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Interactions between Alpine biodiversity, snow and climate change

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Abstract

Mountain and upland areas occupy around 25% of Earth's surface yet they harbour high levels of biodiversity thanks to the diversity of habitats that vary along the elevational gradient. For this reason, uplands are excellent study systems where carry out ecological research under different environmental conditions. These regions, including the Alps, are the result of long-lasting interactions between natural processes and human populations that have deeply shaped mountain landscapes and their associated biodiversity. However, climate and land-use changes are threatening mountains, making them one of the most vulnerable ecosystems worldwide and of major conservation concern. Mountain birds are challenging to study since carrying out research in these environments is not trivial, mainly due to logistical problems, yet little is known about their status and population trends even if they are one of the most threatened bird categories. This thesis concentrates on the upland and mountain bird assemblages found in the European mountains, with a particular focus on the Alps, one of the most iconic mountain chains in Europe. In this thesis, starting from a general perspective on bird populations from the mountain systems present in Europe, I will narrow down my focus on the mountain bird assemblages found in the Alps. I will cover not only the breeding period but also other periods of the bird's life-cycle, in particular taking into account semi-open and open habitat bird species. The first step involved a systematic literature review which allowed to objectively quantify which drivers of environmental change have been most consistently associated with positive or negative population responses in European upland and mountain bird populations. Threats directly affecting bird populations through mortality and fitness had the most significant negative effects, whereas effects from indirect impacts such as climate change were more difficult to detect (Chapter II). Despite their primary ecological role in affecting mountain ecosystem dynamics, snow avalanches, and their effects on animal communities, are highly understudied. However, I underline with my work that

avalanches might actually increase mountain biodiversity levels at certain elevations by creating habitat mosaics which can be considered refugia for many threatened bird species (Chapter III). When I compared a natural source of disturbance (avalanches) with an artificial one (ski pistes; Chapter IV), I found that ski pistes generally harboured low levels of bird abundance and diversity in comparison to avalanche tracks. This is mainly due to the poor habitat structure of ski pistes because woody vegetation, which is fundamental for many semi-open and open habitat species, is removed during piste creation. However, some species might be able to colonize ski pistes which, in a context of vegetation encroachment caused by climate and land-use changes, could act as refugia for farmland birds, yet environmental-friendly practices are necessary for the management of ski pistes. I then focused on a single species from the alpine grasslands, the Northern Wheatear *Oenanthe oenanthe*, to assess the habitat requirements during the pre- and breeding periods of this migratory species (Chapter V). Birds used open areas in the bottom of the valley when arriving from spring migration and early arriving males were able to occupy high-elevation territories when snow cover was still high. For such species, it is fundamental that extensive seasonal grazing activities are maintained, in order to counteract the vegetation encroachment caused by climate change and the abandonment of traditional pastoral activities. In Chapter VI I took into account another key period for birds in the mountains: the post-breeding migration period. For the first time I reported how high-elevation habitats in the Alps are used by a high number of birds as stopover and refuelling sites, even by species which are not tied to mountain habitats during other phases of their annual cycle. The habitat use of high-elevations is probably due to the high levels of trophic resources such as arthropods, which are still exploitable by a wide range of species in late summer and at the beginning of the autumn. In order to conserve mountain biodiversity and keep these ecosystems and their ecological interactions intact, we need to meet bird assemblage requirements and maintain a variety of habitats. To do so, further research about interactions between species and their habitats, as well as

inter-specific interactions, are needed. With this thesis, I have contributed to increasing the knowledge of what drives mountain bird populations across Europe and have investigated previously unknown relationships between mountain bird species and specific habitats in the Alps. The presented studies dealt with bird assemblages along the elevational gradient across different habitats, not only during the breeding season, but also during the pre- and post-breeding periods. On this basis, further studies could increase the knowledge of mountain ecosystems and animal communities by adopting this study designs to study other taxa, or by increasing research effort in periods outside of the breeding season. This is a fundamental requirement in order to promote and develop conservation strategies for mountain biodiversity at 360-degrees.

Riassunto

Le aree montane occupano circa il 25% della superficie terrestre e sono caratterizzate da una ricca biodiversità. Questo è dovuto principalmente alla diversità di habitat, i quali variano lungo il gradiente altitudinale su un'area ristretta. Dunque, queste aree rappresentano ottimi sistemi di studio dove portare avanti ricerche sull'ecologia delle specie in diverse condizioni ambientali. Questi ecosistemi, di cui fanno parte anche le Alpi, sono il frutto di lunghe interazioni che vanno avanti da migliaia di anni tra i processi naturali e le popolazioni umane, le quali hanno plasmato i paesaggi montani e influenzato di conseguenza le specie animali associate. I cambiamenti climatici e di uso del suolo sono tra le più gravi minacce, e rendono le montagne uno tra gli ecosistemi più vulnerabili al mondo ma allo stesso tempo, di grande valore conservazionistico. Le attività di ricerca scientifica sull'avifauna montana non sono semplici da condurre poiché in questi ambienti può risultare difficoltoso pianificare le attività a causa di problemi logistici; tuttavia, le conoscenze che abbiamo sulllo status conservazionistico e sull'andamento delle popolazioni sono scarse, nonostante gli uccelli montani siano tra i più minacciati. Questa tesi si concentra sulle comunità di uccelli presenti nelle aree montuose europee, con un focus particolare sulle Alpi, una delle aree più iconiche d'Europa. Partendo da una prospettiva più generale che prende in considerazione le popolazioni dei sistemi montuosi europei, restringeremo il nostro focus sulle comunità di uccelli alpini. Gli studi non copriranno solamente il periodo riproduttivo, ma anche altri delicati periodi del ciclo annuale, focalizzandosi in maniera particolare sulle specie di habitat semiaperto e aperto. Il primo passo è stato quello di effettuare una revisione della letteratura esistente, la quale ha permesso di condurre una meta-analisi per quantificare oggettivamente quali fattori siano stati associati in modo più consistente a risposte positive o negative nelle popolazioni di uccelli montani europei. I fattori che influenzano direttamente la popolazione di uccelli attraverso la mortalità e il successo riproduttivo (ad es. persecuzione, impatto con infrastrutture

ecc.) mostrano gli effetti negativi più significativi, mentre gli effetti derivanti da impatti indiretti, come ad esempio il cambiamento climatico, sono più difficili da rilevare e quantificare (Capitolo II). Nonostante il ruolo ecologico primario nelle dinamiche degli ecosistemi montani, le valanghe e i loro effetti sulle comunità animali sono ancora poco studiati. Tuttavia, nel nostro studio abbiamo dimostrato come le valanghe possano effettivamente contribuire a mantenere alti livelli di biodiversità a determinate altitudini, dove creano particolari habitat semi-aperti che possono diventare aree di rifugio per molte specie di uccelli (Capitolo III). Confrontando questo disturbo naturale con uno artificiale come le piste da sci (Capitolo IV), abbiamo scoperto come quest'ultime ospitano generalmente un minor numero di individui e di specie rispetto ai tracciati di valanga. Ciò è dovuto principalmente alla bassa complessità strutturale della vegetazione nelle piste da sci, dove la vegetazione arbustiva e arborea, fondamentale per la nidificazione di molte specie, viene rimossa durante la creazione delle piste. Tuttavia, alcune specie hanno dimostrato di essere in grado di colonizzare questi ambienti, i quali, in un contesto di cambiamento climatico e di abbandono dei pascoli, potrebbero fungere da siti di rifugio per gli uccelli di habitat aperto, ma sono comunque necessarie pratiche più sostenibili per la loro gestione. Abbiamo poi condotto uno studio su una specie migratrice in particolare, tipica delle praterie alpine, il culbianco *Oenanthe oenanthe*, al fine di valutarne le esigenze ecologiche durante il periodo primaverile ed estivo (Capitolo V). Abbiamo dimostrato come gli individui utilizzano le aree aperte del fondovalle dopo l'arrivo dai quartieri di svernamento e come i maschi più precoci riescono ad occupare i territori di alta quota quando la copertura nevosa è ancora abbondante. Per la conservazione di questa specie è fondamentale il mantenimento di attività non intensive di pascolo stagionale, al fine di contrastare la colonizzazione della vegetazione verso le alte quote e la chiusura dei pascoli di bassa quota. Nel Capitolo VI abbiamo poi preso in considerazione un altro periodo delicato per il ciclo annuale degli uccelli di montagna: il periodo della migrazione autunnale. Abbiamo dimostrato per la prima volta come gli

habitat di alta quota delle Alpi siano utilizzati da un elevato numero di specie come luoghi di sosta e di foraggiamento, anche da specie che non sono legate agli habitat montani durante le altre fasi del loro ciclo vitale. Questi habitat offrono ai migratori elevati livelli di risorse trofiche, come gli artropodi, che sono sfruttabili da un'ampia varietà di specie da fine estate a inizio autunno. Quindi, per conservare la biodiversità montana nella sua interezza e per mantenere intatti questi ecosistemi e le interazioni tra specie, dobbiamo cercare di soddisfare le esigenze delle comunità ornitiche mantenendo ad esempio la grande varietà di habitat che si rischia di perdere in un futuro prossimo. Per fare questo, sono necessari ulteriori studi sulle interazioni tra le specie e gli habitat, nonché sulle interazioni interspecifiche. Con questa tesi, si è contribuito ad aumentare la conoscenza di quali sono i fattori determinanti per le popolazioni di uccelli di montagna in tutta Europa e sono state dimostrate alcune relazioni specie-habitat precedentemente sconosciute in ambiente alpino. Sono stati riportati risultati sulle comunità di uccelli lungo il gradiente altitudinale attraverso diversi habitat, prendendo in considerazione non solo la stagione riproduttiva ma anche il periodo pre- e post-riproduttivo. Partendo da questa base, futuri studi potranno contribuire ad aumentare la conoscenza degli ecosistemi montani e delle loro comunità faunistiche adottando come modello di studio alcuni lavori presentati in questa tesi. Questi risulteranno utili per studiare altri taxa o altri periodi del ciclo vitale che sono ancora poco indagati nel mondo dell'eclogia alpina. Questo è un requisito fondamentale per riuscire a promuovere e sviluppare strategie di conservazione efficaci per la biodiversità montana a 360 gradi.

List of manuscripts

Alba, R., Kasoar, T., Chamberlain, D., Buchanan, G., Thompson, D., & Pearce-Higgins, J. W. (2022). Drivers of change in mountain and upland bird populations in Europe. *Ibis, 164(3), 635-648*

Alba, R., Oddi, L., Rosselli, D., & Chamberlain, D. (2023). Avalanches create unique habitats for birds in the European Alps. *Journal of Ornithology, 164(2), 377-388*

Dayron, L., Chamberlain, D., Requena, E., Rosselli, D., & **Alba, R.** (2023). Mountain bird assemblages are shaped by differential vegetation dynamics in avalanches and ski pistes. *Submitted to Oecologia*

Alba, R., Chamberlain, D., Rosselli, D., & Sander, M.M. (2023). Habitat quality drives the spatio-temporal occupation of a migratory songbird, the Northern Wheatear *Oenanthe oenanthe*, in alpine grasslands. *Ardeola, 71(1), 61-80*

Alba, R., Sander, M.M., Rosselli, D., & Chamberlain, D. (2023). High-elevation habitats are important for birds during the post-breeding migration period in the Alps. *Journal of Ornithology, 1-11*

Chapter I – Introduction

Mountain and upland areas as biodiversity hotspots

Mountain and upland regions host high relief habitats characterized by high elevations and complex topography that cover around 25% of the world's terrestrial surface (Kapos et al. 2000) and support around one third of global biodiversity (Körner 2004). These areas harbour almost 50% of biodiversity hotspots (Myers et al. 2000) and are of special interest as they contain a unique biodiversity which occurs in a variety of habitats (Nagy and Grabherr 2009). Parameters such as aspect, slope and solar radiation influence climate, with marked changes in temperatures over short distances in elevation (Barry 1992). This makes mountain ecosystems perfect space-for-time substitutes for latitudinal gradients and thus ideal study areas.

Species that depend on and are restricted to high elevation habitats for most of their annual cycle are considered mountain specialists and often show very narrow geographic (and vertical) distributions. In some mountain areas, ranges of mountain specialists may sometimes be restricted to a single mountain or valley (Antonelli et al. 2018), hence mountains have high rates of endemism (Körner et al. 2017) and speciation (Fjeldså et al. 2012; Rahbek et al. 2019). As a consequence, the proportion of threatened species that are found in mountain regions is significantly greater than in other types of habitats (Franzen & Molander 2012). However, also a wide number of generalist species occurs in the mountains, since many species (e.g. farmland birds) have lost their habitat due to anthropogenic impacts at lower elevations (Archaux 2007).

High levels of biodiversity found in mountain regions are the results of complex interactions between climate and topography that need to be considered both at large and fine scales. Geological heterogeneity and long-term fluctuations in climate are the main drivers of high speciation and endemism rates in mountainous regions (Rahbek et al. 2019). When considering a larger scale, tetrapod species

richness is positively correlated with climate (i.e. temperature and precipitation) and topography (Antonelli et al. 2018). At finer scales, the elevational gradient along steep terrain, together with a high variety of micro-climates due to terrain complexity, are the main driver of high levels of biodiversity (Chamberlain et al. 2023).

Elevation is the parameter that best explains the variation in species richness in mountain and upland areas. Different hypotheses exist to explain such patterns, being closely related to those explaining trends in relation to latitude. A stable year-round climate is typical of tropical regions and has contributed to a high biodiversity with high levels of specialization and niche packing. On the contrary, higher latitude environments, with less stable and more fluctuating environmental conditions, facilitate generalists with broad niches. In a similar way, the more fluctuating climatic conditions of higher elevations in mountain areas may contribute to broader niches (Mermillon et al. 2022) and a decrease in species richness along elevation gradients. However, if a decrease in species richness moving towards the poles of the globe is more obvious, there is evidence of an intermediate peak along elevational gradients (Rahbek 1995).

Temperature stands as a fundamental factor influencing biodiversity trends along elevation gradients (Peters et al. 2016; Laiolo et al. 2018). Traditionally, each 100-meter ascent corresponds to an approximate temperature decrease of 0.6°C, with local variations associated with humidity and wind exposure (Dillon et al. 2006; Colwell et al. 2008). Water availability, which includes precipitation but also soil moisture, is another factor that assumes a vital role in shaping climatic conditions (McCain 2009; Antonelli et al. 2018). It is of primary importance in affecting primary productivity, which is inversely correlated with temperature (and consequently elevation). Bird species richness appears closely tied to productivity metrics (e.g., Acharya et al. 2011; Abebe et al. 2019), so it is extremely difficult to find species rich assemblages at high elevations (Newton 2020; Schumm et al. 2020). However, these relationships exhibit substantial geographic variations (Rahbek et al. 2019).

Natural and artificial drivers of Alpine landscapes

Landscapes that are found in the Alps, one of the most iconic mountain ranges in Europe, are the results of long-lasting interactions between natural abiotic processes and human activities (Bebi et al. 2017; Pini et al. 2017; Zimmerer et al. 2017). These processes shaped mountain environments by creating a high diversity of habitat and generating new ecological niches, with potentially positive effects for biodiversity (Araneda et al. 2018). In a natural state without human influence, mountain habitats and associated vegetation are mainly dictated by the rapid change in environmental conditions along the elevational gradient (Nagy & Grabherr 2009). A fairly distinct zonation of vegetation with four general habitats occurs along the gradient: the montane forest is characterized by closed canopy and mature trees and can be composed of broadleaved species at lower elevations or coniferous species at higher elevations; the treeline ecotone is a habitat mosaic transition area above which trees cannot grow due harsh climatic conditions and is characterized by a mixture of trees, shrubs and meadows; alpine grasslands dominate the areas above the treeline and are mainly composed of steppe-like habitats with rocky patches; the nival zone is found at the highest elevations and is characterized by largely unvegetated landscapes with patchy vegetation and snow packs.

Different sources of natural disturbance influence Alpine ecosystem dynamics, such as fire, wind, insect outbreaks and avalanches (Kulakowski and Veblen 2002, Seidl et al. 2011, Kulakowski et al. 2011, Puerta-Piñero et al. 2012, Liu et al. 2015, Flatley et al. 2013). In this thesis, we will focus on avalanches which affect forest ecosystems in particular (Bebi et al. 2009). They have received little research attention in comparison to other types of disturbance despite their important ecological role and the hazard they pose to human settlements (Höller 2007). The high frequency of avalanches contributes to maintaining a semi-open habitat which differs substantially from the surrounding forest, with lower tree density and shorter trees, similar to the treeline ecotone (Bebi et al. 2001; Kulakowski et al. 2006; Requena et al. 2022). This can have

positive effects on gamma mountain biodiversity and these disturbed areas can thus be exploited by a range of animal species such as the Chamois *Rupicapra rupicapra* (Garcia-Gonzalez and Cuartas 1996), Wolverine *Gulo gulo* (Krajick 1998) or Alpine birds such as grouse species (Lieser 1995) or species tied to habitat mosaics like the Rock Bunting *Emberiza cia* (Requena et al. 2022). Nonetheless, effects of avalanches on animal communities have still not been examined in depth.

Humans have been shaping mountain landscapes for millennia. Since the Neolithic period, mountain forests have been cleared and agro-pastoral activities involving livestock management have existed for 7000 years in the European Alps (Schwörer et al. 2014). Nowadays, mountain regions are still exploited by humans for sustenance, through arable and pastoral agriculture (Streifeneder 2016), for leisure activities (Caprio et al. 2011), and even for renewable energy production (Pearce-Higgins et al. 2009) and production of materials (Douglas et al. 2020), with both positive and negative consequences for biodiversity. Large areas used for grazing of livestock are now threatened by both intensification and abandonment, the latter being a particular issue in the last decades in mountain regions (Gehrig-Fasel et al. 2007, Campagnaro et al. 2017). Furthermore, mountains have become popular locations for outdoor leisure activities such as walking, climbing and skiing, which can have negative impacts biodiversity through habitat alteration and disturbance (Arlettaz et al. 2007, Brambilla et al. 2016).

In Europe, winter tourism continues to grow (Wipf et al. 2005) and is expanding into pristine areas at higher elevations due to climate change (Marty 2013; Caprio et al. 2023). The processes involved in the construction and management of ski slopes can be extremely detrimental to the environment (Roux-Fouillet et al. 2011), causing a much more significant impact compared to natural sources of disturbance (Rixen and Rolando 2013). Ski slopes, and winter sports in general, have been found to be harmful to various animal species (Sato et al. 2013), including arthropods (Negro et al. 2009, 2013a), small mammals (Negro et al. 2013b), and birds (e.g. Arlettaz et al.

2007; Rolando et al. 2007; Patthey et al. 2008; Thiel et al. 2008, 2011; Caprio et al. 2011). However, there is potential for ski slopes to be managed in a more environmentally friendly manner to minimize their impacts (Caprio et al. 2023), and when such practices are applied restored ski slopes and natural control grasslands become structurally very similar, with positive effects on biodiversity (Caprio et al. 2016).

Climate change involves alterations in the extended-term climatic patterns that span decades, and the proof that such transformations have occurred is now unequivocal (IPCC 2023). With ongoing climate and land-use changes in mountain regions, open habitats are under significant threat due to vegetation encroachment of abandoned secondary-grasslands and the upwards shift of montane forest (Laiolo et al. 2004; Gehrig-Fasel et al. 2007). The likelihood of these habitats to further decrease in extent is high. Avalanche tracks hold the potential to maintain some degree of habitat diversity, but their existence could be jeopardized by climate change, resulting in reduced avalanche frequency and severity (Eckert et al. 2013). Ski slopes may have a role in preserving open areas, but the extent to which they can compensate for the loss of natural open habitats remains largely uncertain and will be discussed in this thesis (Chapter IV). Farmland and open-habitat bird species are experiencing declines and face significant threats in all mountain ecosystems (Donald et al. 2001; Brambilla et al. 2021). Given the growing human impact, there is an imperative need to integrate human elements with nature for future coexistence. To foster the sustainable coexistence of natural ecosystems and human activities in mountain regions, it is essential to identify the key features of natural habitats that benefit biodiversity and assess whether these attributes can be used in the management of artificial habitats as a strategy to aid the conservation of open habitat species threatened by land use and climate change.

Mountain bird assemblages and conservation issues

Since research activities in mountain areas are particularly challenging, our knowledge of the ecology of many mountain bird species is very poor (Chamberlain et al. 2012; Scridel et al. 2018; Alba et al. 2022). When we look at the number of research articles on mountain birds grouped according to elevation zone (Chamberlain et al. 2023), most of our knowledge comes from studies carried out on montane forest (i.e. lower elevations) whilst higher elevation habitats, such as the ecotone treeline and alpine belt, are largely understudied. However, these habitats host a relatively large number of species related to open habitats, which are threatened by vegetation encroachment due to climate and land-use changes (Chamberlain et al. 2023).

Mountain birds are subject to a variety of extreme environmental conditions during their life-cycle. Breeding birds must cope with highly variable and unpredictable environments, and in response they have evolved a suite of physiological, morphological and behavioural adaptations to survive in these areas. For example, the Rock Ptarmigan *Lagopus muta* which inhabits the alpine and nival zones of the Alps, is one of the most well adapted species to higher elevations and cold temperatures, presenting a thick set of feathers for resisting low temperatures and camouflaged plumage to hide in the surrounding landscapes (Montgomerie & Holder 2020). Unpredictable weather events at higher elevations can have severe consequences for mountain bird populations, for example impacting on breeding success (Martin et al. 2017) or timing of reproduction based on snowmelt (Sander et al. 2021, 2023). In these highly variable environments, a short reproductive season is also a limiting factor that affects food resources for birds, both regarding vegetation (García-González et al. 2016) or invertebrate prey (Resano-Mayor et al. 2019; Barras et al. 2020).

Marked seasonality in mountain regions influences bird activity during the entire annual cycle. Many mountain species (> 75% in temperate mountains) do not remain all year round on the breeding grounds, avoiding harsh environmental conditions in winter (Chamberlain et al. 2023). The majority of research on mountain

bird assemblages has predominantly concentrated on spring and summer periods, leaving a substantial knowledge gap concerning animal life-cycles during other seasons (Martin et al. 2023). Limited investigations have explored the habitat utilization of high-elevation areas by bird communities outside the breeding season, with much of the available work from North American mountain ranges, primarily British Columbia (Wilson & Martin 2005; Martin & Boyle 2015), and some European ringing stations (Hohl 2019; Franzoi et al. 2021). Birds undertake extensive migratory journeys, often spanning thousands of kilometers, from breeding territories to wintering grounds, with many European long-distance migrants facing perilous crossings of the Mediterranean Sea and Sahara Desert. Mountain ranges are generally perceived as ecological barriers for migratory birds (Bruderer & Peter 2022), yet temperate mountains, due to delayed snowmelt and thus a shifted phenology, might be attractive for migrants. Nonetheless, a comprehensive survey of year-round bird communities at high elevations in temperate mountains remains lacking in European settings.

As mentioned before, human activities have significantly shaped mountain environments in the European Alps, with practices like urbanization and deforestation for agriculture and livestock management purposes, having impacts on bird assemblages. These long-lasting transformations did not have only negative effects on biodiversity, but they also created a suite of diverse habitats, potentially generating new ecological niche space for bird species (Araneda et al. 2018). Open habitats created in mountains offer refuge to declining farmland bird populations that colonised mountains from lowlands due to intensive agriculture (Archaux 2007). Nevertheless, traditional practices like agro-pastoral activities are decreasing in many mountain areas, leading to forest encroachment and negative effects on the biodiversity of open habitats (Laiolo et al 2004; Gehrig-Fasel et al. 2007; Campagnaro et al. 2017). Conversely, some areas in the bottoms of the valley are experiencing more intensive management, with the increased use of artificial fertilizers in agricultural lands (Andrey et al. 2014; Assandri et al. 2019), and an expansion of urban areas

(Scolozzi & Geneletti 2012). However, the past century has introduced new pressures, including the leisure industry, with skiing as a major income source for mountain communities, leading to habitat loss and disturbance (Caprio et al. 2011; Rixen and Rolando 2013). Furthermore, power generation, including hydropower and wind energy, is increasingly impacting mountain environments, with consequences for mortality of alpine birds and habitat loss (Aschwanden et al. 2018).

Climate change is posing multiple challenges to mountain birds (Pearce-Higgins et al. 2023). Climate change involves alterations to extended-term climatic patterns that span decades, and the proof that such transformations have occurred is now unequivocal (IPCC 2023). Depending on various factors, including the exposure of species to climate change, species-specific responses to environmental shifts, and species' capacity to adapt to these alterations, climate change might severely threaten certain species by significantly decreasing their range or leading to extinction, while others species may expand their distribution in response to rising temperatures (Bani et al. 2019; Foden et al. 2019). There is increasing evidence of shifts in bird phenology, with species exhibiting earlier breeding dates and migration patterns in the spring, with an advancement of up to 2.2 days per decade (Cohen et al. 2018). Bird species distributions are changing, and there is evidence of a general northward shift in bird species' distributions (Chen et al. 2011; Gillings et al. 2015), and mountain birds are expected to undergo an upwards shift towards higher-elevations (Sekercioglu et al. 2008; Bani et al. 2019).

The combination of these stressors, often interacting with other drivers, threatens high-elevation bird assemblages. To protect vulnerable mountain bird populations, the ecological research community must develop strategies underpinned by sound scientific research.

Aims of this thesis

The general aim of this thesis was to increase the actual knowledge on mountain bird assemblages by filling some knowledge gaps that mountain ecology research presents. In this way, first by covering the bigger picture on European mountains and bird population drivers and subsequently moving to the Alps, analysing the responses of mountain bird assemblages during different stages of the annual cycle, I aimed to provide useful insights and perspectives for future research, but at the same time inspire and suggest conservation strategies for mountain biodiversity.

In **Chapter II** I assessed which drivers have been most consistently associated with positive or negative demographic responses of European mountain birds by using available literature to provide a long-term perspective on changes in these populations. Based on the outcomes, I proposed key priorities for developing conservation strategies for mountain birds. It is essential to understand how changes in management practices at national and continental scales are affecting mountain birds, so that this can inform policy development.

Climate and land-use changes will have severe consequences for open habitats in mountain areas. In **Chapter III** I studiede the role of avalanches in naturally maintaining semi-open habitats and for the first time what were the bird assemblages that colonise avalanche tracks. Furthermore, given the novelty of the study, I was interested in testing if habitats and bird assemblages of avalanche tracks were similar to those found in the treeline ecotone, or whether these tracks formed unique habitats for birds.

I subsequently compared the habitat structure and bird assemblages of avalanche tracks with those found in ski pistes, a similar vertical habitat but of artificial origin (**Chapter IV**). Ski pistes have the potential to become surrogates of other open habitats and hence gain a conservation role, but to what extent these could compensate for the loss of open natural habitats is largely unknown. Furthermore, in order to promote the sustainable coexistence of natural and human activities in the

mountains, it is fundamental to pinpoint which features of avalanches are key for biodiversity, and whether we can use such elements to improve ski pistes as a strategy to aid the conservation of open habitat species and more broadly, mountain biodiversity.

In **Chapter V**, I focused on a bird species, the Northern Wheatear *Oenanthe oenanthe*, which breeds in alpine grasslands and is a long-distance migrant, being thus the perfect model species for studying the effects of climate and land-use changes on open habitats. I investigated the habitat selection during the time between the arrival and breeding period, after individuals arrive from their African wintering grounds. I also described the spatio-temporal patterns of territory selection in order to better understand the role of low elevation open habitats below the treeline (pastures, meadows) and the reason why they either are or not as suitable as those at higher elevations. These could be important in a future in which the current area of alpine grassland breeding habitat is shrinking.

Since the majority of studies on mountain birds are carried out during the breeding season, we need to know more about other crucial life-stages of birds such as the autumn period. In **Chapter VI** I reported for the first time the habitat use of Alpine high-elevation habitats as stopover and fuelling sites for birds migrating through the Alps. Migrants are among the most threatened bird categories and it thus essential to identify the key habitats selected by birds during this delicate period in order to inform conservation strategies that take into account mountain biodiversity during the entire life cycle.

Finally, in **Chapter VII** I discussed the overall implications of the results in a broader context of environmental change and propose the next crucial research steps that are needed in alpine ecology to fill existing knowledge gaps.

References

Abebe, A. F., Cai, T., Wale, M., Song, G., Fjeldså, J., & Lei, F. (2019). Factors determining species richness patterns of breeding birds along an elevational gradient in the Horn of Africa region. Ecology and Evolution, 9(17), 9609-9623.

Acharya, B. K., Sanders, N. J., Vijayan, L., & Chettri, B. (2011). Elevational gradients in bird diversity in the Eastern Himalaya: an evaluation of distribution patterns and their underlying mechanisms. PloS one, 6(12), e29097.

Andrey, A., Humbert, J. Y., Pernollet, C., & Arlettaz, R. (2014). Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. Ecology and evolution, 4(12), 2610-2623.

Antonelli, A., Kissling, W. D., Flantua, S. G., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., ... & Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. Nature Geoscience, 11(10), 718-725.

Araneda, P., Sielfeld, W., Bonacic, C., & Ibarra, J. T. (2018). Bird diversity along elevational gradients in the Dry Tropical Andes of northern Chile: The potential role of Aymara indigenous traditional agriculture. PloS one, 13(12), e0207544.

Archaux, F. (2007). Are mountains refuges for farmland bird species? A case study in the northern French Alps. Bird Study, 54(1), 73-79.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., & Jenni-Eiermann, S. (2007). Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B: Biological Sciences, 274(1614), 1219-1224.

Aschwanden, J., Stark, H., Peter, D., Steuri, T., Schmid, B., & Liechti, F. (2018). Bird collisions at wind turbines in a mountainous area related to bird movement intensities measured by radar. Biological Conservation, 220, 228-236.

Assandri, G., Bogliani, G., Pedrini, P., & Brambilla, M. (2019). Species-specific responses to habitat and livestock management call for carefully targeted conservation

strategies for declining meadow birds. Journal for Nature Conservation, 52, 125757.

Bani, L., Luppi, M., Rocchia, E., Dondina, O., & Orioli, V. (2019). Winners and losers: How the elevational range of breeding birds on Alps has varied over the past four decades due to climate and habitat changes. Ecology and Evolution, 9(3), 1289-1305.

Barras, A. G., Marti, S., Ettlin, S., Vignali, S., Resano-Mayor, J., Braunisch, V., & Arlettaz, R. (2020). The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels Turdus torquatus alpestris. Ibis, 162(2), 505-519.

Barry, R. G. (1992). Mountain weather and climate. Psychology Press.

Bebi, P., Kienast, F., & Schönenberger, W. (2001). Assessing structures in mountain forests as a basis for investigating the forests' dynamics and protective function. Forest Ecology and Management, 145(1-2), 3-14.

Bebi, P., Kulakowski, D., & Rixen, C. (2009). Snow avalanche disturbances in forest ecosystems—State of research and implications for management. Forest ecology and Management, 257(9), 1883-1892.

Bebi, P. S. E. P., Seidl, R., Motta, R., Fuhr, M., Firm, D., Krumm, F., ... & Kulakowski, D. (2017). Changes of forest cover and disturbance regimes in the mountain forests of the Alps. Forest ecology and management, 388, 43-56.

Boyle, W. A., & Martin, K. (2015). The conservation value of high elevation habitats to North American migrant birds. Biological Conservation, 192, 461-476.

Brambilla, M., Pedrini, P., Rolando, A., & Chamberlain, D. E. (2016). Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. Journal of Biogeography, 43(11), 2299-2309.

Brambilla, M., Gubert, F., & Pedrini, P. (2021). The effects of farming intensification on an iconic grassland bird species, or why mountain refuges no longer work for farmland biodiversity. Agriculture, Ecosystems & Environment, 319, 107518.

Bruderer, B., & Peter, D. (2022). Topography and wind moulding directions of autumn migration between Europe and the West African savannas. Journal of Ornithology, 163(2), 357-371.

Campagnaro, T., Frate, L., Carranza, M. L., & Sitzia, T. (2017). Multi-scale analysis of alpine landscapes with different intensities of abandonment reveals similar spatial pattern changes: Implications for habitat conservation. Ecological Indicators, 74, 147-159.

Caprio, E., Chamberlain, D. E., Isaia, M., & Rolando, A. (2011). Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. Biological Conservation, 144(12), 2958-2967.

Caprio, E., Chamberlain, D., & Rolando, A. (2016). Ski-piste revegetation promotes partial bird community recovery in the European Alps. Bird Study, 63(4), 470-478.

Caprio E., Rolando A., Arlettaz R., Chamberlain D. (2023) Anthropogenic activities and mountain birds. In Chamberlain D, Lehikoinen, A, Martin, K (eds) Ecology and Conservation of Mountain Birds, pp 260-295, Cambridge University Press, Cambridge, UK.

Chamberlain, D. E., Negro, M., Caprio, E., & Rolando, A. (2013). Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biological conservation, 167, 127-135.

Chamberlain, D., Lehikoinen, A., Scridel, D., Martin, K. (2023) Mountain birds and their habitats. In Chamberlain D, Lehikoinen, A, Martin, K (eds) Ecology and Conservation of Mountain Birds, pp 1-34, Cambridge University Press, Cambridge, UK.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333(6045), 1024-1026.

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. Nature Climate Change, 8(3), 224-228.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. science, 322(5899), 258-261.

Dillon, G. K., Holden, Z. A., Morgan, P., Crimmins, M. A., Heyerdahl, E. K., & Luce, C. H. (2011). Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere, 2(12), 1-33.

Donald, P. F., Sanderson, F. J., Burfield, I. J., & Van Bommel, F. P. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment, 116(3-4), 189-196.

Douglas, D. J., Groom, J. D., & Scridel, D. 2020. Benefits and costs of native reforestation for breeding songbirds in temperate uplands. Biol. Cons. 244: 108483.

Eckert, N., Keylock, C. J., Castebrunet, H., Lavigne, A., & Naaim, M. (2013). Temporal trends in avalanche activity in the French Alps and subregions: from occurrences and runout altitudes to unsteady return periods. Journal of Glaciology, 59(213), 93-114.

Fjeldså, J., Bowie, R. C., & Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. Annual Review of Ecology, Evolution, and Systematics, 43, 249-265.

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., ... & Huntley, B. (2019). Climate change vulnerability assessment of species. Wiley interdisciplinary reviews: climate change, 10(1), e551.

Franzoi, A., Tenan, S., Sanchez, P. L., & Pedrini, P. (2021). Temporal trends in abundance and phenology of migratory birds across the Italian Alps during a 20-year period. Rivista Italiana di Ornitologia, 91(2), 13-28.

Franzén, M., & Molander, M. (2012). How threatened are alpine environments? A cross taxonomic study. Biodiversity and Conservation, 21, 517-526.

Garcia-Gonzalez, R., & Cuartas, P. (1996). Trophic utilization of a montane/subalpine forest by chamois (Rupicapra pyrenaica) in the Central Pyrenees. Forest Ecology and Management, 88(1-2), 15-23.

García-González, R., Aldezabal, A., Laskurain, N. A., Margalida, A., & Novoa, C. (2016). Influence of snowmelt timing on the diet quality of Pyrenean rock ptarmigan (Lagopus muta pyrenaica): implications for reproductive success. PloS one, 11(2), e0148632.

Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: climate change or land abandonment?. Journal of vegetation science, 18(4), 571-582.

Gillings, S., Balmer, D. E., & Fuller, R. J. (2015). Directionality of recent bird distribution shifts and climate change in Great Britain. Global Change Biology, 21(6), 2155-2168.

Hohl, S. (2019). Jahresbericht 2019 der Beringungsstation Col de Bretolet VS. Sempach: Schweizerishce Vogelwarte.

Höller, P. (2007). Avalanche hazards and mitigation in Austria: a review. Natural Hazards, 43(1), 81-101.

IPCC (2023). Summary for Policymakers. In: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland, pp. 1-34.

Kapos, V., Rhind, J., Edwards, M., Price, M. F., & Ravilious, C. (2000). Developing a map of the world's mountain forests. In Forests in sustainable mountain development: a state of knowledge report for 2000. Task Force on Forests in Sustainable Mountain Development. (pp. 4-19). Wallingford UK: Cabi Publishing.

Körner, C. (2004). Mountain biodiversity, its causes and function. AMBIO: A Journal of the Human Environment, 33(sp13), 11-17.

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K., & M Spehn, E. (2017). A global inventory of mountains for bio-geographical applications. Alpine Botany, 127, 1-15.

Krajick, K. (1998). Animals thrive in an avalanche's wake. Science, 279(5358), 1853-1853.

Kulakowski, D., & Veblen, T. T. (2002). Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. Journal of Ecology, 90(5), 806-819.

Kulakowski, D., Rixen, C., & Bebi, P. (2006). Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. Forest Ecology and Management, 223(1-3), 66-74.

Kulakowski, D., Bebi, P., & Rixen, C. (2011). The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos, 120(2), 216-225.

Laiolo, P., Rolando, A., & Valsania, V. (2004). Responses of birds to the natural re-establishment of wilderness in montane beechwoods of North-western Italy. Acta Oecologica, 25(1-2), 129-136.

Laiolo, P., Pato, J., & Obeso, J. R. (2018). Ecological and evolutionary drivers of the elevational gradient of diversity. Ecology letters, 21(7), 1022-1032.

Lieser, M., 1995. Lebensraumansprueche des Haselhuhns im Schwarzwald. Naturschutzreport 10, 239–255.

Martin, K., Wilson, S., MacDonald, E. C., Camfield, A. F., Martin, M., & Trefry, S. A. (2017). Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. The Auk: Ornithological Advances, 134(3), 696-709.

Martin, K., Chamberlain, D., Lehikoinen, A. (2023) Priorities for information, research and conservation of birds in high mountains. In Chamberlain, D., Lehikoinen,, A.,

Martin, K. (eds) Ecology and Conservation of Mountain Birds, pp 372-406, Cambridge University Press, Cambridge, UK.

Marty, C. (2013). Climate change and snow cover in the European Alps. Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments, Bentham, 30-44.

McCain, C. M. (2009). Vertebrate range sizes indicate that mountains may be 'higher'in the tropics. Ecology letters, 12(6), 550-560.

Mermillon, C., Jähnig, S., Sander, M. M., Alba, R., Rosselli, D., & Chamberlain, D. (2021). Variations in niche breadth and position of alpine birds along elevation gradients in the European Alps. Ardeola, 69(1), 41-58.

Montgomerie, R., Holder, K. (2020). Rock Ptarmigan (Lagopus muta), version 1.0. In Birds of the World (S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Nagy, L., & Grabherr, G. (2009). The biology of alpine habitats. Oxford University Press, USA.

Negro, M., Isaia, M., Palestrini, C., & Rolando, A. (2009). The impact of forest ski-pistes on diversity of ground-dwelling arthropods and small mammals in the Alps. Biodiversity and Conservation, 18, 2799-2821.

Negro, M., Rolando, A., Barni, E., Bocola, D., Filippa, G., Freppaz, M., ... & Palestrini, C. (2013a). Differential responses of ground dwelling arthropods to ski-piste restoration by hydroseeding. Biodiversity and conservation, 22, 2607-2634.

Negro, M., Novara, C., Bertolino, S., & Rolando, A. (2013b). Ski-pistes are ecological barriers to forest small mammals. European Journal of Wildlife Research, 59, 57-67.

Newton, I. (2020). Upland and birds. London: Collins

Patthey, P., Wirthner, S., Signorell, N., & Arlettaz, R. (2008). Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of applied ecology, 45(6), 1704-1711.

Pearce-Higgins, J. W., Stephen, L., Langston, R. H., Bainbridge, I. P., & Bullman, R. (2009). The distribution of breeding birds around upland wind farms. Journal of Applied ecology, 46(6), 1323-1331.

Pearce-Higgins, J. W., Martin, K. (2023) Climate change impacts on mountain birds. In Chamberlain D, Lehikoinen, A, Martin, K (eds) Ecology and Conservation of Mountain Birds, pp 215-259, Cambridge University Press, Cambridge, UK.

Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., ... & Steffan-Dewenter, I. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature communications, 7(1), 13736.

Pini, R., Ravazzi, C., Raiteri, L., Guerreschi, A., Castellano, L., & Comolli, R. (2017). From pristine forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation and landscapes in the western Italian Alps. Journal of Ecology, 105(6), 1580-1597.

Puerta-Piñero, C., Espelta, J. M., Sánchez-Humanes, B., Rodrigo, A., Coll, L., & Brotons, L. (2012). History matters: Previous land use changes determine post-fire vegetation recovery in forested Mediterranean landscapes. Forest Ecology and Management, 279, 121-127.

Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern?. Ecography, 200-205.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J. & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity?. Science, 365(6458), 1108-1113.

Requena, E., Alba, R., Rosselli, D., & Chamberlain, D. (2022). Avalanche tracks are key habitats for the Rock Bunting Emberiza cia in the Alps. Ardeola, 69(2), 203-217.

Resano-Mayor, J., Bettega, C., del Mar Delgado, M., Fernández-Martín, Á., Hernández-Gómez, S., Toranzo, I., ... & Arlettaz, R. (2020). Partial migration of White-winged snowfinches is correlated with winter weather conditions. Global Ecology and Conservation, 24, e01346.

Rixen, C., & Rolando, A. (Eds.). (2013). The impacts of skiing and related winter recreational activities on mountain environments. Soest, the Netherlands: Bentham Science Publishers.

Rolando, A., Caprio, E., Rinaldi, E., & Ellena, I. (2007). The impact of high-altitude ski-runs on alpine grassland bird communities. Journal of applied ecology, 44(1), 210-219.

Roux-Fouillet, P., Wipf, S., & Rixen, C. (2011). Long-term impacts of ski piste management on alpine vegetation and soils. Journal of applied ecology, 48(4), 906-915.

Sander, M. M., Chamberlain, D., Mermillon, C., Alba, R., Jähnig, S., Rosselli, D., ... & Lisovski, S. (2021). Early breeding conditions followed by reduced breeding success despite timely arrival in an alpine migratory songbird. Frontiers in Ecology and Evolution, 9, 676506.

Sander, M. M., Jähnig, S., Lisovski, S., Mermillon, C., Alba, R., Rosselli, D., & Chamberlain, D. (2023). High nest failure but better nestling quality for early breeders in an alpine population of Northern Wheatear (Oenanthe oenanthe). Ibis, 165(1), 125-141.

Sato, C. F., Wood, J. T., & Lindenmayer, D. B. (2013). The effects of winter recreation on alpine and subalpine fauna: a systematic review and meta-analysis. PloS one, 8(5), e64282.

Schumm, M., White, A. E., Supriya, K., & Price, T. D. (2020). Ecological limits as the driver of bird species richness patterns along the east Himalayan elevational gradient. The American Naturalist, 195(5), 802-817.

Schwörer, C., Henne, P. D., & Tinner, W. (2014). A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. Global change biology, 20(5), 1512-1526.

Scolozzi, R., & Geneletti, D. (2012). A multi-scale qualitative approach to assess the impact of urbanization on natural habitats and their connectivity. Environmental Impact Assessment Review, 36, 9-22.

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., ... & Chamberlain, D. (2018). A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. Ibis, 160(3), 489-515.

Sekercioglu, C. H., Schneider, S. H., Fay, J. P., & Loarie, S. R. (2008). Climate change, elevational range shifts, and bird extinctions. Conservation biology, 22(1), 140-150.

Seidl, R., Schelhaas, M. J., & Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology, 17(9), 2842-2852.

Streifeneder, T. (2016). Agriculture first: Assessing European policies and scientific typologies to define authentic agritourism and differentiate it from countryside tourism. Tourism Management Perspectives, 20, 251-264.

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R., & Jenni, L. (2008). Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: a new methodological approach. Journal of applied ecology, 45(3), 845-853.

Thiel, D., Jenni-Eiermann, S., Palme, R., & Jenni, L. (2011). Winter tourism increases stress hormone levels in the Capercaillie Tetrao urogallus. Ibis, 153(1), 122-133.

Wipf, S., Rixen, C., Fischer, M., Schmid, B., & Stoeckli, V. (2005). Effects of ski piste preparation on alpine vegetation. Journal of Applied Ecology, 42(2), 306-316.

Zimmerer, K. S., Córdova-Aguilar, H., Mata Olmo, R., Jimenez Olivencia, Y., & Vanek, S. J. (2017). Mountain ecology, remoteness, and the rise of agrobiodiversity: Tracing the geographic spaces of human–environment knowledge. Annals of the American Association of Geographers, 107(2), 441-455.

Chapter II

Drivers of change in mountain and upland bird populations in Europe

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Abstract

Mountain ecosystems have special significance for biodiversity and are vulnerable to climate and other environmental changes. However, few assessments of drivers of change have been conducted in these areas in comparison to other more accessible biomes. In this study, we developed an objective and broad definition of a mountain bird, and systematically reviewed the existing literature for the 34 European mountain and upland species identified in order to quantify which drivers of environmental change have been most consistently associated with positive or negative demographic responses. Raptors and gamebirds were the most-studied species, whilst mountain specialists and arctic-alpine species were little studied. Using a standardised threat classification, the analyses reported significant negative impacts of hunting, collision with energy generation infrastructures, predation by competitive species, human disturbance, and poisoning. There were significant positive effects or management of non-target species, but less support for effects of drivers operating over longer timescales, such as climate and land-use changes. Analysis of trends in drivers found evidence of increasing temperatures and vegetation encroachment, whereas agricultural impacts decreased, which was largely related to abandonment of grazing. A lack of fine-grained studies investigating ecological mechanisms and population responses to widespread impacts were highlighted. Whilst we have found that some drivers are well studied, we need to collect more detailed and longer-term data on species' requirements and on the impacts that bird populations face to devise priorities for conservation action and research for mountain and upland birds.

Keywords: alpine, climate change, conservation, hunting, threat, trend

Introduction

Mountain and upland regions (hereafter mountain regions) are ecosystems of interest as they harbour a high proportion of global biodiversity and have a high rate of endemism (Antonelli *et* al. 2018, Rahbek *et al.* 2019). However, few assessments of environmental change have been conducted in these areas in comparison to more accessible biomes (Beniston *et al.* 2018). In Europe, mountain regions retain species of conservation concern and are of high cultural and economic importance (Soliva *et al.* 2008, Bonn *et al.* 2009), but they are threatened by ongoing changes in land use and climate (Chamberlain *et al.* 2016a, Lehikoinen *et al.* 2019).

