Università degli Studi di Pavia

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GLI UCCELLI ALPINI E IL CAMBIAMENTO CLIMATICO

ALPINE BIRDS AND CLIMATE CHANGE

Ph.D. Thesis

This doctoral thesis is written according to "Type B" guidelines of the University of Pavia and it is structured in a general introduction, a collection of five papers (accepted/published) 2 manuscripts and a conclusion. Front cover by D. Scridel, Parco Naturale Paneveggio-Pale di San Martino.

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Alpine birds and climate change

Gli uccelli alpini e il cambiamento climatico

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CONTENT

Abstract (ENG)

Although considered globally important areas for birds and biodiversity in general, mountain regions remain poorly studied despite their renowned susceptibility to climatic alterations. Basic knowledge of bird species inhabiting these regions is scarce, and even a univocal definition of mountain regions lacks, as interpretations vary across countries and institutions. These ambiguities may prevent the definition of effective large-scale conservation strategies, and it is urgent to define "mountain birds" and investigate the potential impact of climate change on such species.

In this thesis, we reviewed evidence for impacts of climate change on Holarctic mountain bird populations in terms of physiology, phenology, trophic interactions, demography and observed and projected distribution shifts, including effects of other factors that interact with climate change. We introduced for the first time an objective classification of mountain bird specialists and generalists, presented the results of a systematic review and meta-analysis of the effects of climate change on Holarctic mountain and upland birds, quantifying the general responses to climate change including altitudinal shifts, changes in life history traits and assessment of mitigation actions. Using Italy as a case-study, we demonstrated a relationship between climate and changes in bird distribution in the last 30-years, by comparing net range variation in cold-adapted and closely related control species. In addition, using the white-winged snowfinch *Montifringilla nivalis* (a mountain indicator species sensitive to climate change) as a model species, we aimed at improving the knowledge on biology, ecology and demographic aspects of this species to better elucidate the mechanisms driving declines of mountain birds. Finally, we developed adaptation frameworks for climate change at both large and small scale. For the first case, we established a novel approach for selecting conservation priorities, resistant units and resilient areas in the Italian Alps according to structural connectivity and future distribution for a range of mountain bird species to identify strategies that maximize the chances of species persistence in a changing climate. At a finer scale, we evaluated the role of microhabitats as refugia for climate-threatened species, and developed a theoretical approach based on human-mediated actions (i.e. grazing, mowing) to contain the detrimental effects of climate change on our study species, the white winged-snowfinch.

We identified 2316 bird species breeding in the Holarctic realm, 818 (35.3%) of which were defined as either high-elevation mountain specialists (n = 324 species) or mountain generalists (n = 494 species). We found evidence of biological and ecological responses of mountain birds to climate and environmental change, but little is known about underlying mechanisms or synergistic effects. Meta-analyses did not find a consistent direction in elevation change to track suitable climate but suggested that in the future mountain birds will be significantly more impacted than non-mountain species. In Italy, we found a strong positive correlation between change in range size and species thermal index (STI: average temperature of a species' European range), confirming that recent climatic warming has favoured species of warmer climates and adversely affected species occupying colder areas. A model including STI and birds' associated habitats was not so strongly supported but further suggested that forest species performed better than alpine open habitat and agricultural ones. Regarding our indicator/model species, we found that the white-winged snowfinch selected specific and climate sensitive microhabitat during the nestling rearing period: cool sites with short grass cover,

melting snow margins adjacent to grassland and snow patches. These microhabitats harboured high quality and quantities of invertebrates and snowfinches were able to efficiently tune their microhabitat selection in relation to prey abundance and type, suggesting a high adaptability to resource variation in specie and time, a typical characteristic of high elevation sites. When hindcasting (1976) and forecasting (2066) the suitability of such microhabitats in relation to the observed changes associated to climate change, we found higher suitability in the past and a predicted decline in the future. Grazing activities, which can keep the sward height suitable for snowfinches, could improve the suitability in the present and in the future, but only for population that can have access to extensive grassland areas. For populations confined to more rocky habitats (i.e. subnival and nival), where grassland cover is generally low or even absent, this mitigation may not be applicable and snowfinches living in these habitats could be more at risk from climate change, as they largely rely on snow patches. Measures for adaptation to climate change mostly relied on broad-scale management and extension of protected areas for species already present and for future colonizers from lower elevations. We suggested the development of management/restoration plans in mountain areas that consider threats and opportunities resulting from interactions of climate and land-use changes and encompass different spatial scales, from landscape to microhabitats.

