlikely that ski-pistes will be able to reach the biodiversity levels of avalanche tracks. In part, this is a consequence of the difficulties of re-vegetation dynamics in the harsh climatic conditions in alpine environments (Barni *et al.* 2007). Moreover, the construction of new ski resorts at high elevation must be discouraged at all costs, and any new developments should take into account sensitive areas that are important for mountain bird populations (e.g. Galliformes), where human activities should be limited (Zeitler 2000, Braunisch *et al.* 2011, Arlettaz *et al.* 2013). We have demonstrated that some alpine grassland species are able to colonize the treeline zone in ski-pistes owing to the removal of vegetation in this habitat, but overall effects on the community were negative. The main conclusion of this study is that in the montane forest zone, ski-pistes have great potential as refugia for open habitat species in the face of habitat loss at higher elevations, but sustainable management is necessary. Together with avalanche tracks and other habitats not considered in this study, such as pastures and secondary grasslands, they could help to maintain high levels of biodiversity, and contribute to the conservation of farmland and open-habitat species at a large scale in mountain ecosystems.

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AUTHOR CONTRIBUTIONS

Dayron Lopez: Data curation; investigation; writing – original draft; methodology; formal analysis. **Dan Chamberlain:** Methodology; project administration; supervision; writing – review and editing. **Emmanuel Requena:** Investigation; writing – review and editing. **Domenico Rosselli:** Resources. **Riccardo Alba:** Conceptualization; methodology; data curation; investigation; formal analysis; writing – review and editing; supervision.

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None.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL NOTE

None.

Data Availability Statement

Data used in this study will be provided upon reasonable request to the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Overview of eigenvalues and cumulative variance percentage (Cum. Var. %) and summary of loadings for habitat variables on dimensions 1 and 2 of the PCA on the general dataset and for the three zones. Coordinates for avalanche tracks (A), reference sites (C) and ski-pistes (S) are also reported.

Table S2. Results of Kruskal–Wallis tests for differences in habitat variables between plot types (avalanche tracks (A), reference points (C), ski-pistes (S)) for the general dataset and for the three zones. Chi-square and *P*-values are reported, as well as means ± se.

Table S3. All species detected, including species code, relative abundance, corrected abundance and detection probability, standard deviation, identified surrogate species and species habitat; *indicates use of average detection probability (0.59 ± 0.24). The habitat column reports the classification used by Caprio *et al.* (2016) (SW = shrubs/woodland and GE = grassland/ecotone). Species not reported by Caprio *et al.* (2016) were categorized according to expert opinion.

Table S4. Results of GLMs and LMs carried out on abundance and diversity (expressed as the true Shannon index) for the entire and grassland/ecotone (GE) bird assemblages. Estimates, se and *P*-values are reported. Type indicates plot types:

avalanche tracks (A), ski-pistes (S) and reference points (C), set as the reference level (not shown). Zones: alpine grassland zone (Alp), treeline ecotone zone (Eco) and montane forest (For), set as the reference level (not shown). Autocov stands for the spatially lagged variable added as autocovariate to account for spatial autocorrelation in the models.

Table S5. CCA outputs for each zone with χ^2, F and P values reported. Constrained eigenvalues proportion and species scores are reported according to the two axes (i.e. Dim1 for x-axis, Dim2 for y-axis; see Fig. 4 for biplots and Table S3 for species codes).

Table S6. Results of GLMs carried out on abundance of nine selected grassland/ecotone species abundances (D, Dunnock; LI, Linnet; RN, Rock Bunting; S, Skylark; TP, Tree Pipit; W, Wheatear; WC, Whinchat; WI, Water Pipit; Y, Yellowhammer) between plot types (Type) and zone (Zone) and their interaction term. Chi-square and P-values are shown. Autocov is the spatially lagged variable added as autocovariate to account for spatial autocorrelation in the models.

Figure S1. Overview of the elevational gradient of the three plot types investigated in this study showing different vegetation gradients with elevations (a). Treeline ecotone habitat is fragmented on ski-pistes, resulting in an increase of open habitat towards lower elevations (b). Comparison of the treeline ecotone between a reference site and ski-piste at the same elevation: note the difference in coverage of canopy, shrubs and small trees as well as the marked contrast of the ski-piste edge (c).