Bird species distributions across Europe, as well as their population trends, have been influenced over time by changing environmental and climatic conditions, and human impacts (BirdLife International 2017, Keller *et al.* 2020). Birds face a wide range of threats, and the assessment of drivers and relative impacts on populations is particularly challenging for mountain and upland birds (hereafter mountain birds) because they are less well studied than birds occurring in more accessible locations in the lowlands (Chamberlain *et al.* 2016b).

Across Europe, mountain regions are exploited by humans for sustenance, through arable and pastoral agriculture (Streifeneder 2016), for leisure and recreation (Caprio *et al.* 2011), and also for renewable energy production (Pearce-Higgins *et al.* 2009a) and production of materials (Douglas *et al.* 2020), with both positive and negative consequences for biodiversity. Large areas used for agriculture, particularly grazing of livestock, can be found in mountain regions. Such extensive agriculture has led to many of these areas being considered as "High Nature Value farmland" (Keenleyside *et al.* 2014). These agricultural systems are threatened by both intensification and abandonment, the latter being a particular issue in mountain regions (Gehrig-Fasel *et al.* 2007, Campagnaro *et al.* 2017). In addition to food production, mountains are popular locations for outdoor leisure activities such as walking, climbing and skiing, which can impact biodiversity through habitat alteration

and disturbance (Arlettaz *et al.* 2007, Brambilla *et al.* 2016). Often, increasing urbanization and pollution are associated with tourist infrastructure in mountains, with potential consequences for biodiversity (Scolozzi & Geneletti 2012). In some regions, mountains are also used for recreational hunting, which may include habitat and predator management practices which favour gamebirds and waders (Fletcher *et al.* 2010), but, in some cases, results in illegal persecution of protected species (Newton 2021). Furthermore, renewable energy production (particularly wind) can impact birds through habitat alteration and collisions with turbines and power cables (Vasilakis *et al.* 2016, Arrondo *et al.* 2020).

One of the major threats for temperate mountain species is thought to be climate change (Chamberlain *et al.* 2013, Scridel *et al.* 2018). Studies report that global warming effects are particularly intense in mountain regions (Brunetti *et al.* 2009) where they can act together with other drivers (e.g., land abandonment; Gehrig-Fasel *et al.* 2007) to alter habitats. Woody vegetation encroachment and expansion towards higher elevation are serious threats for some open-habitat mountain species, which often have a negative conservation status (Sekercioglu *et al.* 2008, Viterbi *et al.* 2013). By contrast, these drivers favour forest and ecotonal species (Jähnig *et al.* 2018) and climate change is allowing some species to occupy higher elevations, thus increasing their range (Bani *et al.* 2019).

Management of mountain regions is often strongly influenced by national and international policies. Agriculture within the EU is subsidised via the Common Agricultural Policy, and both agricultural and other forms of management (including forestry and renewable energy generation) may receive payments from the European Agricultural Fund for Rural Development (EAFRD) (European Parliament 2020) and national government incentives. Agri-environment schemes, such as those included in the EAFRD, may help to preserve cultural landscapes, but overall they have not been particularly successful in maintaining either the cultural landscapes or their associated biodiversity (Pe'er *et al.* 2014, Batáry *et al.* 2015). Energy generation, forestry and

recreation are also regulated by national policy, either through state ownership of land or through a diverse range of policy mechanisms and subsidies on privately owned land (Iqtiyanillham *et al.* 2017). As a result, management is subject to rapid change according to the prevailing political landscape.

In the above context, it is essential to understand how changes in management practices at national and continental scales are affecting mountain birds, so that this can inform policy development. A first step is to understand the key drivers and impacts on long-term population trends. Existing reviews and synopses generally focus on specific drivers such as climate change (Scridel *et al.* 2018), are geographically restricted (Pearce-Higgins *et al.* 2009b, Newton 2021), or use expert opinion rather than published results (Chamberlain *et al.* 2016a). To our knowledge, there is no review that objectively quantifies impacts of environmental change on mountain birds at the European scale. Developing this understanding is the main aim of this paper. To do this, we have used an objective method to define mountain birds and then used this as the basis for a literature review to identify and model the impacts that mountain bird populations face in Europe. We quantify which drivers have been most consistently associated with positive or negative demographic responses using all available literature to provide a long-term perspective on changes in these populations. Based on the outcomes, we propose key priorities for developing conservation strategies for mountain birds.

Methods

Mountain bird definition and identification of drivers

This study seeks quantifies the probability that different drivers have statistically significant impacts on the demographic parameters of European mountain bird species, in order to identify the most important drivers. To identify study species, we used two criteria. First, we defined European mountain regions adopting the K3

characterization model reported in Sayre *et al.* (2018), which is derived from the global landforms layer produced by Karagulle *et al.* (2017). This model includes four classes of mountain, characterized by different criteria: high, scattered high, low and scattered low (Fig. A.1). It is thus a fairly broad classification that includes both high elevation alpine mountains and upland areas, such as the British moorlands, that are of relatively lower elevation, but nonetheless show significant relief in relation to the surrounding landscape (see Scridel *et al.* 2018 for further details).

Mountain bird species were defined according to the proportion of their European breeding range that overlapped the defined mountain regions. Using a geographical information system (GIS) software (QGIS, Quantum GIS Development Team 2020), we restricted the K3 characterization model (downloadable from the web-based Global Mountain Explorer tool reported in Sayre *et al.* (2018), https://rmgsc.cr.usgs.gov/gme/) to the European region. Subsequently, we superimposed the vector shapefile (1:1,000,000 scale) of the breeding range of European bird species (BirdLife International 2019) on the mountain region layer. The species for which at least 50% of their breeding range was contained within the borders of the European mountain regions were selected. Secondly, we checked the breeding ecology of the selected species to identify those that occur in mountain regions according to the species factsheets reported by BirdLife International (http://datazone.birdlife.org). We decided to include Golden Eagle *Aquila chrysaetos* and Black Grouse *Lyrurus tetrix* in the list even though they did not quite meet the first selection criterion. Although much of their breeding ranges is represented by northern boreal forests at low altitudes, they occur at high elevations in the southern part of their range and they are considered flagship species for the mountain regions of Europe. The Willow Ptarmigan *Lagopus lagopus* was not included in our study because the species breeds widely in northern Europe and did not meet our first selection criterion, but we included its endemic subspecies, the Red Grouse *Lagopus lagopus scotica*, that represents a species of economic importance (Sotherton *et al.* 2009) and

which is also of major conservation interest as it represents a human-wildlife conflict in upland Britain (Newton 2021).

Following Pearce-Higgins *et al.* (2017a), the list of drivers was adapted from Salafsky *et al.* (2008) to be most informative for our purposes. Some high-level drivers were not listed as they were not relevant, whilst others were split or merged to provide more bespoke information. The final list of drivers and their definitions is given in Table 1.

Table 1. Summary of the impacts used in this study – adapted from Salafsky *et al.* (2008) and Pearce-Higgins *et al.* (2017) as appropriate for the mountain and upland bird focus

Impact	Definition
Residential and commercial development	Residential and commercial development, which includes urban land cover associations, proximity to human settlements.
Transportation and service corridors	Road cover or road proximity associations, disturbance and direct mortality by road traffic
Arable agriculture	Arable/mixed land cover associations, intensification (i.e. change from traditional to intensive management)
Forestry	Coniferous/exotic forest land cover associations, harvesting operations
Pastoral agriculture	Associations with grazed/managed grassland covers, effects of domestic and semi-domestic livestock density/presence, effects of loss of grazing on vegetation if experimental/unequivocal
Energy generation	Disturbance, mortality from wind turbines, solar farms, hydropower but also electrocution and collision with wires
Hunting of target species	Impacts of hunting on mortality or through disturbance – mostly legal edible species (gamebirds, passerines) but also illegal persecution of protected species (raptors)
Management of non-target species	Effects of habitat management aimed specifically at enhancing populations of target species, including killing of competitors or predators
Disturbance	Disturbance from human activities not included in other categories
Fire management	Direct impacts of fire, impacts of burnt areas through vegetation dynamics
Water management	Drainage, canalization flood prevention, not hydropower
Alien species	Impacts from non-native species (plants or animals)
Competitive native species	Impacts from native species (plants or animals) that are expanding their range (due to environmental change) or those that are influenced by human activities
Poisoning	Associations with pollutants or polluted habitats that can have toxic consequences on the target species
Climate change	Correlations with distribution/trend/demographic parameters and temperature or temperature-related variables (e.g. frost days, snow cover, evapotranspiration, NAO). Includes indirect effects of climate change not included in other impacts.
Vegetation encroachment	Woody vegetation and especially forests encroachment on formerly open land that can be caused by several different factors. Includes indirect impact of grazing, climate change and forestry, unless experimental evidence of a link between the impact and vegetation is stated

Literature survey and data extraction

Our study deals with a wide range of drivers that can affect bird species. Consequently, we conducted a broad systematic literature search using ISI Web of Knowledge (www.webofknowledge.com) by searching the species name* OR scientific name* with a period ranging from January 1985 to November 2020. Papers were included in a list of relevant references only if they (i) presented at least one statistical test based on empirical or modelled data (reviews and commentaries not included), (ii) reported the effect of one or more drivers on one or more of our mountain bird species, and (iii) were carried out in Europe. Bird community studies (including measures such as species diversity and species richness) were included if one or more of the study species were present. These were considered as the separate, additional, category 'community'. After the search, which identified 6001 potential papers, we read the title and the abstract and searched for other relevant references missed in the standardized literature search. In the end, we collected 453 papers which were considered relevant for the purposes of this study. A summary of data extraction can be found in the flowchart in Figure 1.

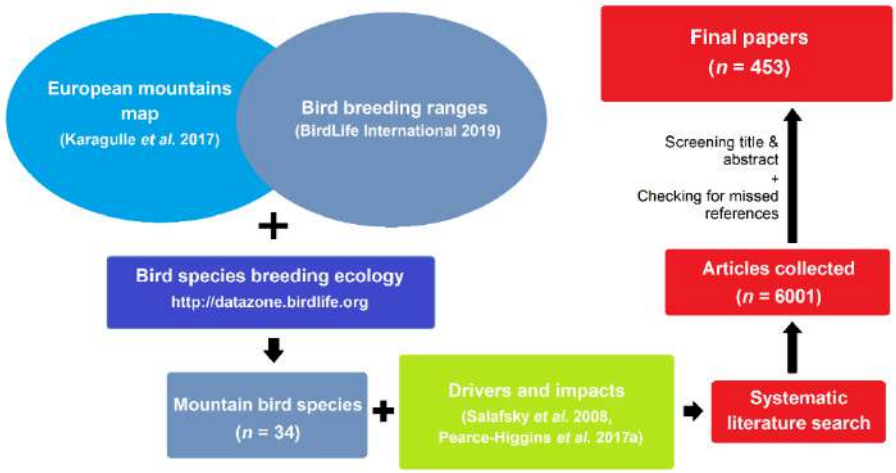

Figure 1. Flow chart showing the methods for this study, from identifying the study species to the systematic literature research and identification of the relevant papers.

A range of information was extracted from each reference, including study species, location, and country. Furthermore, specific statistical parameters were collected: demographic parameter type (occurrence, abundance, breeding success, survival and detection of pollutant level above the threshold, i.e. the response variable for each statistical test, see Table A.1 for the full definition), presence/absence of multivariate tests, whether the study was spatial, temporal, or both, total number of tests undertaken in the study, number of tests undertaken in relation to each driver, and sample size.

An impact was assigned when there was statistical evidence of either a spatial or temporal effect of the level of a given driver on a given demographic parameter of one species. These were summarised as impact scores, defined as drivers having a statistically significant negative (n_n), positive (n_p), or non-statistically significant (n_{ns}) impact on the demographic parameter (as per Pearce-Higgins *et al.* 2015, 2017a). Where a study demonstrated a statistically significant change in a driver over time that was associated with a demographic response, then this was used to score the trend in the driver as either increasing or decreasing. For example, a study that found increased breeding success over time as grazing pressure declined would be considered a significant negative impact for the driver 'Pastoral Agriculture' and also a decreasing trend for the driver 'Pastoral Agriculture' independently of its impact on the species. As studies may report multiple tests of a single driver, for example on breeding success, survival and overall abundance, or on different study populations, we recorded the number of tests which produced significant positive, negative or non-significant results, which totalled the overall number of tests conducted (n) for each species for a given study.

Statistical analysis

The unit of observation was a particular impact for a particular species (or group) in a paper, although this could be based on multiple tests of a single driver for a given

species in a given study, as detailed above. For the purposes of analysis, following Pearce-Higgins *et al.* (2015), binomial scores (S_b) were calculated from the following conversions, which ensure that the data were modelled with an appropriate error structure:

Eq 1) $S_b = (n_{ns} + 2n_p) / 2n$

Final impact scores (S_F), which ensure that the data were appropriately bounded between -1 (all tests statistically significant and negative) and +1 (all tests statistically significant and positive), were calculated as follows:

Eq 2) $S_F = 2(S_b – 0.5)$

Thus, a study reporting three tests, all of which were negative, would produce an $S_b = 0$ and $S_F = -1$. A study with one non-significant, one positive and one-negative test would produce an $S_b = 0.5$ and $S_F = 0$, and a study with two positive and one negative test would produce an $S_b = 0.667$ and $S_F = 0.334$. S_F scores between 0 and -1 show a negative impact on the bird population and from 0 to +1, a positive impact.

With this underpinning, the binomial scores (S_b) were modelled using a logistic regression framework with a binomial error structure and logit link function by modelling '$n_{ns} + 2n_p$' as the numerator and 2n as the denominator (Eq 1). Model outputs were then converted to S_F to aid interpretation using Eq 2.

Using this framework, we first assessed the extent to which methodological differences among studies may have affected the outcomes by testing whether parameter type, multivariate, scale, number of tests and sample size, as nuisance variables, had a significant impact on the score. All models were binomial Generalized Linear Mixed Models (GLMMs), with reference identity and species specified as random effects (function glmer in package lme4, Bates *et al.* 2007) to account for repeated scores from the same publication and the same species. Trends in drivers were coded as 0 for negative, 1 for stable and 2 for increasing, and were modelled

using the same binomial error framework as described previously for the impact scores. Nuisance variables that were significant were retained in subsequent models.

We modelled the impact score as a response variable with a single 13-level categorical variable describing the different drivers in a binomial GLMM, again with reference identity and species specified as random factors. Regarding the trend analysis, drivers were reclassified into six broad categories for trend analysis due to convergence problems associated with a much smaller sample size that reported trends (studies *n* = 108, 24% of the total). These were: agriculture (*n* tests = 33), climate change (*n* = 64), other anthropic pressure (i.e. urban areas and roads, disturbance, forestry and energy production, *n* = 28), habitat and species management (*n* = 34), poisoning (*n* = 25) and vegetation encroachment (*n* = 34). Subsequently, we modelled variation in the trends associated with each driver using a GLMM with the same model structure as above. Trend score was modelled by including a single 6-level categorical variable with the drivers to test the extent to which they were changing through time.

The overall significance of variables was assessed with the function Anova from the R package *car* (Fox & Weisberg 2019). Significance was assessed using 95% credible intervals which were calculated by simulating 2000 random samples from the model parameters using the function *sim* in package *arm* (Gelman *et al.* 2007). Effects were considered significant if the credible interval of the model estimate did not overlap zero (Korner-Nievergelt *et al.* 2015). Estimates and credible intervals were back-transformed to impact scores (i.e. between -1 and +1) when reporting results in the text and to produce forest plots (using the 'forestplot' package in R; Gordon *et al.* 2017). QQ plots of the residuals and of the random effects were checked for each model (Korner-Nievergelt *et al.* 2015), and model fit was adjudged adequate in each case. Publication bias was investigated for each driver by calculating Rosenthal's failsafe number (Table A.2; Rosenthal 1979) which estimates the number of non-significant studies left unpublished that would be needed to suggest Type I errors in the existing sample. Since the estimated numbers were very large, we can conclude

that there was no evidence of publication bias, either for the total number of studies or for any individual driver.

Results

A total of 453 relevant papers were identified which provided 1,205 observations. The studies were widely distributed across Europe, with a particular concentration from southern Europe and the UK (Table 2). There were 36 papers investigating impacts on mountain bird populations at the community level. The most investigated driver was vegetation encroachment (*n* = 126), followed by pastoral agriculture (*n* = 111) and climate change (*n* = 82). The least studied were alien species (*n* = 4) and water management impacts (*n* = 1), both of which were omitted from the analyses. The complete list of the number of studies for each driver is reported in Figure A.2.

Table 2. Number of studies collected from the systematic literature search on the impacts on mountain bird species across the five macro-regions in Europe

Location	**Number of studies**
Southern Europe (Iberia, Southern France, Central and Southern Italy, Balkans)	171
Central Europe (France, Germany, Poland, Czech Republic, Slovakia, Romania)	18
Alps (French Alps, Italian Alps, Switzerland, German Alps, Austria)	55
UK & Ireland	130
Fennoscandia (Denmark, Sweden, Norway, Iceland, Greenland)	74
Europe	5
Total	453

European mountain bird species

According to our criteria, 34 species were considered for this study (Table A.3) that included a variety of species that breed in different habitats, from gamebirds of upland moorlands (e.g. Red Grouse) to alpine specialists breeding in rocky grasslands at high

elevations, e.g. White-winged Snowfinch *Montifringilla nivalis*. The five most studied species were Black Grouse (*n* = 70 studies), Griffon Vulture *Gyps fulvus (n* = 61), Golden Eagle (*n* = 50), Egyptian Vulture *Neophron percnopterus* (*n* = 48) and Red Grouse (*n* = 45). No articles relevant for the purposes of this study were identified for the Wallcreeper *Tichodroma muraria*. The other least studied species were the Gyrfalcon *Falco rusticolus* and Lapland Longspur *Calcarius lapponicus* (*n* = 1 study each), together with the Crag Martin *Ptyonoprogne rupestris,* Horned Lark *Eremophila alpestris*, Long-tailed Skua *Stercorarius longicaudus*, Purple Sandpiper *Calidris maritima* and Snowy Owl *Bubo scandiacus* (*n* = 2 each, see Fig. A.3).

Impacts on bird populations

Of the potential nuisance parameters affecting the detection of significant impacts, parameter type was the only significant variable (X^2_4 = 86.65, P < 0.001*;* see Table A.4 for full results). As a result, it was retained in the impact analyses.

Across all studies, there was significant overall variation in the impacts of different drivers upon species (X^2_{12} = 117.03, P < 0.001), with the mean impacts of 6 drivers being significantly different from zero (see Table A.5a for full results). Hunting of the target species, energy production, competitive native species, poisoning and disturbance were associated with significant negative impacts overall. Management of non-target species was the only significant positive driver (Fig. 2).

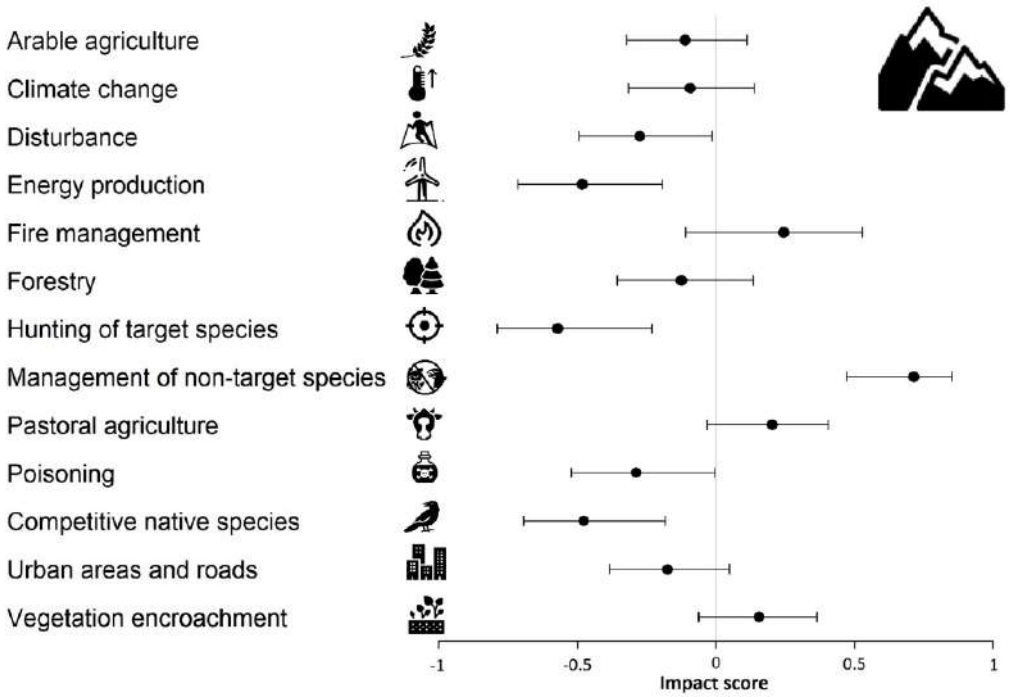

Figure 2. Forest plot with impact scores and 95% credible intervals, derived from back-transformed estimates from the Impact model (see Table A.5a)

Trends in drivers

The random term was dropped from the analysis due to convergence problems and random effects equal to 0, likely due to the much-reduced sample size. We thus modelled trends using binomial GLMs. The model results indicated significant changes over time for three drivers (X^2_5 = 14.81, *P = 0.01)*: agriculture decreased (indicating a decline in extent or intensity), whilst climate change (i.e. temperature increase) and vegetation encroachment increased over time at the European scale (see Table A.5b for full results).

Discussion

This study aimed to identify the main drivers of demographic parameters for European mountain birds and the trends in these drivers to assess their impact on bird

populations. Based on established threat classification schemes, hunting, competitive native species, energy generation, disturbance and poisoning were shown to have the most consistently statistically significant negative impacts on bird populations, whereas there were consistently significant positive effects for management of non-target species. Trend analysis showed that agricultural activities significantly decreased, while climate change and vegetation encroachment increased over the period considered (1985 – 2020).

The impact of competitive native species was the only significant driver that was not explicitly related to human activity, although it may be implicitly related (e.g., Pringle *et al.* 2019). The strong negative effect across species was in many cases caused by predation affecting nesting success. This is thus not a surprising result given that this is the primary cause of nest failure in most bird species (Martin 1993). Other studies show that increasing predation rates by generalist predators are causing declines in many ground-nesting bird species across Europe (Pearce-Higgins *et al.* 2017a, Roos *et al.* 2018) and many mountain and upland bird species have indeed this nesting strategy. Four drivers with negative effects were directly related to human activities. Hunting had the highest magnitude effect size of all drivers, and included both legal hunting activity, which mainly consisted of grouse shooting on managed moorland in UK (e.g. Ludwig *et al.* 2020) or in boreal forests in Fennoscandia (e.g. Lampila *et al.* 2011), and illegal persecution of protected species, such as vultures in Southern Europe (e.g. Carrete *et al.* 2007) and Golden Eagle in the UK (e.g. Whitfield *et al.* 2004). For raptors in particular, historical persecution has severely limited population growth, and even caused local extinction, in many regions of Europe. Whilst prospects for several species are improving (e.g. Fasce *et al.* 2011), there are still areas where populations are unable to establish or grow due to illegal persecution (Murgatroyd *et al.* 2019). Energy generation is known to have negative impacts due to both collision risk with energy infrastructures (Thaxter *et al.* 2017) and habitat alteration and disturbance (Pearce-Higgins *et al.* 2012). The disturbance driver was

defined based on impacts of presence of humans. Many negative effects were from studies of leisure activities, in particular skiing, where it is known that human presence affects habitat use and increases stress (Patthey *et al.* 2012), as well as having impacts on habitat quality (Rolando *et al.* 2007). Negative effects from poisoning and pollution have been reported across Europe, the former mainly for scavengers and the latter especially for the White-throated Dipper *Cinclus cinclus*. Increased mortality and a reduction in fitness were the consequences of physiological dysfunction caused both by lead and pesticide poisoning for raptors (e.g., Sonne *et al.* 2012, Berny *et al.* 2015), and stream acidification for the White-throated Dipper (e.g. Morrissey *et al.* 2014).

Management of non-target species was the only driver to have positive effects on the European scale and included activities such as the legal control of generalist predators. This practice can be beneficial for ground-nesting species such as grouse and waders on uplands, but at the expense of other predators such as mammals or corvids (Ludwig *et al.* 2020), and can be associated with the illegal persecution of raptors (see above).

Vegetation encroachment was the driver with the largest sample size in this study, followed by pastoral agriculture and climate change. It is worth underlining that vegetation encroachment, agriculture (which included mostly studies about pastoral agriculture) and climate change were also the only drivers which showed significant trends over time, with vegetation encroachment and climate change increasing, whilst agriculture was decreasing. These drivers did not, however, have significant consistent impacts on mountain bird populations. Climate change in particular is one of the most studied drivers for bird populations (Pearce-Higgins & Green 2014) and warming is particularly marked in mountain regions (Gobiet *et al.* 2014). However, the impacts on demographic parameters of bird populations might be complex and mediated over longer timescales (Ewing *et al*. 2020), for example through altered species interactions (Ockendon *et al.* 2014), and may be more challenging to detect in comparison to other direct impacts (e.g., hunting). Furthermore, these three drivers are not independent

of one-another. Both climate change and land abandonment may drive vegetation encroachment, often acting in tandem (Gehrig-Fasel *et al.* 2007). For our classification of drivers, we simply accepted the 'proximate' mechanism presented in a given study, but this may of course have been underpinned by other effects (e.g., climate change being a key driver of elevational shifts in the treeline in many regions; Harsch *et al.* 2009). This lack of independence may have to some extent diluted the effect of each individual driver, whilst the large sample sizes could have influenced the detection of significant trends.

For these three drivers, and indeed most of drivers considered here, there will be species that benefit and species that are affected negatively by a given driver, reducing the likelihood of our analysis identifying them as significant drivers of change. For example, loss of open habitats and warmer average temperatures in mountains will likely affect positively forest birds, and negatively affect open-nesting alpine species which are close to their lower thermal limit (Chamberlain *et al.* 2013). However, responses of mountain birds to environmental change can also vary according to species' ecological traits and local conditions (Auer & King 2004, Rocchia *et al.* 2018).

There were geographic and biases in the distribution of studies, the UK and Southern Europe being the most represented regions. The small sample sizes from many geographic regions meant that we were unable to analyse region-specific impacts of drivers (preliminary analyses showed lack of convergence or poor model fit; unpubl. data). However, we might expect some drivers to have more severe effects in some areas. Certainly, population trends of mountain birds vary markedly across different mountain regions in Europe (Lehikionen *et al.* 2019), suggesting that different drivers have different effects according to geographic location. Further studies in some under-represented European mountains would enable a proper assessment of geographic variation in drivers of mountain bird populations.

There were also taxonomic biases; in particular there were many studies of raptors and gamebirds compared to passerines (Fig. A3). There was a lack of studies of alpine specialists, with no studies identified for the Wallcreeper, and very few for other arctic-alpine species such as the Gyrfalcon, the Lapland Longspur or the Snowy Owl, whereas there were many more of groups such as vultures and gamebirds. Such taxonomic biases are well known (Ducatez & Lefebvre 2014), and in this case can be explained by two factors. First, species occurring in extreme environments, like most mountain specialists and arctic species, are more challenging to study than those breeding at lower elevations and in more accessible locations (Chamberlain *et al.* 2012). Second, charismatic flagship species, which are often characterised by a wider distribution and a greater body mass, are more studied (Ducatez & Lefebvre 2014). This highlights the need for greater prioritisation in research, as the least studied species (mountain specialists and those with the smallest distributions) are also the species that are most likely to be impacted in the future, especially by climate change (Hof *et al.* 2017).

In this study we have shown the impacts of a range of drivers on mountain bird populations across Europe. Most of the studies considered dealt with the distribution and occurrence of the species at a broad-scale, and there was a lack of studies considering mechanisms that address ecological requirements and impacts at a finer-scale. Detection of trends in drivers would be more effective if more long-term studies were present in the literature; at the same time, they would enhance the understanding of key drivers and their consequences for bird populations (Lehikoinen *et al.* 2019). Furthermore, we treated all demographic parameters equally, hence there was an implicit assumption that population consequences of the impacts of drivers would be the same for all parameters. However, some demographic parameters may be more important than others in driving mountain bird populations – for example, it may be worth separating the effects of proximate (e.g. breeding success, survival) and ultimate (e.g. population change) drivers in future studies.

Based on our analyses, it is possible to summarise the key conservation challenges for European mountain birds. We have highlighted the strong evidence of impacts that cause direct mortality, such as predation, persecution or collision with renewable energy infrastructure, and affect in particular k-selected species which are highly vulnerable to increases in adult mortality. We recommend that conservation activities for mountain birds in Europe should focus on addressing these direct causes of mortality where they are shown to be driving long-term declines. Furthermore, land-use changes, and particularly forestry, can have dramatic and rapid effects on some taxonomic groups, especially waders, that are associated with open habitats. Drivers likely to cause rapid land-use change, such as large-scale forestry or hydro-electric renewable energy generation, should be spatially planned to avoid concentrations of vulnerable species (Bright *et al.* 2008). The impacts of other drivers such as climate change and pastoral changes may differ between species and operate through multiple mechanisms over long timescales. Addressing the impacts of these pressures may require more detailed research into the effectiveness of interventions that can still operate within an altered management system, such as agri-environment schemes, or that may support species in a changing climate.

We have used a simple classification of drivers that did not take into account the magnitude of a given effect. We consciously decided to follow this approach in order to have sufficient sample sizes on which to base our analyses. Currently, there is insufficient data to undertake a formal meta-analysis based on such a comprehensive range of drivers. Indeed, even for a comparatively well-studied driver such as climate change, there are very few studies on mountain birds on which to base a meta-analysis (Scridel *et al.* 2018), even though mountain and upland birds are regarded as amongst the most vulnerable bird species to climate change (Pearce-Higgins et al. 2017b). However, understanding thoroughly the responses of mountain bird populations to the drivers that we have reviewed is fundamental for developing effective conservation strategies. Mitigation of impacts is needed at the continental scale, yet

any strategies to do so are not feasible without evidence from long-term studies from different regions of Europe. It is crucial to have detailed ecological studies carried out at the same scale for all the species. We thus invite researchers and scientists to put their effort into long-term monitoring of mountain and upland bird populations, their habitats and their drivers, in order to have reliable evidence to inform decision-makers. In this way, efficient conservation measures for bird species occurring in the mountain and upland regions of Europe can be undertaken.

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References

Antonelli, A., Kissling, W. D., Flantua, S. G., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., Kreft, H., Linder, P., Badgley, C., Fjeldså, J., Fritz, S. A., Rahbek, C., Herman, F., Hooghiemstra, H. & Hoorn, C. 2018. Geological and climatic influences on mountain biodiversity. *Nat. Geosci.* 11: 718-725.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., & Jenni-Eiermann, S. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proc. R. Soc. B.* 274: 1219-1224.

Arrondo, E., Sanz-Aguilar, A., Pérez-García, J. M., Cortés-Avizanda, A., Sánchez-Zapata, J. A., & Donázar, J. A. 2020. Landscape anthropization shapes the survival of a top avian scavenger. *Biod. Cons.* 29: 1411-1425.

Auer, S. K., & King, D. I. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob. Eco. Biog.* 23: 867-875.

Bani, L., Luppi, M., Rocchia, E., Dondina, O., & Orioli, V. 2019. Winners and losers: How the elevational range of breeding birds on Alps has varied over the past four decades due to climate and habitat changes. *Ecol. Evol*. 9: 1289-1305.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. 2015. The role of agri-environment schemes in conservation and environmental management. *Cons. Biol.* 29: 1006-1016.

Bates, D., Maechler, M., Bolker, B. 2007. lme4: Linear Mixed-Effects Models using 'Eigen' and S4. Version 1.1-23.

Beniston, M., Farinotti, D., Stoffel, M., Andreassen, L. M., Coppola, E., Eckert, N., Fantini, A., Giacona, F., Hauck, C., Huss, M., Huwald, H., Lehning, M., López-Moreno, J. I., Magnusson, J., Marty, C., Morán-Tejéda, E., Morin, S., Naaim, M., Provenzale, A., Rabatel, A., Six, D., Stötter, J., Strasser, U., Terzago, S. & Vincent, C. 2018. The European mountain cryosphere: a review of its current state, trends, and future challenges. *The Cryosphere*, 12: 759-794.

Berny, P., Vilagines, L., Cugnasse, J. M., Mastain, O., Chollet, J. Y., Joncour, G., & Razin, M. 2015. VIGILANCE POISON: illegal poisoning and lead intoxication are the main factors affecting avian scavenger survival in the Pyrenees (France). *Ecotox. Env. Saf.* 118: 71-82.

BirdLife International and Handbook of the Birds of the World 2019. Bird species distribution maps of the world. Version 2019. Cambridge, UK: BirdLife International

BirdLife International 2017. European birds of conservation concern: populations, trends and national responsibilities Cambridge, UK: BirdLife International.

Bonn, A., Allott, T., Hubacek, K., Stewart, J., & Allott, T. 2009. Drivers of change in upland environments: Concepts, threats and opportunities. Drivers of Environmental Change in Uplands; Bonn, A., Allott, T., Hubacek, K., Stewart, J., Eds, 1-10.

Brambilla, M., Pedrini, P., Rolando, A., & Chamberlain, D. E. 2016. Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *J. Biogeogr.* 43: 2299–2309.

Bright, J., Langston, R., Bullman, R., Evans, R., Gardner, S., & Pearce-Higgins, J. 2008. Map of bird sensitivities to wind farms in Scotland: a tool to aid planning and conservation. *Biol. Cons.* 141: 2342-2356.

Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Bohm, R. & Schoener, W. 2009. Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. Int. *J. Climatol.* 29: 2197–2225.

Campagnaro, T., Frate, L., Carranza, M. L., & Sitzia, T. 2017. Multi-scale analysis of alpine landscapes with different intensities of abandonment reveals similar spatial pattern changes: Implications for habitat conservation. *Ecol. Indic.* 74: 147-159.

Caprio, E., Chamberlain, D. E., Isaia, M., & Rolando, A. 2011. Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. *Biol. Cons*. 144: 2958-2967.

Carrete, M., Grande, J. M., Tella, J. L., Sánchez-Zapata, J. A., Donázar, J. A., Díaz-Delgado, R., & Romo, A. 2007. Habitat, human pressure, and social behavior: Partialling out factors affecting large-scale territory extinction in an endangered vulture. *Biol. Cons.* 136: 143-154.

Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A., & Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. *Ibis* 154: 205-209.

Chamberlain, D. E., Negro, M., Caprio, E., & Rolando, A. 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biol. Cons.* 167: 127-135.

Chamberlain, D. E., Pedrini, P., Brambilla, M., Rolando, A., & Girardello, M. 2016a. Identifying key conservation threats to Alpine birds through expert knowledge. *PeerJ* 4: e1723.

Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P., & Rolando, A. 2016b. Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. *Oecologia* 181: 1139-1150.

Douglas, D. J., Groom, J. D., & Scridel, D. 2020. Benefits and costs of native reforestation for breeding songbirds in temperate uplands. *Biol. Cons*. 244: 108483.

Ducatez, S., & Lefebvre, L. 2014. Patterns of research effort in birds. *PLoS One* 9: e89955.

European Parliament 2020. Second Pillar of the CAP: Rural Development Policy. European Parliament. https://www.europarl.europa.eu/ftu/pdf/en/FTU_3.2.6.pdf

Ewing, S. R., Baxter, A., Wilson, J. D., Hayhow, D. B., Gordon, J., Thompson, D. B. A., Whitfield, D. P. & Van der Wal, R. 2020. Clinging on to alpine life: Investigating factors driving the uphill range contraction and population decline of a mountain breeding bird. *Glob Change Biol*. 26: 3771– 3787

Fasce, P., Fasce, L., Villers, A., Bergese, F., & Bretagnolle, V. 2011. Long-term breeding demography and density dependence in an increasing population of Golden Eagles *Aquila chrysaetos*. *Ibis* 153: 581-591.

Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *J. Appl. Ecol.* 47: 263-272.

Fox, J. & Weisberg, S. 2019. An R Companion to Applied Regression, Third Edition, Sage

Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J. Veg. Sci.* 18: 571-582.

Gelman, A., Su, Y., Yajima, M., Hill, J., Pittau, M., Kerman, J., Zheng, T., Dorie, V. 2007. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. Version 1.11-1

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. 2014. 21st century climate change in the European Alps—A review. *Sci. Tot. Env.*493: 1138-1151.

Gordon, M., Lumley, T., & Gordon, M. M. 2016. Package 'forestplot'. Advanced Forest Plot Using 'grid' Graphics.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Eco. Lett.* 12: 1040-1049.

Hof, A. R., Rodríguez-Castañeda, G., Allen, A. M., Jansson, R., & Nilsson, C. 2017. Vulnerability of Subarctic and Arctic breeding birds. *Eco. Appl.* 27: 219-234.

Iqtiyanillham, N., Hasanuzzaman, M., & Hosenuzzaman, M. 2017. European smart grid prospects, policies, and challenges. Ren. Sust. *En. Rev.* 67: 776-790.

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A., & Chamberlain, D. 2018. The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. *J. Ornithol.* 159: 747-759.

Karagulle, D., Frye, C., Sayre, R., Breyer, S., Aniello,P., Vaughan, R. & Wright, D. 2017. Modeling global Hammond landform regions from 250-m elevation data. *Transact.GIS* 2: 1040-1060

Keller V., Herrando S., Voříšek P., Franch M., Kipson M., Milanesi P., Martí D., Anton M., Klvanova A, Kalyakin M.V., Bauer H.G. & Foppen R.P.B. (eds.) 2020. European Breeding Bird Atlas 2: Distribution, Abundance and Change. *European Bird Census Council & Lynx Edicions*, Barcelona.

Keenleyside, C., Beaufoy, G., Tucker, G., & Jones, G. 2014. High Nature Value farming throughout EU-27 and its financial support under the CAP. *Inst. Euro. Envi. Pol. London*, 10, 91086.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., Korner-Nievergelt, P. 2015. Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan. *Elsevier*.

Lampila, P., Ranta, E., Mönkkönen, M., Lindén, H., & Helle, P. 2011. Grouse dynamics and harvesting in Kainuu, northeastern Finland. *Oikos* 120: 1057-1064.

Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., Grueneberg, C., Haas, F., Harris, S., Herrando, S., Husby, M., Jiguet, F., Kålås, J. A., Lindström, Å., Lorillière, R., Molina, B., Pladevall, C., Calvi, G., Sattler, T., Schmid, H., Sirkiä, P. M., Teufelbauer, N. & Trautmann, S. 2019. Declining population trends of European mountain birds. *Glob. Ch. Bio.* 25: 577-588.

Ludwig, S. C., Roos, S., Rollie, C. J., & Baines, D. 2020. Long-term changes in the abundance and breeding success of raptors and ravens in periods of varying management of a Scottish grouse moor. *Av. Cons. Ecol.* 21: 1-17

Martin, T. E. 1993. Nest predation and nest sites. *BioSc.* 43: 523-532.

Morrissey, C. A., Stanton, D. W., Tyler, C. R., Pereira, M. G., Newton, J., Durance, I., & Ormerod, S. J. 2014. Developmental impairment in Eurasian dipper nestlings exposed to urban stream pollutants. *Env. Tox. Chem.* 33: 1315-1323.

Murgatroyd, M., Redpath, S. M., Murphy, S. G., Douglas, D. J., Saunders, R., & Amar, A. 2019. Patterns of satellite tagged hen harrier disappearances suggest widespread illegal killing on British grouse moors. *Nat. Comm.* 10: 1-8.

Newton, I. 2021. Killing of raptors on grouse moors: evidence and effects. *Ibis* 163: 1-19.

Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner E. V. K. & Pearce-Higgins, J. W.

2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Glob. Ch. Biol.* 20: 2221-2229.

Patthey, P., Signorell, N., Rotelli, L., & Arlettaz, R. 2012. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. *Eu. J. Wil. Res.* 58: 59-70.

Pearce-Higgins, J. W., Stephen, L., Langston, R. H., Bainbridge, I. P., & Bullman, R. 2009a. The distribution of breeding birds around upland wind farms. *J. Appl. Eco.* 46: 1323-1331.

Pearce-Higgins, J.W., Grant, M.C., Beale, C.M., Buchanan, G.M. & Sim, I.M.W. 2009b. International importance and drivers of change of upland bird populations. In Bonn A, Allot T, Hubacek K, Stewart J (eds) Drivers of Environmental Change in Uplands. Routledge, London & New York, Pp 209-227.

Pearce-Higgins, J. W., Stephen, L., Douse, A., & Langston, R. H. 2012. Greater impacts of wind farms on bird populations during construction than subsequent operation: results of a multi-site and multi-species analysis. *J. Appl. Eco.* 49: 386-394.

Pearce-Higgins, J. W., Green, R. E., & Green, R. 2014. Birds and climate change: impacts and conservation responses. *Cambridge University Press*, Cambridge, UK

Pearce-Higgins, J.W., Ockendon, N., Baker, D.J., Carr, J., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J. & Tanner, E.V.J. 2015. Geographical variation in species' population responses to changes in temperature and precipitation. *Proc. Royal Soc. B* 282: 20151561.

Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bellio, M., Bocher, P., Buchanan, G.M., Clay, R.P., Conklin, J., Crockford, N., Dann, P., Elts, J., Friis, C., Fuller, R.A., Gill, J.A., Gosbell, K., Johson, J.A., Marquez-Ferrando, R., Masero,

J.A., Melville, D.S., Millington, S., Minton, C., Mundkur, T., Nol, E., Pehlak, H., Piersma, T., Robin, F., Rogers, D.I., Ruthrauff, D.R., Senner, N.R., Shah, J.N., Sheldon, R.D., Soloviev, S.A., Tomkovich, P.S. & Verkuil, Y.I. 2017a. A global threats overview for Numeniini populations: synthesising expert knowledge for a group of declining migratory birds. *Bird Cons. Int.* 7: 6-34.

Pearce-Higgins, J.W., Beale, C.M., Oliver, T.H., August, T.A., Carroll, M., Massimino, D., Ockendon, N., Savage, J., Wheatley, C.J., Ausden, M.A., Bradbury, R.B., Duffield, S.J., Macgregor, N.A., McClean, C.J., Morecroft, M.D., Thomas, C.D., Watts, O., Beckmann, B.C., Fox, R., Roy, H.E., Sutton, P.G., Walker, K.J. & Crick, H.Q.P. 2017b. A national-scale assessment of climate change impacts on species: assessing the balance of risks and opportunities for multiple taxa. *Biol. Cons.* 213: 124-134

Pe'er, L. Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbé, A., Wulf, F. & Scott, A. V. 2014. EU agricultural reform fails on biodiversity. *Science* 344: 1090-1092.

Pringle, H., Wilson, M., Calladine, J., & Siriwardena, G. 2019. Associations between gamebird releases and generalist predators. *J. Appl. Eco.* 56: 2102-2113.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J. & Fjeldså, J. 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* 365: 1108-1113.

Rocchia, E., Luppi, M., Dondina, O., Orioli, V., & Bani, L. 2018. Can the effect of species ecological traits on birds' altitudinal changes differ between geographic areas? *Acta Oeco*. 92: 26-34.

Rolando, A., Caprio, E., Rinaldi, E., & Ellena, I. 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. *J. Appl. Eco.* 44: 210-219.

Roos, S., Smart, J., Gibbons, D. W., & Wilson, J. D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol. Rev.* 93: 1915-1937.

Rosenthal, R. 1979. The file drawer problem and tolerance for null results. *Psyc. Bull.* 86: 638.

Salafsky, N., Salzer, D., Stattersfield, A. J., Hilton-Taylor, C., Neugarten, R., Butchart, S. H. M., Collen, B., Cox, N., Master, L. L., O'Connor, S. O. and Wilkie, D. 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions*. Cons. Biol.* 22: 897–911.

Sayre, R., Frye, C., Karagulle, D., Krauer, J., Breyer, S., Aniello, P., Wright, D. J., Payne, D., Adler, C., Warner, H., VanSistine, D. P. & Cress, J. 2018 A New High-Resolution Map of World Mountains and an Online Tool for Visualizing and Comparing Characterizations of Global Mountain Distributions. *Mount. Res. Dev.* 38: 240-249

Scolozzi, R., & Geneletti, D. 2012. A multi-scale qualitative approach to assess the impact of urbanization on natural habitats and their connectivity. *Env. Imp. Ass. Rev.* 36: 9-22.

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R. & Chamberlain, D. 2018. A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis* 160: 489-515.

Sekercioglu, C. H., Schneider, S. H., Fay, J. P., Loarie, S. R. 2008 Climate change, elevational range shifts and bird extinctions. *Cons. Biol.* 22: 140–150

Soliva, R., Rønningen, K., Bella, I., Bezak, P., Cooper, T., Flø, B. E., Marty, P. & Potter, C. 2008. Envisioning upland futures: Stakeholder responses to scenarios for Europe's mountain landscapes. *J. Rural Stud.* 24: 56-71.

Sonne, C., Bustnes, J. O., Herzke, D., Jaspers, V. L., Covaci, A., Eulaers, I., Halley, D. J., Moum, T., Ballesteros, M., Eens, M., Ims, R. A., Hanssen, S. A., Erikstad, K. E.,

Johnsen, T. V., Rigét, F. F., Jensen, A. L. & Kjelgaard-Hansen, M. 2012. Blood plasma clinical–chemical parameters as biomarker endpoints for organohalogen contaminant exposure in Norwegian raptor nestlings. *Ecotox. Env. Saf.* 80: 76-83.

Sotherton, N., Tapper, S., & Smith, A. 200). Hen harriers and red grouse: economic aspects of red grouse shooting and the implications for moorland conservation. *J. Appl. Eco.* 46: 955-960.

Streifeneder, T. 2016. Agriculture first: Assessing European policies and scientific typologies to define authentic agritourism and differentiate it from countryside tourism. *Tour. Manag. Persp.* 20: 251-264.

Thaxter, C. B., Buchanan, G. M., Carr, J., Butchart, S. H., Newbold, T., Green, R. E., Tobias, J. A., Foden, W. B., O'Brien, S. & Pearce-Higgins, J. W. 2017. Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proc. R. Soc. B* 284: 20170829.

Vasilakis, D. P., Whitfield, D. P., Schindler, S., Poirazidis, K. S., & Kati, V. 2016. Reconciling endangered species conservation with wind farm development: Cinereous vultures (*Aegypius monachus*) in south-eastern Europe. *Biol. Cons.* 196: 10-17.