Riassunto (ITA)

Le regioni montane, sebbene considerate aree globalmente importanti per gli uccelli e la biodiversità in generale, rimangono scarsamente studiate, nonostante la loro ben nota suscettibilità alle alterazioni climatiche. La conoscenza di base delle specie di uccelli che popolano queste regioni è scarsa, e manca persino una definizione condivisa di "regioni montane", in quanto le interpretazioni variano in base a paesi e istituzioni. Queste ambiguità possono potenzialmente precludere la delineazione di efficaci strategie di conservazione su larga scala, ed è quindi urgente dare una definizione univoca di "avifauna di montagna" per poter indagare il potenziale impatto dei cambiamenti climatici su queste comunità di specie.

In questa tesi abbiamo esaminato le evidenze degli impatti dei cambiamenti climatici sulle popolazioni di avifauna di montagna su scala olartica, riguardo a fisiologia, fenologia, interazioni trofiche, demografia e spostamenti di distribuzione osservati e previsti, considerando anche gli effetti di ulteriori fattori che interagiscono con i cambiamenti climatici, esacerbandone o attenuandone gli effetti. Per la prima volta abbiamo formulato una classificazione oggettiva dell'avifauna di montagna "specialista" e "generalista" e presentato i risultati di una revisione sistematica e di una meta-analisi riguardanti gli effetti dei cambiamenti climatici sugli uccelli montani, quantificando le conseguenze di tali alterazioni, come gli spostamenti altitudinali o i cambiamenti nei tratti biologici, e la valutazione di potenziali azioni mitigatrici e di compensazione degli impatti dovuti alle variazioni nel clima. Utilizzando l'Italia come caso-studio, abbiamo dimostrato l'esistenza di una relazione tra il clima e i cambiamenti nella distribuzione degli uccelli negli ultimi 30 anni, confrontando gli andamenti di occupazione ed abbandono di aree riproduttive da parte di specie legate ad ambienti freddi e di specie-controllo tassonomicamente vicine ma presenti in climi più miti. Inoltre, abbiamo utilizzato il fringuello alpino *Montifringilla nivalis* come specie modello (in quanto particolarmente sensibile ai cambiamenti climatici), al fine di migliorare le attuali conoscenze su biologia, ecologia e aspetti demografici delle specie d'alta quota, e chiarire meglio così i meccanismi che determinano il declino dell'avifauna di montagna. Infine, abbiamo sviluppato degli approcci conservazionistici innovativi per far fronte agli impatti del cambiamento climatico, su larga scala e poi su piccola scala. Nel primo caso, per identificare strategie che massimizzino le possibilità di persistenza delle specie in un clima che cambia, abbiamo stabilito nuove metodologie che hanno consentito di identificare nelle Alpi italiane le specie e le aree prioritarie per la conservazione (unità geografiche resistenti e resilienti ai mutamenti climatici), basandoci su connettività strutturale e previsioni di distribuzione futura di varie specie di avifauna di montagna. A scala più piccola invece abbiamo valutato il ruolo dei microhabitat come siti di rifugio per le specie minacciate dal clima, e sviluppato un approccio teorico basato sulla capacità di alcune attività umane (attività di pascolo e sfalcio) di contenere gli effetti dannosi del cambiamento climatico, con particolare riferimento alla nostra specie studio, il fringuello alpino, e alla struttura del suo habitat di foraggiamento.