Viterbi, R., Cerrato, C., Bassano, B., Bionda, R., von Hardenberg, A., Provenzale, A., Bogliani, G. 2013 Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach. *Comm. Eco.* 14: 18–30

Whitehead, S., Weald, H., & Baines, D. 2021. Post-burning responses by vegetation on blanket bog peatland sites on a Scottish grouse moor. *Eco. Ind.* 123: 107336.

Whitfield, D. P., Fielding, A. H., McLeod, D. R. A., & Haworth, P. F. 2004. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. *Biol. Cons.* 118: 249-259.

Supplementary material

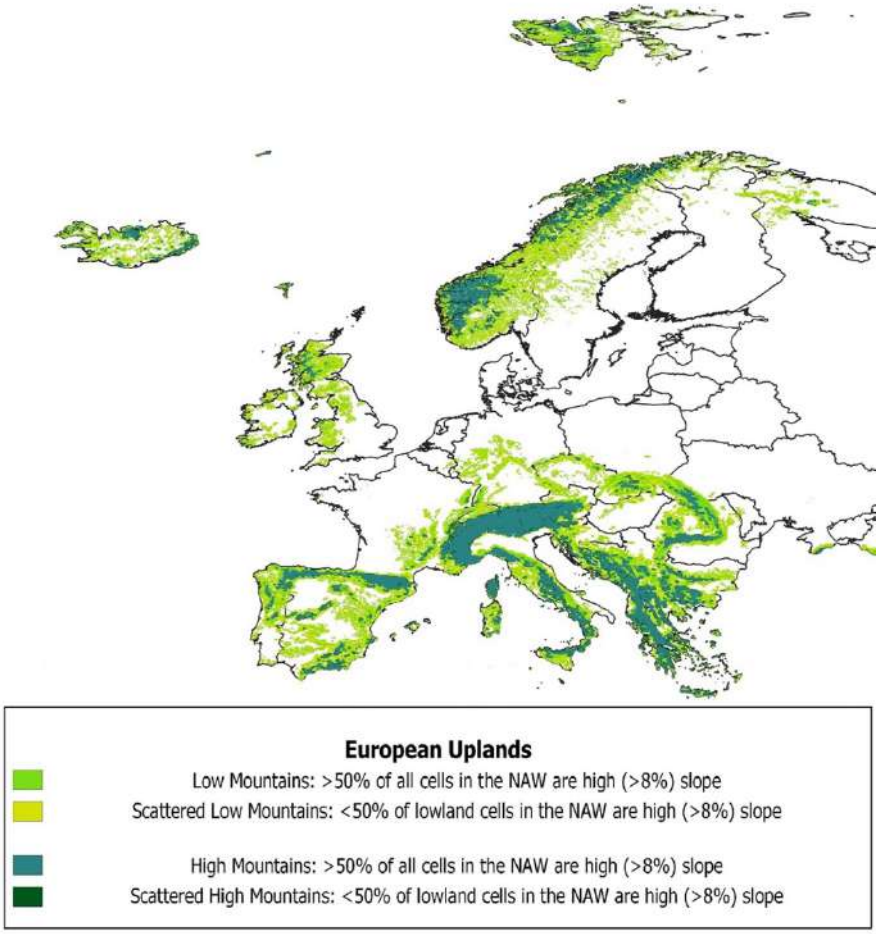

Figure A.1. Mountain systems adapted to the European region. Criteria for defining the 4 mountain classes according to Karagulle *et al.* (2017): slope was averaged from the 250 m pixels in a 3 km neighbourhood analysis window (NAW). Criteria refer to the amount (% area) of high slope (8%) in a 6 km NAW in mountain (higher than the midpoint of the elevation range in the NAW) or lowland (lower than the midpoint of the elevation range in the NAW) pixels. Relative relief (> 900 m for high mountains and scattered high mountains; 301-900 m for low mountains and scattered low mountains, which includes 'uplands' such as heather moorland in the UK) is the absolute value of the difference between the maximum and minimum elevations in a 6 km NAW

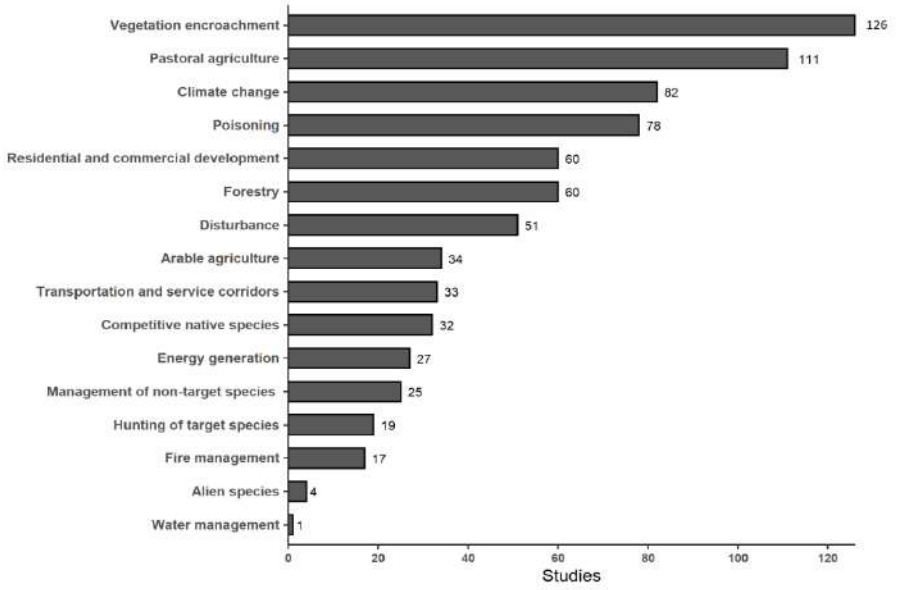

Figure A.2. Variation in the number of studies for each impact

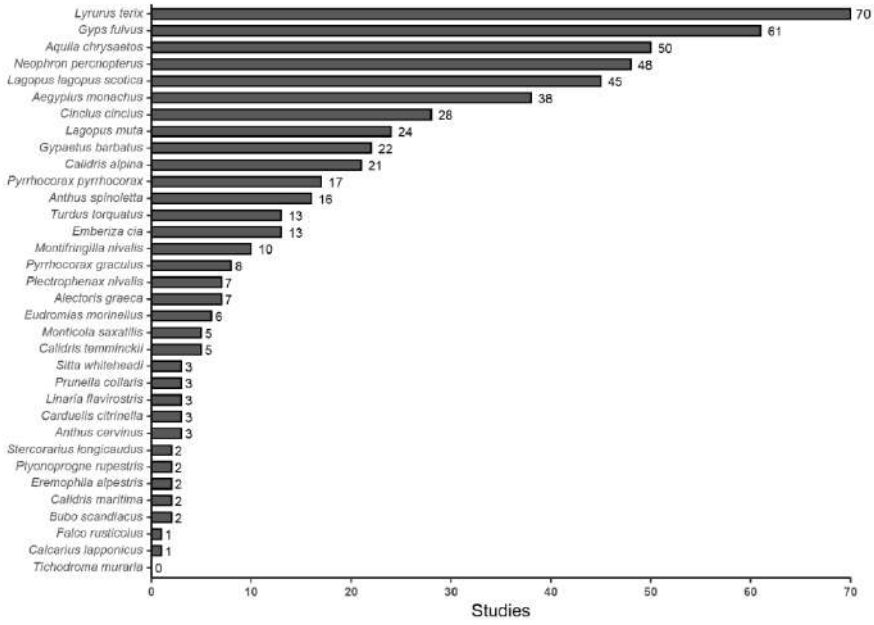

Figure A.3. Variation in the number of studies for each species

Table A.1. Number of tests (n) for each demographic parameter of the nuisance variable 'parameter type'

Demographic parameter	**n**
Occurrence (occurrence, habitat selection)	538
Abundance (abundance, density, population changes)	259
Breeding success (number of fledgelings, nest failure, clutch size)	162
Survival (and mortality)	116
Pollutant level above a given threshold (pesticides, metals, antibiotics, other pollutants) that results in effects on reproductive success (e.g. hatchability of eggs)	84

Table A.2. Publication bias was calculated from Rosenthal's failsafe number (X) for each driver and for the total of studies. X was calculated for studies where a precise value of *P* is unknown as reported in Rosenthal (1979): $X= 19*(n_p + n_n) - n_{ns}$ where n_p is the number of significant positive tests, n_n is the number of significant negative tests and n_{ns} is the number of non-significant tests. n is the number of total tests

Impact	**N**	**n_p**	**n_n**	**n_{ns}**	**X**
Arable agriculture	280	70	37	173	1,860
Forestry	650	80	117	453	3,290
Pastoral agriculture	579	137	108	331	4,324
Urban areas and roads	518	30	124	364	2,562
Energy generation	74	0	41	33	746
Hunting of target species	73	4	40	29	807
Management of non-target species	189	79	19	91	1,771
Disturbance	342	13	93	235	1,779
Fire management	170	71	17	82	1,590

Competitive native species	108	1	63	44	1,172
Poisoning	486	3	240	243	4,374
Climate change	825	87	486	252	10,635
Vegetation encroachment	1,752	284	365	1,099	11,232
Total	6,046	859	1,750	3,429	46,142

Table A.3. Mountain bird species that were selected for this study. Taxonomic order and group are shown, together with the extent of the breeding range (BirdLife International 2019), the IUCN category (www.iucnredlist.org) and population size at the European scale (BirdLife International 2017)

Common name	Scientific name	Order (group)	European breeding range (km^2)	IUCN Category Europe	European population size (pairs)
Alpine Accentor	*Prunella collaris*	Passeriformes (passerines)	597,800	LC	77,900 – 14,9000
Alpine Chough	*Pyrrhocorax graculus*	Passeriformes (passerines)	536,200	LC	108,000 – 253,000
Black Grouse	*Lyrurus terix*	Galliformes (gamebirds)	4,320,200	LC	11,500 – 25,500 (males)
Cinereous Vulture	*Aegypius monachus*	Accipitriformes (raptors)	205,200	LC	2,300 – 2,500
Citril Finch	*Carduelis citrinella*	Passeriformes (passerines)	194,300	LC	250,000 – 283,000
Corsican Nuthatch	*Sitta whiteheadi*	Passeriformes (passerines)	2,300	VU	1,500 – 2,200
Crag Martin	*Ptyonoprogne rupestris*	Passeriformes (passerines)	959,600	LC	182,000 – 342,000
Dotterel	*Eudromias morinellus*	Charadriiformes (waders)	539,700	LC	12,800 – 48,400 (males)
Dunlin	*Calidris alpina*	Charadriiformes (waders)	1,011,800	LC	426,000 – 562,000
Egyptian Vulture	*Neophron percnopterus*	Accipitriformes (raptors)	898,300	EN	3,000 – 4,700
Golden Eagle	*Aquila chrysaetos*	Accipitriformes (raptors)	5,714,000	LC	9,300 – 12,300
Griffon Vulture	*Gyps fulvus*	Accipitriformes (raptors)	366,700	LC	32,400 – 34,400
Gyrfalcon	*Falco rusticolus*	Falconiformes (raptors)	438,500	LC	1,100 – 1,900
Horned Lark	*Eremophila alpestris*	Passeriformes (passerines)	725,000	LC	2,140,000 – 6,510,000
Lammergeier	*Gypaetus barbatus*	Accipitriformes (raptors)	148,300	VU	580 – 790
Lapland longspur	*Calcarius lapponicus*	Passeriformes (passerines)	576,000	LC	5,340,000 – 12,700,000
Long-tailed Skua	*Stercorarius longicaudus*	Charadriiformes (waders)	474,000	LC	19,800 – 53,000
Purple Sandpiper	*Calidris maritima*	Charadriiformes (waders)	366,600	LC	56,700 – 83,000
Red Grouse	*Lagopus lagopus scotica*	Galliformes (gamebirds)	155,900	VU	250,000 – 251,500
Red-billed Chough	*Pyrrhocorax pyrrhocorax*	Passeriformes (passerines)	607,600	LC	40,500 – 86,400

Red-throated Pipit	*Anthus cervinus*	Passeriformes (passerines)	285,700	LC	1,010,000 – 3,020,000
Ring Ouzel	*Turdus torquatus*	Passeriformes (passerines)	1,086,200	LC	299,000 – 598,000
Rock Bunting	*Emberiza cia*	Passeriformes (passerines)	1,235,000	LC	1,930,000 – 4,230,000
Rock Partridge	*Alectoris graeca*	Galliformes (gamebirds)	547,600	NT	41,800 – 73,400
Rock Ptarmigan	*Lagopus muta*	Galliformes (gamebirds)	812,250	NT	257,000 – 1,010,000
Rock Thrush	*Monticola saxatilis*	Passeriformes (passerines)	1,060,000	LC	88,900 – 283,000
Snow Bunting	*Plectrophenax nivalis*	Passeriformes (passerines)	446,600	LC	1,230,000 – 2,310,000
Snowy Owl	*Bubo scandiacus*	Strigiformes (raptors)	360,160	LC	700 – 2,300
Temminck's Stint	*Calidris temminckii*	Charadriiformes (waders)	660,100	LC	58,100 – 167,000
Twite	*Linaria flavirostris*	Passeriformes (passerines)	215,300	LC	164,000 – 756,000
Wallcreeper	*Tichodroma muraria*	Passeriformes (passerines)	570,100	LC	29,000 – 69,700
Water Pipit	*Anthus spinoletta*	Passeriformes (passerines)	379,000	LC	1,620,000 – 3,160,000
White-throated Dipper	*Cinclus cinclus*	Passeriformes (passerines)	2,591,000	LC	131,000 – 292,000
White-winged Snowfinch	*Montifringilla nivalis*	Passeriformes (passerines)	357,600	LC	129,000 – 568,000

Table A.4. Outputs from the nuisance variable models. Models were binomial GLMMs with Sf as response variable, each nuisance variable as explanatory variable and reference id and species as random terms. Effects were considered significant if 95 % credible intervals (CrI) of the estimates did not include zero. Significant effects in bold

			Estimate (CrI)	**df**	***X²***	***P***
Nuisance variable models *Sf ~ nuisance variable + (1|reference id) + (1|species)*	Parameter type (categorical)			**4**	**86.65**	**<0.001**
		Intercept	**-0.26 (-0.50 – -0.03)**			
		Breeding success	**-0.34 (-0.66– -0.02)**			
		Occurrence	-0.02 (-0.27–0.21)			
		Pollutant level	**-1.57 (-2.04– -1.10)**			
		Survival	**-1.37 (-1.75– -0.96)**			
	Multivariate (categorical)			1	0.01	0.916
		Intercept	**-0.53 (-0.70– -0.36)**			
		Multivariate	-0.01 (-0.22–0.19)			
	Scale (categorical)			2	6.02	0.059
		Intercept	**-0.83 (-1.09– -0.58)**			
		Spatial	0.37 (0.04–0.59)			
		Temporal	0.40 (-0.20–1.00)			
	Number of tests (numeric)			1	1.78	0.182
		Intercept	**-0.56 (-0.70– -0.43)**			
		Number of tests	0.005 (-0.003– 0.013)			
	Sample size (numeric)			1	0.87	0.351
		Intercept	**-0.61 (-0.80– -0.42)**			
		Sample size	0.001 (-0.001– 0.002)			

Table A.5. Outputs from the impact and trend analyses. Impacts were modelled according to binomial GLMMs with Sf as the response variable, impact as the explanatory variable, parameter type as a nuisance variable and reference id and species as a random terms. Trends were modelled according to binomial GLMs with Trend as response variable and impact as the explanatory variable. Levels were considered significant if 95 % credible intervals (CrI) of the estimates did not include zero. Significant levels are highlighted in bold

			Estimate (CrI)
a)	Impact model *Sf ~ impact + (parameter type) + (1|reference id) + (1|species)*	Intercept	-0.23 (-0.65 – 0.21)
		Impact	
		Disturbance	**-0.55 (-1.06 – -0.05)**
		Energy production	**-1.06 (-1.78 – -0.36)**
		Management of non-target species	**1.79 (1.04 – 2.54)**
		Hunting of target species	**-1.29 (-2.16 – -0.41)**
		Competitive native species	**-1.02 (-1.69 – -0.35)**
		Poisoning	**-0.59 (-1.17 – -0.03)**
		Climate change	-0.19 (-0.67 – 0.27)
		Fire management	0.48 (-0.22 – 1.18)
		Forestry	-0.24 (-0.72 – 0.25)
		Pastoral agriculture	0.41 (-0.05 – 0.85)
		Urban areas and roads	-0.34 (-0.78 – 0.12)
		Vegetation encroachment	0.31 (-0.14 – 0.78)
b)	Trend model *Trend ~ impact*	**Intercept**	**-0.69 (-1.11 – -0.28)**
		Impact	
		Climate change	**0.68 (0.21 – 1.18)**
		Vegetation encroachment	**0.63 (0.07 – 1.20)**
		Anthropic pressure	0.49 (-0.06 – 1.09)
		Habitat and species management	0.34 (-0.21 – 0.90)

Chapter III

Avalanches create unique habitats for birds in the European Alps

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Abstract

Mountain regions harbour dynamic ecosystems that have been historically shaped by interactions between natural abiotic processes and human activities, but nowadays they are threatened by climate change. Avalanches are one of the main sources of natural disturbance in mountain areas, creating habitat mosaics with a high vegetation heterogeneity that can be exploited by a suite of animal species. Since snow precipitation regimes in mountain regions will be altered by climate change, it is fundamental to study the interactions between avalanches and biodiversity. We carried out surveys on 240 points to study birds and habitats across horizontal and vertical transects in the Western Italian Alps to assess the differences in habitat and bird assemblage composition and ecological traits between avalanche tracks and control points. Differences in both habitat and in bird assemblages were more pronounced at lower elevations and became less obvious towards alpine grasslands. Avalanche tracks were characterized by a higher structural vegetation diversity with a greater cover of rocks, shrubs and a higher number of small trees. Bird assemblages differed between avalanche tracks and adjacent control points, with the former being more diverse and characterised by a higher proportion of species typical of open habitats and migrants. Importantly, the avalanche track bird assemblage differed from both forest and treeline ecotone assemblages, showing that these heterogeneous areas are unique, harbouring a mixture of bird species from different habitats. Future environmental change that may affect the frequency of avalanches thus has the potential to affect broader-scale diversity in mountains, and hence should be a priority for alpine ecological research.

Key words: avalanche, disturbance, climate change, indicator species, bird assemblage, Alps

Introduction

High-elevation habitats are subject to a range of different pressures, but climate change is one of the major current threats (Nogués-Bravo et al. 2007; Loarie et al. 2009; Gobiet and Kotlarski 2020), with potentially serious consequences for animal and plant communities (Thuiller et al. 2005; Bellard et al. 2012; Pacifici et al. 2018). Mountains are characterised by dynamic landscapes that are shaped by the interaction of natural abiotic processes (Bebi et al. 2017) and human activities (Pini et al. 2017; Zimmerer et al. 2017), which have contributed to promoting biodiversity where environmentally-friendly agricultural practices were adopted (e.g., Princé and Jiguet 2013). However, a decrease in the landscape heterogeneity is likely leading to negative consequences for biodiversity through both climate and land use changes (Johansson et al. 2018; Ingty 2021).

Avalanches are one of the main sources of disturbance in mountain areas, affecting forest ecosystems in particular (Bebi et al. 2009). Despite their primary ecological role in shaping mountain forest dynamics (Kulakowski et al. 2017), and the hazard they pose to human settlements (Höller 2007), they have received little research attention in comparison to other types of disturbance. The effects of avalanche activity are mostly visible in the upper forest close to the treeline and downwards, where the frequency of avalanches can span from centuries of inactivity to several events within the same year, especially on steep slopes (Laternser and Schneebeli 2003). Subalpine forest is the most impacted habitat, yet at the same time it plays a major role in influencing the magnitude of avalanche damage (Bebi et al. 2017). Forest stand structure stabilizes snowpacks on slopes and reduces wind speed, which prevents the accumulation of snow in gullies (Viglietti et al. 2010; Teich et al. 2012). Forests also prevent hazards by reducing the speed of low magnitude avalanches (Brang et al. 2006; Getzner et al. 2017). Other drivers of avalanche occurrence are terrain and snow features, with contributions of wind conditions, solar radiation and slope orientation (McClung and Schaerer 1993; Kulakowski et al. 2017).

The high frequency of avalanche events on a given track contributes to maintaining a particular habitat which often differs substantially from the surrounding forest, being characterized by lower tree density and shorter trees with slow growth rates (Bebi et al. 2001; Kulakowski et al. 2006). Frequently disturbed areas have an increased compositional and structural vegetation diversity (Rixen et al. 2007) and avalanches not only contribute to depressing the treeline below the climatic limit (Mietkiewicz et al. 2017), but they also promote habitat heterogeneity and increase vascular plant richness (Rixen and Brugger 2004). This can have cascading effects on mountain biodiversity and the impacted areas can thus be exploited by a range of animal species such as the Chamois *Rupicapra rupicapra* (Garcia-Gonzalez and Cuartas 1996), Wolverine *Gulo gulo* (Krajick 1998) or alpine birds such as grouse species (Lieser 1995). Nonetheless, effects of avalanches on animal communities have still not been examined in depth.

Frequent avalanche activity can create semi open-habitats which are normally found at higher elevations in the mountain landscapes (i.e., the treeline ecotone), and may offer an appropriate habitat for high-elevation bird species. These will be the most threatened in Alpine regions in the near future by climate (e.g. Chamberlain et al. 2013) and land-use changes (Laiolo et al. 2004) and might exploit these disturbed, more open, areas present at lower elevations when the higher elevation habitat is degraded.

As climate change effects are particularly pronounced in mountain areas (Gobiet et al. 2014; IPCC 2022), avalanche activity is predicted to change in the future, although there is no agreement on the direction or magnitude of these changes; avalanche frequency might decrease due to lower snow cover (e.g., Gądek et al. 2017; Bormann et al. 2018) or increase due to warmer winters and earlier springs (e.g., Ballesteros-Cánovas et al. 2018) and higher precipitation in February and March (e.g., Laute and Beylich 2018). Furthermore, in recent decades, a progressive expansion of forest in mountain regions has occurred in response to climate change and the

abandonment of agricultural activities (Gehrig-Fasel et al. 2007). Therefore, there is uncertainty as to how the importance of avalanche disturbance in controlling forest cover and naturally maintaining semi-open habitats will change in the near future.

The main aim of this paper is to assess if avalanche tracks are colonized by bird species which are normally found at higher elevations, and thus whether they contribute to increasing bird gamma diversity due to their habitat characteristics. Therefore, we aimed (i) to assess the differences in habitat structure between avalanche tracks and the surrounding non-disturbed habitat; (ii) to identify the characteristic bird species that occur in avalanche tracks and how they are distributed along the elevational gradient, and (iii) to test if the habitat and bird assemblage of avalanche tracks is similar to that found in the treeline ecotone, or whether these tracks form unique habitats for birds.

Methods

Study area and point selection

The study area was located in the western Italian Alps in the province of Torino, from the Viù Valley in the North (45° 13' 58" N 7° 13' 34" E) to the Germanasca Valley in the South (44° 52' 1" N 7° 2' 24" E) and ranged from 1400 m to 2500 m (Fig. 1). Along an altitudinal gradient, the area is dominated by broadleaved trees, such as Beech *Fagus sylvatica*, Ash *Fraxinus excelsior* and Norway Maple *Acer platanoides*, at lower elevations, which are replaced by forests of Larch *Larix decidua* and shrubs such as Juniper *Juniperus communis* and Alpenrose *Rhododendron ferrugineum* at higher elevations. Alpine grasslands and rocky habitats occur above c. 2300 m, although open habitats such as pastures and secondary grasslands are present at lower elevation.

Using Geographic Information Systems (GIS) software, QGIS 3.14.15 'Pi' (QGIS Development Team 2020), suitable locations for survey sites were identified from a DTM and the avalanche tracks shapefile provided by SIVa – Sistema Informativo Valanghe (Arpa Piemonte 2020), both downloaded from Geoportale Piemonte

(geoportale.piemonte.it). This 1:25.000 scale shapefile provides a range of mapped avalanche tracks resulting from both in-situ surveys and historical archive data; every avalanche polygon is linked to an online database containing information on the frequency of avalanche activity, reports of damage caused by avalanches and photos. For this study, a suite of points on avalanche tracks was selected (*n* = 120), based on their accessibility and on the level of human disturbance (i.e., urban areas and ski-pistes were avoided); the same number of control points was then selected in the proximity of the avalanche tracks.

Using this shapefile, horizontal transects were placed to assess differences between control points and avalanche tracks at the same elevation, whilst vertical transects assessed differences along the altitudinal gradient (Fig. 1). Horizontal transects were characterized by an equal number of points located in the avalanche tracks and the surrounding forests at the same elevation (control points), with a minimum distance of 200 m between points (4-6 points per transect). Vertical transects investigated the altitudinal gradient through 3 different elevation belts (i.e., mountain forest 1400-2200 m, treeline ecotone 2000-2300m and alpine grassland 2100-2500m) and consisted of two parallel transects (i.e., one along the avalanche tracks, one along the undisturbed forest-alpine grassland gradient) of 3 points each, with a minimum distance of 200 m between points. A total of 240 points was surveyed, of which half (*n* = 120) were surveyed in the horizontal transects (*n* = 23) and the other half in the vertical ones (*n* = 20). Points were visited in 2020 during the breeding period (i.e., 15-May to 15-July) where point counts and habitat surveys (intended as vegetation cover and structure) were carried out.

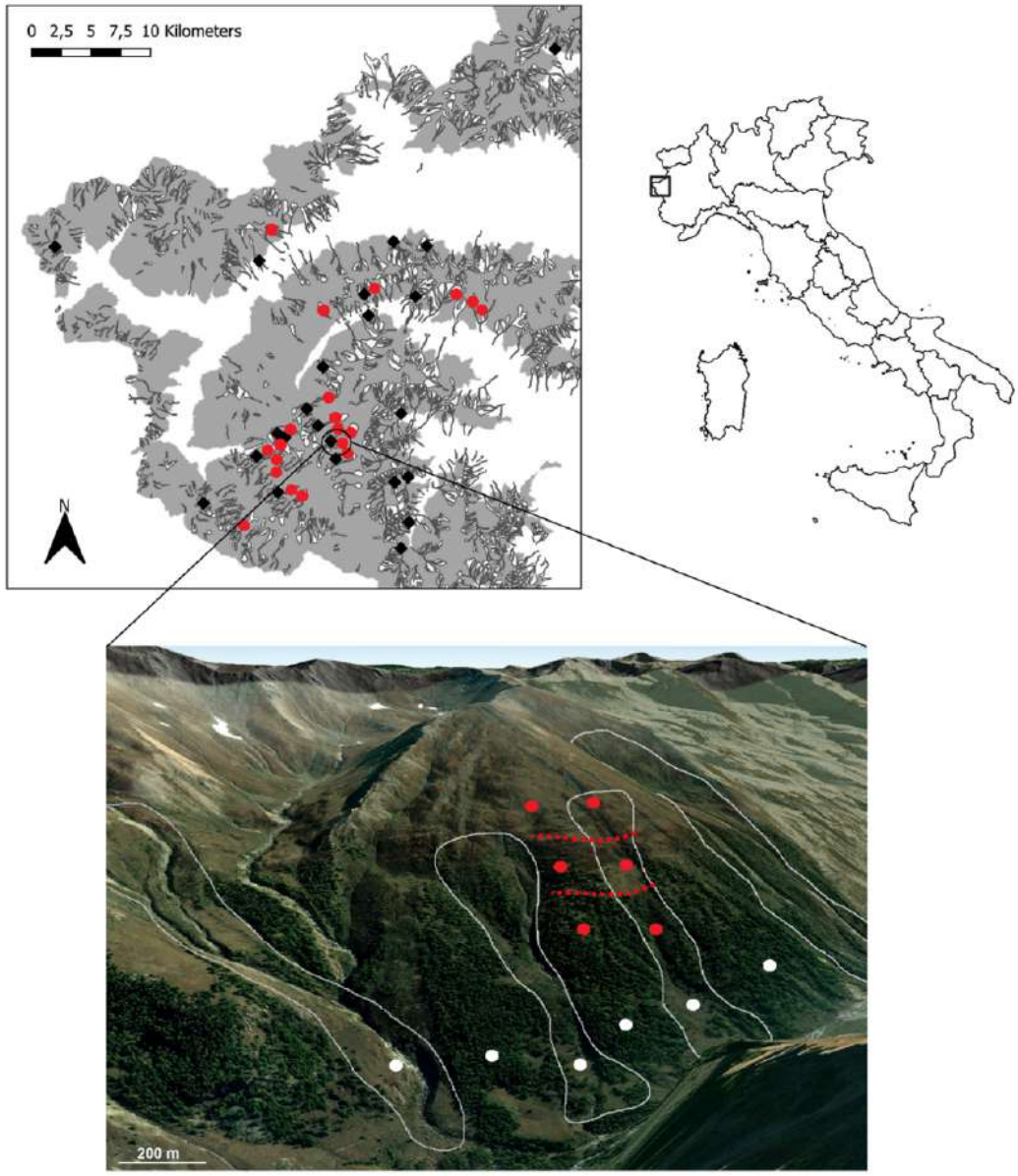

Figure 1. Study area and study design in the western Italian Alps. The area above 1700m of elevation is shown in grey, avalanche tracks are in white, and horizontal transects are shown with black rhombi whilst vertical transects with red circles. In the overview in the lower panel from Troncea Valley, the study design is shown with avalanche tracks in grey, horizontal transect points in white and vertical transect points and elevational belt borders in red (3D photo from Google Earth).

Habitat and vegetation

We estimated by sight the percentage cover of high canopy (≥ 4 m height), low canopy (between 4 and 2 m height), shrubs (woody vegetation ≤ 2 m height), grass and rocks (scree and bare areas included) within a 100 m radius from the centre of each point. Furthermore, the number of small trees (trees ≤ 2 m height) were counted within a 50 m radius. These measures have proven relevant for modelling bird species distribution in previous studies (see Jähnig et al. 2018). Distances from the observer were estimated with a laser range finder.

Bird assemblage

Point counts were carried out following the methods reported in Bibby et al. (2000), using a 10 min count period, divided into 3 time intervals of 3-2-5 min each to enable testing and incorporation of detection biases (Alldredge et al. 2007) and to model detectability (see below). The observer (who was the same for all surveys) recorded all birds seen and heard within a 100 m radius, noting for each individual detected the time interval in which it was contacted and its activity using standard activity codes (Bibby et al. 2000). For each survey, the distance from the observer was estimated with a laser range finder. Point counts were carried out from 1–1.5 h after sunrise until 1100 h and took place in opportune weather conditions (i.e. good visibility, no rain or high winds).

Statistical analysis

Habitat and vegetation

To visualize the differences in the habitat structure of avalanche tracks and control points, we carried out four Principal Component Analyses (PCAs) using the R package *factoextra* (Kassambara and Mundt 2017). One PCA was performed on the general dataset and the others on each habitat belt separately. For the mountain forest belt, we used the points surveyed along the horizontal transects and the lower points of the vertical transects. For the treeline ecotone belt, we used the points located in the

intermediate belt of the vertical transects, and for the alpine grassland belt, we used the highest points of the vertical transects (see Fig. 1 for the study design). Habitat variables were scaled to minimize the effects of measurements in different units before the analyses. Factor loadings and 99% confidence ellipses were calculated to assess variable contributions to each principal component and to visualize the variability of a mean point and allow visual comparison between the groups. Significant differences between the two groups (avalanche track and control) for each PCA were calculated with Permutational Multivariate Analyses of Variance (PERMANOVAs) with the function 'adonis' from the R package *pairwiseAdonis* (Martinez Arbizu 2019) by running 999 permutations. In order to check for assumptions and homogeneity of variances between the two groups (Anderson 2006), we used the function 'betadisper' from the *vegan* package (Oksanen et al. 2013). Moreover, we carried out an extra PERMANOVA between the points in the undisturbed treeline belt and the points in the lowest belt of avalanche tracks in order to assess if the habitat created by avalanche activity in the forest was comparable to the treeline habitat.

Bird assemblage

Detectability

Before the analysis, we modelled detectability with the R package *detect* (Sólymos et al. 2013a) for each contacted species in our point count surveys in order to assess how detectability varied according to the duration of the point count by adding the day of the year (JDAY), the time of the day (TSSR) and the percentage cover of high canopy (HC) as covariates. In this way, we accounted for likely sources of variation in detectability, i.e. change in behaviour as the breeding season progresses and over each sampling day, in particular due to variations in singing rates (Sólymos et al. 2018), and effects of habitat structure on detectability across the forest-avalanche gradient, high canopy cover being the most descriptive parameter for this gradient (see below). Thus, we fitted removal models with no covariates (habitat- and time-invariant

models) and with covariates (habitat- and time-varying models) and then carried out model selection based on Akaike's Information Criterion (AIC) to select the best model.

In these models, the rate parameter of the Poisson process (φ) was used to estimate the singing rates of birds during a point count with three time intervals for a total of 10 minutes (Alldredge et al. 2007). Each detected individual from point counts was included in these models. Subsequently, it was possible to calculate the detection probability (p) within a time interval (t) for each species (Sólymos et al. 2013b) as:

$$p = 1 - \exp(-t\,\varphi)$$

The detection probability (p) was then used to correct species abundances (n) and estimate adjusted counts (N) in the area of interest (Diefenbach et al. 2007):

$$N = n/p$$

We used adjusted counts (N) for each species in the subsequent analyses.

It was possible to calculate reliable detection probabilities (p) for 19 species due to sample sizes ($n > 40$ individuals). For the other less common species, we used detection probabilities of surrogate species based on expert opinion, following the approach of Davey et al. (2012) (Appendix S1 for the full list of species).

Mean detection probabilities ranged from 0.99 ± 0.10 SD for the Red Crossbill *Loxia curvirostra* to 0.36 ± 0.18 SD for the Mistle Thrush *Turdus viscivorus*. All species reached maximum detectability before 10-minutes, suggesting that this is an adequate time interval for this type of survey (see examples in Fig. S1).

Differences between bird assemblages

We carried out PERMANOVAs between the bird assemblages found in avalanche tracks and control points, first on the general dataset, then for the three elevation belts separately, and finally between the undisturbed treeline habitat and the avalanche track in the lowest belt, following the same methods that we used for the habitat and vegetation analyses. This allowed to test for significant differences between the avian assemblages. We also calculated Shannon–Weiner index to compute the diversity of

bird assemblages in avalanche and control points. Diversity index between the two groups was then compared using Hutcheson's t test using the R package *ecolTest* (Salinas & Ramirez-Delgado 2021).

Subsequently, we undertook Indicator Species Analyses using the R package *indicspecies* (De Caceres et al. 2015) with the function 'multipatt' to determine which species were mostly associated with the different habitat types. Indicator Species Analysis is particularly useful for investigating unknown habitats and ecosystems and their associated biodiversity (De Cáceres et al. 2010). We thus calculated Indicator Values (IndVal), adopting the group-based approach to understand which species were most closely associated with a given habitat (in our case, avalanche tracks or control points) based on corrected species abundances. IndVals are used to measure the degree of association between a species and a group of sites (from 0 to 1); values are calculated for each species and each site group and then the associations are checked for the highest association values. Finally, the statistical significance of these relationships was tested using a permutation test using 9999 permutations to calculate *P-values*. Subsequently, we used the function 'strassoc' (De Caceres and Legendre 2009) to describe the degree of association of each detected species with the habitat categories. We then assigned each species to one of the two habitat categories (i.e., avalanche tracks and control) based on the species IndVal (e.g., Chaffinch with IndVal Avalanche = 0.46, IndVal Control = 0.71 was assigned to the control category). In order to analyse the differences between the two habitats from a functional point-of-view, we tested how the proportions of ecological traits (habitat density, migration strategy and trophic niche, retrieved by AVONET database (Tobias et al. 2022) varied by carrying out a two-proportions Z-Test. All the analyses were carried out with R version 3.4.1 (R Development Core Team 2021).

Results

Habitat and vegetation

When considering all points together (Fig. 2a), there was a clear and significant difference in terms of habitat composition between avalanche tracks and control points (PERMANOVA, R^2 = 0.13, P = 0.001, see also Requena et al. 2022 for further analyses on the habitat). By looking at factor loadings for each variable (Tab. S1), it is evident that avalanche tracks were characterized by higher rock and shrub cover, with a greater number of small trees and higher grass cover. High and low canopy were more associated with control points, which accounted for more forested habitats. Separate PCAs demonstrated how the magnitude of habitat differences between avalanche tracks and control points varied along the elevation gradient (Figs. 2b-d). Differences were strongest in the forest belt (R^2 = 0.27, P = 0.001): forests were characterized by a high canopy cover, and areas which were impacted by avalanches had higher grass and rock cover with abundant small trees. In the treeline ecotone belt, differences between the two habitats were less extreme (R^2 = 0.07, P = 0.04), but the principal components still showed a clear difference between more forested habitat on control points and rocky open habitats on avalanche tracks. In the alpine grassland belt, differences between the two habitats were not significant (R^2 = 0.02, P = 0.57), also shown by the near complete overlap of the 99% ellipses (Fig. 2d). The last analysis between treeline points and those in avalanche tracks in the lowest elevation belt showed a fairly slight but significant difference (R^2 = 0.02, P = 0.04), indicating that avalanche track habitat does show some differences from the treeline habitat.

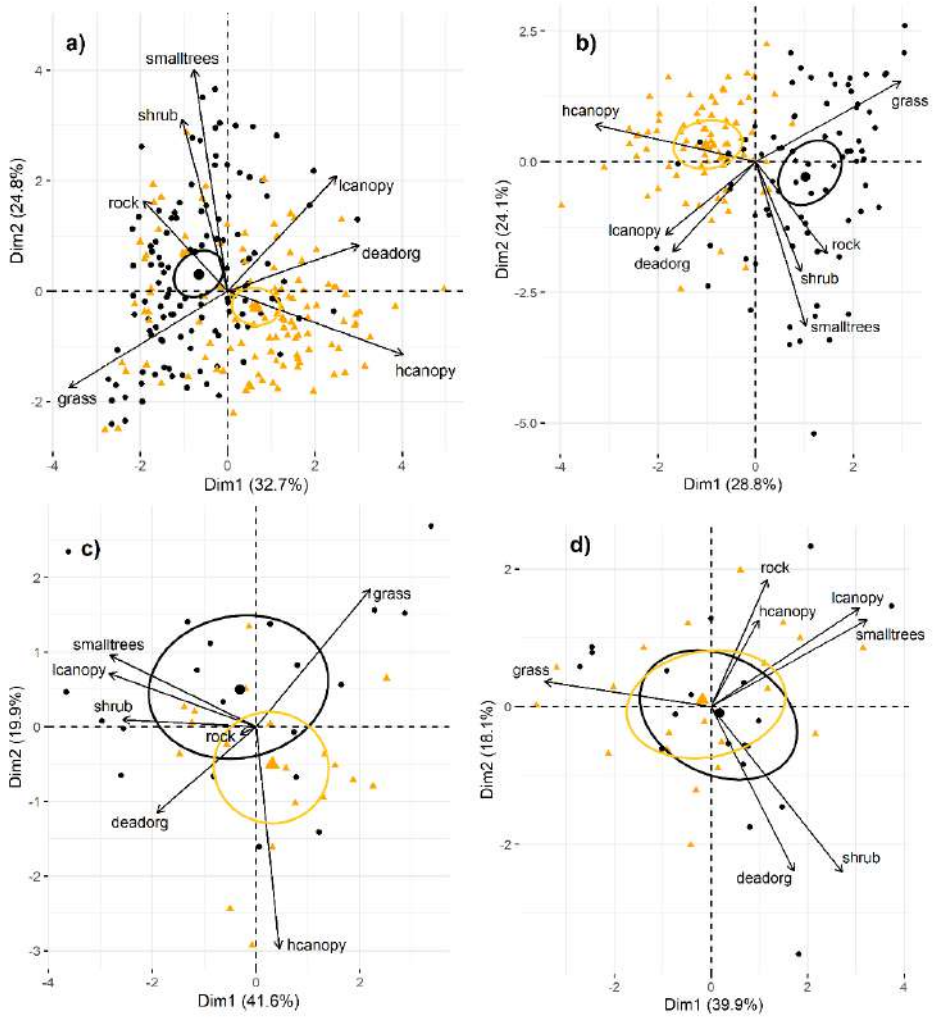

Figure 2. Principal Component Analyses (PCAs) for the habitat variables *(*hcanopy = High canopy %, lcanopy = Low canopy %, shrub = Shrubs %, rock = Rock %, grass = Grass %, deadorg = Dead organic material %, smalltrees = Number of small larches) of avalanche tracks and control points for the general dataset (a), n = 240) and at the three different habitat belts (b), montane forest belt 1400-2200m, n = 160; c) treeline ecotone 2000-2300m, n = 40; d) alpine grasslands 2100-2500m, n = 40). Points on avalanche tracks are shown with black circles and control points with yellow triangles. 99% confidence ellipses are represented for each group. Habitat variables and their contribution are represented with black arrows. Details and statistics are given in Table S1.

Bird assemblage

During the surveys, 68 bird species were detected. In the avalanche tracks, a total of 62 species was contacted, with 53 species in the lowest belt, 35 in the middle belt and 33 in the highest. In the control points, a total of 55 species was contacted, with 44 species in the lowest belt, 25 in the middle belt and 27 in the highest. The most commonly detected species in the surveys were Common Chaffinch *Fringilla coelebs* (*n* = 291), Rock Bunting *Emberiza cia* (*n* = 149), Tree Pipit *Anthus trivialis* (*n* = 138), Common Linnet *Linaria cannabina* (*n* = 100) and Eurasian Wren *Troglodytes troglodytes* (*n* = 93).

Bird assemblages differed significantly between avalanche tracks and control points overall (PERMANOVA, R^2 = 0.03, P = 0.001), with bird assemblages found in avalanche tracks being more diverse than control points (Hutcheson's t-test on Shannon–Weiner diversity index; t = 2.0888, P = 0.037). Based on species ecological trait analysis, avalanche tracks harboured more open habitat (X^2 = 22.26, p-value < 0.001) and migratory species (X^2 = 5.12, p-value = 0.024), whilst control points had a higher proportion of species typical of dense habitat (X^2 = 8.00, p-value = 0.005, see Figure 3). Avalanche tracks accounted for a more diverse bird assemblage based on the trophic niche, with species such as the Black Grouse *Lyrurus tetrix* being a terrestrial herbivore, the White-throated Dipper *Cinclus cinclus* as an aquatic predator and the Griffon Vulture *Gyps fulvus* as a scavenger (see Appendix S1 for details on species). When considering separate belts, highly significant differences were evident between the assemblages of the forest belt (PERMANOVA, R^2 = 0.07, P = 0.001), whilst differences between the assemblages of the treeline belt were less marked, but still significant (PERMANOVA, R^2 = 0.05, P = 0.01). No significant differences were found between the assemblages in the alpine belt (PERMANOVA, R^2 = 0.02, P = 0.74), suggesting that avalanche activity does not affect alpine grassland bird assemblage composition. The analysis between the bird assemblages of the undisturbed treeline and of the avalanche track in the lowest belt showed a highly significant difference (R^2

= 0.04, *P* = 0.001), showing that the bird assemblage found in avalanche track differed from that of the treeline.

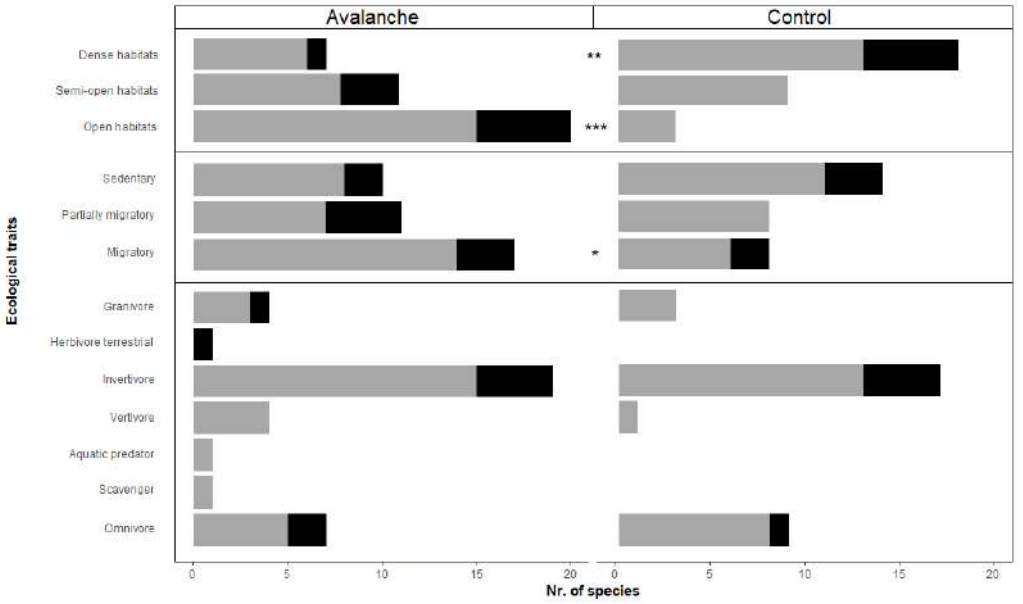

Figure 3. Differences in the number of species among ecological trait categories between avalanche tracks and control points. Indicator species are shown in black. The two-proportions Z-Test was used to test for differences in the proportion of species between the two habitats (*** = p-value < 0.001, * = p-value < 0.05, * not present = non-significant differences).

Indicator Species Analyses supported a difference in bird assemblages between avalanche tracks and control points (Tab. 1) and between the undisturbed treeline and of the avalanche track in the lowest belt (Tab. 2). In the analysis carried out on the whole dataset, 11 indicator species were identified, 6 for avalanche tracks and 5 for control points. For the montane forest belt, 11 indicator species were identified and were in general similar to those for the whole data set, with species typical from forest habitats for the control points and species from ecotone and more open habitats for the avalanche tracks. In the treeline ecotone belt, 2 indicator species were identified on avalanche tracks (Whinchat *Saxicola rubetra*, Black Redstart

Phoenicurus ochruros) and none on control points. There were no indicator species identified for either avalanche or control points in the alpine belt. Thus, this analysis supports the decrease in differences between the two bird assemblages along the elevational gradient, reflecting the differences between the habitats (Fig. 2). Identified indicator species for avalanche tracks were Rock Bunting, Whinchat, Grey Wagtail *Motacilla cinerea*, Common Linnet, Black Redstart, Yellowhammer *Emberiza citrinella*, Garden Warbler *Sylvia borin* and Black Grouse *Lyrurus tetrix*. Indicator Species Analysis between the undisturbed treeline and of the avalanche track in the lowest belt identified 5 indicator species, 2 for the avalanche tracks (Eurasian Blackcap *Sylvia atricapilla* and Coal Tit *Periparus* ater) and and 3 for the undisturbed treeline ecotone (Red Crossbill *Loxia curvirostra*, Mistle Thrush *Turdus viscivorus*, Ring Ouzel *Turdus torquatus*) supporting the results from PERMANOVA and thus the hypothesis that avalanches harbour slightly different bird assemblages from those found at the treeline level.

Table 1 Outputs from Indicator Species Analyses for the general analysis and for the elevational belts for both avalanche tracks and control points. No indicator species were detected for the alpine grassland belt. Indicator species, Indicator Values, *p-values* and sample sizes are reported.

Species	**IndVal**	**P-value**	**Species**	**IndVal**	**P-value**
Avalanche tracks			**Control Points**		
General dataset, n = 240					
WC	0.46	< 0.001	WT	0.49	< 0.001
BX	0.41	0.002	GS	0.40	0.005
Y	0.38	0.004	TC	0.39	0.002
GRW	0.38	< 0.001	ST	0.32	0.019
GW	0.27	0.035	FC	0.24	0.035
BG	0.24	0.013			
Montane forest belt, n = 160					
RN	0.71	< 0.001	WT	0.56	< 0.001
TP	0.59	< 0.001	GS	0.47	0.002
GRW	0.44	< 0.001	TC	0.45	0.001

LI	0.40	< 0.001	ST	0.39	0.016
WC	0.40	< 0.001	FC	0.30	0.034
Y	0.39	0.001			
BX	0.34	0.005			
GW	0.33	0.029			
Treeline ecotone belt, n = 40					
WC	0.72	0.001			
BX	0.56	0.039			

WC = Whinchat (Saxicola rubetra), GRW = Grey Wagtail (Motacilla cinerea), BX = Black Redstart (Phoenicurus ochruros), Y = Yellowhammer (Emberiza citronella), GW = Garden Warbler (Sylvia borin), BG = Black Grouse (Lyrurus tetrix), WT = Willow Tit (Poecile montanus), GS = great-spotted woodpecker (Dendrocopos major), TC = Eurasian Treecreeper (Certhia familiaris), ST = Song Thrush (Turdus philomelos), FC = Common Firecrest (Regulus ignicapilla), RN = Rock Bunting (Emberiza cia), TP = Tree Pipit (Anthus trivialis), LI = Common Linnet (Linaria cannabina).

Table 2 Outputs from Indicator Species Analyses between the forest belt on avalanche tracks and treeline ecotone on control points. Indicator species, Indicator Values, *p-values* and sample sizes are reported.

Species	**IndVal**	**P-value**	**Species**	**IndVal**	**P-value**
Avalanche forest belt			**Control treeline ecotone**		
BC	0.57	0.013	CR	0.59	< 0.001
CT	0.50	0.030	M	0.58	0.024
			RZ	0.47	0.004

BC = Eurasian Blackcap (*Sylvia atricapilla*), CT = Coal Tit (*Periparus ater*), CR = Red Crossbill (*Loxia curvirostra*), M = Mistle Thrush (*Turdus viscivorus*), RZ = Ring Ouzel (*Turdus torquatus*).

Discussion

In our study, we highlighted how avalanche tracks create a characteristic habitat, with features that differ from the surrounding undisturbed habitat, in terms of vegetation structure and composition of the bird assemblages. Avalanches create open habitat at lower elevations, thus habitat differences between avalanche and control points were

more enhanced in the montane forest belt and became more similar at higher elevations. These changes were reflected in the bird community, whereby avalanche tracks had some species that were characteristic of more open, higher elevation habitat, but also species from a range of elevations, contributing thus to increase bird gamma diversity in the montane forest belt. Importantly, however, both the habitat and the bird assemblage of avalanche tracks differed from that of the treeline ecotone, showing that avalanches create unique bird habitats in mountain environments, rather than simply creating treeline habitats at lower elevations. Changes in the frequency and severity of avalanches due to climate change will therefore have consequences for gamma (i.e., landscape-level) biodiversity in the forest and treeline belts.

Avalanche-impacted areas were characterized by a habitat mosaic, with higher rock cover, more shrubs and more small trees as consequence of avalanche activity, whilst undisturbed areas in the surroundings were mainly represented by high-canopy forests (in the lower belt) or more, larger trees (at the treeline). Avalanche and control points above the treeline were indistinguishable. These differences in habitat were also reflected in the associated bird assemblages. The greatest differences were in the forest belt, where the two assemblages were quite distinct. Indeed, the highest number of indicator species for both habitat categories was found in this belt, with 5 indicator species for control points and 7 for avalanche tracks. The former was composed of typical high canopy forest species (e.g., Great Spotted Woodpecker *Dendrocopos major*, Song Thrush *Turdus philomelos*, Treecreeper *Certhia familiaris*), while the latter included both treeline species (Black Grouse, Tree Pipit, Linnet, Rock Bunting) and species more associated with open habitats both at lower (Whinchat, Yellowhammer) and higher (Black Redstart) elevations.

The key point is that the habitat created by avalanches was clearly different from that of the treeline. In our study area, the treeline ecotone shows consistent characteristics, both in terms of habitat structure and bird species, with a highly heterogeneous habitat of small trees and shrubs. In comparison, avalanche habitat can

be highly variable depending on a suite of variables that are influenced by avalanche frequency (Vacchiano et al. 2015). Tracks that are characterized by higher vegetation encroachment, due to a longer span between avalanche events, are suitable breeding habitat for shrub nesting species which are not found at higher elevations, such as the Eurasian Blackcap and the Garden Warbler which tends to select Green Alder *Alnus alnobetula*, a shrub species that thrives in avalanche tracks (Bischof 1984). Areas impacted by an intermediate frequency of avalanches might indeed have similar features to the treeline ecotone, but tracks which are regularly disturbed tend to have a more open-habitat structure with fewer shrub patches and a higher grass cover (Rixen et al. 2007). These areas can also be exploited by local mountain communities as pasture or cultivated areas (Stocker 2009) and may be colonized by species related to mountain agro-ecosystems such as the Whinchat and the Yellowhammer (Bazzi et al. 2015; Assandri et al. 2019a). This is important, because managed avalanche tracks could thus operate as refuges for such species, since the ongoing changes in traditional farming have negatively impacted semi-natural grassland where these species were typically found (Archaux 2007; Assandri et al., 2019b). At the same time, vegetation encroachment, which is caused both by the abandonment of traditional activity (Gellrich et al. 2007) and climate change (Dullinger et al. 2003), is an additional threat to these habitats and their species (Chamberlain et al. 2013). During our surveys, we also contacted two bird species which are linked to alpine streams, the Grey Wagtail (n = 22 individuals) and the White-Throated Dipper (n = 2) that find suitable habitat in streams of avalanche gullies.

Climate change threatens mountain habitats and mountain birds at the European scale (Scridel et al. 2018; Alba et al. 2022) and it is predicted to affect snow precipitation and snow cover in the near future (Schöner et al. 2018; Gobiet and Kotlarski 2020). Climate change will affect avalanche activity (Strapazzon et al. 2021), but the projections of future avalanche frequency and severity still unclear due to uncertainties regarding the response of snow cover to climate change (Eckert et al.

2010). Nevertheless, due to the buffering effect of subalpine forest on avalanche severity (Bebi et al. 2017), any environmental change that brings about an increase in forest cover at higher elevation, such as grazing abandonment or shifts in vegetation zones due to climate change (Gehrig-Fasel et al. 2007), is likely to reduce the impacts of avalanches at lower elevations. In a scenario of decreasing disturbance, avalanche tracks will undergo a process of vegetation encroachment, with negative consequences for some species linked to these areas. Furthermore, it is predicted that the decrease will be amplified at lower elevations (Castebrunet et al. 2014) where we showed the most characteristic species are found. Shrub nesting bird species might be favoured at the beginning of the process, at the expense of semi-open habitat species that will need to shift upwards to seek suitable habitats. This might be an additional threat not considered before; these species are already in danger from climatic and land-use changes such as the upshifting treeline and the abandonment of agropastoral activities (Chamberlain et al. 2013; Bani et al. 2019).

In conclusion, we suggest that more research is needed to analyse in detail how the frequency of avalanche activity shapes bird assemblages in mountain regions and what will be the consequences for mountain biodiversity in a climate change scenario where avalanche activity will change. Other taxa (e.g., lepidoptera) might use avalanche impacted areas as suitable areas during their life cycle. Therefore, a similar study design to what we described in this work could be adapted to study the ecological interactions between other mountain animal communities and avalanche tracks in order to fully assess the contribution of avalanches to gamma diversity in alpine regions.

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References

Alba R, Kasoar T, Chamberlain D, Buchanan G, Thompson D, Pearce-Higgins JW (2022) Drivers of change in mountain and upland bird populations in Europe. Ibis https://doi.org/10.1111/ibi.13043

Alldredge MW, Pollock KH, Simons TR, Collazo JA, Shriner SA (2007) Time-of-Detection Method for Estimating Abundance From Point-Count Surveys. Auk 124, 653

Anderson MJ (2006) Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62, 245–253

Archaux F (2007) Are mountains refuges for farmland bird species? A case study in the northern French Alps. Bird Study 54, 73–79.

Arpa Piemonte (2020) Sistema Informativo Valanghe – SIVa. Available at http://webgis.arpa.piemonte.it/. Accessed on 09.03.2020

Assandri G, Bogliani, G, Pedrini P, Brambilla M (2019a) Species-specific responses to habitat and livestock management call for carefully targeted conservation strategies for declining meadow birds. J Nat Conserv 52, 125757

Assandri G, Bogliani G, Pedrini P, Brambilla M (2019b) Toward the next Common Agricultural Policy reform: Determinants of avian communities in hay meadows reveal current policy's inadequacy for biodiversity conservation in grassland ecosystems. J Appl Ecol 56, 604–617

Ballesteros-Cánovas JA, Trappmann D, Madrigal-González J, Eckert N, Stoffel M (2018) Climate warming enhances snow avalanche risk in the Western Himalayas. Proc Natl Acad Sci U S A 115, 3410–3415

Bani L, Luppi M, Rocchia E, Dondina O, Orioli V (2019) Winners and losers: How the elevational range of breeding birds on Alps has varied over the past four decades due to climate and habitat changes. Ecol Evol 9, 1289–1305

Bazzi G, Foglini C, Brambilla M, Saino N, Rubolini D (2015) Habitat management effects on Prealpine grassland bird communities. Ital J Zool 82, 251–261

Bebi P, Kienast F, Schönenberger W (2001) Assessing structures in mountain forests as a basis for investigating the forests' dynamics and protective function. For Ecol Manage 145, 3–14

Bebi P, Kulakowski D, Rixen C (2009) Snow avalanche disturbances in forest ecosystems-State of research and implications for management. For Ecol Manage 257, 1883–1892

Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, Conedera M, Ginzler C, Wohlgemuth T, Kulakowski D (2017) Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For Ecol Manage 388, 43–56

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15, 365–377

Bibby CJ, Burgess ND, Hillis DM, Hill DA, Mustoe S (2000) Bird census techniques. Elsevier

Bischof N (1984) Pflanzensoziologische Untersuchungen von Sukzessionen aus gemähten Magerrasen in der subalpinen Stufe der Zentralalpen vol 60 Beiträge zur geobotanischen Landesaufnahme der Schweiz Flück-Wirth, Switzerland

Bormann KJ, Brown RD, Derksen C, Painter TH (2018) Estimating snow-cover trends from space. Nat Clim Change 8(11), 924-928.

Brang P, Schönenberger W, Frehner M, Schwitter R, Thormann JJ, Wasser B (2006) Management of protection forests in the European Alps: An overview. For Snow Landsc Res 80, 23–44

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574

De Cáceres M, Legendre P, Moretti M (2010) Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684

De Cáceres M, Jansen F (2015) Package 'indicspecies' (Version 176) http://cranr-projectorg/web/packages/indicspecies/indicspeciespdf

Castebrunet H, Eckert N, Giraud G, Durand Y, Morin S (2014) Projected changes of snow conditions and avalanche activity in a warming climate: The French Alps over the 2020-2050 and 2070-2100 periods. Cryosphere 8, 1673–1697

Chamberlain D, Negro M, Caprio E, Rolando A (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol Conserv 167, 127–135

Davey CM, Chamberlain D, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: Evidence for climate driven homogenization in avian communities. Glob Ecol Biogeogr 21, 568–578

Diefenbach DR, Marshall MR, Mattice JA, Brauning DW (2007) Incorporating Availability for Detection in Estimates of Bird Abundance. Auk 124, 96–106

Eckert N, Parent E, Kies R, Baya H, Eckert N, Parent E, Morse E (2010) A spatio-temporal modelling framework for assessing the fluctuations of avalanche occurrence resulting from climate change: application to 60 years of data in the northern French Alps. Clim Change 101, 515–553

Gądek B, Kaczka RJ, Rączkowska Z, Rojan E, Casteller A, Bebi P (2017) Snow avalanche activity in Żleb Żandarmerii in a time of climate change (Tatra Mts, Poland). Catena 158, 201–212

Garcia-Gonzalez R, Cuartas P (1996) Trophic utilization of a montane/subalpine forest by chamois (Rupicapra pyrenaica) in the Central Pyrenees. For Ecol Manage 88, 15–23

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment?. J Veg Sci 18, 571–582

Gellrich M, Bauer P, Zimmermann NE, Koch B (2007) Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. Agricult Ecosyst Environ 118: 93-108

Getzner M, Gutheil-Knopp-Kirchwald G, Kreimer E, Kirchmeir H, Huber M (2017) Gravitational natural hazards: valuing the protective function of Alpine forests. Forest Policy Econ, 80, pp 150-159

Gobiet A, Kotlarski S (2020) Future Climate Change in the European Alps. Oxford Res Encycl Clim Sci

Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21st century climate change in the European Alps—a review. Sci Tot Environ 493:1138–1151

Höller P (2007) Avalanche hazards and mitigation in Austria: a review. Nat Haz, 43(1), 81-101

Ingty T (2021) Pastoralism in the highest peaks: Role of the traditional grazing systems in maintaining biodiversity and ecosystem function in the alpine Himalaya. PLoS One 16, e0245221

IPCC (2022) Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. In Press.

Jähnig S, Alba R, Vallino C, Rosselli D, Pittarello M, Rolando A, Chamberlain D (2018) The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. J Ornithol 159, 747–759

Johansson MU, Frisk CA, Nemomissa S, Hylander K (2018) Disturbance from traditional fire management in subalpine heathlands increases Afro-alpine plant resilience to climate change. Glob Chang Biol 24, 2952–2964

Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of Shrub Invasion into High Mountain Grasslands of the Northern Calcareous Alps, Austria. Arctic, Antarct Alp Res 35, 434–441

Kassambara A, Mundt F (2017) Factoextra: extract and visualize the results of multivariate data analyses R package version, 1(5), 337-354

Krajick K (1998) Animals thrive in an avalanche's wake. Science 80 279, 1853

Kulakowski D, Rixen C, Bebi P (2006) Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. For Ecol Manage 223, 66–74

Kulakowski D, Seidl R, Holeksa J, Kuuluvainen T, Nagel TA, Panayotov M, Svoboda M, Thorn S, Vacchiano G, Whitlock C, Wohlgemuth T, Bebi P (2017) A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. For Ecol Manage 388, 120–131

Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. J Appl Ecol 41, 294–304

Laternser M, Schneebeli M (2003) Long-term snow climate trends of the Swiss Alps (1931-99). Int J Climatol 23, 733–750

Laute K, Beylich AA (2018) Potential effects of climate change on future snow avalanche activity in western Norway deduced from meteorological data. Geogr Ann Ser A, Phys Geogr 100, 163–184

Lieser M, (1995) Lebensraumansprüche des Haselhuhns im Schwarzwald. Naturschutzreport 10, 239–255

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 4627276 462, 1052–1055

Martinez Arbiz P (2017) PairwiseAdonis: Pairwise Multilevel Comparison Using Adonis Available online at: https://githubcom/pmartinezarbizu/pairwiseAdonis

McClung D, Schaerer P (1993) The Avalanche Handbook. The Mountaineers, Seattle

Mietkiewicz N, Kulakowski D, Rogan J, Bebi P (2017) Long-term change in sub-alpine forest cover, tree line and species composition in the Swiss Alps. J Veg Sci 28, 951–964

Nogués-Bravo D, Araújo MB, Errea MP, Martínez-Rica JP (2007) Exposure of global mountain systems to climate warming during the 21st Century. Glob Environ Chang 17, 420–428

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara R, Simpson GL, Solymos P, Henry M et al. (2013) Package 'Vegan' Community Ecology Package, Version 2 Available at: http://CRANR-projectorg/package=vegan

Pacifici M, Visconti P, Rondinini C (2018) A framework for the identification of hotspots of climate change risk for mammals. Glob Chang Biol 24, 1626–1636

Pini R, Ravazzi C, Raiteri L, Guerreschi A, Castellano L, Comolli R (2017) From pristine forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation and landscapes in the western Italian Alps. J Ecol 105, 1580–1597

Princé K, Jiguet F (2013) Ecological effectiveness of French grassland agri-environment schemes for farmland bird communities. J Env Management, 121, 110-116

QGIS Development Team (2020) QGIS Geographic information system QGIS 31415 'Pi' Open-source geospatial foundation project.

R Core Team (2021) R: A language and environment for statistical computing R Foundation for Statistical Computing. Available at: https://wwwR-projectorg/

Requena E, Alba R, Rosselli D, Chamberlain D (2022) Avalanche tracks are key habitats for the Rock Bunting Emberiza cia in the Alps. Ardeola, 69(2), 203-217

Rixen C, Brugger S (2004) Naturgefahren - ein Motor der Biodiversität In: Eidg Forschungsanstalt WSL (Ed), Schutzwald und Naturgefahren, Forum für Wissen 2004, pp 67–71

Rixen C, Haag S, Kulakowski D, Bebi P (2007) Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. J Veg Sci 18, 735–742

Salinas H, Ramirez-Delgado D (2021) ecolTest: Community Ecology Tests.

Schöner W, Koch R, Matulla C, Marty C, Tilg A M (2019) Spatiotemporal patterns of snow depth within the Swiss-Austrian Alps for the past half century (1961 to 2012) and linkages to climate change. Int J Clim, 39(3), 1589-1603

Scridel D, Brambilla M, Martin K, Lehikoinen A, Iemma A, Matteo A, Jähnig S, Caprio E, Bogliani G, Pedrini P, Rolando A, Arlettaz R, Chamberlain D (2018) A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. Ibis 160, 489–515

Solymos P, Moreno M, Lele SR (2013a) Detect: analyzing wildlife data with detection error R package version 03. Available at: http://CRANR-projectorg/package=detect

Sólymos P, Matsuoka SM, Bayne EM, Lele SR, Fontaine P, Cumming SG, Stralberg D, Schmiegelow FKA, Song SJ (2013b) Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. Methods Ecol Evol 4, 1047–1058

Sólymos P, Matsuoka SM, Cumming SG, Stralberg D, Fontaine P, Schmiegelow FKA, Song SJ, Bayne EM (2018) Evaluating time-removal models for estimating availability of boreal birds during point count surveys: Sample size requirements and model complexity. Condor 120, 765–786

Stocker E (2009) Geomorphic responses to landuse changes on steep slopes in timberline environment; Central Alps, Austria. Rom Journ Geogr 53, 91–106

Strapazzon G, Schweizer J, Chiambretti I, Brodmann Maeder M, Brugger H, Zafren K (2021) Effects of Climate Change on Avalanche Accidents and Survival. Front Physiol 12, 450

Teich M, Marty C, Gollut C, Grêt-Regamey A, Bebi P (2012) Snow and weather conditions associated with avalanche releases in forests: Rare situations with decreasing trends during the last 41years. Cold Reg Sci Technol 83–84, 77–88

Thuiller W, Lavorel S, Araú Jo MB, Sykes MT, Prentice IC, Mooney HA (2005) Climate change threats to plant diversity in Europe. Natl Acad Sci 102

Tobias JA, Sheard C, Pigot AL, et al (2022) AVONET: morphological, ecological and geographical data for all birds. Ecol Lett 25:581–597. https://doi.org/10.1111/ELE.13898Vacchiano G, Maggioni M, Perseghin G, Motta R (2015) Effect of avalanche frequency on forest ecosystem services in a spruce–fir mountain forest. Cold Reg Sci Technol 115, 9–21

Viglietti D, Letey S, Motta R, Maggioni M, Freppaz M (2010) Snow avalanche release in forest ecosystems: A case study in the Aosta Valley Region (NW-Italy). Cold Reg Sci Technol 64, 167–173

Zimmerer KS, Córdova-Aguilar H, Mata Olmo R, Jiménez Olivencia Y, Vanek SJ (2017) Mountain Ecology, Remoteness, and the Rise of Agrobiodiversity: Tracing the Geographic Spaces of Human-Environment Knowledge. Ann Am Assoc Geogr 107, 441–455

Supplementary Material

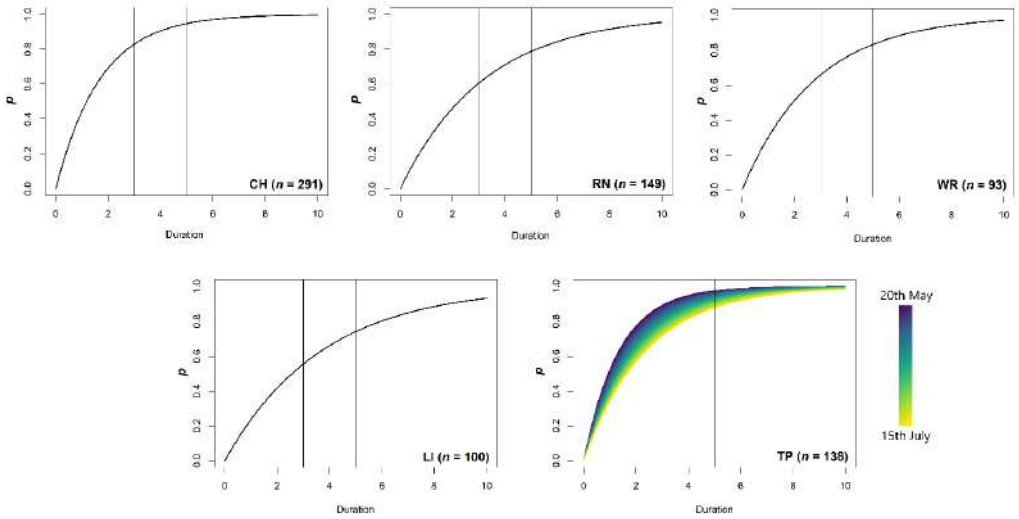

Figure S1 Detection probabilities (*p*) from time-invariant removal models for five selected species: CH (Common Chaffinch *Fringilla coelebs*, mean *p* = 0.83, SD = 0.24), RN (Rock Bunting *Emberiza cia*, mean *p* = 0.69, SD = 0.26) and WR (Eurasian Wren *Troglodytes troglodytes*, mean *p* = 0.73, SD = 0.26), LI (Eurasian Linnet *Linaria* cannabina, mean *p* = 0.65, SD = 0.26) and from time-varying removal models for TP (Tree Pipit *Anthus trivialis*, mean *p* = 0.76, SD = 0.26). Colour scale shows variation in availability probabilities according to the day of the year. Vertical black lines show time intervals during point counts.

Table S1 Factor loadings of the first 3 principal components based on 7 habitat variables for the general dataset (*n* = 240), montane forest (*n* = 160), treeline ecotone (*n* = 40) and alpine grassland (*n* = 40) belts

		High canopy %	Low canopy %	Shrubs %	Rock %	Grass %	Dead organic material %	Small larches	Cumulative Variance
General dataset	PC1	0.57	0.35	-0.15	-0.27	-0.51	0.43	-0.11	0.33
	PC2	-0.19	0.34	0.51	0.27	-0.28	0.14	0.65	0.57
	PC3	0.07	0.10	0.43	-0.75	0.01	-0.49	0.04	0.72

Montane forest belt	PC1	0.60	0.33	-0.17	-0.27	-0.54	0.31	-0.19	0.29
	PC2	-0.14	0.28	0.42	0.35	-0.31	0.34	0.63	0.53
	PC3	0.15	-0.11	0.67	-0.46	-0.20	-0.51	0.07	0.68
Treeline ecotone belt	PC1	0.08	-0.51	-0.46	-0.05	0.39	-0.34	-0.50	0.42
	PC2	-0.77	0.18	0.02	-0.03	0.48	-0.30	0.25	0.62
	PC3	0.25	0.17	0.17	-0.86	0.03	-0.36	0.07	0.79
Alpine grassland belt	PC1	0.15	0.46	0.41	0.18	-0.52	0.26	0.48	0.40
	PC2	-0.28	-0.32	0.53	-0.41	-0.08	0.53	-0.28	0.58
	PC3	0.25	-0.40	-0.15	0.68	-0.25	0.38	-0.29	0.75

Chapter IV

Mountain bird assemblages are shaped by differential vegetation dynamics in avalanches and ski pistes

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Abstract

Mountain landscapes are the result of long-lasting interactions between natural processes and human activities but, due to climate and land use change, open habitats are shrinking. Snow avalanches are a natural source of disturbance that maintain habitats open, and ski pistes can be considered their artificial counterpart. Although these are ubiquitous features in many temperate mountains, the biological communities that they harbour and how these differ from relatively undisturbed habitats is largely unknown. In this study, we carried out habitat surveys and point counts along elevation transects on avalanche tracks, ski pistes and control areas. Results showed that avalanche tracks supported high levels of bird diversity and abundance whilst ski pistes had lower values of biodiversity, especially at higher elevations. However, few grassland specialists managed to colonize treeline ecotone in ski pistes, where woody vegetation is artificially removed. Avalanche tracks were characterized by higher vegetation diversity, whereas ski pistes had high grass cover and poor vegetation structure. Shrub-related species were thus negatively affected by the land use changes caused by the creation of ski pistes, but they found suitable habitats in the avalanche tracks at lower elevations. In a context of climate change, where a reduction in avalanche activity and treeline upshifts are predicted, open habitats and associated biodiversity are threatened. The conservation potential of ski pistes could be improved as long as sustainable management practices are implemented, including the introduction of habitat elements from avalanche tracks. This would contribute to the conservation and maintenance of alpine biodiversity.

Keywords: Alpine birds, climate change, disturbance, farmland birds, mountain conservation, treeline ecotone

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). The interactions between human activities, such as agro-pastoral activities, and natural processes have shaped the landscapes and animal communities in the European Alps over the last millennia (Pini et al., 2017; Von Scheffer et al., 2019). However, after World War II, human-made open habitats started shrinking due to vegetation encroachment, caused mainly by abandonment of traditional pastures (Laiolo et al., 2004; Lasanta et al., 2017). Climate change, acting synergically with land-use changes, favours the colonization of trees and shrubs towards higher elevations, leading to further 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 (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). Despite their impact on vegetation, they are not considered high intensity perturbations because not all tracks are affected to the same degree (Bebi et al., 2009). 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 is likely to be important. Studies on mammals, such as Brown Bears *Ursus arctos horribilis* (Mace et al., 1996), Caribous *Rangifer tarandus*, Wolverines *Gulo gulo* (Krajick, 1998) and Chamois *Rupicapra pyrenaica* (Garcia-Gonzalez and 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 nowadays 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), both due to habitat loss and fragmentation caused by an increase in urban and ski piste extent, and to direct disturbance caused by humans (Arlettaz et al., 2007; Larson et al., 2019). In Europe, the area affected by winter tourism is still expanding (Mountain Agenda, 1999; Wipf et al., 2005), and is moving into currently undisturbed areas at higher elevations due to 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 and Rolando, 2013). Machine-grading, artificial snow and the use of chemical products have pronounced effects on soil structure (Bayfield, 1996; Burt and Rice, 2009) and associated microbial communities (Gros et al., 2004). Ski pistes 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 the latter, 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 and Moss, 2004; Buffet and Dumont-Dayot, 2013), and species richness and diversity (Laiolo and Rolando, 2005; Rolando et al., 2007; Caprio et al., 2011). However, there is some potential for ski pistes to be managed in a more environmental-friendly way to minimise impacts (Caprio et al., 2023). Where such management practices are applied, restored ski pistes and natural control grasslands become structurally very similar, and species richness and abundance is 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 have an impact on skiing activity, making some (usually lower elevation) areas no longer viable (Rixen et al., 2011). Effects of climate change on avalanches are not clear (Eckert et al., 2010) and their frequency could either decrease due to lower precipitation (Gądek et al., 2017; Bormann et al., 2018) or increase due to later spring snowfalls and instability of snowpacks caused by higher temperatures (Ballesteros-Cánovas et al., 2018). In a scenario of climate change with an expansion of the forest area towards higher elevations and a decrease of avalanches due 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 the impacts directly attributable to climate change (Chamberlain et al., 2013). It is therefore important to develop strategies to minimise impacts of ski pistes on alpine biodiversity.

With undergoing 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 to what extent these can compensate for the loss of open natural habitats is largely unknown. Considering past investigations concerning ski pistes (Laiolo and Rolando, 2005; Rolando et al., 2007;

Caprio et al., 2011), we believe is important to compare these two vertical open habitats and to argue how mountain biodiversity will respond to future land- and climate changes. Farmland and open-habitat bird species are declining and are highly threatened in all mountain ecosystems (Donald et al., 2001; Brambilla et al., 2021). At higher elevations, where sensitive habitats are found, the impact of ski pistes has been shown to be negative a few years after their construction (Wipf et al., 2005; Roux-Fouillet et al., 2011), but the status of habitats and bird assemblages should be assessed after a longer period has passed. Furthermore, due to increasing human pressure, there is a necessity to integrate anthropic elements and nature for future coexistence. In order to promote the sustainable coexistence of natural and human activities in the mountains, it is fundamental to pinpoint which features of avalanches are key for biodiversity, and whether we can use such features in a management context to improve ski pistes as a strategy to aid the conservation of open habitat species that are threatened by land use and climate change.

Combining data on habitats and bird assemblages collected on avalanche tracks, ski pistes and control plots during the breeding season in the Italian Alps, the aims of this work are: (1) to compare habitat differences between the three different plot types; (2) to assess how bird abundance and diversity vary among plot types; and more specifically (3) to assess the effects on individual grassland and ecotone bird species.

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 m and 2769 m. At lower elevations, broadleaved forests are common (typically beech *Fagus sylvatica*, ash *Fraxinus excelsior*, Norway maple *Acer platanoides*). At higher elevations larch *Larix decidua* is the dominant forest tree. 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. 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 single pistes.

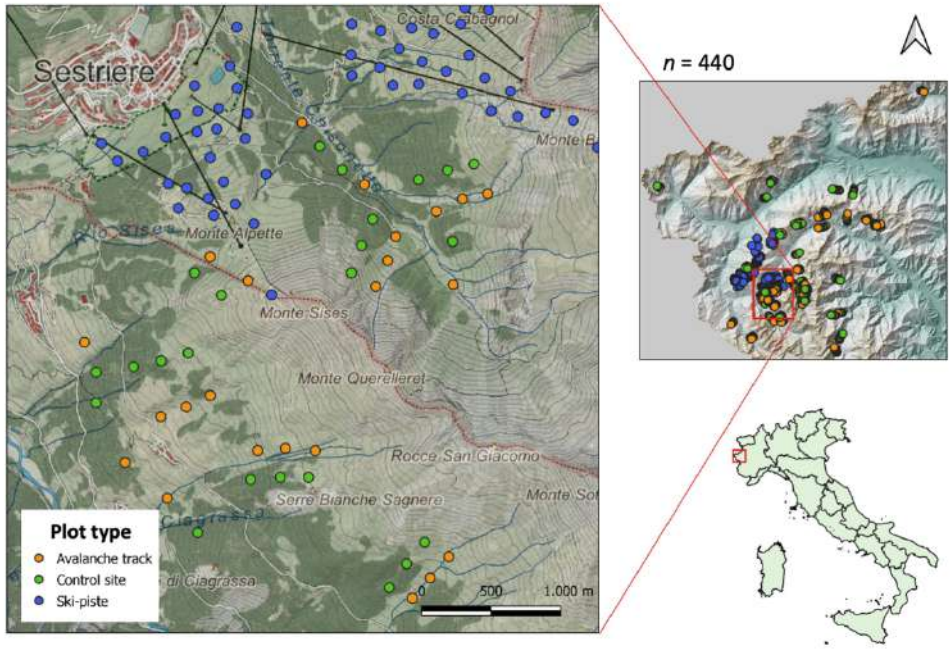

Figure 1. Map of the study area located in north-western Italy, showing the 440 points investigated in this study. Orange points show avalanche tracks, green points control sites and light blue points ski pistes.

Using a 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 3 different locations (hereafter "plot types"): 180 on ski pistes, 130 on avalanche tracks and 130 on control 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 control areas outside the track. Points were also defined according to three elevational belts along the elevation gradient: mountain forest, *n* = 240; treeline ecotone, *n* = 100; alpine grassland, *n* = 100 . Points were placed at least 200 m apart in order to avoid overlap and were visited in 2021 and 2022 during the breeding period (i.e. from 15-May to 15-July). See Alba et al., (2023) for further details on study design, elevational belt classification and field methods.

Habitat and vegetation

From the centre of each point, we recorded elevation and estimated by eye the percent cover of habitat variables within a 100 m radius measured with a laser range finder (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). Presence/absence of water, gulleys, roads, tracks, paths, settlements, dung (old/fresh) and stanchions (only ski pistes) were also recorded.

Bird assemblages

Point counts were carried out using a 10 min count period (Bibby et al., 2000), divided into 3 time-intervals of 3-2-5 min each to model detectability (Alldredge et al., 2007). All birds seen or heard within a 100 m radius, and for each individual the time interval in which it was detected, were noted. Surveys were carried out in suitable weather conditions (i.e. good visibility, no rain or strong winds) from 1–1.5 h after sunrise until 11.00 A.M., when bird activity is highest.

Statistical analyses

Habitat and vegetation

We used the R package *factoextra* (Kassambara and Mundt, 2017) to carry out Principal Component Analyses (PCAs), first on the general dataset and then one for each elevational belt to visually identify variables mostly associated with each plot type at different elevations. 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

We used the same approach described in Alba et al. (2023) to model detectability for each contacted bird species using the *detect* package (Sólymos et al., 2013) in R software and to correct species abundances. Models were integrated with covariates that could have a potential effect on bird detectability during the breeding season (Sólymos et al., 2018) such as the day of year ("JDAY") and the time of day ("TSSR"). 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 probabilitiesy 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 couldn't 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 control 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 (3-levels) and elevational belt (3-levels) and their interaction as predictors by fitting a GLM with a Poisson distribution and an LM respectively. We then modelled abundance

and diversity using a subset of the previous dataset only containing grassland/ecotone (hereinafter GE) species as we were particularly interested in the response of the open-habitat bird assemblages to avalanche and ski piste impacts. 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 the last analysis, we modelled species-specific responses of 9 GE bird species, since individual species might respond differently to disturbance pressure based on their degree of association degree with specific open habitats. These species were whinchat *Saxicola rubetra*, yellowhammer *Emberiza citrinella*, rock bunting *Emberiza cia*, tree pipit *Anthus trivialis*, linnet *Linaria cannabina*, dunnock *Prunella modularis*, skylark *Alauda arvensis*, wheatear *Oenanthe oenanthe* and water pipit *Anthus spinoletta*. We decided to use these species as they had large sample sizes ($n > 60$) and were relevant for this analysis as they represent well the ecotone/grassland bird community. As above, we fitted Poisson GLMs using abundance as response variable with plot types, elevational belts and their interaction as predictors. All analyses were carried out in R software version 4.3.1 (R Core Team 2023).

Results

Habitat and vegetation

PCAs carried out on the general dataset showed a clear distinction between ski piste points, avalanche tracks and control points (Tab S1, Fig 2A). However, in the PCAs produced for each elevational belt, the similarity between avalanches and controls increased along the elevation gradient, whilst ski pistes remained clearly separated (Fig 2B-D). Results from Kruskall-Wallis tests highlighted statistically significant differences for the majority of habitat variables (Tab 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. Control points were mainly characterized by a higher canopy cover. These differences became less clear along the elevational gradient, especially between avalanche tracks and control points.

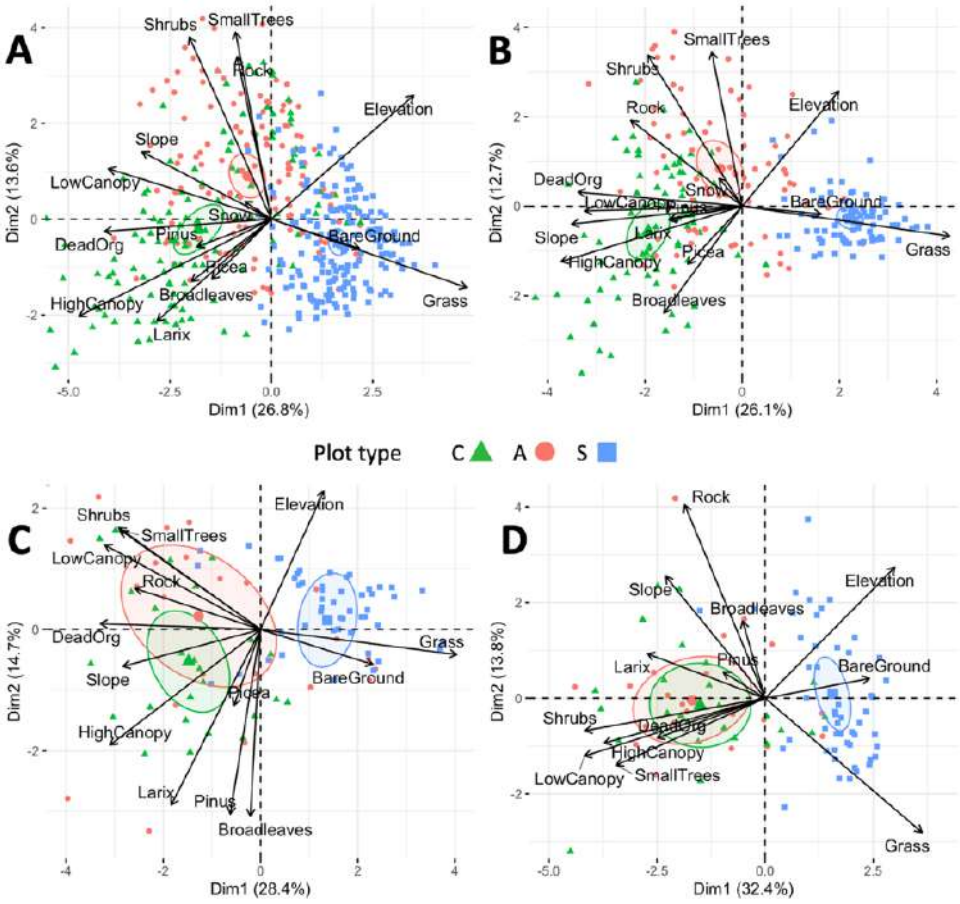

Figure 2. Biplots of the PCAs performed on the general dataset (A), and on the montane forest (B), ecotone treeline (C) and alpine grassland (D) datasets. Arrows represent continuous environmental variables. 99% confidence ellipses are shown for each plot type. C stands for control points, A for avalanche tracks and S for ski pistes. Full results and details on habitat variable names are in Tab S1.

Bird assemblages

Overall, 81 bird species were detected in the study area during the two breeding seasons (see Tab S3 for species, abundances and detectability). Analyses showed that abundance did not vary significantly according to plot type (X^2 = 2.64, P = 0.267), but showed significant differences between elevational belts (X^2 = 8.54, P = 0.014) and a significant interaction between the two terms (X^2 = 23.04, P < 0.001). Diversity was significantly different between plot types (R^2 = 0.18, $F_{(2,430)}$ = 4.95, P = 0.007) and elevational belts (R^2 = 0.18, $F_{(2,430)}$ = 31.06, P < 0.001) and there was a significant interaction between them (R^2 = 0.18 ,$F_{(4,430)}$ = 3.43, P = 0.009). Overall, ski pistes had lower abundance and diversity in the alpine belt (Fig 3A, Tab S4). GE species abundance and diversity were significantly different according to plot type (X^2 = 71.23, P < 0.001; X^2 = 41.86, P < 0.001), elevational belt (X^2 = 141.90, P < 0.001; X^2 = 123.23, P < 0.001) and there was an interaction between them (X^2 = 65.04, P < 0.001; X^2 = 98.17, P < 0.001). Abundance and diversity were lower in control points in the montane forest belt and diversity was lower on ski pistes in the alpine belt. Positive effects for the two open habitats (ski pistes and avalanche tracks) were evident in the ecotone treeline and montane forest belts (Fig 3B, Tab S4).

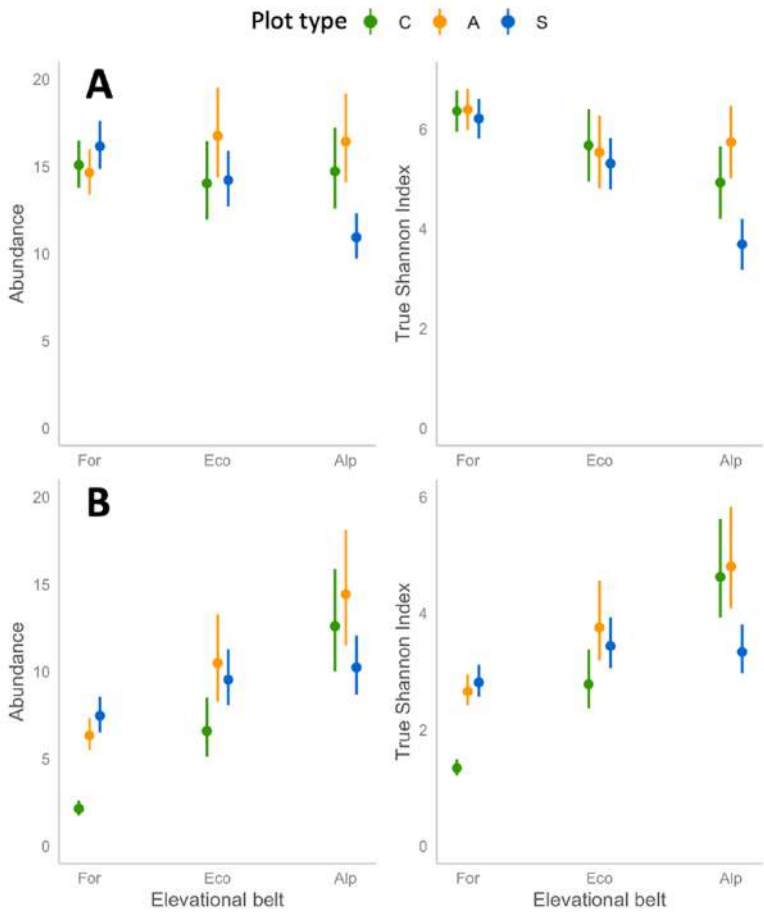

Figure 3. Plots showing the relationship between abundance and diversity (i.e. True Shannon Index) according to plot type and elevational belt for the entire bird assemblage (A) and for grassland/ecotone bird assemblage (B). C stands for control points, A for avalanche tracks and S for ski pistes. For stands for montane forest, Eco for treeline ecotone and Alp for alpine grassland belt. Full results are in Tab S4.

Species-specific responses were reported for the 9 GE species according to plot type and elevational belt (Fig. 4, Tab S5). In the montane forest, whinchat and tree pipit were abundant in ski pistes whilst rock bunting was strongly associated with avalanche tracks. In the treeline ecotone, whinchat was more abundant in avalanches and ski pistes, whilst species typical of alpine grasslands such as skylark and water pipit

were significantly more abundant in ski pistes. In the alpine grasslands, species linked to habitat mosaics like tree pipit, rock bunting, linnet and dunnock were significantly less abundant on ski pistes.

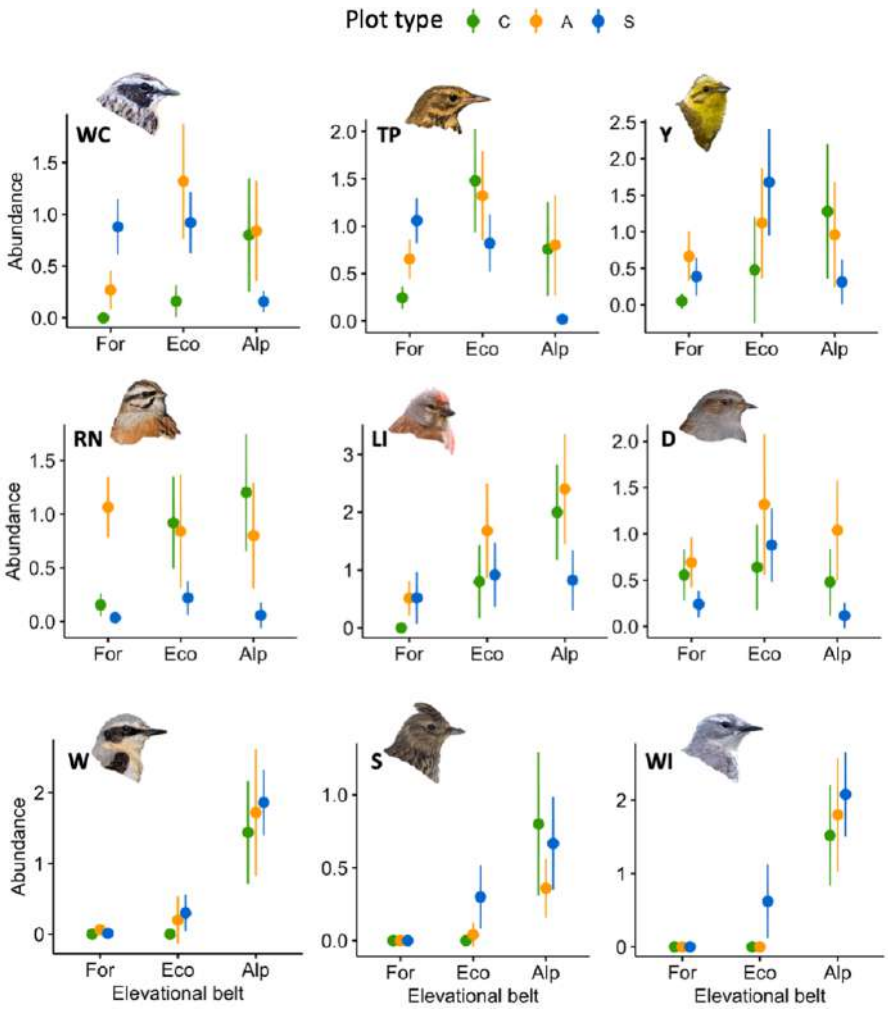

Figure 4 Plots showing the relationship between abundance and the interaction between plot type and elevational belt for the 9 selected grassland/ecotone species (WC = whinchat, TP = tree pipit, Y = yellowhammer, RN = rock bunting, LI = linnet, D = dunnock, W = wheatear, S = skylark, WI = water pipit). C stands for control points, A for avalanche tracks and S for ski pistes. For stands for montane forest, Eco for treeline ecotone and Alp for alpine grassland belt. Full results are in Tab S5.