Abbiamo identificato 2316 specie avifaunistiche che si riproducono nell'Olartico, 818 (35,3%) delle quali sono state divise secondo le nostre definizioni in specialiste d'alta quota (n = 324 specie) o generaliste di montagna (n = 494 specie). Abbiamo poi riscontrato evidenze di reazioni biologiche ed ecologiche degli uccelli di montagna al cambiamento climatico ed ambientale, ma l'influenza di meccanismi ed effetti sinergici di altre

variabili sono ancora poco conosciuti. Una meta-analisi svolta per valutare gli spostamenti altitudinali degli uccelli di montagna in risposta alle anomalie termali, non ha trovato una direttrice costante nel cambiamento di quota, ma una seconda meta-analisi riguardante le previsioni future ha suggerito che proprio le specie montane saranno significativamente più impattate dai cambiamenti climatici rispetto a specie non-montane. In Italia, abbiamo trovato una forte correlazione positiva tra variazione delle dimensioni degli areali riproduttivi e l'indice termale delle specie (STI: temperatura media di presenza di una specie a scala europea), a conferma del fatto che il recente riscaldamento climatico ha favorito specie di climi più caldi e sfavorito quelle legate ad ambienti più freddi. Un modello che includeva STI e habitat associati agli uccelli è risultato poco supportato, ma ha anche suggerito che le specie forestali hanno avuto variazioni più positive rispetto a specie legate agli habitat aperti alpini o agricoli. Per quanto riguarda la nostra specie modello, abbiamo scoperto che il fringuello alpino durante il periodo riproduttivo, seleziona per il foraggiamento luoghi freddi, caratterizzati da copertura erbosa bassa, margini di neve in scioglimento adiacenti al prato e macchie di neve: microhabitat sensibili al cambiamento climatico e che ospitano un'alta qualità e quantità di invertebrati. I fringuelli alpini sono in grado di selezionare con grande efficienza questi microhabitat in relazione all'abbondanza e al tipo di prede, dimostrando un'alta adattabilità alla variabilità delle risorse trofiche nello spazio e nel tempo, caratteristica tipica delle specie proprie di ambienti d'alta quota. Modellizzando l'idoneità di foraggiamento di questi microhabitat rispetto ai cambiamenti climatici osservati rispetto al passato (1976) e previsti per il futuro (2066), abbiamo riscontrato un'idoneità maggiore di tali siti nel passato e un previsto calo della stessa per il futuro. Le attività di pascolo, in grado di mantenere il manto erboso ad un'altezza adatta ai fringuelli alpini, potrebbero migliorare l'idoneità strutturale attuale e futura di tali microhabitat di foraggiamento, almeno per le popolazioni presenti in habitat adiacenti a prati alpini adibiti a pascolo. Per le popolazioni confinate invece in habitat rocciosi (ad esempio sub-nivali e nivali), dove la copertura erbosa è generalmente bassa o addirittura assente, questa mitigazione non potrà essere applicata, ed i fringuelli alpini di questi habitat, dipendendo principalmente dalla presenza di macchie di neve, potrebbero essere più colpiti/minacciati dai cambiamenti climatici. Le misure per mitigare e compensare gli effetti dei cambiamenti climatici si basano principalmente su una gestione a vasta scala che dovrebbe estendere le attuali aree protette per favorire le specie già presenti ed anche quelle future colonizzatrici provenienti da quote più basse. Abbiamo dunque suggerito lo sviluppo di piani di gestione delle aree montuose che considerino le minacce e le opportunità derivanti dalle interazioni fra cambiamenti climatici, uso del suolo a diverse scale spaziali e conservazione di ambienti chiave dal macro al micro habitat.