Discussion

In this study, we analysed the effects of two different sources of disturbance that have a strong influence in shaping many mountain landscapes and, as a consequence, biodiversity. We analysed data from 440 point counts and habitat surveys carried out in undisturbed habitat (i.e. control points), avalanche tracks and ski pistes. Analyses revealed how avalanche tracks were characterized by high vegetation diversity with high cover of rocks, shrubs and small trees and hosted relatively high levels of bird abundance and diversity. Ski pistes had high grass and bare ground cover and harboured lower levels of bird diversity and abundance, especially in the alpine grassland belt (see Fig 5A for overviews of the 3 plot types). However, it is interesting to note how some species such as the skylark, water pipit, whinchat and tree pipit were able to colonize ski pistes. For the former two species, this represented the creation of suitable habitat at and below the treeline at elevations where the species would not usually occur under natural conditions (Fig 5B). 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 belt.

The negative effects of ski pistes on biodiversity were evident on the bird community as a whole, all parameters being notably lower than avalanche and control points. It is interesting to compare our results with previous studies carried out in the same area (Laiolo and Rolando, 2005; Rolando et al., 2007); after almost 20 years, pistes still harbour low levels of biodiversity. Even if grass growth might have provided a partial restoration during the years after ski piste creation (Roux-Fouillet et al., 2011), vegetation cover on high-altitude ski pistes has probably remained unchanged due to heavy management practices and the difficulty for the vegetation to grow at these elevations (Barni et al., 2007). Such substantial impacts at high elevations acquire even more relevance, since the number of threatened bird species (and other sensitive taxa) is higher in these fragile habitats (Viterbi et al. 2013). Regarding ski pistes at lower elevations in the montane forest, we assume they underwent a faster vegetation

growth (especially on ski piste edges), since the bird assemblages are more diverse in comparison to previous studies where higher bare ground cover and poor vegetation structure were described (Laiolo and Rolando, 2005).

Ski pistes had the most negative impacts on species related to shrub cover in the alpine belt. This is not surprising as the artificial removal of trees, shrubs, rocks and even the topsoil (Bayfield, 1996; Rixen and 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 linnet, were significantly lower in ski pistes in the alpine belt in comparison to avalanche areas, where a heterogenous vegetation is 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), canopy and small trees for tree pipit and whinchat (Fonderflick et al., 2013; Fischer et al. 2013), shrubs for dunnock and a high overall habitat complexity for linnet and more broadly for all shrub-related species (Caplat and Fonderflick, 2009; Jähnig et al., 2018).

However, whinchat and tree pipit were significantly more abundant in ski pistes in the montane forest belt. Whinchats were mostly observed using small larches on the sides of less heavily managed ski pistes, whilst tree pipit, which needs the presence of both grass and trees (Fonderflick et al., 2013), finds a suitable habitat in pistes where a marked contrast between forests and open habitats is found. Grassland specialists like the skylark and water pipit also seemingly benefit from ski pistes at lower elevations as they were able to expand their range into the treeline ecotone in ski pistes. Treeline fragmentation caused by piste creation allows these species to colonize lower elevations. Some species were even able to exploit ski piste infrastructures, including rock sparrows *Petronia petronia,* white-winged snowfinches *Montifringilla nivalis* and alpine choughs *Pyrrhocorax graculus*, which were observed using buildings and pylons in ski pistes as nesting sites.

Changes in snow precipitation and consequently in avalanche activity, which are forecast in a context of climate change (Beniston et al., 2018; Hock et al., 2019), are expected to have negative consequences for open habitats and associated biodiversity. Our results have highlighted how avalanche tracks harbour 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 the importance of this natural disturbance factor for mountain ecosystems. Whinchat, tree pipit, yellowhammer, rock bunting, 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 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 like wheatear, 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.

Management implications

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 harbour low levels of biodiversity, we argue that pistes 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. Since our results are based on a large sample of points scattered over a large 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.

In order to lower the negative impact of pistes and make them more biodiversity-friendly, we suggest that a higher number of natural elements that contribute to the quality of avalanche tracks (e.g. small trees, shrubs and small rocks) and some vegetation patches (see 'safety islands' in Urbanska, 1997) should be retained during the construction of ski pistes, or implemented during their management. Maintaining a more natural ski piste edge (see Fig 5C) and re-seeding newly constructed pistes might potentially have positive effects on bird communities, without any repercussions on piste functionality. This is important, especially at higher elevations, where the bird community is impacted the most.

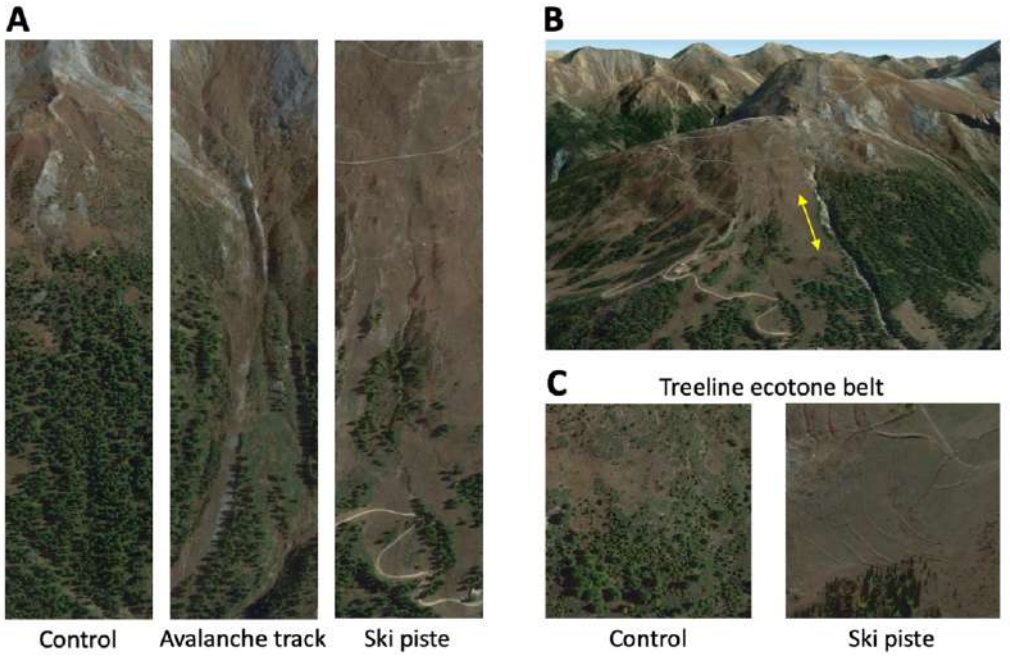

Figure 5. Overview of the elevational gradient of the 3 plot types investigated in this study showing different vegetation gradients with elevations (A). Treeline ecotone habitat is fragmented on ski pistes, resulting in an increase of open habitat towards lower elevations which can be exploited by skylark *Alauda arvensis* and water pipit *Anthus spinoletta* (see Fig 4)

(B). Comparison of the treeline ecotone between a control 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).

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 due to the difficulties of re-vegetation dynamics due to 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 banned (Zeitler, 2000; Braunisch et al., 2011; Arlettaz et al., 2013). In the montane forest belt, ski pistes have an extremely valuable 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 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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References

Alba, R., Kasoar, T., Chamberlain, D., Buchanan, G., Thompson, D., & Pearce-Higgins, J. W. (2022). Drivers of change in mountain and upland bird populations in Europe. Ibis, 164(3), 635-648.

Alba, R., Oddi, L., Rosselli, D., & Chamberlain, D. (2023). Avalanches create unique habitats for birds in the European Alps. Journal of Ornithology, 164(2), 377-388.

Alldredge, M. W., Simons, T. R., & Pollock, K. H. (2007). A field evaluation of distance measurement error in auditory avian point count surveys. The Journal of Wildlife Management, 71(8), 2759-2766.

Antonelli, A., Kissling, W. D., Flantua, S. G., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., Kreft, H., Linder, H. P., Badgley, C., Fjeldså, J., Fritz, S. A., Rahbek, C., Herman, F., Hooghiemstra, H. & Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. Nature Geoscience, 11(10), 718-725.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., & Jenni-Eiermann, S. (2007). Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B: Biological Sciences, 274(1614), 1219-1224.

Arlettaz, R., Patthey, P., & Braunisch, V. (2013). Impacts of outdoor winter recreation on alpine wildlife and mitigation approaches: a case study of the Black Grouse. The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments (eds C. Rixen & A. Rolando), S, 137-154.

Arpa Piemonte (2020). Sistema Informativo Valanghe – SIVa. Available at http://webgis.arpa.piemonte.it/

Ballesteros-Cánovas, J. A., Trappmann, D., Madrigal-González, J., Eckert, N., & Stoffel, M. (2018). Climate warming enhances snow avalanche risk in the Western Himalayas. Proceedings of the National Academy of Sciences, 115(13), 3410-3415.

Barni, E., Freppaz, M., & Siniscalco, C. (2007). Interactions between vegetation, roots, and soil stability in restored high-altitude ski runs in the Alps. Arctic, Antarctic, and Alpine Research, 39(1), 25-33.

Bayfield, N. G. (1996). Long-term changes in colonization of bulldozed ski pistes at Cairn Gorm, Scotland. Journal of Applied Ecology, 1359-1365.

Bebi, P., Kulakowski, D., & Rixen, C. (2009). Snow avalanche disturbances in forest ecosystems—State of research and implications for management. Forest ecology and Management, 257(9), 1883-1892.

Beniston, M., Farinotti, D., Stoffel, M., Andreassen, L. M., Coppola, E., Eckert, N., Fantini, A., Giacona, F., Hauck, C., Huss, M., Huwald, H., Lehning, M., López-Moreno, J. I., Magnusson, J., Marty, C., Morán-Tejéda, E., Morin, S., Naaim, M., Provenzale, A., Rabatel, A., Six, D., Stötter, J., Strasser, U., Terzago, S., & Vincent, C. (2018). The European mountain cryosphere: a review of its current state, trends, and future challenges. The Cryosphere, 12(2), 759-794.

Bibby, C. J. (1999). Making the most of birds as environmental indicators. Ostrich, 70(1), 81-88.

Bibby, C. J. (2000). Bird census techniques. Elsevier.

Bormann, K. J., Brown, R. D., Derksen, C., & Painter, T. H. (2018). Estimating snow-cover trends from space. Nature Climate Change, 8(11), 924-928.

Brambilla, M., Pedrini, P., Rolando, A., & Chamberlain, D. E. (2016). Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. Journal of Biogeography, 43(11), 2299-2309.

Brambilla, M., Gubert, F., & Pedrini, P. (2021). The effects of farming intensification on an iconic grassland bird species, or why mountain refuges no longer work for farmland biodiversity. Agriculture, Ecosystems & Environment, 319, 107518.

Braunisch, V., Patthey, P., & Arlettaz, R. (2011). Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecological Applications, 21(3), 955-967.

Buffet, N., & Dumont-Dayot, E. (2013). Bird collisions with overhead ski-cables: a reducible source of mortality. The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments, 123.

Burt, J. W., & Rice, K. J. (2009). Not all ski slopes are created equal: Disturbance intensity affects ecosystem properties. Ecological Applications, 19(8), 2242-2253.

Caplat, P., & Fonderflick, J. (2009). Area mediated shifts in bird community composition: a study on a fragmented Mediterranean grassland. Biodiversity and Conservation, 18(11), 2979-2995.

Caprio, E., Chamberlain, D. E., Isaia, M., & Rolando, A. (2011). Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. Biological Conservation, 144(12), 2958-2967.

Caprio, E., Chamberlain, D., & Rolando, A. (2016). Ski-piste revegetation promotes partial bird community recovery in the European Alps. Bird Study, 63(4), 470-478.

Caprio E., Rolando A., Arlettaz R., Chamberlain D. (2023) Anthropogenic activities and mountain birds. In Chamberlain D, Lehikoinen, A, Martin, K (eds) Ecology and Conservation of Mountain Birds, pp 260-295, Cambridge University Press, Cambridge, UK.

Catalan, J., Ninot, J. M., & Aniz, M. M. (2017). High mountain conservation in a changing world. Springer Nature.

Chamberlain, D. E., Negro, M., Caprio, E., & Rolando, A. (2013). Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biological conservation, 167, 127-135.

Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. (2012). Rise of the generalists: evidence for climate driven homogenization in avian communities. Global Ecology and Biogeography, 21(5), 568-578.

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London. Series B: Biological Sciences, 268(1462), 25-29.

Eckert, N., Baya, H., & Deschatres, M. (2010). Assessing the response of snow avalanche runout altitudes to climate fluctuations using hierarchical modeling: application to 61 winters of data in France. Journal of Climate, 23(12), 3157-3180.

Eckert, N., Keylock, C. J., Castebrunet, H., Lavigne, A., & Naaim, M. (2013). Temporal trends in avalanche activity in the French Alps and subregions: from occurrences and runout altitudes to unsteady return periods. Journal of Glaciology, 59(213), 93-114.

Erschbamer, B. (1989). Vegetation on avalanche paths in the Alps. Vegetatio, 80, 139-146.

Fischer, K., Busch, R., Fahl, G., Kunz, M., & Knopf, M. (2013). Habitat preferences and breeding success of Whinchats (Saxicola rubetra) in the Westerwald mountain range. Journal of Ornithology, 154, 339-349.

Fonderflick, J., Besnard, A., & Martin, J. L. (2013). Species traits and the response of open-habitat species to forest edge in landscape mosaics. Oikos, 122(1), 42-51.

Gądek, B., Kaczka, R. J., Rączkowska, Z., Rojan, E., Casteller, A., & Bebi, P. (2017). Snow avalanche activity in Żleb Żandarmerii in a time of climate change (Tatra Mts., Poland). Catena, 158, 201-212.

Garcia-Gonzalez, R., & Cuartas, P. (1996). Trophic utilization of a montane/subalpine forest by chamois (Rupicapra pyrenaica) in the Central Pyrenees. Forest Ecology and Management, 88(1-2), 15-23.

Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: climate change or land abandonment?. Journal of vegetation science, 18(4), 571-582.

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st century climate change in the European Alps—A review. Science of the total environment, 493, 1138-1151.

Gregory, R. D., Noble, D., Field, R., Marchant, J., Raven, M., & Gibbons, D. W. (2003). Using birds as indicators of biodiversity. Ornis hungarica, 12(13), 11-24.

Gros, R., Monrozier, L. J., Bartoli, F., Chotte, J. L., & Faivre, P. (2004). Relationships between soil physico-chemical properties and microbial activity along a restoration chronosequence of alpine grasslands following ski run construction. Applied Soil Ecology, 27(1), 7-22.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology letters, 12(10), 1040-1049.

Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., Jackson, M., Kääb, A., Kang, S., Kutuzov, S., Milner, A., Molau, U., Morin, S., Orlove, B., Steltzer, H., Allen, S., Arenson, L., Baneerjee, S., Barr, I., Bórquez, R., Brown, L., Cao, B., Carey, M., Cogley, G., Fischlin, A., de Sherbinin, A., Eckert, N., Geertsema, M., Hagenstad, M., Honsberg, M., Hood, E., Huss, M., Jimenez Zamora, M., Kotlarski, S., Lefeuvre, P.M., Ignacio López Moreno, J., Lundquist, J., McDowell, G., Mills, S., Mou, C., Nepal, S., Noetzli, J., Palazzi, E., Pepin, N., Rixen, C., Shahgedanova, M.,McKenzie Skiles, S., Vincent, C., Viviroli, D., Gesa A Weyhenmeyer, Yangjee Sherpa, P., Weyer, N., Wouters, B., Yasunari, T., You, Q., & Zhang, Y. (2019). High mountain areas. In IPCC special report on the ocean and cryosphere in a changing climate (pp. 131-202). Pörtner, H.O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, Z., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (eds.).

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A., & Chamberlain, D. (2018). The contribution of broadscale and finescale habitat structure to the

distribution and diversity of birds in an Alpine forest-shrub ecotone. Journal of Ornithology, 159, 747-759.

Kassambara, A., & Mundt, F. (2017). Package 'factoextra'. Extract and visualize the results of multivariate data analyses, 76(2).

Klaus, S., Bock, W., Gorner, M., Seibt, E. (1985). Zur Ökologie des Auerhuhns in Thüringen. Acta Ornithologica, 1: 3–36.

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K., & M Spehn, E. (2017). A global inventory of mountains for bio-geographical applications. Alpine Botany, 127, 1-15.

Krajick, K. (1998). Animals thrive in an avalanche's wake. Science, 279(5358), 1853-1853.

Kulakowski, D., Rixen, C., & Bebi, P. (2006). Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. Forest Ecology and Management, 223(1-3), 66-74.

Laiolo, P., Dondero, F., Ciliento, E., & Rolando, A. (2004). Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. Journal of Applied Ecology, 41(2), 294-304.

Laiolo, P., & Rolando, A. (2005). Forest bird diversity and ski-runs: a case of negative edge effect. Animal Conservation Forum, 8(1), 9-16.

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2019). A meta-analysis of recreation effects on vertebrate species richness and abundance. Conservation Science and Practice, 1(10), e93.

Lasanta, T., Errea, M. P., & Nadal-Romero, E. (2017). Traditional agrarian landscape in the Mediterranean mountains. A regional and local factor analysis in the Central Spanish Pyrenees. Land Degradation & Development, 28(5), 1626-1640.

Lieser, M. (1995) Lebensraumansprüche des Haselhuhns im Schwarzwald. Naturschutzreport 10:239–255.

Ingold, P., Huber, B., Neuhaus, P., Mainini, B., Marbacher, H., Schnidrig-Petrig, R., & Zeller, R. (1993). Tourism and sport in the Alps-a serious problem for wildlife? *Revue Suisse de Zoologie*, *100*(3), 529-545.

Mace, R. D., Waller, J. S., Manley, T. L., Lyon, L. J., & Zuuring, H. (1996). Relationships among grizzly bears, roads and habitat in the Swan Mountains Montana. Journal of Applied ecology, 1395-1404.

Marty, C. (2013). Climate change and snow cover in the European Alps. Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments, Bentham, 30-44.

Montevecchi, W. A. (1993). Birds as indicators of change in marine prey stocks. Birds as monitors of environmental change, 217-266.

Mountain Agenda (1999). Mountains of the world: tourism and sustainable mountain development. Mountain Agenda.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Negro, M., Isaia, M., Palestrini, C., & Rolando, A. (2009). The impact of forest ski-pistes on diversity of ground-dwelling arthropods and small mammals in the Alps. Biodiversity and Conservation, 18, 2799-2821.

Negro, M., Rolando, A., Barni, E., Bocola, D., Filippa, G., Freppaz, M., Isaia, M., Siniscalco, C., & Palestrini, C. (2013a). Differential responses of ground dwelling arthropods to ski-piste restoration by hydroseeding. Biodiversity and conservation, 22, 2607-2634.

Negro, M., Novara, C., Bertolino, S., & Rolando, A. (2013b). Ski-pistes are ecological barriers to forest small mammals. European Journal of Wildlife Research, 59, 57-67.

Patthey, P., Wirthner, S., Signorell, N., & Arlettaz, R. (2008). Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of applied ecology, 45(6), 1704-1711.

Pini, R., Ravazzi, C., Raiteri, L., Guerreschi, A., Castellano, L., & Comolli, R. (2017). From pristine forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation and landscapes in the western Italian Alps. Journal of Ecology, 105(6), 1580-1597.

QGIS Development Team (2020). QGIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Requena, E., Alba, R., Rosselli, D., & Chamberlain, D. (2022). Avalanche tracks are key habitats for the Rock Bunting Emberiza cia in the Alps. Ardeola, 69(2), 203-217.

Rixen, C., Haag, S., Kulakowski, D., & Bebi, P. (2007). Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. Journal of Vegetation Science, 18(5), 735-742.

Rixen, C., Teich, M., Lardelli, C., Gallati, D., Pohl, M., Pütz, M., & Bebi, P. (2011). Winter tourism and climate change in the Alps: an assessment of resource consumption, snow reliability, and future snowmaking potential. Mountain Research and Development, 31(3), 229-236.

Rixen, C., & Rolando, A. (Eds.). (2013). The impacts of skiing and related winter recreational activities on mountain environments. Soest, the Netherlands: Bentham Science Publishers.

Rolando, A., Caprio, E., Rinaldi, E., & Ellena, I. (2007). The impact of high-altitude ski-runs on alpine grassland bird communities. Journal of applied ecology, 44(1), 210-219.

Roux-Fouillet, P., Wipf, S., & Rixen, C. (2011). Long-term impacts of ski piste management on alpine vegetation and soils. Journal of applied ecology, 48(4), 906-915.

Sato, C. F., Wood, J. T., & Lindenmayer, D. B. (2013). The effects of winter recreation on alpine and subalpine fauna: a systematic review and meta-analysis. PloS one, 8(5), e64282.

Solymos, P., Moreno, M., Lele, S.R. (2013). Detect: analyzing wildlife data with detection error R package version 03. http://CRAN.R-project.org/package=detect

Sólymos, P., Matsuoka, S.M., Cumming, S.G., Stralberg, D., Fontaine, P., Schmiegelow, F.K.A., Song, S.J., Bayne, E.M. (2018). Evaluating time-removal models for estimating availability of boreal birds during point count surveys: sample size requirements and model complexity. Condor 120:765–786

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R., & Jenni, L. (2008). Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: a new methodological approach. Journal of applied ecology, 45(3), 845-853.

Thiel, D., Jenni-Eiermann, S., Palme, R., & Jenni, L. (2011). Winter tourism increases stress hormone levels in the Capercaillie Tetrao urogallus. Ibis, 153(1), 122-133.

Urbanska, K. M. (1997). Restoration ecology research above the timberline: colonization of safety islands on a machine-graded alpine ski run. Biodiversity & Conservation, 6, 1655-1670.

Viterbi, R., Cerrato, C., Bassano, B., Bionda, R., Hardenberg, A. V., Provenzale, A., & Bogliani, G. (2013). Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach. Community Ecology, 14(1), 18-30.

Von Scheffer, C., Lange, A., De Vleeschouwer, F., Schrautzer, J., & Unkel, I. (2019). 6200 years of human activities and environmental change in the northern central Alps. E&G Quaternary Science Journal, 68(1), 13-28.

Watson, A., Moss, R. (2004). Impacts of ski-development on ptarmigan (Lagopus mutus) at Cairn Gorm, Scotland. Biological Conservation, 116: 267–275.

Wipf, S., Rixen, C., Fischer, M., Schmid, B., & Stoeckli, V. (2005). Effects of ski piste preparation on alpine vegetation. Journal of Applied Ecology, 42(2), 306-316.

Zeitler, A. (2000). Human disturbance, behaviour and spatial distribution of black grouse in skiing areas in the Bavarian Alps. Cahiers d'Ethologie, 20, 381-400.

Supplementary material

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 3 elevational belts. Coordinates for avalanche tracks (A), control sites (C) and ski pistes (S) are also reported.

		General		**Montane forest**		**Treeline ecotone**		**Alpine grassland**	
		Dim.1	*Dim.2*	*Dim.1*	*Dim.2*	*Dim.1*	*Dim.2*	*Dim.1*	*Dim.2*
Eigenvalue		4.02	2.04	3.92	1.9	3.98	2.06	4.21	1.79
Cum. Var. %		26.77	40.39	26.13	38.79	28.41	43.12	32.42	46.18
Elevation	Elevation in meters	0.618	0.455	0.413	0.535	0.275	0.482	0.582	0.531
Slope	Slope in grades	-0.562	0.248	-0.729	-0.083	-0.596	-0.129	-0.447	0.494
HighCanopy	% cover of high canopy	-0.836	-0.357	-0.774	-0.258	-0.652	-0.401	-0.722	-0.182
LowCanopy	% cover of low canopy	-0.708	0.185	-0.672	-0.022	-0.675	0.294	-0.810	-0.234
Shrubs	% cover of shrubs	-0.356	0.670	-0.403	0.703	-0.615	0.354	-0.807	-0.131
Rock	% cover of rocks	-0.148	0.597	-0.476	0.400	-0.543	0.143	-0.361	0.784
BareGround	% cover of bare ground	0.383	-0.060	0.338	-0.037	0.488	-0.122	0.468	0.080
Snow	% cover of snow	-0.115	0.063	-0.098	0.130	\	\	\	\
Grass	% cover of grass	0.849	-0.252	0.887	-0.139	0.851	-0.087	0.703	-0.544

DeadOrg	% cover of dead organic material	-0.725	-0.045	-0.702	0.066	-0.694	0.020	-0.483	-0.162
Larix	Number of *Larix* trees	-0.497	-0.375	-0.314	-0.064	-0.387	-0.611	-0.528	0.180
Pinus	Number of *Pinus* trees	-0.322	-0.101	-0.308	-0.057	-0.131	-0.641	-0.188	0.105
Picea	Number of *Picea* trees	-0.259	-0.221	-0.232	-0.270	-0.115	-0.264	\	\
Broadleaves	Number of broadleaf trees	-0.347	-0.229	-0.334	-0.496	-0.044	-0.649	-0.101	0.312
SmallTrees	Number of small trees	-0.155	0.688	-0.129	0.718	-0.605	0.344	-0.668	-0.272
A	Avalanche track	-0.593	0.905	-0.451	0.839	-1.270	0.220	-1.680	-0.042
C	Control point	-1.790	-0.214	-1.930	-0.557	-1.480	-0.527	-1.500	-0.146
S	Ski piste	1.650	-0.482	2.220	-0.272	1.380	0.154	1.560	0.092

Table S2 Results of Kruskal-Wallis tests for differences in habitat variables between plot types (A avalanche tracks, C control points, S ski pistes) for the general dataset and for the 3 elevational belts. Chi-square and *P-values* are reported, as well as means ± standard errors.

			High Canopy	**Shrubs**	**Rock**	**Grass**	**Bare Ground**	**Small trees**
General	X^2		151.22	144.60	101.56	178.26	112.56	32.18
	P		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	A	Mean ± SE	22.15 ± 1.46	30.85 ± 1.84	18.71 ± 1.17	37.46 ± 1.91	0.35 ± 0.12	54.82 ± 5.16
	C		52.44 ± 2.55	26.42 ± 1.92	13.22 ± 1.23	25 ± 1.71	0.08 ± 0.05	24.73 ± 2.86
	S		11.22 ± 0.93	6.87 ± 1.02	6.68 ± 1.02	63.29 ± 1.46	4.30 ± 0.54	23.20 ± 2.07
Montane forest	X^2		155.94	84.15	126.1	137.24	36.12	44.02
	P		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	A	Mean ± SE	28.33 ± 1.63	28.14 ± 2.19	17.24 ± 1.52	33.01 ± 2.21	0.38 ± 0.15	53.41 ± 6.77
	C		71.49 ± 1.49	22.79 ± 2.50	10.13 ± 1.31	15.39 ± 1.13	0.13 ± 0.09	12.17 ± 2.20

	S		20.18 ± 1.29	4.33 ± 1.07	0.06 ± 0.06	63.67 ± 2.02	2.59 ± 0.49	19.29 ± 3.45
Treeline ecotone	X^2		48.23	14.02	18.58	25.27	24.70	3.03
	P		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.219
	A	Mean ± SE	19.4 ± 3.49	34 ± 4.83	15.8 ± 2.30	42.6 ± 5.41	0.2 ± 0.2	64.4 ± 11.71
	C		39.8 ± 3.04	28.6 ± 3.93	13.8 ± 2.91	30 ± 2.92	0 ± 0	42.52 ± 6.76
	S		7.7 ± 1.26	15.9 ± 2.91	4.9 1.04	57.6 ± 3.01	2.8 ± 0.52	34.14 ± 3.39
Alpine grassland	X^2		41.65	61.97	7.28	21.26	43.62	12.54
	P		< 0.001	< 0.001	0.026	< 0.001	< 0.001	0.002
	A	Mean ± SE	5.6 ± 1.48	36.2 ± 4.24	26.2 ± 2.44	46.2 ± 3.71	0.4 ± 0.4	49.64 ± 10.98
	C		6.4 ± 1.24	35.4 ± 4.06	22.2 ± 3.21	49.6 ± 4.43	0 ± 0	45.64 ± 8.61
	S		0.09 ± 0.09	2.16 ± 0.76	19.21 ± 2.83	68.23 ± 2.76	8.53 ± 1.58	18.98 ± 3.27

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 stands for shrubs/woodland and GE corresponds to grassland/ecotone; species not reported by Caprio et al. (2016) were categorized according to expert opinion.

Code	Species	Abundance	Corrected Abundance	Detectability	SD	Surrogate	Habitat
CH	*Fringilla coelebs*	467	509	0.84	0.24	\	SW
TP	*Anthus trivialis*	258	312	0.76	0.26	\	GE
WC	*Saxicola rubetra*	186	227	0.73	0.26	\	GE
LI	*Linaria cannabina*	174	347	0.52	0.23	\	GE
RN	*Emberiza cia*	168	210	0.7	0.26	\	GE
W	*Oenanthe oenanthe*	152	200	0.67	0.26	\	GE
CT	*Periparus ater*	141	251	0.62	0.26	\	SW
M	*Turdus viscivorus*	141	282	0.49	0.23	\	GE
WT	*Poecile montanus*	137	274	0.53	0.24	\	SW

LW	*Curruca curruca*	135	245	0.66	0.26	\	SW
D	*Prunella modularis*	129	260	0.45	0.21	\	GE
CR	*Loxia curvirostra*	124	293	0.41	0.2	\	SW
BX	*Phoenicurus ochruros*	107	211	0.57	0.25	\	GE
WR	*Troglodytes troglodytes*	105	115	0.71	0.26	\	SW
CC	*Phylloscopus collybita*	99	99	0.85	0.24	\	SW
R	*Erithacus rubecula*	98	196	0.52	0.24	\	SW
IW	*Phylloscopus bonelli*	92	110	0.78	0.26	\	SW
WI	*Anthus spinoletta*	78	220	0.4	0.2	\	GE
BC	*Sylvia atricapilla*	74	161	0.41	0.2	\	SW
Y	*Emberiza citrinella*	71	284	0.24	0.13	\	GE
GS	*Dendrocopos major*	70	131	0.6	0.25	\	SW
S	*Alauda arvensis*	67	79	0.68	0.26	\	GE
RZ	*Turdus torquatus*	56	72	0.72	0.26	\	GE
FF	*Turdus pilaris*	55	90	0.62	0.26	\	GE
TC	*Certhia familiaris*	46	48	0.71	0.26	\	SW
C	*Corvus corone*	40	70	0.6	0.25	GS	GE
CK	*Cuculus canorus*	39	66	0.59	0.24	*	GE
NC	*Nucifraga caryocatactes*	38	70	0.6	0.25	GS	SW
AC	*Phyrrocorax graculus*	37	63	0.59	0.24	*	GE
CRT	*Lophophanes cristatus*	35	65	0.62	0.26	CT	SW
GF	*Carduelis carduelis*	34	68	0.52	0.23	LI	GE
ST	*Turdus philomelos*	34	68	0.49	0.23	M	SW
RS	*Petronia petronia*	30	51	0.59	0.24	*	GE
WH	*Motacilla alba*	24	41	0.59	0.24	*	GE
GRW	*Motacilla cinerea*	23	39	0.59	0.24	*	GE
SE	*Serinus serinus*	22	44	0.52	0.23	LI	GE
CG	*Phyrrocorax phyrrocorax*	22	37	0.59	0.24	*	GE
MN	*Montifringilla nivalis*	21	37	0.57	0.25	BX	GE
GT	*Parus major*	19	38	0.53	0.24	WT	SW
LT	*Aegithalos caudatus*	19	32	0.62	0.26	CT	SW
GW	*Sylvia borin*	19	40	0.41	0.2	BC	SW
BB	*Turdus merula*	19	38	0.49	0.23	M	SW

J	*Garrulus glandarius*	18	33	0.6	0.25	GS	SW
HM	*Delichon urbicum*	18	31	0.59	0.24	*	GE
K	*Falco tinnunculus*	15	25	0.59	0.24	*	GE
BG	*Lyrurus tetrix*	14	24	0.59	0.24	*	GE
RO	*Monticola saxatilis*	13	23	0.57	0.25	BX	GE
BU	*Pyrrhula pyrrhula*	13	13	0.84	0.24	CH	SW
GO	*Picus viridis*	12	24	0.6	0.25	GS	SW
BT	*Cyanistes caeruleus*	12	22	0.62	0.26	CT	SW
CM	*Ptyonoprogne rupestris*	12	20	0.59	0.24	*	GE
SH	*Lanius collurio*	12	20	0.59	0.24	*	GE
GC	*Regulus regulus*	11	22	0.53	0.24	WT	SW
RE	*Phoenicurus phoenicurus*	11	22	0.57	0.25	BX	SW
CF	*Carduelis citrinella*	9	18	0.52	0.23	LI	SW
RP	*Alectoris graeca*	9	15	0.59	0.24	*	GE
FC	*Regulus ignicapilla*	9	18	0.53	0.24	WT	SW
WL	*Lullula arborea*	7	9	0.76	0.26	TP	GE
RA	*Corvus corax*	6	10	0.59	0.24	*	GE
WN	*Jynx torquilla*	5	8	0.59	0.24	*	SW
GE	*Aquila chrysaetos*	4	7	0.59	0.24	*	GE
SW	*Apus apus*	4	7	0.59	0.24	*	GE
WD	*Cinclus cinclus*	3	5	0.59	0.24	*	SW
GV	*Gyps fulvus*	3	5	0.59	0.24	*	GE
GR	*Chloris chloris*	3	4	0.84	0.24	CH	SW
BW	*Dryocopus martius*	2	4	0.6	0.25	GS	SW
OB	*Emberiza hortulana*	2	8	0.24	0.13	Y	GE
WP	*Columba palumbus*	2	3	0.59	0.24	*	SW
HB	*Pernis apivorus*	2	3	0.59	0.24	*	SW
NH	*Sitta europaea*	1	1	0.71	0.26	TC	SW
WW	*Phylloscopus sibilatrix*	1	1	0.78	0.26	IW	SW
BZ	*Buteo buteo*	1	2	0.59	0.24	*	GE
GH	*Accipiter gentilis*	1	2	0.59	0.24	*	SW
SP	*Accipiter nisus*	1	2	0.59	0.24	*	SW
TAP	*Anthus campestris*	1	3	0.4	0.2	WI	GE

AA	*Prunella collaris*	1	2	0.57	0.25	BX	GE
BS	*Hirundo rustica*	1	2	0.59	0.24	*	GE
CV	*Aegypius monachus*	1	2	0.59	0.24	*	GE
IS	*Passer italiae*	1	2	0.59	0.24	*	GE
STE	*Circaetus gallicus*	1	2	0.59	0.24	*	GE
CW	*Sylvia communis*	1	2	0.66	0.26	LW	GE

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, standard errors (SE) and P-values are reported. Type indicates plot type, with avalanche tracks reported as A, Ski pistes as S, whilst C as control points which was set as the reference level and is not shown. Belt indicates elevational belt, with Alp referring to alpine grassland belt, Eco to treeline ecotone belt and For as montane forest, which was set as the reference level and is not shown.

		Entire bird assemblage						**GE bird assemblage**					
		Abundance			Diversity			Abundance			Diversity		
		Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
	(Intercept)	2.713	0.045	< 0.001	6.363	0.211	< 0.001	0.762	0.097	< 0.001	0.745	0.038	< 0.001
Type													
	A	-0.023	0.064	0.717	0.030	0.297	0.921	1.086	0.122	< 0.001	-0.369	0.043	< 0.001
	S	0.070	0.063	0.265	-0.154	0.293	0.599	1.249	0.120	< 0.001	-0.390	0.042	< 0.001
Belt													
	Alp	-0.019	0.092	0.840	-1.433	0.426	0.001	1.772	0.152	< 0.001	-0.529	0.043	< 0.001
	Eco	-0.071	0.093	0.442	-0.686	0.426	0.108	1.125	0.162	< 0.001	-0.386	0.050	< 0.001
Type*Belt													
	A:Alp	0.136	0.129	0.293	0.783	0.602	0.194	-0.949	0.205	< 0.001	0.361	0.051	< 0.001
	S:Alp	-0.359	0.118	0.002	-1.087	0.538	0.044	-1.457	0.187	< 0.001	0.474	0.050	< 0.001
	A:Eco	0.205	0.129	0.113	-0.170	0.602	0.777	-0.623	0.214	0.004	0.276	0.059	< 0.001
	S:Eco	-0.053	0.117	0.652	-0.215	0.539	0.690	-0.880	0.196	< 0.001	0.322	0.056	< 0.001

Table 5 Results of GLMs carried out on abundance of 9 selected grassland/ecotone species abundances (WC = whinchat, RN = rock bunting , LI = linnet, Y = yellowhammer, D = dunnock, TP = tree pipit, W = wheatear, WI = water pipit, S = skylark) between plot types (Type) and elevational belt (Belt) and their interaction term. Chi-square and p-values are shown.

Species code	Variable	X^2	*P*
WC	Type	41.51	< 0.001
	Belt	19.37	< 0.001
	Type*Belt	111.20	< 0.001
RN	Type	144.21	< 0.001
	Belt	12.11	0.002
	Type*Belt	50.14	< 0.001
LI	Type	34.62	< 0.001
	Belt	143.57	< 0.001
	Type*Belt	74.42	< 0.001
Y	Type	20.98	< 0.001
	Belt	74.77	< 0.001
	Type*Belt	75.32	< 0.001
D	Type	36.32	< 0.001
	Belt	29.58	< 0.001
	Type*Belt	21.26	< 0.001

TP	Type	4.51	0.105
	Belt	36.64	< 0.001
	Type*Belt	93.50	< 0.001
W	Type	5.71	0.058
	Belt	382.89	< 0.001
	Type*Belt	16.10	0.002
WI	Type	13.08	0.001
	Belt	443.93	< 0.001
	Type*Belt	32.86	< 0.001
S	Type	7.72	0.021
	Belt	144.20	< 0.001
	Type*Belt	12.95	0.012

Chapter V

Habitat quality drives the spatio-temporal occupation of a migratory songbird, the Northern Wheatear *Oenanthe oenanthe*, in alpine grasslands

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Abstract

Birds of open alpine grasslands are threatened by the degradation and contraction of their breeding habitat. To assess potential impacts of environmental change in alpine environments, basic ecological knowledge, such as habitat requirements during pre-breeding and breeding periods, is needed. We conducted territory and habitat mapping of a population of the Northern Wheatear Oenanthe oenanthe breeding in alpine grasslands and lower elevation open habitats in the Western Italian Alps during two consecutive breeding seasons (2019–2020). For territory mapping, a study area of over 160ha was visited five times, covering an elevation gradient from 1,600 to 2,700m asl. Low elevation grasslands in the valley were exploited by birds as arrival habitat after spring migration, but were not selected as breeding territories. On territories, birds avoided areas with numerous small trees, selecting patchy habitats with high rock cover. Early arriving males first occupied the territories at lower elevations, and those with taller ground vegetation, but avoided overall higher vegetation cover. Birds were able to initiate the breeding season when snow cover was still high, as long as forbs and grass were present. The expected decrease in the area of open alpine grassland due to shrub encroachment will probably reduce the availability of suitable territory habitat and thus threatens the alpine population. Extensive seasonal grazing could help to maintain alpine grasslands above the treeline, and may provide suitable, but lower quality, habitat even at lower elevations by keeping the area open.

Keywords: Alps, birds, climate change, habitat selection, Oenanthe, snowmelt, treeline

Introduction

High elevation habitats are breeding grounds, migration stopovers or wintering sites for several bird species, and are thus identified as important elements for full life-cycle conservation (Boyle & Martin, 2015). Mountain habitats and their bird communities are particularly threatened by land-use change (Inouye et al., 2000; Lehikoinen et al., 2018; Scridel et al., 2018), and by climate change, as the rate of warming is more than double that in lowland habitats in many mountain ranges (Brunetti et al., 2009; Oyler et al., 2015; Wang et al., 2016; Scridel et al., 2017). Upward shifts in the treeline, abandonment of extensive grazing activities and shrub encroachment all contribute to decreases in the extent of open grasslands (Chamberlain et al., 2013; Smith et al., 2013; Lehikoinen et al., 2018; Scridel et al., 2018; Ewing et al., 2020). Furthermore, these habitats are threatened by degradation through unsustainable land-use due to transformation into ski-pistes and disturbance from other touristic activities (Caprio et al., 2011; Herrando et al., 2016). Range contractions and increased extinction risks of high elevation species have been observed across continents, highlighting the need for additional knowledge on species' distributions and their adaptive capacities (La Sorte & Jetz, 2010). At the same time, the assessment of species distributions and population trends in mountain regions is highly under-represented in the ecological literature, which is related to the logistical constraints faced in these areas (Chamberlain et al., 2012).

For some high-elevation species, long-term monitoring (Brambilla et al., 2020; Ewing et al., 2020), the use of museum specimens (Delgado et al., 2019) and fossil records (Smith et al., 2013) have facilitated a better understanding of the effects of climate change and its consequences by projecting future species distributions, and of potential phenotypic adaptability to environmental change. When such data are not available, which is mostly the case in mountain systems, basic ecological information, such as current species distributions, drivers of habitat selection and reproductive success, is essential to assess the vulnerability and resilience of species, and to predict

their responses to future environmental changes (Chamberlain et al., 2012; Scridel et al., 2018).

High-elevation breeding requires a set of adaptations to the particular conditions such as a short vegetation period, large temperature differences between day and night, higher precipitation compared to lowland habitats, low air pressure and unpredictable early season weather events. To increase individual fitness as a function of reproductive success and survival, territories are selected for their quality in providing food resources, nesting possibilities and other factors such as a favourable microclimate and reduced predation risk (Martin, 1995; Martin & Wiebe, 2004; Currie et al., 2008). Early settlement in breeding territories is typically advantageous, as individuals select high quality habitats for nesting and foraging, and also increase their chances of pairing with higher quality mates (Møller, 1994; Currie et al., 2008). For example, the high-elevation breeding Water Pipit Anthus spinoletta was found to settle first in prey-rich territories, which was related to snow cover (Bollmann et al., 1997). Consequently, in territorial migratory birds, there is a strong selection for early arrival in spring, although this is limited by departure from the wintering grounds, overall migration speed and stopover duration (Schmaljohann & Both, 2017; Morbey & Hedenström, 2020). For many migratory birds worldwide, there is an evident trend of earlier arrival at the breeding grounds in order to that tracks advancing springs caused by climate change, although increasing phenological mismatches at the breeding grounds have been observed (Mayor et al., 2017; Koleček et al., 2020). Related to the overall earlier timing of migration, an earlier spring passage at stopover sites has been noted for Afro-Palaearctic migrants, such as the Northern Wheatear Oenanthe oenanthe, henceforth 'Wheatear' (Desaever & Bairlein, 2020; Maggini et al., 2020). This species is distributed across the Holarctic, and breeds in open habitats from sea level to uplands at northerly latitudes whilst is mostly confined to high elevations in Southern Europe (Conder, 1989; Bairlein et al., 2012). Although globally classified as 'least concern', the population trend is decreasing (BirdLife International, 2022), and

populations are declining regionally, e.g. in Swedish farmlands (Arlt et al., 2008, Wretenberg et al. 2006), Dutch dune grasslands (Oosten et al., 2014), French coastal grasslands (Henry & Ollivier 2015), and in the European mountain regions of south-western Iberia and Fennoscandia (Lehikoinen et al., 2018). In Afro-Palaearctic migrants, population declines are strongly related to the degradation of breeding habitat (Vickery et al., 2014).

Details of key habitat features are unknown for mountain populations of many widely distributed migratory birds, such as the Wheatear, whereas their lowland breeding habitats, and in some cases, their wintering habitats, are well studied (Table 1). In general, Wheatears are assumed to use vegetation structures to assess the quality of the habitat prior to nesting (Tye, 1992). In Swedish agricultural landscapes (Arlt & Pärt, 2008; Arlt et al., 2008), Dutch coastal dunes (Oosten et al., 2014) and English Breckland (Tye, 1992), this species selects short vegetation, despite the greater prey biomass in grassy habitats with taller vegetation. In their wintering grounds, preferably savannah habitats, the density and height of trees plays a major role, as Wheatears choose sites in which trees provide shade and perches (Wilson & Cresswell, 2010). Within the mountain bird community, Wheatears are classified as generalists in terms of niche position and width (Mermillon et al., 2021), although they have a preference for nest sites on sun-exposed slopes, far from the treeline, with warmer microclimates (Jähnig et al., 2020). In Spanish mountains, the species was found to select nest sites in rocky microhabitats that differed from the surrounding territory that was used for all other activities, such as foraging (Zamaro, 1990). Breeding success was related to spring phenology by being lower in early springs, and in less 'green' nest sites, and was thus assumed to be affected by the seasonal abundance and availability of invertebrate food resources (Sander et al., 2021, 2022).

Table 1. Studies describing the habitat of the Northern Wheatear *Oenanthe oenanthe* during the breeding season and in their wintering range.

Population	Season	Habitat	Habitat features considered	Main findings	References
Swedish lowlands	Breeding	Agricultural landscape: cropfields, ungrazed grasslands, pastures, farmyards, grazing (rabbits)	Vegetation/land-use type and vegetation height: 'short' vs. 'tall' habitat	Negative population growth rates in 'tall' habitat (cropfield, ungrazed grassland) acting as sinks, whereas 'short' habitats, such as pastures and farmyards, are sources (high-quality territories); beneficial effect of grazing	(Arlt & Pärt, 2008; Arlt *et al.*, 2008; Öberg *et al.*, 2014; Paquet *et al.*, 2019)
Dutch lowlands	Breeding	Dune grassland	Vegetation structures: 'pioneer', 'short', 'tall' grassland	Territories are mosaics of all three structures, prey abundance highest in 'tall' vegetation, but birds prefer to forage in 'short' and 'pioneer'	(Oosten *et al.*, 2014)
British moorland/ Breckland	Breeding	Open: grassland, bracken, heather, grazing (rabbits)	Vegetation height ('short' ('bare', 'turf'), 'tall') & community classification; Occupation date used to rank territory quality	Prey abundance highest in 'turf', but biomass in 'tall', early occupied territories had higher prey abundance & were in 'short' habitat; Older and early arriving birds occupied higher ranked territories and had higher breeding success	(Conder, 1989; Tye, 1992; Currie *et al.*, 2008)
Sahel, West Africa	Wintering	Savannah, agricultural sites, woodland	Tree species, density, height; shrub species, density	Occurrence: highest in savannah, preference for sites with scattered large trees (shelter, perching)	(Wilson & Cresswell, 2010)
Italian Alps	Breeding	Open alpine grassland, treeline ecotone, grazing (cows)	Temperature, slope, elevation, shrub cover, canopy, vegetation green-up/snowmelt	Occurrence: preference for SW slopes & high elevations, greater distance to treeline, intermediate shrub cover, warmer micro-climate; Nest survival: lower in early springs, in early season, at higher elevations & higher for nests with more vegetated surroundings; Nestling condition: higher in early broods	(Jähnig *et al.*, 2018, 2020; Sander *et al.*, 2021, 2022)

In this study, we describe spatio-temporal patterns of territory selection in an alpine population of the Wheatear. We investigate in detail: 1. whether and to what extent the habitat during the arrival period differs from the breeding habitat at higher elevations; 2. which environmental variables are important for the selection of territories in our alpine population, and 3. which environmental factors determine the timing of territory occupation (henceforth "occupation timing"). We assume that early occupied territories are generally of higher quality (as per Bollmann et al., 1997), as

first arriving individuals can choose between all the yet-unoccupied territories (Currie et al., 2008). Therefore, we expect that early snow-free territories will be selected first in our strongly seasonal alpine study system. Here, we aim to understand whether low-elevation breeding territories below the treeline (pastures, meadows) are as suitable as those in open alpine grasslands and will thus assess whether they would be an adequate alternative in a future in which the current area of alpine grassland breeding habitat is shrinking.

Methods

Study species and area

In our study area, territories of the Wheatear are generally found in open alpine grasslands at 1,900–2,800m asl. This species nests in rock crevices or holes in the ground, covered by dwarf shrubs (Juniperus nana, Rhododendron ferrugineum; henceforth juniper and rhododendron). Its occurrence on the breeding grounds is restricted to the period from mid-late May (arrival from Sub-Saharan wintering grounds) to early-mid September (post-breeding moult and departure) (Sander et al., 2021).

Data were collected in 2019 and 2020 during the pre-breeding and breeding seasons, from May to August, in Val Troncea Natural Park, 44°57’28’’N, 6°56’28’E, Western Alps, Piedmont, Italy. The study area covers an elevational gradient, ranging from 1,560 to 2,700m asl (Supplementary material Figure A1). The treeline varies locally but is typically at around 2,200m asl. The landscape structure of the valley is characterised by forest, predominantly larch Larix decidua, with patches of green alder Alnus viridis at lower elevations. The ecotone around the treeline is formed by larch, rhododendron, juniper, common bilberry Vaccinuium myrtillus and bog bilberry Vaccinium uliginosum. Above the treeline, open grassland (dominated by Festuca ovina, Carex foetida, Nardus stricta, Phleum raeticum, Pseudolysimachion sp., B. Schöpke pers. comm.) and rocky areas predominate. The vegetation structure of the

valley is influenced by seasonal cattle grazing which contributes to maintaining open habitats and creating patches with different sward heights during the breeding season (Jähnig et al., 2018, 2020).

Arrival habitat mapping

From 20 May to 10 June 2019, we surveyed a line transect of 200m width (i.e. 100m to either side of the transect) along a c.19km route covering 380ha in the bottom of the valley. Meadows and pastures below the treeline (1,560-2,200m asl) were assumed to be used by the Wheatears as arrival habitat after migration (Supplementary material Figure A1). The complete transect was visited for the first time across three consecutive days (20 to 22 May) and twice four days later (26 to 29 May). Afterwards, specific points were visited as long as Wheatears were found at those points along the route, to define the point in time of the abandonment of the arrival habitats. GPS points were taken where Wheatears were sighted and habitat parameters were collected within a 100m radius of each point; following methodology used in previous studies (Jähnig et al., 2018, 2020; Sander et al., 2021, 2022). We recorded: elevation; cover of snow, "grass" (green ground-level vegetation), rock, shrubs (juniper, rhododendron, bilberry and other occasional species), bare ground, boulders (rocks taller than 1.5m); canopy, and grass height (five measurements along the radius with a random angle), number of habitat structures (shrub, forest, boulder and snow patches, gulleys), number of mature trees (20cm or more diameter, within 50m radius), and number of small larches (lower than 2m, see Supplementary material, Table A1).

Breeding territory mapping

We defined four sectors between 29 and 48ha (a total area of 161ha) located above the treeline within the study area for the breeding territory (henceforth "territory") mapping and the control point survey, by using QGIS (version 3.10) and Google Earth (Supplementary material, Figure A1). The sectors were selected in open grassland

covering a broad elevational gradient, in areas with a known high density of breeding Wheatear pairs. We defined a route for each sector (total 6km), along which we set points at 200m intervals for the control point survey (6–8 points per sector, 30 in total). These points were thus independent of bird activity and gave a measure of the general habitat available in each sector (Supplementary material, Figure A1). In 2019, on the same days as the first arrival habitat mapping was conducted (20 to 22 May), snow cover was estimated from a distance for the control points within the territory mapping study area. In both years, territory mapping and the control point surveys were conducted over five visits across the breeding season, as soon as the area was accessible by foot, from 27 May in 2019 and 14 May in 2020, until 21 July in 2019 and 10 July in 2020. During each visit, habitat parameters (the same used for arrival mapping; see above and Supplementary material, Table A1) were measured for each control point (covering an area of 200 x 200m) and for each territory. In total, territory mapping was carried out by three observers, who conducted the first visit in each year and sector together to calibrate the method and the estimation of habitat parameters.

The first territory mapping was carried out in 2019, from sunrise around 8am until 12pm at the latest, in suitable weather conditions, following the methodology of Südbeck & Weick (2005). On each visit, positions of males sighted along the route were marked with a GPS device. Male behaviour and movements in relation to this position were recorded, with distances measured with a laser range finder. After each visit, estimated territories were digitalised by drawing polygons on a geo-referenced map (taking into account positions and movements noted on paper in the field). These are referred to as territory polygons. The direction of walking the route was changed between visits in order to account for the potential effect of time of day on bird activity. Final unique territories were drawn and identified after the fifth visit by taking into account the territory polygons drawn after each visit, male behaviour (e.g. singing, interactions with female, chasing of other males (but see Südbeck & Weick, 2005) and the overlap of the polygons (see Supplementary material, Figure A1, for an example).

In 2020, we identified unique territories by comparing mapped territories with those defined in the same area in 2019. Territorial males were mapped on territory boundaries identified from the previous year, and the surrounding habitat was recorded as described above. We assumed that territory boundaries were the same in both years, as shown in previous studies on the Wheatear (Arlt & Pärt, 2007; Currie et al., 2008; Öberg et al., 2014). Territories were defined as occupied when territorial behaviour and/or nests were recorded in the same territory polygon on at least two of the five visits. Additional territories (not recorded in 2019) were identified if territorial behaviour or nest sites were recorded in close proximity to each other on at least three visits (without overlapping previous polygons and recorded simultaneously in the same visit as previously identified neighbouring territories).

Statistical analyses

All statistical analyses were carried out in R Project (version 4.2.2). Before analyses, all continuous variables were scaled and centred in order that effect sizes could be directly compared. Furthermore, we reduced collinearity by removing variables that showed strong inter-correlation using the standard threshold of $r > 0.6$ found in Zuur et al. (2009).

Differentiation between arrival and territory habitats

In order to visualize the habitat differences between arrival points, control points and territories, we carried out a Principal Component Analysis (PCA) using the prcomp function (package stats). Here, we only used the habitat data collected in the first week of June, when habitat surveys were carried out simultaneously for the three habitat categories. It was thus possible to compare the temporally varying habitat parameters snow-melt and vegetation phenology for the different categories at the same time, reflecting the choice of habitat available to birds at that moment.

Territory characterisation

General linear mixed models (GLMM) and Bayesian model averaging, (as described by Korner-Nievergelt et al., 2015) were carried out to test which environmental variables were important for territory selection. We used a binomial GLMM (i.e. 0 for control points as pseudo-absence points and 1 for territories as selected points) using the lme4 package (Bates et al., 2007), with the same habitat variables as used in the PCA as predictors and visit date as a categorical random effect in order to account for seasonal effects (since repeated observations taken on the same date are not strictly independent). Here, observations of control points and territories from all five visits were analysed. Initially, we included the unique territory ID (n = 68) as a random effect, but models did not converge. We thus could not account for the non-independence between the territory polygons. Non-linear effects of ecologically relevant variables (all scaled) were tested and subsequently Bayesian model averaging was carried out using the bms function, which fits all possible models and calculates posterior inclusion probabilities (PIP), using the BMS package (Zeugner, 2015). The variables were ordered according to their PIPs, with the highest PIP for variables most closely associated with the selection of the territory. Posterior model probabilities (PMP) were calculated with the topmodels.bma function, which gives 1 for variables included in the best models and 0 for excluded variables. Within the five best models, we selected the final model based on the highest PMP, which was used to describe the effects of habitat variables on the probability to be selected as a territory.

Occupation timing

The dataset for the occupation timing analysis only included the dates on which each unique territory was first recorded. We transformed date into a numeric variable (day of year (doy), 1 = 1 January) and centred it within its year subset to account for inter-annual variability of spring phenology. This was thus expressed as a measure of relative arrival at the unique territory, as we were interested in the order in which territories were occupied independently of the overall spring phenology of the respective year.

Territory recordings after the third quartile of doy of the respective breeding season (doy > 3rd quartile of doy) were excluded from the data set, as they were not considered as newly occupied territories but as territorial behaviour after nest failure. We selected the habitat parameters considered important for territory selection (see Territory characterisation) and elevation to build a full model. As for the analyses of the whole dataset, all habitat variables were centred and scaled prior to the analysis and checked for collinearity. We modelled the influence of habitat parameters and their quadratic terms on occupation timing (response variable) with a generalized linear model (GLM) using the glm function. The best performing model was selected by comparing AICs (equal performance when $\Delta AIC < 2$).

For both territory characterisation and occupation timing, the interpretation of final model results followed the Bayesian framework proposed by Korner-Nievergelt et al. (2015) using improper priors, with $p(\beta) \propto 1$ for the coefficients, and $p(\sigma) \propto 1/\sigma$ for the variance parameters. The posterior distribution was approximated by simulating 2,000 values from the joint posterior distribution of the model parameters using the sim function of the arm package (Gelman and Hill, 2007). An effect was considered significant if the credible interval of the model estimate did not include zero. For all models, model assumptions were assessed following Korner-Nievergelt et al. (2015) (i.e. residual analysis, overdispersion and zero-inflation checks).

Results

Within the first arrival habitat mapping round, we recorded 70 individuals at 18 locations. The last birds were recorded on 29 May at single locations. In total, we recorded 370 territory polygons (N = 181 in 2019 and N = 189 in 2020). These were summed across all visits and included repeated measurements for the same unique territory which were identified after the fifth visit. We identified 67 unique territories in 2019 and 59 in 2020 in the area of 161ha, constituting an average density of 0.4 breeding pairs/ha. Mapping started about two weeks earlier in 2020 as there was less

snow cover and birds did not stay at lower elevations during the arrival period as observed in 2019. The largest increase in the number of territory polygons was observed between the second and third visit (within one week) in 2019, and between the first and second visit (within one week) in 2020. It should be noted that the general trend in the increase and decrease (between the third and fourth visits in 2019, and between the second and third visits in 2020) of territory polygons was the same as the previous year, but that the occupation of the breeding area was advanced by approximately one week in 2020. Occupation in 2020 appeared to be more rapid than in 2019, and there was a strong decrease in territorial behaviour after the fourth visit at the beginning of July, whereas in 2019, territorial behaviour was still very evident during the last visit at the end of July (Figure 1).

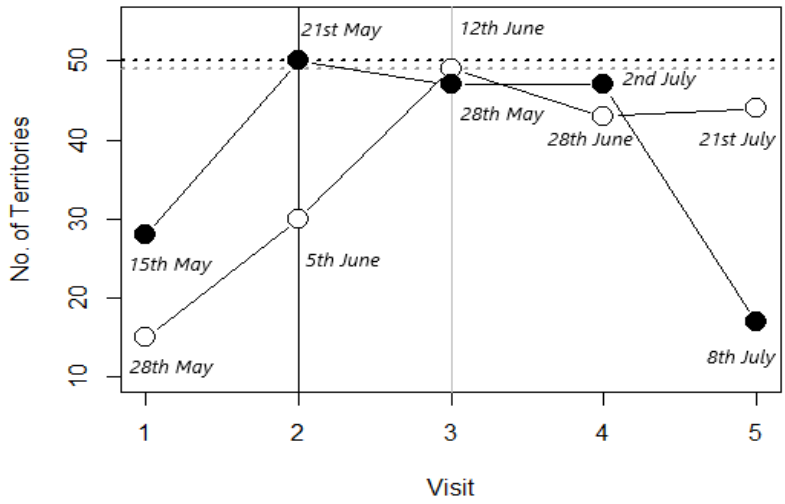

Figure 1. Total number of territories recorded per visit per year (white: 2019, black: 2020). Dates for each visit differed between years. Horizontal dashed lines (grey: 2019, black: 2020) represent the maximum number of territories recorded in a single visit, indicated by vertical lines (grey: 2019, black: 2020), respectively.

Differences between arrival and territory habitats

The first principal component, explaining 26% of total variance, was negatively correlated with grass height ("grassh") and, to a lesser extent, with grass cover

("grass"). The second principal component, explaining 16% of total variance, was positively correlated with snow cover ("snow"). The third component, explaining 15% of total variance, was negatively correlated with rhododendron cover ("rhod") whereas the fourth principal component, explaining 9% of total variance, was positively correlated with the number of small larches ("slarix"). The results of the PCA show that the three categories were clustered to some degree: in the first week of June at the time the birds chose to move to breeding territories, arrival points were characterised by high grass cover, taller grass and the presence of trees (canopy cover) and small larches. Control points and territories were less clearly discriminated, but control points were positively associated with snow and rhododendron cover ("rhod"), whereas territories were positively associated with rock ("rock") and juniper cover ("jun"), as well as greater numbers of boulders and more bare ground ("bare") (Supplementary material, Table A2, Figure 2).

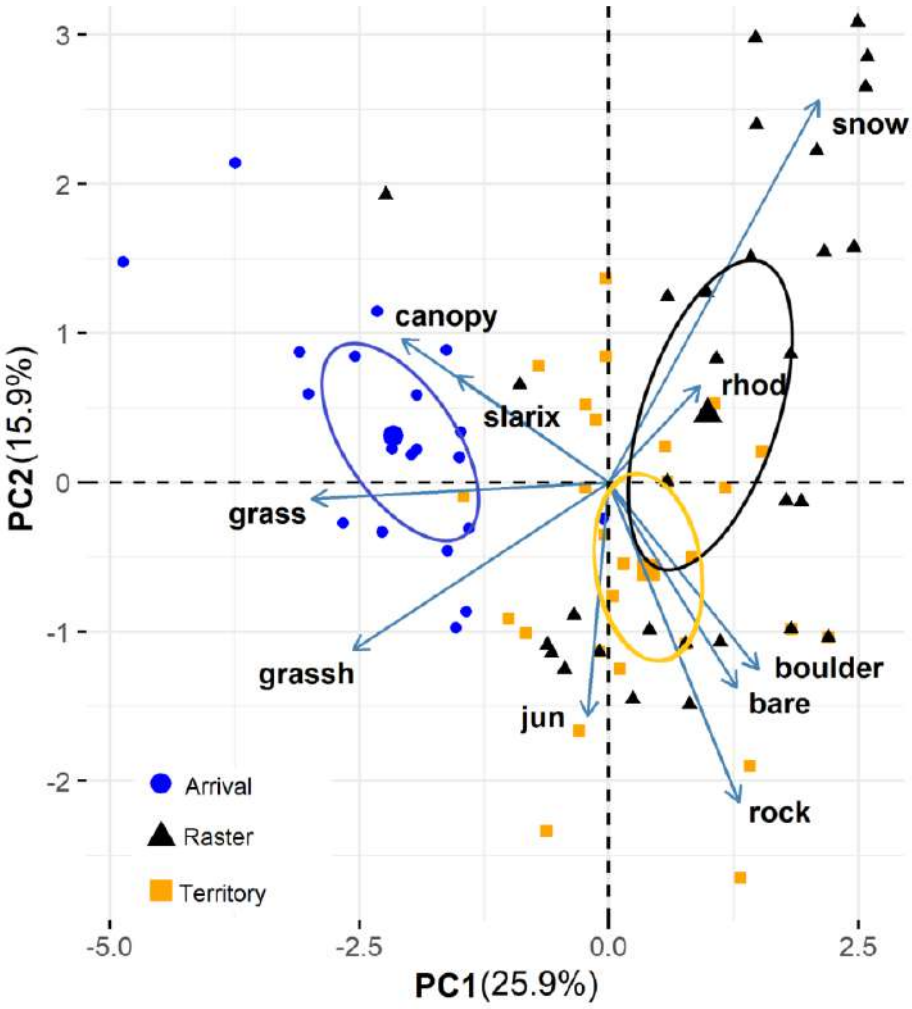

Figure 2. Principal components 1-2 for habitat variables of the three habitat types. Arrival points are represented by *circles*, control points by *triangles* and territories by *squares* (symbol size represents the number of points included). 99% confidence ellipses shown for each group (black: arrival, black dashed: control, grey: territory). Habitat variables and their contribution are represented by grey arrows.

Territory characteristics

Posterior inclusion probabilities (PIP) showed grass height as the most important habitat variable in territory selection, followed by the quadratic term of grass height, the number of small larches, rock cover and the number of boulders. These variables

were included in the best model that was then used to describe their effects: Grass height and rock cover (linear) had a positive effect on territory selection, whereas number of small larches and boulders reduced the probability for a point to be selected as a territory (Figure 3, Supplementary material, Table A3).

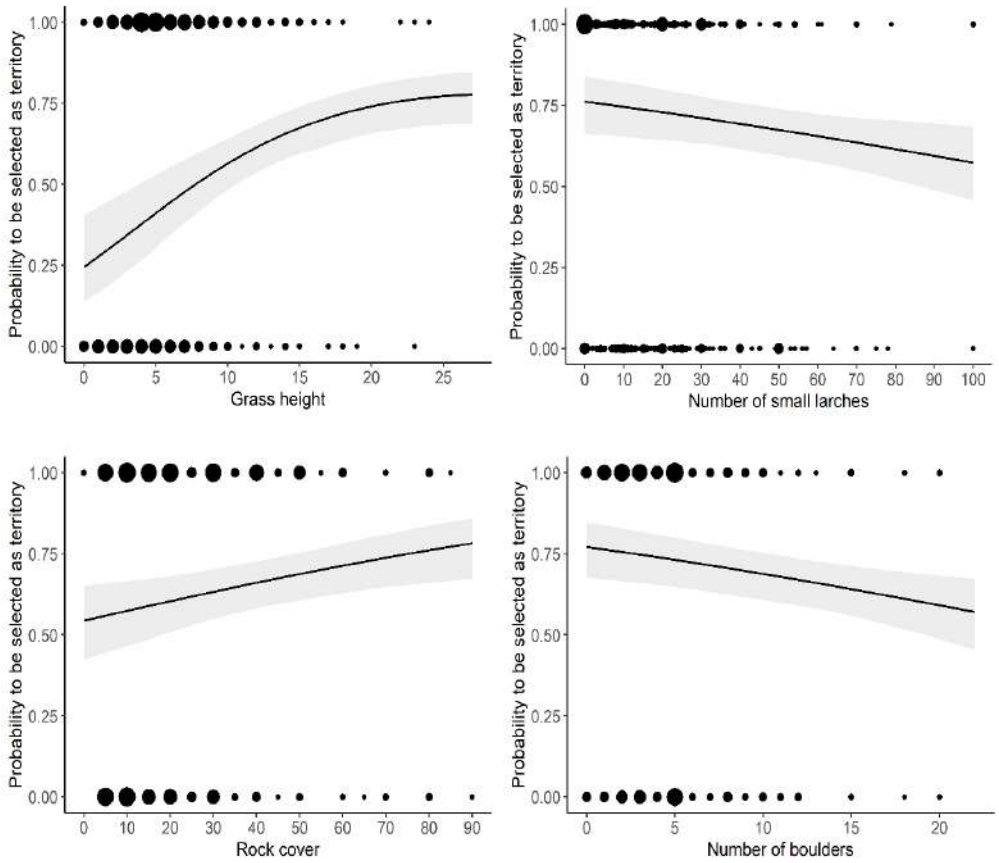

Figure 3. Relationship between grass height (cm), number of small larches, rock cover (%) and number of boulders from the best model and the probability for territory selection. Black circles represent the presence/absence of the territory in relation to the habitat parameter, and circle size is proportional to the number of points for a given category of presence/absence at a certain level of habitat parameter extension. Lines represent the fitted values and grey shaded areas the 95% CrI of the models given in Supplementary material, Table A3.

Occupation timing

For the model of occupation timing, we included only those observations that were recorded before doy = 164 (2019) and before doy = 142 (2020), and for which the habitat measurements were complete. The resulting data set included 71 observations in unique territories for both years combined. When controlling for collinearity and correlations between the fixed effects, all variables were below the threshold for VIF < 4, and correlation coefficients were below 0.6 (Supplementary material, Table A4, A5). Four models (three including snow cover with its quadratic term) performed equally well. As the quadratic term of snow cover was never significant, it was removed in the final model, whereas the other six variables were retained (Supplementary material, Table A6). The final model showed that occupation timing was positively associated with elevation (linear term), as territories at higher elevations were occupied at later dates, and that in later occupied territories, grass cover (linear and quadratic terms) was greater. Conversely, early-occupied territories showed high snow cover (linear term), but also taller grass (linear and quadratic term) (Table 2, Figure 4).

Table 2. Effects of habitat variables and elevation (scaled) on territory occupation date (doy, scaled) modelled with the final GLM (N = 71, Table A6). Estimates were considered significant if bold: P < 0.05, and 95% credible intervals (CrI) of the model estimates did not include zero.

Variables	Estimates (95% CrI)	±SE	P
Intercept	**0.445 (0.264 – 0.632)**	0.091	**<0.001**
Small larches	-0.147 (-0.309 – 0.015)	0.082	0.071
Elevation	**0.243 (0.058 – 0.414)**	0.090	**0.009**
Snow cover	**-0.307 (-0.513 – -0.107)**	0.102	**0.004**
Grass cover	**0.300 (0.073 – 0.548)**	0.121	**0.015**
Grass cover^2	**-0.216 (-0.331 – -0.099)**	0.059	**<0.001**
Grassheight	**-0.253 (-0.450 – -0.052)**	0.103	**0.017**
Grassheight^2	**0.137 (0.023 – 0.251)**	0.058	**0.019**

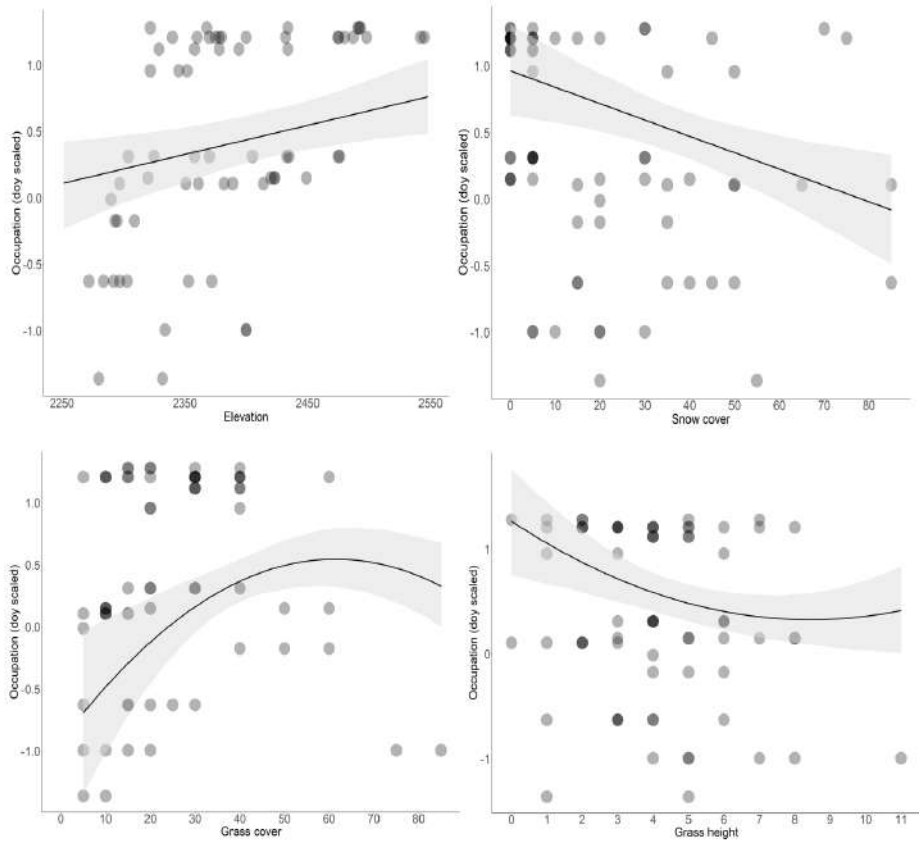

Figure 4. Occupation timing in relation to elevation (m asl), snow and grass cover (%), and grass height (cm), modelled with GLMs for data from 2019–2020. Note that the y-axis is the scaled day of year (doy), with early occupation < 0 and late occupation > 0. Lines represent the fitted values and grey shaded areas the 95% CrI of the models given in Table 2. Darker points represent several points that are overlapping.

Discussion

Contemporaneous observations in potential habitats below and above the treeline showed that birds first arrived in spring at low elevations in the valley bottom, when snow cover was still high overall. Our observation was recently verified with the help of geolocators collecting not only light levels, but also atmospheric pressure (pressure loggers) (Rime et al. 2023). As soon as higher elevations became partly snow-free, most

arrival sites were abandoned and higher elevation territories above the treeline were occupied. In our study period in 2019, Wheatears encountered complete snow cover at the high-elevation breeding sites upon arrival (Sander et al., 2021). They are assumed to arrive in lean body condition and need immediate access to food resources after migration, as this species' migration strategy is to fly with daily stopovers for refuelling, without carrying large energy stores unless barriers, such as the Mediterranean Sea, have to be crossed (Delingat et al., 2006; Maggini et al., 2013). Further studies on Wheatears have shown that the conditions encountered upon arrival, and thus for recovering after spring migration and gaining energy stores prior to egg laying (arrival-breeding interval), determine breeding phenology and success (Low et al., 2019; Sander et al., 2021). The two habitat types (arrival and territory) differed in grass height and grass cover, which were both higher in arrival points. High elevation habitats (control and territory) clearly showed higher rock and lower grass cover. As arrival points were subsequently abandoned, we assume that these open habitats, with their high vegetation cover (including ground and woody vegetation), their proximity to the forest (number of trees) and generally low rock cover, are not as suitable for nesting as sites above the treeline.

Control points and territory polygons differed mainly in snow and rhododendron cover, which were lower in the territories. This suggests that Wheatears avoided areas with high snow and rhododendron covers. Conversely, territories were also situated in areas with greater juniper cover. These two shrub species usually occur in very different microclimates, with juniper growing on south-facing slopes that are sun-exposed, and rhododendron on north-facing slopes, which are covered in snow for longer. This supports previous findings on open grassland birds in our study area, indicating that, at a small-scale, Wheatears prefer sun-exposed and warmer sites for nesting (Jähnig et al., 2020). Additionally, juniper shrubs in our study area are short, providing a more open habitat than sites dominated by rhododendron.

Models used for territory characterisation showed clearly that grass height was the most important habitat variable for territory selection, a similar finding to previous studies on lowland Wheatears in Sweden, the United Kingdom and The Netherlands. However, in contrast to the above mentioned lowland populations, where territories with short field layers (<5cm) had a higher prey availability, lower predation rates, higher fledgling production and overall higher breeding success and fitness (Tye, 1992; Pärt, 2001; Arlt et al., 2008; Currie et al., 2008; Öberg et al., 2014; Paquet et al., 2019), Wheatears in our high-elevation study area preferred sites with taller grass up to 20cm. This is supported by previous findings on nest survival within our population, which was higher with relatively taller grass (Sander et al., 2022). Whereas the habitats of Northern European populations are generally well vegetated, the high-elevation population breeds in relatively poorly vegetated open habitat (across all recorded territories, grass cover was 32 ± 16 % on average), within a habitat mosaic of areas with high scree and rock cover. The remaining vegetation is therefore distributed in a patchy manner. These patches may provide invertebrate food resources Most of the grassland is grazed later in the season, when the majority of the chicks have fledged or are about to fledge (mid-July; Sander et al., 2021), so that grasses and forbs are potentially growing up to their maximum height. On average, the grass in the territories was 7 ± 4 cm tall. We do not have direct information regarding prey availability, prey abundance or predation risk in relation to vegetation height, but as lower failure rates were found at sites with taller grass (Sander et al., 2022), we infer that there is no negative effect of taller grasses on breeding success, as was found in the Swedish lowland populations. In contrast to lowland habitats, we thus assume a beneficial effect of tall grass during spring that presumably holds a much higher invertebrate diversity and abundance than lowland 'tall' habitats characterised by intensive agricultural landscapes with denser and more uniform swards where fertilizers and pesticides decrease insect abundance and diversity (Archaux, 2007; Arlt and Pärt, 2007; Arlt et al., 2008).

The occurrence and abundance of small larches had a negative effect on territory selection. Small larches provide a measure of the degree of shrub encroachment in the Alpine region, similar to other woody species, e.g. Salix, Pinus mugo, rhododendron and juniper (Jähnig et al., 2018; Malfasi & Cannone, 2020; Cannone et al., 2022), whose spread is reducing the area of grasslands above the treeline (Gehrig-Fasel et al., 2007). The Wheatear, and other open habitat species, is thus expected to be threatened by a range contraction in our study area due to the increasing number of small larches and shrubs such as rhododendron and juniper. This effect is likely to be even stronger if pastures in the area are abandoned, since seasonal grazing currently keeps the area around the treeline open (Jähnig et al., 2018). The negative effect of boulders on territory selection may result from the general preference of the species for an open area without visual barriers (Conder, 1989), which is assumed to be the same reason for the avoidance of large numbers of small larches. However, a few larches and boulders may provide perches or shelter, as happens with the scattered trees in the Wheatear's wintering grounds (Wilson & Cresswell, 2010).

Territory occupation by male Wheatears in our study area was earliest at lower elevations (above the treeline), but did not exclude areas with high snow cover. As these early occupied territories also had taller grass, it suggests that arriving males selected territories that already offered food resources, even when large areas were still inaccessible due to snow cover. During territory establishment and prior to egg laying, the availability and abundance of food is essential for later breeding success (Tye, 1992). Tall grass, but at the same time low grass cover and high snow cover, was characteristic of early-occupied territories, which are assumed to be of higher quality (Currie et al., 2008). Although grass and snow cover were not significantly correlated, there could be a unit-sum constraint between these two variables that additionally changes across the season. Thus, we assume that the high snow cover and low grass cover in the early territories is to some extent a seasonal effect and may not be driven

by the preference of males for these habitat characteristics in general. These territories may also be occupied first due to environmental constraints (i.e. the extent of snow and plant cover) on the accessibility of food resources and nest sites. We therefore conclude that the only true indicator of territory quality (as inferred from occupation timing) is tall, patchily-distributed grass and extensive rock cover that influence respectively prey abundance (Oosten et al., 2014), nest site availability and concealment from predators in a landscape with many potential nest holes (Zamaro, 1990).

The relationship between occupation timing and environmental variables offers insight into the behavioural adaptation of the Wheatear to its alpine breeding habitat and the constraints of the early season. High energy demands for egg production and territory defence while temperatures are still low and the partial inaccessibility of nest sites and invertebrate food resources force arriving Wheatears to settle at lower elevations first, where the ground is partially accessible and ground vegetation is developed, despite overall high snow cover. Predicting territory quality by assessing the vegetation structure prior to nesting may be difficult when large areas are covered in snow upon arrival, as shown in a previous study (Sander et al. 2021). Additional cues are expected to be used by male Northern Wheatears, as seen in Cyprus Wheatears Oenanthe cypriaca in which breeding territory selection has been found to depend on the locations of post-fledging dispersal movements, during which young birds may assess the quality of their potential future breeding sites (Patchett et al., 2022).

In our alpine study area, both the territory selection models as well as the occupation timing model show a clear preference by the Wheatear for open alpine grasslands over highly vegetated pastures and meadows below the treeline. However, the pressure loggers revealed that some individuals perform daily movements between their high elevation territories and lower elevation foraging grounds (Rime et al., 2023). Extensive rock cover and greater distance from forest structures (indicated

by the avoidance of higher numbers of small larches) in the open alpine grassland seem to be the most important habitat features that differentiate this breeding habitat from the pre-breeding foraging grounds at lower elevations. Nevertheless, a few territories (9%;18 of 201 nests during 2019–2022) were occupied below the treeline in our valley and were used for at least four consecutive years. Clearly this population could also breed at low-elevation sites in alpine valleys as long as open habitats with high rock cover and a large distance to the nearest forest patch are present. Predation risk may be higher in these lower elevation habitats due to their proximity to forest (Masoero et al., 2016; Sasvári & Hegyi, 2011). Furthermore, at low elevations, disturbance due to human recreational activities is more frequent and cows graze earlier in the season here, i.e. before Wheatear fledging. This could affect reproductive success as our population showed a trend towards smaller nestlings at low elevations (Sander et al., 2022). On the other hand, nests that were established earlier when vegetation development was enhanced due to higher temperatures and earlier snow melt had higher survival probabilities (Sander et al., 2022).

Despite the apparently lower quality, we conclude that extensively managed grasslands at low elevations (alpine pastures, meadows) may be an alternative nesting habitat for birds breeding in alpine grasslands that are shrinking due to current environmental change: shrub encroachment and abandonment of grazing. We thus consider the maintenance of extensive grazing practices in the Alps as beneficial for grassland birds by both preventing further shrub encroachment around the treeline and sustaining breeding habitats at low elevations.

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References

Archaux, F. (2007). Are mountains refuges for farmland bird species? A case study in the northern French Alps. Bird Study 54, 73–79. doi: 10.1080/00063650709461458.

Arlt, D., Forslund, P., Jeppsson, T., and Pärt, T. (2008). Habitat-Specific Population Growth of a Farmland Bird. PLoS ONE 3, e3006. doi: 10.1371/journal.pone.0003006.

Arlt, D., and Pärt, T. (2007). NONIDEAL BREEDING HABITAT SELECTION: A MISMATCH BETWEEN PREFERENCE AND FITNESS. Ecology 88, 792–801. doi: 10.1890/06-0574.

Arlt, D., and Pärt, T. (2008). Post-breeding information gathering and breeding territory shifts in northern wheatears. J. Anim. Ecol. 77, 211–219. doi: 10.1111/j.1365-2656.2007.01329.x.

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J. W., et al. (2012). Cross-hemisphere migration of a 25 g songbird. Biol. Lett. 8, 505–507. doi: 10.1098/rsbl.2011.1223.

Bollmann, K., Reyer, H. U., and Brodmann, P. A. (1997). Territory quality and reproductive success: can Water Pipits Anthus spinoletta assess the relationship reliably? Ardea 63, 1179–1191. doi: 10.5167/uzh-168.

Boyle, W. A., and Martin, K. (2015). The conservation value of high elevation habitats to North American migrant birds. Biol. Conserv. 192, 461–476. doi: 10.1016/j.biocon.2015.10.008.

Brambilla, M., Resano-Mayor, J., Arlettaz, R., Bettega, C., Binggeli, A., Bogliani, G., et al. (2020). Potential distribution of a climate sensitive species, the White-winged Snowfinch Montifringilla nivalis in Europe. Bird Conserv. Int., 1–11. doi: 10.1017/S0959270920000027.

Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R., et al. (2009). Climate variability and change in the Greater Alpine Region over the last two centuries

based on multi-variable analysis. Int. J. Climatol. 29, 2197–2225. doi: 10.1002/joc.1857.

Cannone, N., Guglielmin, M., Casiraghi, C., and Malfasi, F. (2022). Salix shrub encroachment along a 1000 m elevation gradient triggers a major ecosystem change in the European Alps. Ecography, ecog.06007. doi: 10.1111/ecog.06007.

Caprio, E., Chamberlain, D. E., Isaia, M., and Rolando, A. (2011). Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. Biol. Conserv. 144, 2958–2967. doi: 10.1016/j.biocon.2011.08.021.

Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A., et al. (2012). The altitudinal frontier in avian climate impact research. Ibis 154, 205–209.

Chamberlain, D. E., Negro, M., Caprio, E., and Rolando, A. (2013). Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol. Conserv. 167, 127–135. doi: 10.1016/j.biocon.2013.07.036.

Conder, P. (1989). The Wheatear. 1st ed. London: Christopher Helm.

Currie, D., Thompson, D. B. A., and Burke, T. (2008). Patterns of territory settlement and consequences for breeding success in the Northern Wheatear Oenanthe oenanthe. Ibis 142, 389–398. doi: 10.1111/j.1474-919X.2000.tb04435.x.

Delgado, M. del M., Bettega, C., Martens, J., and Päckert, M. (2019). Ecotypic changes of alpine birds to climate change. Sci. Rep. 9, 16082. doi: 10.1038/s41598-019-52483-0.

Delingat, J., Dierschke, V., Schmaljohann, H., Mendel, B., and Bairlein, F. (2006). Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear. 14.

Desaever, R., and Bairlein, F. (2020). Earlier spring passage of 'Greenlandic' Northern Wheatears Oenanthe o. leucorhoa on the coast of Belgium. Ringing Migr., 1–5. doi: 10.1080/03078698.2019.1759907.

Ewing, S. R., Baxter, A., Wilson, J. D., Hayhow, D. B., Gordon, J., Thompson, D. B. A., et al. (2020). Clinging on to alpine life: Investigating factors driving the uphill range contraction and population decline of a mountain breeding bird. Glob. Change Biol. 26, 3771–3787. doi: 10.1111/gcb.15064.

Gehrig-Fasel, J., Guisan, A. and Zimmermann, N.E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? J. Veg. Sci. 18, 571–582.

Gelman, A., and Hill, J. (2007). Data analysis using regression and hierarchical/multilevel models. N. Y. NY Camb.

Henry, P.-Y., and Ollivier, P. (2015). Low Immigration and High Local Recruitment in an Isolated, Coastal Population of a Declining Grassland Passerine, the Northern Wheatear Oenanthe oenanthe. Acta Ornithologica 50, 193–203. 10.3161/00016454AO2015.50.2.007.

Herrando, S., Brotons, L., Anton, M., Páramo, F., Villero, D., Titeux, N., et al. (2016). Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. Environ. Conserv. 43, 69–78. doi: 10.1017/S0376892915000260.

Inouye, D. W., Barr, B., Armitage, K. B., and Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. Proc. Natl. Acad. Sci. 97, 1630–1633.

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A., et al. (2018). The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. J. Ornithol. 159, 747–759. doi: 10.1007/s10336-018-1549-9.

Jähnig, S., Sander, M. M., Caprio, E., Rosselli, D., Rolando, A., and Chamberlain, D. (2020). Microclimate affects the distribution of grassland birds, but not forest

birds, in an Alpine environment. J. Ornithol. 161, 677–689. doi: 10.1007/s10336-020-01778-5.

Kassambara, A., and Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. Available at: https://CRAN.R-project.org/package=factoextra [Accessed February 16, 2022].

Koleček, J., Adamík, P., and Reif, J. (2020). Shifts in migration phenology under climate change: temperature vs. abundance effects in birds. Clim. Change 159, 177–194. doi: 10.1007/s10584-020-02668-8.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., and Korner-Nievergelt, P. (2015). Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan. Elsevier doi: 10.1016/B978-0-12-801370-0.18001-3.

La Sorte, F. A., and Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. Proc. R. Soc. B Biol. Sci. 277, 3401–3410. doi: 10.1098/rspb.2010.0612.

Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., et al. (2018). Declining population trends of European mountain birds. Glob. Change Biol. 25, 577–588. doi: 10.1111/gcb.14522.

Low, M., Arlt, D., Knape, J., Pärt, T., and Öberg, M. (2019). Factors influencing plasticity in the arrival-breeding interval in a migratory species reacting to climate change. Ecol. Evol., ece3.5716. doi: 10.1002/ece3.5716.

Maggini, I., Cardinale, M., Sundberg, J. H., Spina, F., and Fusani, L. (2020). Recent phenological shifts of migratory birds at a Mediterranean spring stopover site: Species wintering in the Sahel advance passage more than tropical winterers. PLOS ONE 15, e0239489. doi: 10.1371/journal.pone.0239489.

Maggini, I., Spina, F., Voigt, C. C., Ferri, A., and Bairlein, F. (2013). Differential migration and body condition in Northern Wheatears (Oenanthe oenanthe) at a Mediterranean spring stopover site. J. Ornithol. 154, 321–328. doi: 10.1007/s10336-012-0896-1.

Malfasi, F., and Cannone, N. (2020). Climate Warming Persistence Triggered Tree Ingression After Shrub Encroachment in a High Alpine Tundra. Ecosystems 23, 1657–1675. doi: 10.1007/s10021-020-00495-7.

Martin, K., and Wiebe, K. L. (2004). Coping Mechanisms of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience. Integr. Comp. Biol. 44, 177–185. doi: 10.1093/icb/44.2.177.

Martin, T. E. (1995). Avian Life History Evolution in Relation to Nest Sites, Nest Predation, and Food. Ecol. Monogr. 65, 101–127. doi: 10.2307/2937160.

Masoero, G., Maurino, L., Rolando, A., and Chamberlain, D. (2016). The effect of treeline proximity on predation pressure: an experiment with artificial nests along elevational gradients in the European Alps. Bird Study 63, 395–405. doi: 10.1080/00063657.2016.1214106.

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., et al. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Sci. Rep. 7, 1902. doi: 10.1038/s41598-017-02045-z.

Mermillon, C., Jähnig, S., Sander, M. M., Alba, R., Rosselli, D., and Chamberlain, D. (2021). Variations in Niche Breadth and Position of Alpine Birds along Elevation Gradients in the European Alps. Ardeola 69, 41–58. doi: 10.13157/arla.69.1.2022.ra3.

Møller, A. P. (1994). Phenotype-dependent arrival time and its consequences in a migratory bird. Behav. Ecol. Sociobiol. 35, 115–122. doi: 10.1007/BF00171501.

Morbey, Y. E., and Hedenström, A. (2020). Leave Earlier or Travel Faster? Optimal Mechanisms for Managing Arrival Time in Migratory Songbirds. Front. Ecol. Evol. 7, 492. doi: 10.3389/fevo.2019.00492.

Öberg, M., Pärt, T., Arlt, D., Laugen, A. T., and Low, M. (2014). Decomposing the seasonal fitness decline. Oecologia 174, 139–150. doi: 10.1007/s00442-013-2763-z.

Oosten, H. H. van, van den Burg, A. B., Versluijs, R., and Siepel, H. (2014). Habitat Selection of Brood-Rearing Northern Wheatears Oenanthe oenanthe and Their Invertebrate Prey. Ardea 102, 61–69. doi: 10.5253/078.102.0111.

Oyler, J. W., Dobrowski, S. Z., Ballantyne, A. P., Klene, A. E., and Running, S. W. (2015). Artificial amplification of warming trends across the mountains of the western United States. Geophys. Res. Lett. 42, 153–161. doi: https://doi.org/10.1002/2014GL062803.

Paquet, M., Arlt, D., Knape, J., Low, M., Forslund, P., and Pärt, T. (2019). Quantifying the links between land use and population growth rate in a declining farmland bird. Ecol. Evol. 9, 868–879. doi: 10.1002/ece3.4766.

Pärt, T. (2001). The effects of territory quality on age-dependent reproductive performance in the northern wheatear, Oenanthe oenanthe. Anim. Behav. 62, 379–388. doi: 10.1006/anbe.2001.1754.

Patchett, R., Styles, P., Robins King, J., Kirschel, A. N. G., and Cresswell, W. (2022). The potential function of post-fledging dispersal behavior in first breeding territory selection for males of a migratory bird. Curr. Zool., zoac002. doi: 10.1093/cz/zoac002.

Rime, Y., Nussbaumer, R., Briedis, M., Sander, M. M., Chamberlain, D., Amrhein, V., et al. (2023). Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant. Mov Ecol 11, 19. doi: 10.1186/s40462-023-00381-6.

Sander, M. M., Chamberlain, D., Mermillon, C., Alba, R., Jähnig, S., Rosselli, D., et al. (2021). Early Breeding Conditions Followed by Reduced Breeding Success Despite Timely Arrival in an Alpine Migratory Songbird. Front. Ecol. Evol. 9, 676506. doi: 10.3389/fevo.2021.676506.

Sander, M. M., Jähnig, S., Lisovski, S., Mermillon, C., Alba, R., Rosselli, D., et al. (2022). High nest failure but better nestling quality for early breeders in an alpine

population of Northern Wheatear (Oenanthe oenanthe). Ibis n/a. doi: 10.1111/ibi.13133.

Sander, M. M., Jähnig, S., Lisovski, S., Mermillon, C., Alba, R., Rosselli, D., et al. Reproductive trade-offs for early breeders at high elevations in a long-distance migrant, the Northern Wheatear Oenanthe oenanthe.