SECTION I

- *General Introduction* -

Glacier in the Ortler Apls (Stelvio National Park), between Tuckett Mountain (3.464 m) and Punta degli Spiriti (3.467m). Photo: D. Scridel

I.a The problem of anthropogenic climate change

"You can deny environmental calamity until you check the facts" George Monbiot

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Anthropogenic climate change is one of the greatest pressures to biodiversity of recent times (Thomas *et al.* 2004), and it is increasingly threatening ecosystems and species worldwide (Bellard *et al.* 2012). During the history and evolution of life on Earth the climate has always changed with both warmer and cooler phases than those we are currently experiencing (Petit *et al.* 1999). Such variations were natural (e.g. non-anthropogenic) in origin and mostly caused by orbital wobbles, volcanic activity, rock weathering, solar activity (IPCC 2007). Ecosystems and species have moved to track such changes and have evolved within this climatic history (Atkinson *et al.* 1987, Blois *et al.* 2013). However, these prehistoric changes differ substantially from what we are currently experiencing, as the current changes involve a new natural forcing defined as greenhouse emission by anthropogenic activity. The greenhouse effect was firstly described by Tyndall and Arrhenius at the end of the XIX Century as the process by which radiation, from a planet's atmosphere, warms the globe's surface to a temperature above what it would be without its atmosphere (IPCC 2007). The denser the atmosphere the more energy it can trap thanks to the higher concentration of energy-holding molecules such as water vapour and carbon dioxide. Without this natural greenhouse effect (as opposed to anthropogenic), life on earth would be vastly different, or even non-existent as conditions will be similar to our moon (given its similar distance to the sun as the earth is). However, since the Industrial Revolution, the burning of fossil fuels has grown at unprecedented rates, further increasing the concentration of various greenhouse gases in the atmosphere most notably carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O; Figure 1 & 2). According to the results of IPCC (2014), the level of greenhouse gases has surpassed the highest levels of concentrations on earth over the last 800,000 years. If considering atmospheric CO_2 alone, human activities alongside natural forces have driven at its highest level over 15 million years (Tripati & Darmi 2018). Like climate, also CO_2 has fluctuated over time. During pre-industrial revolution, natural forces caused fluctuations of CO_2 between 180-280 parts per million (ppm). It took 5.000 to 20.000 years to increase by 100ppm, but since the industrial revolution it took only 120 years to increase 100ppm due to human activity. The changes in atmospheric composition, alongside changes in land use cover, has led to an increase in radiative forcing, a metric that indicates changes in global radiation balance.

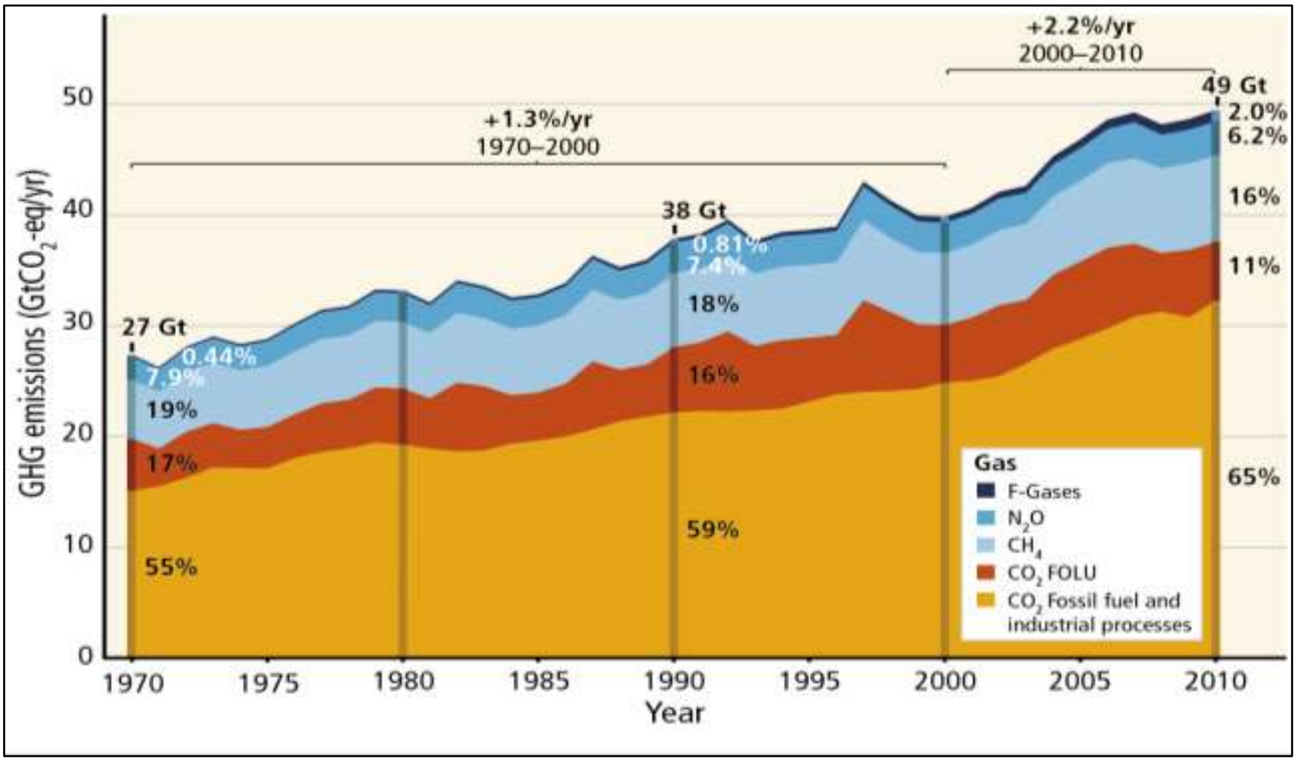

Figure 1 Total annual anthropogenic greenhouse gas (GHG) emissions (gigatonne of CO2-equivalent per year, GtCO2-eq/yr) for the period 1970 to 2010 by gases: CO2 from fossil fuel combustion and industrial processes; CO2 from Forestry and Other Land Use (FOLU); methane (CH4); nitrous oxide (N2O); fluorinated gases covered under the Kyoto Protocol (F-gases). Adapted from (IPCC 2014 available at: http://www.ipcc.ch/report/ar5/syr/)