Sasvári, L., and Hegyi, Z. (2011). Predation Risk of Tawny Owl Strix aluco Nests in Relation to Altitude, Breeding Experience, Breeding Density and Weather Conditions. Ardea 99, 227–232. doi: 10.5253/078.099.0213.

Schmaljohann, H., and Both, C. (2017). The limits of modifying migration speed to adjust to climate change. Nat. Clim. Change 7, 573–576. doi: 10.1038/nclimate3336.

Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., von Hardenberg, A., and Brambilla, M. (2017). Thermal niche predicts recent changes in range size for bird species. Clim. Res. 73. doi: 10.3354/cr01477.

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., et al. (2018). A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. Ibis 160, 489–515. doi: 10.1111/ibi.12585.

Smith, S. E., Gregory, R. D., Anderson, B. J., and Thomas, C. D. (2013). The past, present and potential future distributions of cold-adapted bird species. Divers. Distrib. 19, 352–362. doi: 10.1111/ddi.12025.

Südbeck, P., and Weick, F. (2005). Methodenstandards zur Erfassung der Brutvögel Deutschlands. Radolfzell: Mugler.

Tye, A. (1992). Assessment of territory quality and its effects on breeding success in a migrant passerine, the Wheatear Oenanthe oenanthe. Ibis 134, 273–285. doi: 10.1111/j.1474-919X.1992.tb03810.x.

Vickery, J., Ewing, S., Smith, K., Pain, D., Bairlein, F., Škorpilová, J., et al. (2014). The decline of Afro-Paleartic migrants and an assessment of potential causes. Ibis 156. doi: 10.1111/ibi.12118.

Wang, Q., Fan, X., and Wang, M. (2016). Evidence of high-elevation amplification versus Arctic amplification. Sci. Rep. 6, 19219. doi: 10.1038/srep19219.

Wilson, J. M., and Cresswell, W. (2010). The Northern Wheatear Oenanthe oenanthe in the Sahel of West Africa: distribution, seasonal variation in abundance and habitat associations. Ostrich 81, 115–121. doi: 10.2989/00306525.2010.488432.

Wretenberg J, Lindström A, Svensson S, Thierfelder T, Pärt T (2006) Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. J Appl Ecol 43: 1110–1120.

Zamaro, R. (1990). Nest-Site Selection of the Common Wheatear in High Mountain Areas of Southeastern Spain. 102, 3.

Zeugner, M. F. and S. (2015). BMS: Bayesian Model Averaging Library. Available at: https://CRAN.R-project.org/package=BMS [Accessed February 16, 2022].

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). "Violation of Independence – Part I," in Mixed effects models and extensions in ecology with R Statistics for Biology and Health., eds. A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith (New York, NY: Springer), 143–160. doi: 10.1007/978-0-387-87458-6_6.

Supplementary material

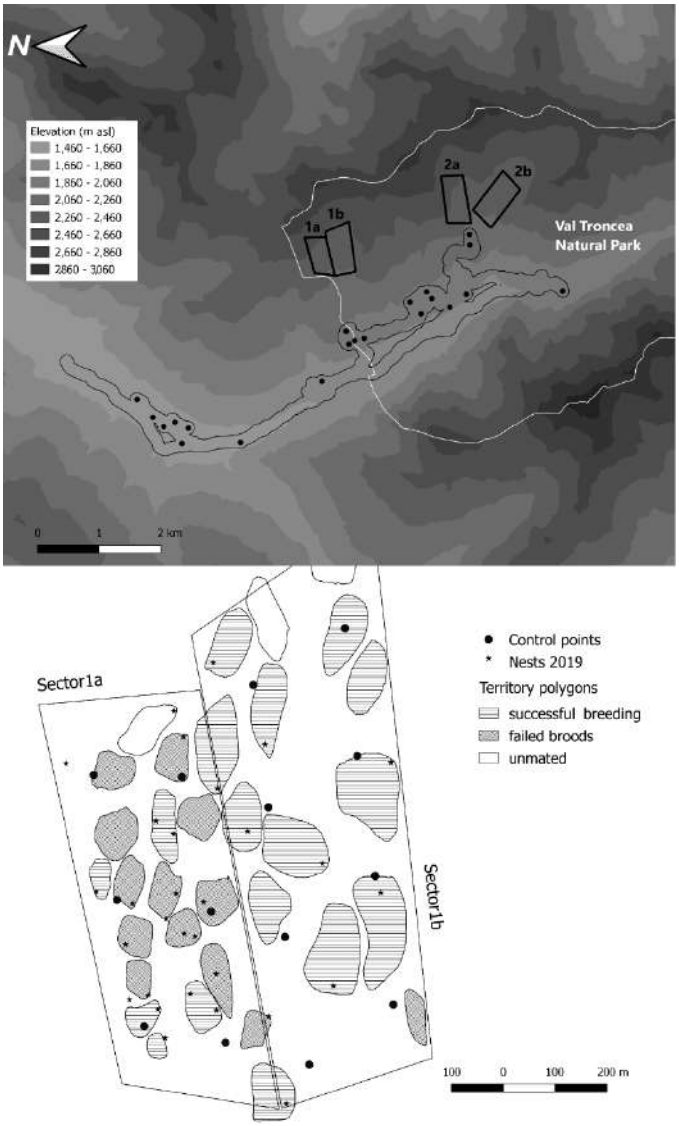

Figure A1. Study design projected on a digital elevation map. Borders of the Val Troncea Natural Park are shown as a white line. Black points show positions of recorded Wheatears within the surveyed arrival habitat (buffer of 200m) below treeline. Sectors (1a, 1b, 2a, 2b) for territory and control point surveys at high elevations (May – July) are shown as black boxes (above). The lower figure is an example of the territory mapping in 2019 in two sectors (1a and 1b), showing territory polygons control points and nest sites.

Table A1. Habitat parameters sampled for arrival points, control points and territories.

Variable	Details
elev	Elevation (m asl)
canopy	Canopy cover (%)
rhod	Rhododendron cover (%)
jun	Juniper cover (%)
vacc	*Vaccinium* cover (%)
oth	Other shrubs cover (%)
grass	Grass cover (%)
grassh	Grass height (cm)
rock	Rock cover (%)
bare	Bare ground cover (%)
snow	Snow cover (%)
boulderc	Boulder cover (%)
shrp	Number of shrub patches
forestp	Number of forest patches
boulderp	Number of boulders
gullp	Number of gulleys
snowp	Number of snow patches
trees	Number of mature tress
cow	Presence/absence of cattle
dung	Presence/absence of cattle dung
build	Presence/absence of buildings
trail	Presence/absence of trails
water	Presence/absence of water
slarix	Number of small larches
road	Presence/absence of roads

Table A2. Factor loadings of the first four principal components based on ten habitat variables for arrival points, control points and territories (N = 84). Factor loadings calculated with the *stats* R package are equal to the coordinates of the variables divided by the square root of the eigenvalue associated with the component.

Habitat Variable	PC1	PC2	PC3	PC4
Canopy cover	-0.361	0.214	-0.212	0.352
Rhododendron cover	0.159	0.144	-0.594	-0.054
Juniper cover	-0.037	-0.349	-0.518	0.218
Grass cover	-0.518	-0.025	0.187	-0.316
Grass height	-0.447	-0.250	-0.120	-0.271
Rock cover	0.227	-0.477	0.377	0.395
Bare ground cover	0.223	-0.306	-0.365	-0.249

Snow cover	0.366	0.570	0.023	-0.063
Boulders	0.260	-0.279	0.022	0.081
Small larches	-0.267	0.159	-0.090	0.651
Proportion of variance	0.259	0.159	0.147	0.097
Cumulative proportion of variance	0.259	0.418	0.565	0.662

Table A3. Output from the model averaging and best models for the probability to be selected as territory according to habitat variables (N = 641). Posterior inclusion probabilities (PIP) are shown, with Posterior means and standard deviations of the model-averaged parameters. Five best ranked-models with the inclusions of the variables (1 included, 0 not included) and posterior model probabilities (PMPs) are shown. Estimates of the best model were considered significant if 95% credible intervals (CrI) did not include zero (in bold). 'Visit' was included as random term in the GLMM (not shown).

Habitat variable	**PIP**	**Post Mean**	**Post SD**	**Best model**	**2nd model**	**3rd model**	**4th model**	**5th model**	**Best model Estimate (CrI)**
Intercept									0.73 (0.38 – 1.08)
Grass height	0.87	0.20	0.10	1	1	1	1	1	0.68 (0.40 – 0.97)
Grass height^2	0.83	-0.16	0.09	1	1	1	1	1	-0.22 (-0.35 - -0.11)
Small larches	0.66	-0.05	0.04	1	0	1	1	0	-0.28 (-0.49 - -0.09)
Rock cover	0.64	0.04	0.04	1	1	1	0	1	0.32 (0.10 – 0.55)
Boulders	0.63	-0.04	0.03	1	1	0	0	1	-0.25 (-0.46 - -0.05)
Canopy cover	0.38	-0.02	0.03	0	1	0	0	0	
Snow cover	0.17	-0.01	0.03	0	0	0	0	0	
Juniper cover	0.09	-0.002	0.01	0	0	0	0	0	
Bare ground cover	0.08	0.002	0.01	0	0	0	0	0	
Rhododendron cover	0.07	-0.001	0.01	0	0	0	0	0	
Grass cover	0.05	0.000	0.01	0	0	0	0	0	
PMP (Exact)				0.15	0.09	0.07	0.06	0.05	
PMP (MCMC)				0.15	0.09	0.07	0.06	0.05	

Table A4. Correlation between explanatory variables in the occupation timing model, calculated with the *cor* function. All correlation coefficients are below the 0.6 threshold and were thus included in the models. Variable abbreviations shown in Supplementary material, Table A1.

	slarix	boulderp	Elevation	grass	grassh	snow
slarix	1.00	-0.11	-0.36	-0.20	0.02	-0.11

boulderp	-0.11	1.00	0.34	-0.10	-0.29	-0.04
elevation	-0.36	0.34	1.00	-0.15	-0.42	0.00
grass	-0.20	-0.10	-0.15	1.00	0.54	-0.48
grassh	-0.11	-0.29	-0.42	0.54	1.00	-0.51
snow	-0.11	-0.04	0.00	-0.48	-0.51	1.00

Table A5. Collinearity of explanatory variables in the linear occupation timing models, calculated with the *vif* (Variance Inflation Factor) function. Variable abbreviations shown in Supplementary material, Table A1.

	slarix	**boulderp**	**elev**	**grass**	**grassh**	**snow**	**rock**
Final model	1.38		1.62	1.70	2.06	1.80	
Full model	1.45	1.21	2.09	2.03	2.22	3.13	2.69

Table A6. General linear models with occupation date (doy, scaled) as response variable, and habitat variables (all scaled, for abbreviations see Supplementary material, Table A1) as fixed effects. N = 71. AICs (function AIC) for model selection shown. The AIC (Akaike information criterion) of the models with a difference in AIC < 2 shown in bold and are considered as equally good. The final model is in bold.

Model for occupation date (doy, scaled within year)	**AIC**
~ slarix + snow + grass + grassh + elev + I(grass^2) + I(grassh^2) + I(snow^2)	**133.1**
~ slarix + snow + grass + grassh + elev + I(grass^2) + I(grassh^2)	**134.5**
~ snow + grass + grassh + elev + I(grass^2) + I(snow^2) + I(grassh^2)	**134.7**
~ slarix + grassh + snow + grass + elev + I(grass^2) + I(snow^2)	**134.9**
~ slarix + snow + grass + elev + I(grass^2) + I(snow^2)	135.5
~ slarix + boulderp + rock + snow + grass + grassh + elev + I(grass^2) + I(grassh^2) + I(snow^2) + I(rock^2)	136.0
~ slarix + snow + grass + grassh + elev + I(grass^2)	138.8
~ slarix + snow + grass + grassh + elev	145.0
~ snow + rock + grassh + grass + elev + boulderp + slarix	146.9
~ slarix + snow + grass + grassh + elev + I(grass^2) + I(grassh^2) + year	163.5

Chapter VI

High-elevation habitats are important for birds during the post-breeding migration period in the Alps

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Abstract

Mountain habitats harbour significant breeding populations of alpine bird species, yet they can also be important from a biodiversity conservation point of view outside the breeding season. High-elevations are likely important fuelling habitats for birds during the post-breeding period due to seasonal peaks in arthropod abundance being later relative to lowlands. There is no detailed study of bird communities using high-elevations in the post-breeding migration period in Europe. In this study, we recorded birds on line transects from August to October in 2021 and 2022 across an elevational gradient in the Western Italian Alps in order to assess how the abundance and diversity of birds varied in time and space during the autumn migration period. We detected 104 species in total, representing 22% of the Italian list of terrestrial bird species, showing that a wide range of bird species exploit these habitats. The highest bird diversity and abundance were found during the early migration period at the end of August when long-distance migrants use high-elevations. Treeline habitats and south-facing slopes held the highest abundance of migrants, probably due to the high structural diversity and relatively high solar radiation which might affect thermoregulation and prey activity. We suggest that future management of protected areas in the mountains should take these parameters into account in order to protect mountain bird diversity, not only during the breeding season, but also in other key periods of the annual cycle, such as post-breeding migration. It is also essential to counteract the effects of climate and land-use change in mountain habitats by promoting conservation strategies for Alpine biodiversity, including migrants, over the entire year.

Keywords: alpine birds, climate change, migrants, protected areas, treeline.

Introduction

Mountain regions are considered hotspots of biodiversity at the global scale (Kier et al. 2009; Noroozi et al. 2018; Körner 2019) and the interactions between natural processes and historical human land use have given rise to a significant diversity of habitats and species (Nagy et al. 2003; Fischer et al. 2008). Although the crucial role of high-elevation ecosystems in the conservation of a wide range of taxa has been acknowledged (Schirpke et al. 2018; Ramel et al. 2020), these areas have received less research attention in comparison to other more accessible habitat types (Chamberlain et al. 2016). Furthermore, the vast majority of the studies carried out in mountain regions have focussed on the spring and summer periods and there is a general knowledge-gap about animal life-cycles in the other periods (Martin et al. 2023). Very few studies have investigated the habitat use of high-elevation areas by bird communities outside the breeding season, most of our knowledge coming from studies carried out in the North American mountain ranges such as British Columbia (Wilson and Martin 2005.; Ogden et al. 2013) or from data collected at ringing stations in Europe (Bairlein 1983; Franzoi et al. 2021). Boyle and Martin (2015), in the only comprehensive survey of year-round bird communities at high elevation in temperate mountains, found that a large proportion of the North American avifauna (c. 35%) use mountains at some point in their annual cycle, even if many do not breed in mountains. No such similar study has been carried out in European mountains.

Birds are able to perform flights of thousands of kilometres during their migratory journeys from their breeding territories to the wintering grounds and vice versa (Newton 2007); long-distance migrants in Europe cross the Mediterranean Sea and the Sahara Desert to reach their African wintering grounds and are amongst the most threatened migratory species (Vickery et al. 2013; BirdLife International 2021). Whilst studies on pre-breeding migration have received much research attention, focussing in particular on phenology (Both and Visser 2001; Møller et al. 2008), post-breeding migration is often neglected, possibly due to a wider range of species-specific

phenological patterns and less stringent time constraints on departure in comparison to spring migration (Lawrence et al. 2022).

Mountain ranges are generally considered as ecological barriers for migratory birds. When migrants pass through mountains, they tend to channel into valleys, crossing via lower passes and avoiding higher peaks which require a greater energetic demand to cross (Panuccio et al. 2012; Bruderer and Peter 2022). Birds that migrate during the autumn period following a south-westerly direction from continental Europe tend to follow the highest northern ridges of the Alps. However, some birds manage to circumvent the Alps from the east and enter and fly through Northern Italy, crossing the Western Italian Alps into France (Bruderer and Peter 2022).

Bird species are known to exploit high-elevation habitats as stop-over sites for resting and refuelling (Wilson et al. 2005; Bottoni et al. 2011; Ogden et al. 2013).Temperate mountains are characterized by delayed snow melt and colder temperatures in spring, thus there is a shifted phenology, meaning that peaks in arthropod abundance are later relative to lowlands (Leingärtner et al. 2014). Higher prey availability during the late summer makes alpine grasslands attractive fuelling sites for both birds stopping during migration (i.e. not breeding in the area but using the site as stopover and fuelling site (Bruderer and Jenni 1990; Ogden et al. 2013)) and breeding birds still present on territories (Vallino et al. 2020; Resano-Mayor et al. 2019) that need to gain weight before departure. These birds are in most cases linked to an insectivorous diet, such as most long-distance migrants.

Migratory birds depend on a network of interconnected sites during migration, but threats encountered during the journey can cause steep population declines. Runge et al. (2015) showed that just 9% of 1451 migratory birds worldwide are adequately covered by protected areas (PAs) during their entire annual cycle which is thought to be one of the main reasons for the global conservation crisis of migratory birds. As approximately 25% of European terrestrial land and inland waters are protected, Europe has the world's most extensive network of PAs among the

continents and they are considered to play a substantial role in buffering the effects of climate and land-use changes (Gaston et al. 2008; Araújo et al. 2011). PAs are fundamental for biodiversity and for ecosystems of high conservation value, in addition to providing a variety of direct and indirect ecosystem services to our societies and economies (Jones-Walters and Čivić 2013; Pröbstl-Haider and Haider 2014). However, the services of PAs are threatened by climate change (Rannow et al. 2014; Ranius et al. 2022), especially in those regions where its rate and magnitude are high, such as the Alpine biogeographical region (Schirpke et al. 2021). In order to promote year-round conservation of mountain biodiversity in Europe and counteract the effects of climate change, it is thus fundamental to assess the spatio-temporal habitat use of animals not only during the breeding season, but also during other periods of the year, and to evaluate the effects of PAs on the conservation of migrants. In particular, we need to know more about the habitat use of mountain areas in the post-breeding period, especially in relation to migration strategy, given that migrants, and in particular long-distance migrants, are amongst the most declining bird categories (Vickery et al. 2013). We also need to identify the key habitats used by migrants during this delicate period of the life-cycle in order to inform management strategies for migrants in mountains.

Thus, the main aims of this study were: i) to assess the number, density and temporal patterns of the bird species that use high-elevation habitats during the post-breeding migration period, and whether these patterns vary according to migration strategy; ii) to test how bird abundance and diversity vary during the migration period, in different habitats along the elevational gradient and according to aspect and habitat diversity; iii) to test if PAs play a role in affecting the species diversity and abundance of migratory and protected species in the Western Italian Alps.

Methods

Study area and transect location

The study area was located in the western Italian Alps in the Susa, Chisone and respective smaller secondary valleys (44°59'58.9"N 6°55'07.4"E, Fig. 1) and focused exclusively on high-elevation habitats, ranging from 1900m to 2500m. Starting from the montane forest and going upwards along the elevation gradient, the area is dominated by Larch Larix decidua forests at lower elevations, with a few patches of Spruce Picea abies and Swiss Pine Pinus cembra. The treeline ecotone is characterised by a mix of sparse coniferous trees of different heights with shrubs such as Juniper Juniperus communis nana, Alpenrose Rhododendron ferrugineum, Vaccinium spp. and, locally, Bog Pine Pinus uncinata. Alpine grasslands and rocky habitats occur above c. 2300-2400 m, although open anthropogenic habitats such as pastures and secondary grasslands can be found at lower elevations.

Using Geographic Information Systems (GIS) software, QGIS 3.14.15 'Pi' (QGIS Development Team 2020), suitable locations for survey sites were identified from a Digital Terrain Model and satellite photos based on their accessibility, and on the level of human disturbance (i.e., urban areas and valley bottoms were avoided). In this way, 10 vertical line transects with a 100m buffer on each side (mean length ± SD = 781 ± 189 m, covered transect area = 156ha, elevation range = 1900-2500m), each one consisting of three continuous small-transects (ST hereafter, mean length ± SD = 260 ± 65 m), were identified to survey bird assemblages along the elevation gradient. Three different habitats were surveyed within each transect (each for one ST): montane forest, treeline ecotone and alpine grasslands. Montane forest was defined as tall coniferous forests, with a cover of >60% high canopy (i.e., above 4 m height); the treeline ecotone had an intermediate canopy cover (5-60 % high canopy) with shrub patches interspersed with rocks and small larches; alpine grasslands were characterized by few or absent trees (<5% high canopy) with a high grass cover, rocky areas and few small larches. In order to study the variation in habitat use by birds, we

placed transects in the primary valley (n = 6, i.e. Chisone Valley) and in secondary valleys (n = 4, i.e. Troncea Valley, Argentera Valley and Chisonetto Valley) and on slopes with different aspects to test if habitat selection was influenced by this parameter. We had no transect located on north-oriented slopes due to problems with accessibility in our study area (see Discussion). To test if PAs played a role in influencing habitat use, we placed transects inside (n = 6) and outside (n = 4) PAs of the Natura 2000 network (see Fig. 1 for details on transect position and study design).

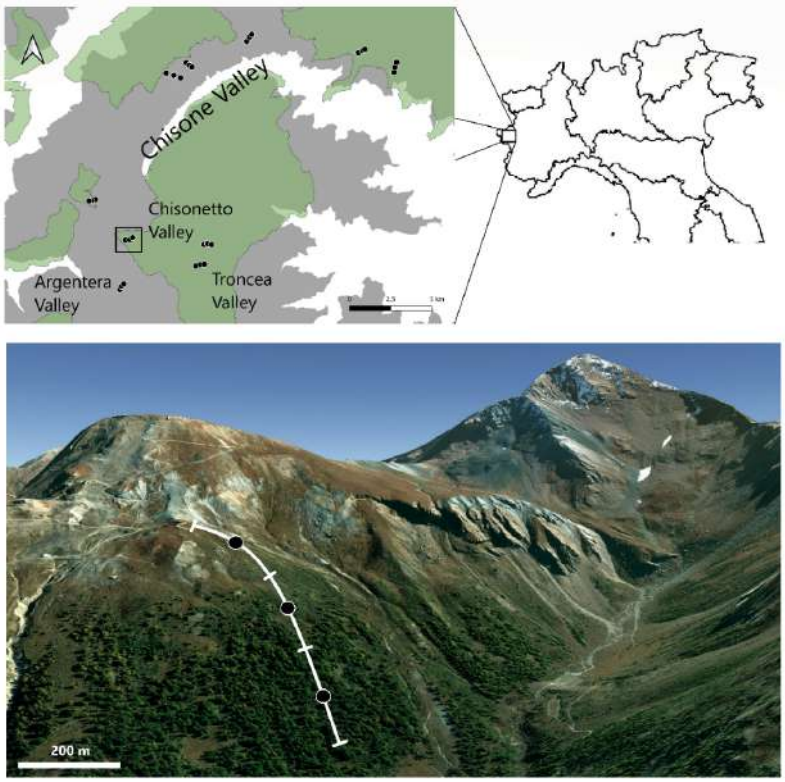

Figure 1. Map of the study area (above) and study design of each transect (below) in the Western Italian Alps. In the study area, transects are shown with three black dots per transect (one per habitat type), the Natura 2000 Protected Areas (PAs) are shown in green, whilst the area above 1700 m is shown in grey. In the study design, the small transects (STs) through the montane forest, the treeline ecotone and alpine grasslands are represented by a white line. The centre of each ST from where habitat surveys were conducted is shown with a black dot. A

scale is reported on bottom-left to show the buffer width for the transect (100m each side). Maps elaborated with QGIS and Google Earth.

Bird and habitat surveys

Bird surveys were conducted in 2021 and 2022, avoiding days with extreme weather conditions such as heavy rain. Transects were surveyed during the morning (7:00-12:00) or afternoon (15:00-18:00) over six different time periods between late August and mid-October (1 = 20 Aug.-29 Aug. 2021, 2 = 30 Aug.-9 Sept. 2022, 3 = 14 Sept.-19 Sept. 2021, 4 = 20 Sept.-29 Sept. 2022, 5 = 1 Oct.-10 Oct. 2022, 6 = 12 Oct.-17 Oct. 2021) in random order for a total of 180 surveys on STs. These time periods were defined to cover the periods of known maximum migration for the majority of species likely to be encountered. We explicitly decided not to sample in July or early August as breeding birds are still active in our study area. We decided to carry out bird surveys not only during the morning as most surveys carried out during the breeding period do, but also during the afternoon as bird activity during migration is not linked to singing activity in the morning period and a second activity-peak is known during the late afternoon (Boyle and Martin 2015). During the surveys, the observer walked at a slow pace (ST mean duration ± SD = 34 ± 8 min), identifying and counting every bird that was seen or heard within a buffer of 100m each side of the transect using specific activity codes (calling, foraging, perched), estimating the distance from the observer with a rangefinder to calculate perpendicular distances from the transect. Birds that flew over without interacting with the habitat were recorded and included in the overall species list, but were not used in the statistical analyses of habitat use. During the line transects, cloudiness, strength of the wind and visibility were recorded on a discrete scale from 0 (absence) to 4 (maximum).

From the centre of each ST, we collected a suite of habitat variables, estimating by sight the percentage cover of high canopy (≥ 4 m height), shrubs (juniper and rhododendron), grass, rocks and dead organic material on the ground within a 100

m radius, and the number of small trees (trees ≤ 2 m height) within a 50 m radius (see Jähnig et al. 2018 for details).

Analyses

We used distance sampling techniques from the R package 'Detect' (Miller et al. 2019) to have more accurate estimates of abundances and to see if the incorporation of detectability had any effect on the results compared to using raw data. We fitted different combinations of models using half-normal and hazard-rate (i.e. accounting for evasive movements) key detection functions and by incorporating group size as a covariate in order to counteract the effect of size bias (i.e. larger groups of birds are easier to detect than single individuals). Goodness-of-fit of each model was assessed by the Cramer von-Mises test along with a quintile-quantile plot, and model selection was carried out by comparing AICs. It was possible to calculate detection probability with distance sampling only for 16 species for which the sample size was sufficient (n of detections > 40, see Table S1 for the species and the detection probabilities based on model selection). We adjusted counts for these species and used the mean detection probability (i.e. 0.91) to adjust the counts for the other species. Subsequently, we ran models (GLMMs and LMMs, see below) with adjusted data and raw data to test for significant differences. There were no statistically significant differences highlighted between the models (see Table 2 and S2), suggesting incorporation of detectability did not affect our conclusions. We therefore present outputs only from models based on raw count data in the main paper (results using data adjusted for detectability are given in the supplementary material, Table S2).

We classified each species as resident (R), short-distance (S) or long-distance migrant (L) adapting the classification of Storchová and Hořák (2018). Altitudinal migrants (e.g. Water Pipit Anthus spinoletta) were included in the S category. We also classified species based both on the IUCN category at the European level included in the European Red List of Birds ([Birdlife International 2021) and on the inclusion in

Annex I of the EU Birds Directive (2009/147/EC). Using Kruskal-Wallis tests, we then assessed how habitat use varied according to migration strategy by testing the mean number of R, S and L species within each ST between habitat types (montane forest, treeline ecotone and alpine grasslands), periods of the year (6 levels) and the interaction between the two terms. We also tested for differences in species richness for each migration strategy inside and outside PA. Using the same variables, we also assessed how species richness varied for protected vs. non-protected species, testing first all protected species and subsequently only protected Alpine resident species.

We used the 'lme4' package (Bates et al. 2015) to model bird abundance (i.e. summed individuals in each ST) with a GLMM specifying a Poisson distribution, and the 'nlme' package to model species diversity expressed as the True Shannon diversity index (i.e. exp (Shannon diversity index H'), an estimate of the effective number of species, calculated with 'vegan' package (Oksanen et al. 2013) with an LMM. Site was specified as a random factor (10 levels) in each model. Explanatory variables included categorical variables such as habitat type, period of the year, inclusion in PA, aspect (5 levels) and habitat diversity (calculated as Shannon Index of habitat variables, see Table S3 for means ± sd of each variable). We also included nuisance variables such as time of the day (morning or afternoon) and weather parameters collected in the field (cloudiness, wind, visibility) to account for their effects on the response variables. Multicollinearity between ordinal variables and nominal variables was checked with Spearman rank correlation coefficients and chi-square tests respectively, whilst we used Variance Inflation Factors (VIFs) for numeric variables. Model selection was carried out by comparing AICs (Burnham and Anderson 2004).

Results

We detected 104 species belonging to 33 families in our study area. A total of 75 species were contacted in the montane forest, 67 in the treeline ecotone and 64 in the alpine grasslands. Of the 104 species, 27 were long-distance migrants, 32 were

residents and 45 were short-distance migrants, whilst two species were listed as Vulnerable at the European level (Italian Sparrow Passer italiae and Red-footed Falcon Falco vespertinus) and two listed as Near Threatened (Common Swift Apus apus and Rock Partridge Alectoris graeca). There were 19 species protected by the EU Birds Directive (2009/147/EC) (see Table S4 for species detected, the total number of individuals contacted in the surveys and the densities calculated as n individuals/hectare for each habitat and each time period).

There were 87 species (84% of the total) detected in the transects actively using the habitat (i.e. not including fly-overs and detections before and after starting the transect), with a total of 5571 individuals counted over the two years. Spatio-temporal patterns of habitat use by migrants, in terms of mean number of species per ST, varied according to migration strategy (Table 1, Fig. 2). Long-distance migrants had an earlier peak, showing the highest species richness on the first survey period ($X2 = 114.93$, $P < 0.001$). Short-distance migrant species, after a slight increase at the beginning of the surveys, showed the highest species richness in the sixth survey period ($X2 = 23.40$, $P< 0.001$). Short-distance migrant species were fewer in the alpine belt than in the forest and ecotone ($X2 = 33.88$, $P< 0.001$). Resident species showed a higher peak on the first time period but also shorter ones during the third and sixth visits ($X2 = 23.11$, $P< 0.001$). Their species richness was greater in the forest belt, decreasing towards higher elevations ($X2 = 45.27$, $P< 0.001$). No significant differences in mean richness for each migratory strategy were detected when we tested for the interactions between period and elevational belt. Similarly, no significant differences were detected outside or inside PAs neither for each migratory strategy, nor for protected species (first including all species and then only Alpine residents).

Table 2 Mean number of species ± standard error per transect according to migration strategy for habitat type and period. Time periods are 1 = 20 Aug.-29 Aug., 2 = 30 Aug.-9 Sept., 3 = 14 Sept.-19 Sept., 4 = 20 Sept.-29 Sept., 5 = 1 Oct.-10 Oct., 6 = 12 Oct.-17 Oct.

	Habitat			Period						Protected areas	
Migration strategy	Montane forest	Treeline ecotone	Alpine grasslands	1	2	3	4	5	6	PA	Non-PA
Long-distance migrants	0.9 ± 0.17	1.1 ± 0.21	1.1 ± 0.17	3.2 ± 0.25	1.8 ± 0.20	0.8 ± 0.20	0.2 ± 0.07	0.2 ± 0.10	0.1 ± 0.05	1 ± 0.13	1.1 ± 0.18
Short-distance migrants	5.5 ± 0.31	6.0 ± 0.4	3.3 ± 0.25	5.7 ± 0.45	4.1 ± 0.34	4.3 ± 0.48	4.2 ± 0.44	4.4 ± 0.51	7.0 ± 0.58	5.2 ± 0.27	4.6 ± 0.32
Residents	4.5 ± 0.27	3.4 ± 0.24	1.8 ± 0.25	4.6 ± 0.42	2.6 ± 0.39	3.5 ± 0.33	2.6 ± 0.46	2.5 ± 0.35	3.8 ± 0.39	3.2 ± 0.22	3.3 ± 0.27

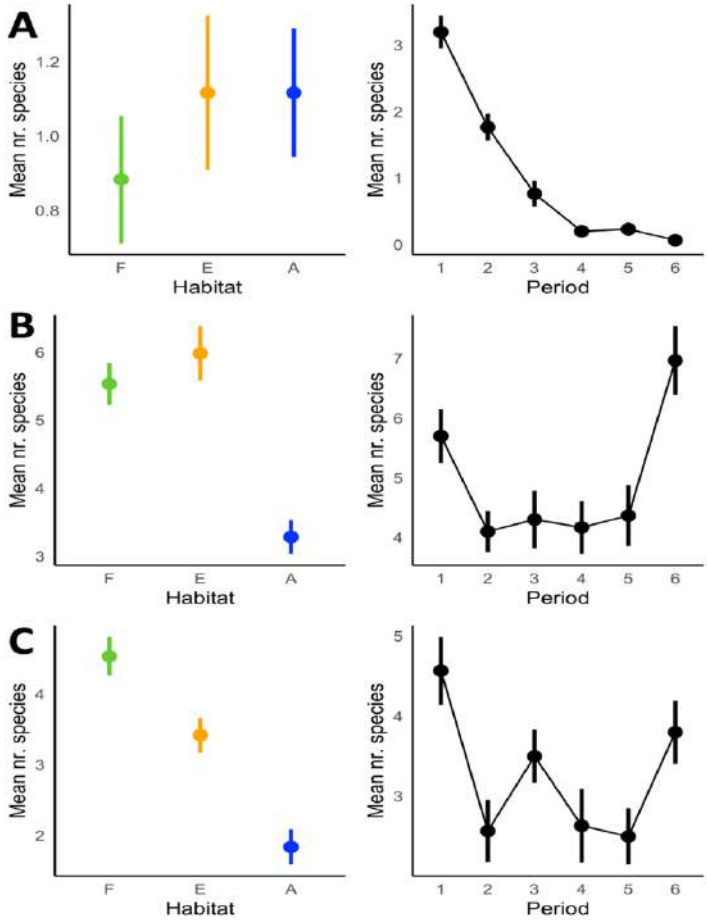

Figure 2. Plots showing spatio-temporal trends of habitat use by birds according to the migration strategy (A long-distance migrants, *n species* = 22; B short-distance migrants, *n species* = 41; C residents *n species* = 24). Means of the number of species in each ST for a given

category and standard error bars are reported. Habitat categories are classified as F = montane forest, E = ecotone treeline and A = alpine grasslands. Time periods are 1 = 20 Aug.-29 Aug., 2 = 30 Aug.-9 Sept., 3 = 14 Sept.-19 Sept., 4 = 20 Sept.-29 Sept., 5 = 1 Oct.-10 Oct., 6 = 12 Oct.-17 Oct.

GLMM and LMM results for bird abundance and diversity are shown in Table 2. Both bird abundance and diversity varied significantly according to habitat type and time period. The treeline ecotone harboured the highest bird abundance (n = 29.03, 95% CI = 27.48-30.66), whilst alpine grassland had the lowest diversity (H' = 4.99, 95% CI = 4.00-5.99). The end of August was the time period with the highest species diversity (H' = 9.30, 95% CI = 8.17-10.43) and the highest migrant abundance (n = 49.07, 95% CI = 46.24-52.06). Slope orientation had a strong significant effect, with east- (n = 43.97, 95% CI = 40.91-47.26) and southeast- (n = 33.76, 95% CI = 29.48-38.65) oriented slopes accounting for the highest bird numbers, but no effect on diversity was found. There were no significant effects of inclusion in PAs or habitat diversity for either bird abundance or diversity.

Nuisance weather variables had a strong significant effect on abundance (cloudiness $X2 = 77.61$, p-value < 0.001, wind $X2 = 28.1792$, p-value < 0.001, visibility $X2 = 41.57$, p-value < 0.001) and the morning period accounted not only for a significantly higher number of individuals ($X2 = 33.32$, p-value < 0.001, n morning = 34.6, n afternoon = 19.3), but also a more diverse bird assemblage (F-value = 15.30, p-value < 0.001, H' morning = 7.8, H' afternoon = 5.0) in comparison to the afternoon.

Table 2. GLMM and LMM outputs for abundance and true Shannon index diversity (Bird diversity) data (*n* = 180). Variables, chi-squared, F-values and relative p-values are reported. Levels (only for categorical variables), their estimates and standard errors, z (GLMM) and t (LMM) values and relative p-values are reported. Reference levels not shown are alpine grasslands for Type, period 1 for Period, east for Aspect, not protected for Protected area. Significant results are shown in bold

		Bird abundance						**Bird diversity**					
Variable	**Levels**	**X^2**	**p-value**	**Estimate**	**SE**	**z value**	**p-value**	**F-value**	**p-value**	**Estimate**	**SE**	**t value**	**p-value**
	Intercept			**4.03**	**0.13**	**30.82**	**<0.001**			**6.46**	**2.09**	**3.10**	**0.002**
Type		**26.20**	**<0.001**					**53.77**	**<0.001**				
	Alpine grassland												
	Treeline ecotone			**0.29**	**0.04**	**4.77**	**<0.001**			**3.00**	**0.52**	**5.71**	**<0.001**
	Montane forest			0.08	0.04	1.81	0.070			**3.32**	**0.52**	**5.71**	**<0.001**
Period		**688.59**	**<0.001**					**13.65**	**<0.001**				
	1												
	2			**-1.05**	**0.05**	**-21.23**	**<0.001**			**-3.25**	**0.65**	**-5.04**	**<0.001**
	3			**-0.41**	**0.05**	**-8.82**	**<0.001**			**-2.80**	**0.64**	**-4.35**	**<0.001**
	4			**-0.92**	**0.06**	**-17.46**	**<0.001**			**-2.95**	**0.66**	**-4.46**	**<0.001**
	5			**-0.93**	**0.06**	**-15.97**	**<0.001**			**-2.52**	**0.73**	**-3.46**	**<0.001**
	6			**-0.49**	**0.04**	**-11.16**	**<0.001**			**-1.67**	**0.65**	**-2.56**	**0.011**
Aspect		**274.97**	**<0.001**					0.33	0.842				
	East												
	South			**-0.62**	**0.08**	**-8.09**	**<0.001**			-2.79	1.80	-1.55	0.197
	Southeast			**-0.26**	**0.07**	**-3.58**	**<0.001**			1.00	1.80	0.56	0.608
	Southwest			**-0.68**	**0.07**	**-9.92**	**<0.001**			0.78	1.57	0.50	0.645
	West			**-0.74**	**0.06**	**-12.09**	**<0.001**			-1.70	1.45	-1.17	0.306
Protected area		0.59	0.443					1.56	0.280				

	Non-protected												
	Protected			0.06	0.07	0.767	0.443			1.78	1.81	0.99	0.380
Habitat diversity		1.13	0.288	0.10	0.09	1.06	0.287	0.03	0.863	0.33	1.29	0.25	0.801

Discussion

This study is the first to explicitly describe habitat use by birds during the migration period in the high-elevation habitats of the European Alps. We found that a high number of species use these areas during post-breeding migration (22% of 471 terrestrial species recorded in Italy, without taking into account birds strictly tied to wetland and marine habitats such as Anseriformes, Podicipediformes, Phoenicopteriformes, Gaviiformes, Procellariiformes and Suliformes (Baccetti and Fracasso 2021), thus suggesting that Alpine habitats are important for a wide range of European species. Boyle and Martin (2015) found an even greater percentage (35%) of North American species using mountains at some point in their annual cycle based on an extensive literature review. Given the relatively restricted geographic and elevational range and sample size of our study, we expect that our estimate of 22%, even though it represents an impressive proportion of the Italian terrestrial avifauna, is under-estimated at the national scale, further underlining the importance of high elevation habitats for birds in the post-breeding period.

We showed that the highest number of individuals and the highest species diversity were reached at the beginning of the migration period (end of August), when long-distance migrants are still largely present and using the area. These comprised both species that breed in the area (local breeders and potentially other migrants from other breeding areas, e.g. Northern Wheatear Oenanthe oenanthe, Tree Pipit Anthus trivialis, Whinchat Saxicola rubetra), and species that do not breed in the area but which use the sites as fuelling areas on the way to their African wintering grounds (e.g. Pied Flycatcher Ficedula hypoleuca, Willow Warbler Phylloscopus trochilus). These

species are often linked to an insectivorous diet, since dependence on seasonally variable resources, such as arthropods, necessitates seasonal movements (Levey and Stiles 1992). The highest bird abundances were found in the treeline ecotone, which also accounted for the highest bird diversity along with montane forest; the heterogeneity in the vegetation found in the treeline ecotone and the mature trees found in the coniferous forest might offer higher food resources, as well as a more stable microclimate throughout the migration period in comparison to alpine grasslands. Previous studies carried out during the breeding period (Jähnig et al. 2018; Altamirano et al. 2020), showed how habitat mosaics (e.g. the treeline ecotone) accounted for high levels of avian diversity due to the higher number of ecological niches found in these complex habitats, although we found no significant effect of habitat diversity on the bird assemblages.

We recorded 19 protected species in our transects: these were mostly migratory raptors, including some species not breeding in the area such as the Red-footed Falcon Falco vespertinus and the Lesser Kestrel Falco naumanni, which were observed to actively use the high-elevation open habitat for hunting Orthoptera, which make up a large part of their diet, especially during migration periods (Bounas and Sotiropoulos 2017) (see Table S4 for all protected species recorded). Bird abundance and diversity did not significantly vary inside and outside PAs. Nonetheless, we argue that an efficient PA network is essential to protect mountain biodiversity and it might be useful in providing stepping-stones of suitable habitats that can facilitate range shifts towards higher elevations that are predicted for a wide range of taxa due to climate change (Thomas and Gillingham 2015; Vitasse et al. 2021). It is thus crucial to continue monitoring the role of PAs in the conservation of biodiversity, not only during the breeding season, but also during key stages of species' life-cycles, such as post-breeding moult and migration periods.

Migrants' habitat use was also influenced by aspect. We showed how east- and southeast-oriented slopes had the highest bird abundance and diversity, although

we did not sample north-facing slopes in our study area, as access was much harder with few easily accessible or appropriate footpaths or trails. However, we are confident that we sampled the habitats that were of most importance to migrants given that other studies have shown that the onset and magnitude of solar radiation received by a mountain slope during the day can affect prey availability (i.e. arthropods) and consequently bird activity (Robbins 1981). As a result, migrants might select for east- and southeast-oriented slopes as they receive the earliest and the highest solar radiation during the morning when bird activity is high, in order to reduce thermoregulatory costs and optimize foraging activity when temperatures are low (Huertas and Díaz 2001; Villén-Pérez et al. 2014). Nevertheless, it would be interesting to undertake a similar survey on sites with a wider range of slope aspect.

In conclusion, we have provided evidence that high-elevation areas in the Alps are important sites for a large number of bird species outside the breeding period, and we have described for the first time the habitat use during post-breeding migration in the Alps. As the treeline ecotone was identified as one of the most important habitats for migrating birds, it is fundamental to maintain landscape heterogeneity in order to counteract vegetation shifts and subsequent loss of open habitats caused by climate and land-use changes (Chamberlain et al. 2016). Ensuring adequate protection of key habitat (i.e. treeline ecotone) and topographically suitable areas (i.e. east-southeast slopes) in mountains as part of the PA network will provide benefits to migrant birds. We argue that a well-functioning PA network is crucial to buffer the negative effects of environmental change on mountain biodiversity during the whole annual cycle. Only in this way will it be possible to promote sustainable strategies that take into account the conservation value of alpine biodiversity at all levels.

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References

Altamirano TA, de Zwaan DR, Ibarra JT, Wilson S, Martin K (2020) Treeline ecotones shape the distribution of avian species richness and functional diversity in south temperate mountains. Sci Rep 10:1–13

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. Ecology Letters 14:484–492

Baccetti N, Fracasso G (2021) CISO-COI Check-list of Italian birds - 2020. Avocetta 45:21–82

Bairlein F (1983) Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations (Lake Constance, Germany). Ornis Scandinavica 14:239–245

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48

BirdLife International (2021) European Red List of Birds 2021. Compiled by BirdLife International.

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 2001 411:6835 411:296–298

Bottoni L, Massa R, Fornasari L (2011) The migration of the Robin Erithacus rubecula in the central pre-Alps of Italy. Ringing & Migration, 12(1), 48-53

Bounas A, Sotiropoulos K (2017) Change of feeding strategy prior to migration: a comparative diet analysis in the Lesser Kestrel (Falco naumanni). Avian Biology Research 10:2017

Boyle WA, Martin K (2015) The conservation value of high elevation habitats to North American migrant birds. Biological Conservation 192:461–476

Bruderer B, Jenni L (1990) Migration Across the Alps. Bird Migration 60–77

Bruderer B, Peter D (2022) Topography and wind moulding directions of autumn migration between Europe and the West African savannas. Journal of Ornithology 163:357–371

Burnham KP, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304

Chamberlain DE, Pedrini P, Brambilla M, Rolando A, Girardello M (2016) Identifying key conservation threats to Alpine birds through expert knowledge. PeerJ 2016:1–21

Franzoi A, Tenan S, Lorenzo Sanchez P, Pedrini P (2021) Temporal trends in abundance and phenology of migratory birds across the Italian Alps during a 20-year period. Rivista Italiana di Ornitologia 91:13–28

Gaston KJ, Jackson SF, Nagy A, Cantú-Salazar L, Johnson M (2008) Protected Areas in Europe. Annals of the New York Academy of Sciences 1134:97–119

Huertas DL, Díaz JA (2001) Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. Canadian Journal of Zoology, 79(2), 279-284

Jones-Walters L, Čivić K (2013) European protected areas: Past, present and future. Journal for Nature Conservation 21:122–124

Kier G, Kreft H, Tien ML, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America 106:9322–9327

Körner C (2019) Mountain biodiversity, its causes and function: An overview. Mountain Biodiversity: A Global Assessment 3–20

Lawrence KB, Barlow CR, Bensusan K, Perez C, Willis SG (2022) Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. Global Change Biology 28:375–389

Leingärtner A, Krauss J, Steffan-Dewenter I (2014) Elevation and experimental snowmelt manipulation affect emergence phenology and abundance of soil-hibernating arthropods. Ecological Entomology 39:412–418

Levey D, Stiles G (1992) Evolutionary Precursors of Long-Distance Migration: Resource Availability and Movement Patterns in Neotropical Landbirds Author(s): Douglas J . Levey and F . Gary Stiles Published by : The University of Chicago Press for The American Society of Natura. 140:447–476

Martin K, Chamberlain, D, Lehikoinen, A (2023) Priorities for information, research and conservation of birds in high mountains. In Chamberlain D, Lehikoinen, A, Martin, K (eds) Ecology and Conservation of Mountain Birds, pp 372-406, Cambridge University Press, Cambridge, UK.