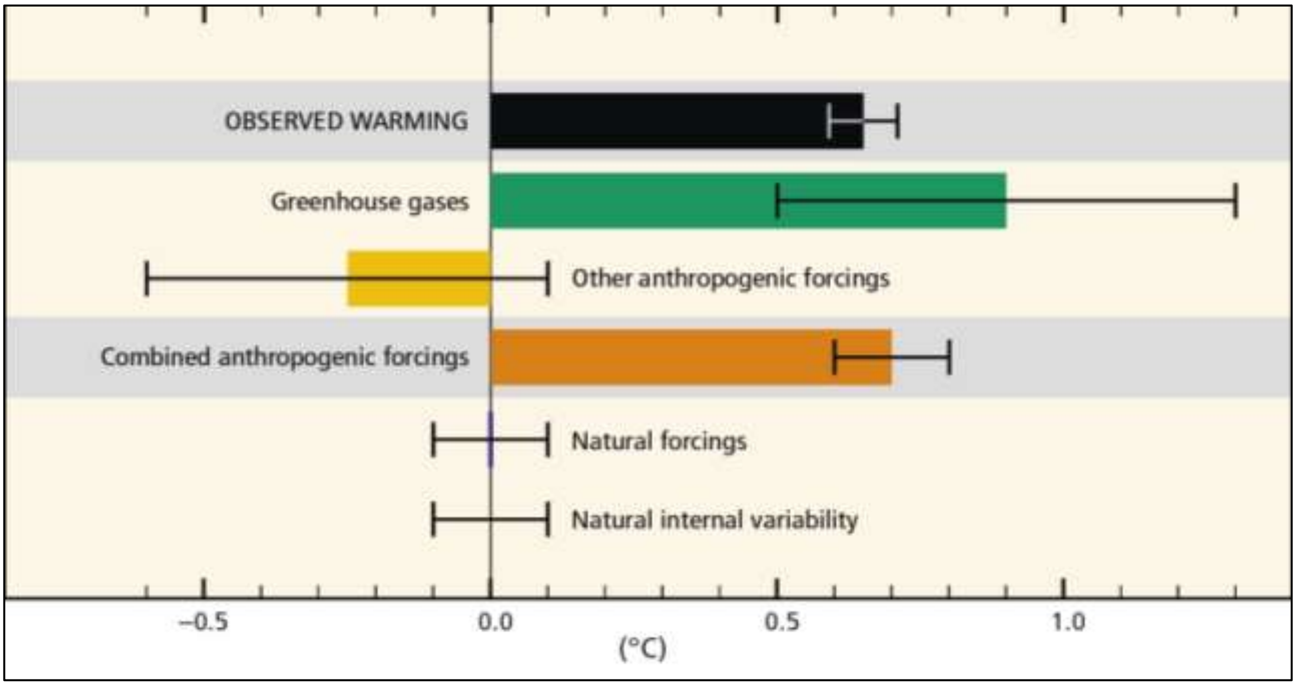

Figure 2 Contribution to observed surface temperature change over the period 1951-2010. Adapted from (IPCC 2014, available at: http://www.ipcc.ch/report/ar5/syr/).

A primary consequence of this is that global mean surface temperature increased by 0.7–0.9 °C per century (calculated from 1901), but the rate of warming has nearly doubled since 1975 to 1.5–1.8 °C per century, with the 10th warmest years on record occurred since 1998 (Sánchez-Lugo *et al.* 2017). Apart the warming effect *per se*, what really concerns scientists is the rapidity of such changes. A recent study by Gaffney & Steffen (2017) estimated that humans are causing climate to change 170 times faster than natural forces alone. The rate of change can vary in space and time due to different factors. The land is warming faster than the oceans, with Northern Hemisphere land surface temperatures increasing at around 0.3 °C per decade between 1979 and 2005, compared to increases of around 0.2 °C per decade for ocean temperatures over the same period (IPCC 2007). Additionally, climatic changes have influenced the global atmospheric circulation and precipitation patterns, but in a less predictable manner, with some areas experiencing drier conditions and others wetter, whilst both heavy rainfall and drought frequency have increased (Trenberth *et al.* 2007). Rapid changes in temperature have been accompanied by an increase in the frequency, intensity and duration of unpredictable weather events such as floods, hurricanes, heatwaves or droughts (IPCC 2001, EEA 2004). Diffenbaugh (2017) found that historical global warming has increased the severity and probability of the hottest monthly and daily events at more than 80% of the observed area and has increased the probability of the driest and wettest events at approximately half of the observed area. These changes are already affecting physical, biological and human systems (Rosenzweig *et al.* 2007), and even if we stopped all emissions tomorrow, climate change will continue in the foreseeable future due to gasses already emitted (Raftery *et al.* 2017).

Understanding and predicting climate change impacts is therefore an important and necessary aspect of climate change research. In this regard, Global Climate Models (also known as General Circulation models both abbreviate as GCMs) aim to describe climate behaviour by integrating a variety of atmospheric, oceanic, cryospheric and land surface processes and represent the most advanced tool currently available for simulating the response of the global climate system to increasing emission or radiation scenarios (IPCC 2007). Emission scenarios are built upon estimates of the development of the world economy, population growth, globalisation, increasing use of green technology, etc. In the past IPCC assessments, the most widely used scenarios were SRES (Special Report on Emission Scenarios (Nakićenović *et al.* 2000)). More recently, IPCC has applied a new set of scenarios, named Representative Concentration Pathways (RCPs) which differentiate from SRES as they account for potential climate change mitigation policies to limit emissions and are expressed in approximate radiative forcing relative to the pre-industrial period achieved either in the year 2100, or at stabilization after 2100 (Moss *et al.* 2010; Figure 3). Over the past ten years, observed emissions have been close to the most carbon intensive of the SRES scenarios—A1FI emphasizing how complex is to stabilize carbon emissions for our society and that extreme scenarios are unlikely to be unrealistic (Figure 3).

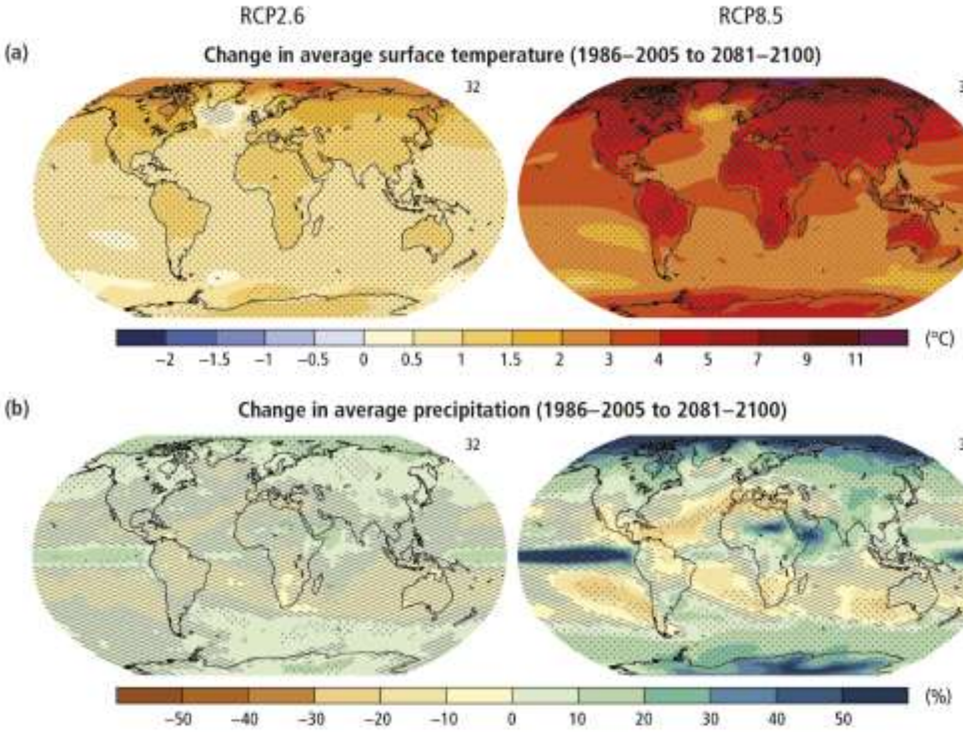

Figure 3 Change in average surface temperature **(a)** and precipitation **(b)** based on multi-model mean projections for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarios. Available from Climate Change 2014 Synthesis Report Summary for Policymakers.