Miller DL, Rexstad E, Thomas L, et al (2019) Distance Sampling in R. Journal of Statistical Software 89:1–28

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105: 16195-16200

Newton I (2007) The Migration Ecology of Birds. The Migration Ecology of Birds. Elsevier

Noroozi J, Talebi A, Doostmohammadi M, Rumpf SB, Linder HP, Schneeweiss GM (2018) Hotspots within a global biodiversity hotspot-areas of endemism are associated with high mountain ranges. Scientific Reports 8:1–10

Ogden LJE, Martin K, Williams TD (2013) Elevational differences in estimated fattening rates suggest that high-elevation sites are high-quality habitats for fall migrants. The Auk 130:98–106

Panuccio M, Agostini N, Premuda G (2012) Ecological barriers promote risk minimisation and social learning in migrating short-toed snake eagles. Ethology Ecology & Evolution, 24(1), 74-80

Pröbstl-Haider U, Haider W (2014) The role of protected areas in destination choice in the european alps. Zeitschrift fur Wirtschaftsgeographie 58:144–163

Ramel C, Rey PL, Fernandes R, Vincent C, Cardoso AR, Broennimann O, Pellissier L, Pradervand JN, Ursenbacher S, Schmidt BR, Guisan A (2020) Integrating ecosystem services within spatial biodiversity conservation prioritization in the Alps. Ecosystem Services 45:101186

Ranius T, Widenfalk LA, Seedre M, Lindman L, Felton A (2022) Protected area designation and management in a world of climate change: A review of recommendations. Ambio 1–13

Rannow S, Macgregor NA, Albrecht J, et al (2014) Managing Protected Areas Under Climate Change: Challenges and Priorities. Environmental Management 54:732–743

Resano-Mayor J, Korner-Nievergelt F, Vignali S, et al (2019) Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change. Biodiversity and Conservation 28:2669–2685

Robbins (1981) Bird Activity Levels Related to Weather. Studies in Avian Biology 6:301-310.

Runge CA, Watson JEM, Butchart SHM, et al (2015) Protected areas and global conservation of migratory birds. Science 350:1255–1258

Schirpke U, Meisch C, Tappeiner U (2018) Symbolic species as a cultural ecosystem service in the European Alps: insights and open issues. Landscape Ecology 33:711–730

Schirpke U, Wang G, Padoa-Schioppa E (2021) Editorial: Mountain landscapes: Protected areas, ecosystem services, and future challenges. Ecosystem Services 49:101302

Storchová L, Hořák D (2018) Life-history characteristics of European birds. Global Ecology and Biogeography 27:400–406

Thomas CD, Gillingham PK (2015) The performance of protected areas for biodiversity under climate change. Biological Journal of the Linnean Society 115:718–730

Vallino C, Caprio E, Genco F, Chamberlain D, Palestrini C, Roggero A, Bocca M, Rolando A (2020) Flocking of Foraging Yellow-Billed Choughs Pyrrhocorax Graculus Reflects the Availability of Grasshoppers and the Extent of Human Influence in High Elevation. Ardeola 68(1):53-70

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, Gregory RJ (2013) The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156:1–22

Villén-Pérez S, Carrascal LM, Gordo O (2014) Wintering forest birds roost in areas of higher sun radiation. European Journal of Wildlife Research 60:59–67

Vitasse Y, Ursenbacher S, Klein G, Bohnenstengel T, Chittaro Y, Delestrade A, Monnerat C, Rebetez M, Rixen C, Strebel N, Schmidt BR, Wipf S, Wohlgemuth T, Yoccoz NG, Lenoir J (2021) Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. Biological Reviews brv.12727

Wilson S, Martin K (2005) Songbird use of high-elevation habitat during the fall post-breeding and migratory periods. Ecoscience 12:561-568

Supplementary material

Table S1. Model selection table for each species where *n* represents the number of detections. Key detection functions, model formula (~1 = no covariates, ~group size = with group size covariate included), CvM (Cramer von-Mises test) p-value for goodness of fit, P as detection probability, SE(P) as standard error of detection probability and ΔAIC (Akaike Information Criterion) for the selection of the best model are reported.

Model	**Key function**	**Formula**	**CvM p-value**	**P**	**SE(P)**	**ΔAIC**
Dendrocopos major (n = 45)						
1	Half-normal	~1	0.146	0.914	0.161	0.000
2	Hazard-rate	~1	0.133	0.900	0.113	1.111
3	Half-normal	~group size	0.150	0.910	0.160	1.160
4	Hazard-rate	~group size	0.128	0.887	0.136	2.959
Erithacus rubecola (n = 45)						
1	Half-normal	~1	0.097	0.821	0.142	0.000
2	Hazard-rate	~1	0.126	0.858	0.086	0.263
3	Half-normal	~group size	0.181	0.880	0.061	1.167
4	Hazard-rate	~group size	0.111	0.816	0.142	1.848
Phoenicurus ochruros (n = 46)						
1	Half-normal	~1	0.01	1.000	0.001	0.000
2	Hazard-rate	~1	0.01	0.998	0.000	1.845
3	Half-normal	~group size	0.01	1.000	0.114	2.000
4	Hazard-rate	~group size	0.01	1.000	0.112	3.974
Phylloscopus collybita (n = 46)						
1	Half-normal	~1	0.123	0.979	0.171	1.867
2	Hazard-rate	~1	0.098	0.932	0.136	3.413
3	Half-normal	~group size	0.066	0.851	0.177	0.000
4	Hazard-rate	~group size	0.128	1.000	0.029	5.883
Linaria cannabina (n = 49)						
1	Half-normal	~1	0.004	1.000	0.001	0.000
2	Hazard-rate	~1	0.004	0.998	0.000	1.835
3	Half-normal	~group size	0.004	0.998	496.660	1.993
4	Hazard-rate	~group size	0.004	1.000	0.168	3.994
Nucifraga caryocatactes (n = 54)						
1	Half-normal	~1	0	1.000	0.001	0.000
2	Hazard-rate	~1	0	0.998	0.000	1.819
3	Half-normal	~group size	0	1.000	0.056	2.000

4	Hazard-rate	~group size	0	1.000	0.000	3.975
Emberiza cia (n = 54)						
1	Half-normal	~1	0.361	0.729	0.099	0.000
2	Hazard-rate	~1	0.440	0.801	0.095	1.558
3	Half-normal	~group size	0.425	0.729	0.100	1.960
4	Hazard-rate	~group size	0.495	0.816	0.087	3.538
Anthus trivialis (n = 54)						
1	Half-normal	~1	0.036	1.000	0.001	0.000
2	Hazard-rate	~1	0.035	0.998	0.000	1.181
3	Half-normal	~group size	0.036	1.000	0.096	2.000
4	Hazard-rate	~group size	0.036	1.000	0.002	3.979
Lophophanes cristatus (n = 55)						
1	Half-normal	~1	0.088	0.901	0.149	0.156
2	Hazard-rate	~1	0.065	0.880	0.085	0.000
3	Half-normal	~group size	0.097	0.948	2099.579	0.885
4	Hazard-rate	~group size	0.067	0.880	0.085	1.999
Certhia familiaris (n = 61)						
1	Half-normal	~1	0.017	0.804	0.127	4.134
2	Hazard-rate	~1	0.012	0.808	0.066	0.000
3	Half-normal	~group size	0.021	0.786	0.131	4.571
4	Hazard-rate	~group size	0.019	1.000	0.026	10.675
Loxia curvirostra (n = 66)						
1	Half-normal	~1	0.047	1.000	0.002	0.000
2	Hazard-rate	~1	0.021	0.952	0.067	1.157
3	Half-normal	~group size	0.045	0.995	25.601	1.917
4	Hazard-rate	~group size	0.018	0.940	0.061	2.120
Turdus viscivorus (n = 74)						
1	Half-normal	~1	0.002	1.000	0.001	0.000
2	Hazard-rate	~1	0.002	0.998	0.000	1.751
3	Half-normal	~group size	0.002	1.000	0.103	2.000
4	Hazard-rate	~group size	0.002	1.000	0.092	3.996
Fringilla coelebs (n = 75)						
1	Half-normal	~1	0.027	0.889	0.124	1.494
2	Hazard-rate	~1	0.017	0.865	0.075	0.000
3	Half-normal	~group size	0.026	0.846	0.119	1.228
4	Hazard-rate	~group size	0.035	1.000	0.040	6.356
Anthus spinoletta (n = 76)						
1	Half-normal	~1	0.015	1.000	0.002	0.000
2	Hazard-rate	~1	0.006	0.948	0.074	1.169

3	Half-normal	~group size	0.010	0.961	0.120	1.677
4	Hazard-rate	~group size	0.007	0.942	0.005	2.162
Poecile montanus (n = 91)						
1	Half-normal	~1	0.024	0.908	0.116	1.043
2	Hazard-rate	~1	0.015	0.884	0.072	0.000
3	Half-normal	~group size	0.035	0.914	0.172	1.274
4	Hazard-rate	~group size	0.026	0.887	0.067	1.439
Periparus ater (n = 105)						
1	Half-normal	~1	0	0.796	0.111	18.755
2	Hazard-rate	~1	0	0.805	0.033	0.000
3	Half-normal	~group size	0	0.791	0.112	20.005
4	Hazard-rate	~group size	0	0.800	0.031	0.501

Table S2. GLMM and LMM outputs for abundance and true Shannon index diversity (Bird diversity) with adjusted count data (i.e. abundances were corrected with mean detection probability = 0.91). Variables, chi-squared, F-values and relative p-values are reported. Levels (only for categorical variables), their estimates and standard errors, z (GLMM) and t (LMM) values and relative p-values are reported. Reference levels not shown are alpine grasslands for Type, period 1 for Period, east for Aspect, not protected for Protected area. Significant results are shown in bold

		Bird abundance						**Bird diversity**					
Variable	Levels	X^2	p-value	Estimate	SE	z value	p-value	F-value	p-value	Estimate	SE	t value	p-value
	Intercept			**4.10**	**0.13**	**31.20**	**<0.001**			**6.51**	**2.01**	**3.22**	**0.002**
Type		**31.61**	**<0.001**					**53.77**	**<0.001**				
	Alpine grassland												
	Treeline ecotone			**0.22**	**0.04**	**5.42**	**<0.001**			**2.91**	**0.51**	**5.76**	**<0.001**
	Montane forest			0.10	0.04	2.58	0.051			**3.13**	**0.50**	**6.31**	**<0.001**
Period		**735.35**	**<0.001**					**13.65**	**<0.001**				
	1												
	2			**-1.05**	**0.05**	**-22.04**	**<0.001**			**-3.20**	**0.62**	**-5.16**	**<0.001**
	3			**-0.40**	**0.04**	**-9.09**	**<0.001**			**-2.75**	**0.62**	**-4.43**	**<0.001**
	4			**-0.90**	**0.05**	**-17.93**	**<0.001**			**-2.89**	**0.64**	**-4.53**	**<0.001**
	5			**-0.91**	**0.06**	**-16.40**	**<0.001**			**-2.53**	**0.70**	**-3.61**	**<0.001**
	6			**-0.49**	**0.04**	**-11.67**	**<0.001**			**-1.61**	**0.63**	**-2.56**	**0.011**
Aspect		**240.76**	**<0.001**					0.33	0.842				

	East												
	South			**-0.62**	**0.08**	**-7.50**	**<0.001**			-2.73	1.76	-1.55	0.195
	Southeast			**-0.27**	**0.08**	**-3.34**	**<0.001**			0.93	1.75	0.53	0.623
	Southwest			**-0.69**	**0.07**	**-9.40**	**<0.001**			0.66	1.53	0.43	0.688
	West			**-0.75**	**0.07**	**-11.33**	**<0.001**			-1.70	1.41	-1.20	0.295
Protected area		0.48	0.488					1.56	0.280				
	Non-protected												
	Protected			0.05	0.08	0.693	0.488			1.65	1.76	0.93	0.404
Habitat diversity		1.22	0.269	0.10	0.09	1.10	0.269	0.03	0.863	0.29	1.25	0.24	0.814

Table S3. Mean ± SD of habitat variables according to the habitat type

Habitat	**% High Canopy**	**% Juniper**	**% Rhododendron**	**% Rock**	**% Grass**	**% Dead organic material**	**Nr. of small trees**
Montane forest	69 ± 7	18 ± 17	8 ± 12	10 ± 13	15 ± 10	9 ± 7	14 ± 22
Treeline ecotone	38 ± 12	31 ± 19	4 ± 8	10 ± 9	33 ± 14	2 ± 5	60 ± 32
Alpine grassland	3 ± 5	29 ± 16	4 ± 8	21 ± 14	54 ± 19	0 ± 2	16 ± 22

Table S4. Abundance of 104 bird species detected between August and October in the monitored sites in the Western Italian Alps. Species protected by the EU Birds Directive (2009/147/EC) are shown in bold. We show the migratory status of species extracted and adapted from Storchová and Hořák (2018), denoted as residents (R), short-distance migrants (S), and long-distance migrants (L). IUCN category at the European regional level extracted from the the European Red List of Birds (BirdLife International 2021) is reported. Total individuals detected, % of surveys in which the species was detected and mean density (individuals/ha) are shown. Habitat categories (montane forest (M), treeline ecotone (E) and alpine grasslands (A)) and temporal periods (1 = 20 Aug.-29 Aug., 2 = 30 Aug.-9 Sept., 3 = 14 Sept.-19 Sept., 4 = 20 Sept.-29 Sept., 5 = 1 Oct.-10 Oct., 6 = 12 Oct.-17 Oct.) are reported. Missing values in total individuals, % of surveys and mean density data represent species only detected in the study area outside the transects; ✓ symbol represents the elevational belt where the species was detected. The % of surveys in which a species was detected includes fly-overs within the transect.

Common name	Scientific name	Mig stat	Eu IUCN cat	Tot ind	% surveys detected			Mean density								
					Habitat			Habitat			Temporal period					
					M	E	A	M	E	A	1	2	3	4	5	6
PHASIANIDAE																
Rock Ptarmigan	***Lagopus muta helveticus***	R	LC	2	-	-	✓	-	-	-	-	-	-	-	-	-
Black Grouse	***Lyrurus tetrix***	R	LC	31	6.7	18.3	0.0	0.029	0.169	0.000	0.008	0.008	0.066	0.052	0.015	0.043
Rock Partridge	***Alectoris graeca***	R	NT	10	0.0	6.7	5.0	0.000	0.031	0.044	0.014	0.000	0.039	0.024	0.000	0.000
ARDEIDAE																
Grey Heron	*Ardea cinerea*	S	LC	1	✓	-	-	-	-	-	-	-	-	-	-	-
ACCIPITRIDAE																
Griffon Vulture	***Gyps fulvus***	R	LC	13	0.0	0.0	11.7	0.000	0.000	0.065	0.054	0.000	0.006	0.004	0.007	0.000
Golden Eagle	***Aquila chrysaetos***	R	LC	15	1.7	8.3	16.7	0.005	0.034	0.061	0.046	0.014	0.036	0.000	0.007	0.013
Red Kite	***Milvus milvus***	S	LC	1	-	-	✓	-	-	-	-	-	-	-	-	-
Common Buzzard	*Buteo buteo*	S	LC	7	1.7	1.7	5.0	0.000	0.000	0.031	0.031	0.000	0.000	0.000	0.000	0.000
Honey Buzzard	***Pernis apivorus***	L	LC	14	1.7	3.3	16.7	0.000	0.019	0.032	0.051	0.000	0.000	0.000	0.000	0.000
Short-toed Eagle	***Circaetus gallicus***	L	LC	4	0.0	0.0	11.7	0.000	0.000	0.015	0.015	0.000	0.000	0.000	0.000	0.000
Northern Goshawk	*Accipiter gentilis*	R	LC	5	3.3	3.3	1.7	0.012	0.010	0.008	0.004	0.000	0.006	0.000	0.008	0.012
Eurasian Sparrowhawk	*Accipiter nisus*	S	LC	6	1.7	0.0	8.3	0.006	0.000	0.032	0.016	0.000	0.022	0.000	0.000	0.000
Marsh Harrier	***Circus aeroginosus***	L	LC	3	0.0	0.0	3.3	0.000	0.000	0.015	0.000	0.000	0.016	0.000	0.000	0.000
FALCONIDAE																
Peregrine Falcon	***Falco peregrinus***	R	LC	3	0.0	0.0	5.0	0.000	0.000	0.018	0.001	0.000	0.014	0.000	0.000	0.000
Common Kestrel	*Falco tinnunculus*	R	LC	41	3.3	20.0	28.3	0.016	0.126	0.208	0.141	0.026	0.097	0.005	0.032	0.008
Lesser Kestrel	***Falco naumanni***	L	LC	1	0.0	0.0	1.7	0.000	0.000	0.008	0.000	0.000	0.008	0.000	0.000	0.000
Red-footed Falcon	***Falco vespertinus***	L	VU	4	0.0	1.7	5.0	0.000	0.006	0.004	0.006	0.000	0.000	0.004	0.000	0.000
CHARADRIIDAE																
Eurasian Dotterel	***Eudromias morinellus***	S	LC	2	0.0	0.0	1.7	0.000	0.000	0.015	0.015	0.000	0.000	0.000	0.000	0.000
COLUMBIDAE																
Wood Pigeon	*Columba palumbus*	S	LC	12	3.3	3.3	1.7	0.014	0.063	0.010	0.039	0.000	0.024	0.000	0.008	0.016
Collared Dove	*Streptopelia decaocto*	R	LC	3	✓	-	-	-	-	-	-	-	-	-	-	-
CUCULIDAE																
Common Cuckoo	*Cuculus canorus*	L	LC	1	0.0	0.0	1.7	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000	0.000
STRIGIDAE																
Pygmy Owl	***Glaucidium passerinum***	R	LC	1	1.7	0.0	0.0	0.008	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000
Tengmalm's Owl	***Aegolius funereus***	R	LC	1	✓	-	-	-	-	-	-	-	-	-	-	-
Long-eared Owl	*Asio otus*	S	LC	1	1.7	0.0	0.0	0.006	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000
APODIDAE																
Common Swift	*Apus apus*	L	NT	20	0.0	0.0	1.7	0.000	0.000	1.282	0.128	0.000	0.000	0.000	0.000	0.000
Alpine Swift	*Tachymarptis melba*	L	LC	8	-	-	✓	-	-	-	-	-	-	-	-	-
UPUPIDAE																
Eurasian Hoopoe	*Upupa epops*	L	LC	1	0.0	1.7	0.0	0.000	0.005	0.000	0.005	0.000	0.000	0.000	0.000	0.000
PICIDAE																
Black Woodpecker	***Dryocopus martius***	R	LC	3	3.3	1.7	0.0	0.014	0.006	0.000	0.000	0.000	0.006	0.014	0.000	0.000
Great-spotted Woodpecker	*Dendrocopos major*	R	LC	51	41.7	33.3	0.0	0.074	0.117	0.000	0.075	0.056	0.022	0.041	0.057	0.034
Green Woodpecker	*Picus viridis*	R	LC	35	43.3	10.0	0.0	0.098	0.022	0.000	0.085	0.018	0.029	0.032	0.036	0.036
Eurasian Wryneck	*Jynx torquilla*	L	LC	2	✓	✓	-	-	-	-	-	-	-	-	-	-
ALAUDIDAE																
Eurasian Skylark	*Alauda arvensis*	S	LC	8	0.0	1.7	8.3	0.000	0.007	0.040	0.020	0.000	0.006	0.000	0.019	0.008
HIRUNDINIDAE																
House Martin	*Delichon urbicum*	L	LC	100	0.0	6.7	5.0	0.000	0.435	0.228	0.326	0.000	0.150	0.000	0.187	0.000
Barn Swallow	*Hirunda rustica*	L	LC	33	1.7	3.3	5.0	0.015	0.048	0.130	0.175	0.000	0.000	0.000	0.000	0.018
Crag Martin	*Ptyonoprogne rupestris*	S	LC	13	0.0	3.3	6.7	0.000	0.030	0.066	0.030	0.000	0.000	0.000	0.050	0.016
MOTACILLIDAE																
Water Pipit	*Anthus spinoletta*	S	LC	369	3.3	40.0	85.0	0.043	0.476	1.479	0.331	0.224	0.574	0.302	0.248	0.582

Meadow Pipit	*Anthus pratensis*	S	LC	36	0.0	1.7	15.0	0.000	0.015	0.200	0.000	0.000	0.000	0.000	0.030	0.192
Tree Pipit	*Anthus trivialis*	L	LC	81	26.7	36.7	26.7	0.201	0.227	0.284	0.316	0.221	0.163	0.014	0.008	0.008
White Wagtail	*Motacilla alba*	S	LC	6	0.0	0.0	6.7	0.000	0.000	0.030	0.005	0.010	0.000	0.000	0.006	0.008
Grey Wagtail	*Motacilla cinerea*	S	LC	3	0.0	0.0	5.0	0.000	0.000	0.008	0.000	0.000	0.008	0.000	0.000	0.000
CINCLIDAE																
White-throated Dipper	*Cinclus cinclus*	R	LC	3	✓	-	-	-	-	-	-	-	-	-	-	-
TROGLODYTIDAE																
Eurasian Wren	*Troglodytes troglodytes*	S	LC	33	43.3	20.0	0.0	0.146	0.070	0.000	0.073	0.081	0.072	0.080	0.028	0.016
PRUNELLIDAE																
Dunnock	*Prunella modularis*	S	LC	40	20.0	26.7	3.3	0.103	0.155	0.016	0.021	0.029	0.102	0.067	0.053	0.053
Alpine Accentor	*Prunella collaris*	R	LC	21	0.0	0.0	13.3	0.000	0.000	0.153	0.054	0.000	0.000	0.000	0.086	0.013
TURDIDAE																
Song Thrush	*Turdus philomelos*	S	LC	91	28.3	15.0	3.3	0.308	0.106	0.121	0.085	0.015	0.081	0.035	0.024	0.361
Redwing	*Turdus iliacus*	S	LC	2	1.7	0.0	1.7	0.008	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.014
Mistle Thrush	*Turdus viscivorus*	S	LC	583	38.3	61.7	23.3	1.036	2.201	0.629	1.343	0.680	0.860	0.434	0.243	0.344
Fieldfare	*Turdus pilaris*	S	LC	151	15.0	16.7	6.7	0.233	0.710	0.131	0.512	0.012	0.278	0.017	0.022	0.235
Blackbird	*Turdus merula*	S	LC	12	6.7	6.7	1.7	0.035	0.041	0.008	0.016	0.000	0.008	0.000	0.000	0.060
Ring Ouzel	*Turdus torquatus*	S	LC	61	5.0	28.3	10.0	0.044	0.274	0.074	0.282	0.036	0.041	0.046	0.008	0.000
Rock Thrush	*Monticola saxatilis*	L	LC	6	0.0	0.0	5.0	0.000	0.000	0.044	0.021	0.000	0.008	0.000	0.005	0.000
MUSCICAPIDAE																
Pied Flycatcher	*Ficedula hypoleuca*	L	LC	43	21.7	11.7	3.3	0.124	0.133	0.011	0.214	0.064	0.000	0.000	0.000	0.000
European Robin	*Erithacus rubecola*	S	LC	62	50.0	23.3	0.0	0.259	0.156	0.000	0.051	0.054	0.023	0.066	0.068	0.149
Common Redstart	*Phoenicurus phoenicurus*	L	LC	3	1.7	3.3	0.0	0.007	0.010	0.000	0.011	0.010	0.000	0.000	0.000	0.000
Black Redstart	*Phoenicurus ochruros*	S	LC	76	5.0	31.7	40.0	0.023	0.178	0.352	0.119	0.069	0.107	0.018	0.069	0.235
Whinchat	*Saxicola rubetra*	L	LC	27	5.0	8.3	6.7	0.057	0.082	0.051	0.000	0.000	0.005	0.010	0.006	0.008
Northern Wheatear	*Oenanthe oenanthe*	L	LC	88	1.7	3.3	46.7	0.016	0.022	0.550	0.367	0.131	0.093	0.033	0.024	0.000
SYLVIIDAE																
Garden Warbler	*Sylvia borin*	L	LC	2	3.3	0.0	0.0	0.012	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000
Blackcap	*Sylvia atricapilla*	S	LC	1	1.7	0.0	0.0	0.006	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000
Lesser Whitethroat	*Curruca curruca*	L	LC	22	6.7	13.3	1.7	0.045	0.100	0.008	0.074	0.072	0.006	0.000	0.000	0.000
ACROCEPHALIDAE																
Reed/Marsh Warbler	*Acrocephalus sp.*	L	LC	1	✓	-	-	-	-	-	-	-	-	-	-	-
LOCUSTELLIDAE																
Grasshopper Warbler	*Locustella naevia*	L	LC	1	✓	-	-	-	-	-	-	-	-	-	-	-
PHYLLOSCOPIDAE																
Willow warbler	*Phylloscopus trochilus*	L	LC	35	18.3	13.3	1.7	0.128	0.080	0.006	0.156	0.037	0.008	0.000	0.000	0.005
Wood Warbler	*Phylloscopus sibilatrix*	L	LC	1	0.0	1.7	0.0	0.000	0.006	0.000	0.006	0.000	0.000	0.000	0.000	0.000
Bonelli's Warbler	*Phylloscopus bonellii*	L	LC	2	1.7	1.7	0.0	0.008	0.008	0.000	0.016	0.000	0.000	0.000	0.000	0.000
Chiffchaff	*Phylloscopus collybita*	S	LC	81	43.3	31.7	1.7	0.361	0.192	0.008	0.099	0.152	0.084	0.159	0.138	0.092
REGULIDAE																
Goldcrest	*Regulus regulus*	S	LC	4	8.3	0.0	0.0	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.006
Firecrest	*Regulus ignicapilla*	S	LC	2	✓	-	-	-	-	-	-	-	-	-	-	-
PARIDAE																
Great Tit	*Parus major*	S	LC	9	6.7	6.7	0.0	0.026	0.036	0.000	0.000	0.000	0.000	0.032	0.000	0.030
Coal Tit	*Periparus ater*	S	LC	414	91.7	75.0	1.7	1.271	0.949	0.016	0.420	0.349	0.519	0.453	0.393	0.368
Blue Tit	*Cyanistes caeruleus*	S	LC	42	6.7	13.3	1.7	0.074	0.212	0.016	0.000	0.000	0.020	0.010	0.022	0.250
Crested Tit	*Lophophanes cristatus*	R	LC	140	65.0	23.3	0.0	0.480	0.257	0.000	0.181	0.075	0.142	0.182	0.109	0.183
Willow Tit	*Poecile montanus*	R	LC	369	80.0	66.7	5.0	1.137	0.804	0.074	0.307	0.343	0.417	0.325	0.358	0.516
AEGITHALIDAE																
Long-tailed Tit	*Aegithalos caudatus*	S	LC	45	6.7	3.3	0.0	0.181	0.060	0.000	0.000	0.000	0.000	0.123	0.073	0.024
CERTHIIDAE																
Eurasian Treecreeper	*Certhia familiaris*	R	LC	94	68.3	31.7	0.0	0.247	0.110	0.000	0.088	0.110	0.081	0.062	0.123	0.102

TICHODROMIDAE																
Wallcreeper	*Tichodroma muraria*	R	LC	1	-	-	✓	-	-	-	-	-	-	-	-	-
LANIIDAE																
Red-backed Shrike	***Lanus collurio***	L	LC	2	1.7	0.0	0.0	0.015	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000
CORVIDAE																
Eurasian Magpie	*Pica pica*	R	LC	3	✓	-	-	-	-	-	-	-	-	-	-	-
Eurasian Jay	*Garrulus glandarius*	R	LC	56	28.3	23.3	1.7	0.170	0.127	0.012	0.082	0.060	0.083	0.044	0.020	0.039
Spotted Nutcracker	*Nucifraga caryocactates*	R	LC	130	40.0	43.3	16.7	0.262	0.380	0.182	0.303	0.164	0.072	0.116	0.037	0.169
Red-billed Chough	***Pyrrhocorax pyrrhocorax***	R	LC	150	0.0	8.3	43.3	0.000	0.024	0.780	0.509	0.000	0.065	0.015	0.014	0.206
Alpine Chough	*Pyrrhocorax graculus*	R	LC	142	0.0	6.7	35.0	0.000	0.000	0.837	0.604	0.000	0.086	0.023	0.016	0.129
Carrion Crow	*Corvus corone*	R	LC	121	26.7	18.3	13.3	0.075	0.068	0.680	0.549	0.172	0.012	0.012	0.037	0.055
Hooded Crow	*Corvus cornix*	R	LC	1	0	0	1.7	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000	0.000
Common Raven	*Corvus corax*	R	LC	64	6.7	3.3	33.3	0.028	0.097	0.321	0.030	0.015	0.247	0.039	0.000	0.058
PASSERIDAE																
Tree Sparrow	*Passer montanus*	R	LC	2	1.7	0.0	0.0	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015
Italian Sparrow	*Passer italiae*	R	VU	5	✓	-	-	-	-	-	-	-	-	-	-	-
Rock Sparrow	*Petronia petronia*	S	LC	17	1.7	3.3	0.0	0.000	0.045	0.000	0.045	0.000	0.000	0.000	0.000	0.000
White-winged Snowfinch	*Montifringilla nivalis*	R	LC	5	-	-	✓	-	-	-	-	-	-	-	-	-
FRINGILLIDAE																
Common Chaffinch	*Fringilla coelebs*	S	LC	314	75.0	65.0	15.0	0.926	0.673	0.052	0.646	0.267	0.205	0.165	0.111	0.412
Brambling	*Fringilla montifringilla*	S	LC	15	3.3	6.7	0.0	0.051	0.008	0.000	0.000	0.000	0.000	0.000	0.008	0.051
Common Linnet	*Linaria cannabina*	S	LC	151	1.7	48.3	60.0	0.023	0.231	0.615	0.252	0.231	0.239	0.079	0.079	0.142
Lesser Redpoll	*Acanthis cabaret*	S	LC	1	1.7	0.0	0.0	0.008	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000
European Goldfinch	*Carduelis carduelis*	S	LC	57	16.7	16.7	8.3	0.045	0.046	0.314	0.032	0.060	0.301	0.000	0.000	0.022
European Greenfinch	*Chloris chloris*	S	LC	7	1.7	1.7	0.0	0.024	0.008	0.000	0.008	0.000	0.000	0.000	0.000	0.000
Eurasian Siskin	*Spinus spinus*	S	LC	133	28.3	25.0	0.0	0.455	0.401	0.000	0.330	0.000	0.106	0.000	0.120	0.386
European Serin	*Serinus serinus*	S	LC	2	1.7	1.7	0.0	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006
Citril Finch	*Carduelis citronella*	S	LC	5	0.0	1.7	1.7	0.000	0.038	0.000	0.000	0.000	0.000	0.000	0.000	0.038
Eurasian Bullfinch	*Pyrrhula pyrrhula*	S	LC	10	8.3	1.7	0.0	0.056	0.006	0.000	0.042	0.000	0.000	0.000	0.006	0.014
Red Crossbill	*Loxia curvirostra*	R	LC	449	80.0	58.3	8.3	1.012	1.386	0.026	0.625	0.187	0.671	0.635	0.162	0.546
Hawfinch	*Coccothraustes coccothraustes*	S	LC	-	✓	✓	-	-	-	-	-	-	-	-	-	-
EMBERIZIDAE																
Yellowhammer	*Emberiza citronella*	S	LC	45	8.3	18.3	11.7	0.074	0.094	0.121	0.046	0.000	0.016	0.024	0.028	0.153
Rock Bunting	*Emberiza cia*	S	LC	120	20.0	50.0	33.3	0.168	0.339	0.237	0.202	0.076	0.077	0.092	0.097	0.214
Ortolan Bunting	***Emberiza hortulana***	L	LC	2	✓	✓	-	-	-	-	-	-	-	-	-	-

Chapter VII - General Discussion

The works presented in this thesis contributed to the knowledge of the ecology of mountain and upland birds. I assessed how different factors shape their populations in European mountain ranges (Chapter II; Alba et al. 2022) and assemblage compositions in the Alps (Chapters III-VI; Alba et al. 2023a, Lopez et al. submitted, Alba et al. 2023b, Alba et al. in revision), taking into consideration not only the breeding season (Chapters III-V; Alba et al. 2023a, Lopez et al. submitted, Alba et al. 2023b), but also during different periods of the annual cycle (Chapters V-VI; Alba et al. 2023b, Alba et al. in revision). I presented for the first time results about the habitat use of some mountain habitats in the Alps that might play a substantial role in the conservation of mountain birds and that were previously neglected (Alba et al. 2023b). At the same time, I explored the high-elevation habitat use of birds during delicate phases of species' life-cycles, which are largely understudied in comparison to the breeding period (Alba et al. in revision). In the *Discussion* section the main findings of each chapter were briefly discussed whilst in the subsequent section *Conservation of mountain birds: challenges and opportunities* I presented the major challenges and research ideas for the future of mountain bird ecology research.

Discussion

In first place, I identified the primary drivers influencing the demographic responses of European mountain birds and examined the trends in these drivers to evaluate their impact on bird populations (Chapter II; Alba et al. 2022). Whilst the management of non-target species, such as the legal control of predators, had a consistently positive effect on bird populations, several key drivers affected negatively and directly European mountain bird populations. These were: hunting; competitive native species; energy generation (involving collision risks and habitat loss); disturbance

caused by human presence (especially in leisure activities like skiing); and, poisoning or pollution. Hunting had the most significant negative impact, and it involved legal activities like grouse shooting in the UK (Ludwig et al. 2020) and illegal persecution of protected species, mostly raptors (Whitfield et al. 2004). Energy generation also negatively affected bird populations due to collisions and habitat alteration (Pearce-Higgins et al. 2012; Thaxter et al. 2017) whilst disturbance from human activities like skiing had detrimental effects on habitat use and stress levels (Patthey et al. 2012). Poisoning and pollution, mainly from lead and pesticides, harmed raptors especially (Berny et al. 2015). Other drivers like vegetation encroachment, climate change and pastoral agriculture did not consistently impact mountain bird populations, with climate change being a complex factor with long-term effects which are difficult to objectively quantify. However, these drivers exhibited significant trends over time and whilst the first two were increasing, agro-pastoral activities decreased in upland and mountain areas across time. The study acknowledged geographic and taxonomic biases in the available data, with UK and Southern Europe being the most represented regions, limiting the possibility to analyse region-specific impacts, and raptors and gamebirds being more studied than passerines, with alpine and arctic specialists largely underrepresented. I concluded that spatial planning is necessary to mitigate the impacts of drivers causing rapid land-use changes, like large-scale forestry, whilst more detailed research is needed to analyse the effects of climate change and abandonment of pastoral activities on mountain birds.

When I moved to study the habitats and bird assemblages found in avalanche tracks, I found that avalanches created distinct habitats compared to undisturbed areas, with varying vegetation structure and different bird species (Chapter III; Alba et al. 2023a). I highlighted differences in habitat in comparison to undisturbed areas with avalanche-impacted areas characterized by more rocks, shrubs, and small trees resulting from avalanche activity. These differences were more pronounced at lower elevations in the montane forest with high-canopy forest species in undisturbed areas

and a mix of treeline and open habitat species in avalanche tracks. At these elevations avalanches contributed to maintain high levels of bird diversity. This highlighted the primary role of avalanche disturbance in affecting ecological processes in mountain areas, since avalanches create unique bird habitats rather than merely shifting treeline habitats to lower elevations. Changes in avalanche frequency and severity due to climate change might potentially affect biodiversity at a landscape-level. However, the exact impact on avalanche frequency and severity remains uncertain (e.g., Gądek et al. 2017; Bormann et al. 2018). Increased forest cover at higher elevations due to climate change, grazing abandonment and lower snow precipitation may reduce avalanche impacts at lower elevations, leading to vegetation encroachment and potential negative consequences for some species.

I then compared the effects of natural disturbances such as avalanches with an artificial one like ski pistes (Chapter IV; Lopez et al. submitted) and I found that, whilst avalanche tracks exhibited high vegetation diversity, with substantial rock, shrub, and small tree cover, ski pistes were characterized by high grass and bare ground cover and hosted lower bird diversity and abundance, particularly in alpine grasslands. However, some grassland species like the Skylark, Water Pipit, Whinchat and Tree Pipit were less impacted by ski pistes, managing to colonize these habitats. Ski pistes had the most adverse effects on species dependent on shrub cover in the alpine belt, where the artificial removal of trees, shrubs, and topsoil significantly impact vegetation dynamics and biodiversity. I emphasized the importance of managing ski pistes more sustainably, retaining natural elements like small trees, shrubs, and small rocks during piste construction or management. This could potentially improve bird communities without affecting piste functionality, especially at higher elevations where bird species are most impacted (Chamberlain et al. 2013).

I assessed the ecological requirements of a migratory open habitat species, the Northern Wheatear *Oenanthe oenanthe* (Chapter V; Alba et al. 2023b). Contemporaneous observations were made in potential habitats both below and

above the treeline to understand the bird's arrival patterns and territory selection. The findings suggested that Wheatears first arrive in spring at low elevations in the valley bottom, and as higher elevations become partly snow-free, the birds abandon the lower arrival sites and occupy territories above the treeline. This arrival pattern was crucial for the Wheatears, which arrive in lean body condition and require immediate access to food resources. Territory selection models indicated that taller grass was the most important habitat variable for territory selection. In contrast to lowland populations (e.g. Arlt et al. 2008; Oosten et al. 2014), where territories with short grass layers were preferred, Wheatears in the alpine study area showed a preference for sites with taller grass (up to 20cm). The presence of small larches had a negative effect on territory selection, indicating that shrub encroachment in the alpine region, including small larches, poses a threat to the Wheatears and other open habitat species. Extensive rock cover and greater distance from forest structures were the key habitat features distinguishing high-elevation breeding grounds from lower-elevation foraging areas. However, a small portion of territories were occupied below the treeline, highlighting that these birds could breed at low elevations as long as open habitats with high rock cover and a significant distance from the nearest forest patch were present. Despite the lower quality of low-elevation habitats due to predation risk, disturbance, and grazing pressure, I suggested that extensively managed grasslands at lower elevations, such as alpine pastures and meadows, could serve as alternative nesting habitats for Wheatears. The maintenance of extensive grazing practices in the Alps is considered beneficial for grassland birds (Laiolo et al. 2004), helping prevent further shrub encroachment around the treeline and sustaining breeding habitats at lower elevations.

Mountain areas can also be important for birds during post-breeding migration. In my research (Chapter VI; Alba et al. in revision) we showed that approximately 22% of the terrestrial bird species recorded in Italy used these high-elevation habitats during this period, underscoring their significance for a wide range

of European bird species. The highest number of individuals and species diversity was recorded at the beginning of the migration period, around the end of August when both local breeders and migrants use these areas, some as stopover sites before continuing their journey to the wintering grounds. These species often rely on an insectivorous diet, thus habitat use is linked to the seasonal variation in resources. The treeline ecotone and montane forests were identified as the areas with the highest bird diversity and abundance, suggesting that the heterogeneity of vegetation and mature trees might offer stable microclimates and high levels of trophic resources, making them attractive for migratory birds. While I found no significant difference in bird abundance and diversity inside and outside protected areas, I stressed the importance of a well-structured protected area network in safeguarding mountain biodiversity, not only for breeding species, but also for migrants that use mountain habitats in other periods of the year. Slopes facing east and southeast accounted for greater bird abundance and diversity; these slopes received the earliest and highest solar radiation during the morning and might hence affect prey availability, such as arthropods. Migratory birds were likely to select these slopes to optimize foraging activity when temperatures were lower, minimizing thermoregulatory costs. In conclusion, in this study I showed the important role of high-elevation habitats in the Alps for a diverse range of bird species during their post-breeding migration. The treeline ecotone was identified as a critical habitat for these birds and I underlined the need to maintain landscape heterogeneity to counteract shifts in vegetation caused by climate and land-use changes.

Conservation of mountain birds: challenges and opportunities

In the last decades, upland and mountain areas have increased in conservation value as wildlife habitats since low-elevations have undergone severe transformations due to human activities. When I summed up the knowledge on the main drivers of upland and mountain bird populations through a systematic literature research, I found a general lack of detailed ecological studies for the majority of mountain areas in Europe. Such studies are fundamental to deliver effective conservation strategies and implement management actions. Furthermore, since I showed the presence of taxonomic and geographic biases, we need a higher number of studies on mountain specialists and from poorly covered mountain regions. I thus encourage researchers across Europe to carry on long-term and detailed studies on mountain and upland bird populations to gather reliable evidence to inform decision-makers and develop effective conservation measures for these vulnerable bird species.

In this thesis, I presented for the first time insights into the role of avalanche tracks in influencing ecosystem dynamics and animal communities and their contribution to maintaining high levels of biodiversity in mountain environments. I discussed their role as refugia for semi-open habitat species in a context of climate and land-use changes, but further research is needed to explore more in depth how the frequency of avalanche activity shapes bird communities in mountain regions and what will be the consequences for biodiversity of a decrease/increase in avalanche activity. Furthermore, my study design could be adapted to investigate other animal communities (e.g. lepidoptera, small mammals) in avalanche tracks and could thus contribute to a more comprehensive understanding of the role of avalanches for mountain biodiversity. While ski pistes may not reach the biodiversity levels of avalanche tracks, I showed their potential to act as refugia for open habitat species. I explicitly suggest that new ski resort developments at high elevations should be discouraged since future projections showed potential conflicts between ski activity and alpine specialist distribution in a context of climate change (Brambilla et al. 2016).

Furthermore, sensitive areas important for mountain bird populations should be protected and excluded from off-piste skiing. I conclude that ski pistes could act as valuable surrogates of other open habitats in mountain ecosystems, as long as environmental-friendly practices are applied to their management and construction.

When I studied the habitat selection of the Northern Wheatear, I provided insights into its adaptive behaviour and habitat preferences in alpine environments, highlighting the importance of open grasslands for this species, particularly in the face of environmental changes such as shrub encroachment and habitat loss. Such fine-grained studies are essential to know the details of the ecological requirements of open habitat species which is fundamental for developing effective conservation strategies. The maintenance of habitat heterogeneity is essential not only for breeding birds but also for migrants, as I showed in my study. It is needed to counteract shifts in vegetation caused by climate and land-use changes, and protected areas should take into account species requirements also during other critical period of species life-cycle, such as the autumn migration. In this way, it would be possible to promote sustainable conservation strategies that consider the value of alpine biodiversity throughout the year.

Mountains regions hold profound importance for human populations that developed thoughout thousands of years of history. Majestic peaks, serene landscapes, and diverse ecosystems always fascinated the human kind and the rich biodiversity in mountain areas, encompassing unique plant and animal species, adds to their allure. These ecosystems provide crucial ecosystem services, such as water regulation, carbon storage, and cultural inspiration, benefiting millions of people at the global scale. Preserving mountain biodiversity is essential for sustainable living and ensuring the well-being of future generations which should be an overarching priority. Conservation efforts must prioritize these ecosystems, acknowledging their intrinsic value and the interconnected relationship between humans and the landscapes that mountains embody.

References

Alba, R., Kasoar, T., Chamberlain, D., Buchanan, G., Thompson, D., & Pearce-Higgins, J. W. (2022). Drivers of change in mountain and upland bird populations in Europe. Ibis, 164(3), 635-648

Alba, R., Oddi, L., Rosselli, D., & Chamberlain, D. (2023a). Avalanches create unique habitats for birds in the European Alps. Journal of Ornithology, 164(2), 377-388

Alba, R., Chamberlain, D., Rosselli, D., & Sander, M.M. (2023b). Habitat quality drives the spatio-temporal occupation of a migratory songbird, the Northern Wheatear Oenanthe oenanthe, in alpine grasslands. Ardeola, 71(1), 61-80

Alba, R., Sander, M.M., Rosselli, D., & Chamberlain, D. High-elevation habitats are important for birds during the post-breeding migration period in the Alps. In revision in Journal of Ornithology

Arlt, D., Forslund, P., Jeppsson, T., and Pärt, T. (2008). Habitat-Specific Population Growth of a Farmland Bird. PLoS ONE 3, e3006.

Berny, P., Vilagines, L., Cugnasse, J. M., Mastain, O., Chollet, J. Y., Joncour, G., & Razin, M. 2015. VIGILANCE POISON: illegal poisoning and lead intoxication are the main factors affecting avian scavenger survival in the Pyrenees (France). Ecotox. Env. Saf. 118: 71-82.

Bormann, K. J., Brown, R. D., Derksen, C., & Painter, T. H. (2018). Estimating snow-cover trends from space. Nature Climate Change, 8(11), 924-928.

Brambilla, M., Pedrini, P., Rolando, A., & Chamberlain, D. E. (2016). Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. Journal of Biogeography, 43(11), 2299-2309.

Chamberlain, D. E., Negro, M., Caprio, E., and Rolando, A. (2013). Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol. Conserv. 167, 127–135. doi: 10.1016/j.biocon.2013.07.036.

Dayron, L., Chamberlain, D., Requena, E., Rosselli, D., & Alba, R. Mountain bird assemblages are shaped by differential vegetation dynamics in avalanches and ski pistes. Submitted to Biodiversity and Conservation

Gądek, B., Kaczka, R. J., Rączkowska, Z., Rojan, E., Casteller, A., & Bebi, P. (2017). Snow avalanche activity in Żleb Żandarmerii in a time of climate change (Tatra Mts., Poland). Catena, 158, 201-212.

Laiolo, P., Dondero, F., Ciliento, E., & Rolando, A. (2004). Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. Journal of Applied Ecology, 41(2), 294-304.

Ludwig, S. C., Roos, S., Rollie, C. J., & Baines, D. (2020). Long-term changes in the abundance and breeding success of raptors and ravens in periods of varying management of a Scottish grouse moor.

Oosten, H. H. van, van den Burg, A. B., Versluijs, R., and Siepel, H. (2014). Habitat Selection of Brood-Rearing Northern Wheatears Oenanthe oenanthe and Their Invertebrate Prey. Ardea 102, 61–69.

Patthey, P., Wirthner, S., Signorell, N., & Arlettaz, R. (2008). Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of applied ecology, 45(6), 1704-1711.

Pearce-Higgins, J. W., Stephen, L., Douse, A., & Langston, R. H. (2012). Greater impacts of wind farms on bird populations during construction than subsequent operation: results of a multi-site and multi-species analysis. Journal of Applied Ecology, 49(2), 386-394.

Thaxter, C. B., Buchanan, G. M., Carr, J., Butchart, S. H., Newbold, T., Green, R. E., ... & Pearce-Higgins, J. W. (2017). Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. Proceedings of the Royal Society B: Biological Sciences, 284(1862), 20170829.

Whitfield, D. P., Fielding, A. H., McLeod, D. R. A., & Haworth, P. F. (2004). The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. Biological Conservation, 118(2), 249-259.

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