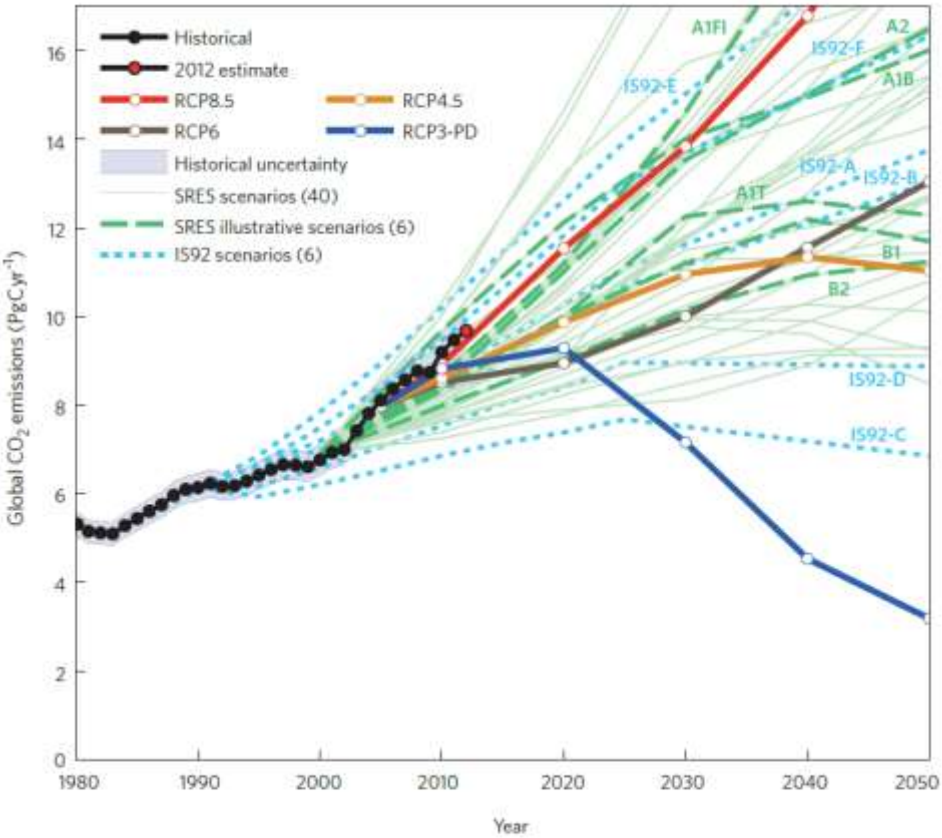

Figure 4 Coloured lines represent different scenarios of estimated historical and projected increase in carbon dioxide emissions according to various scenarios (SRES, RCPs). Graph available from Peters *et al.* (2013).

I.b Mountain biodiversity and ecosystem services

"Here not palaces, neither theatre nor loggia, but in their place a fir, a beech, a pine, between the green grass and the beautiful mountain nearby. They lift from Earth to Heaven our mind" Francesco Petrarca

Although considered globally important areas for biodiversity, mountain and upland regions remain amongst the most poorly studied systems to the point that we lack even a univocal definition for mountain regions, which are subject to different interpretations vary across countries and institutions. According to Kapos *et al.* (2000), 25% of the Earth's surface is covered by mountains which support ¼ of terrestrial biodiversity and contain about 50% of the world's biodiversity hotspots (Myers *et al.* 2000, Körner & Ohsawa 2006). In Europe, mountains are important biodiversity hotspot for plants holding 20% vascular plants of the continent (Väre *et al.* 2003) and host many endemic species (Dirnböck *et al.* 2011). The reasons for the high biological diversity can be explained by the interaction of unique ecological characteristics typical of mountain areas (Table 1 & Figure 4).

Table 1 Some of the peculiar features influencing biodiversity in mountain systems (adapted and further implemented from Spehn *et al.* 2012).

Climate	Antonelli *et al.* (2018), found that temperature and total annual precipitation are the two most important predictors of tetrapod species richness in mountains regions and their contribution vary greatly depending on the regions considered.
Compressed climatic zones	Create a variety of habitats and species otherwise only seen over several thousands of kilometres of latitudinal distance. Climbing a 100 meters mountain can offer a climatic variety equal to travelling 100 km across a flat terrain. For this reason, the alpine life zone is richer in species than might be expected from the size of its area (Körner 2004).
Geology	Plant communities on calcareous soils have higher plant richness than on siliceous substrates (Wohlgemuth 2002). Similar patterns are likely to be found for invertebrate and vertebrate communities. Antonelli *et al.* (2018) found that species richness in mountain regions correlated with erosion rates and heterogeneity of soil types, with a varying response across continents.
Exposure, slope and relief	Forms a variety of microclimatic situations which, combined with various substrates and associated water and nutrient regimes, create a heterogeneity of microhabitats, often occupied by endemic organisms.
Altitudinal isolation	Imposes isolation of species which has led over time to speciation events (allopatric speciation).
Migratory corridors	Allow intra and interspecies immigration and emigration therefore maintaining genetic diversity. Common examples are the east-west forest connection of the Alps and along the southern slopes of the Himalayas.
Disturbances	Such as landslides, avalanches, grazing by large herbivores and/or wildfires creating further habitat heterogeneity
Anthropogenic activity	Livestock grazing, forest management, leisure activities influence significantly biodiversity in many alpine regions. For instance, human activity in the Alps and Pyrenees has been recorded since Neolithic times. Despite anthropogenic presence in mountain systems, its intensity is generally low, allowing to retain higher levels of wilderness compared to other systems (Catalan *et al.* 2017).

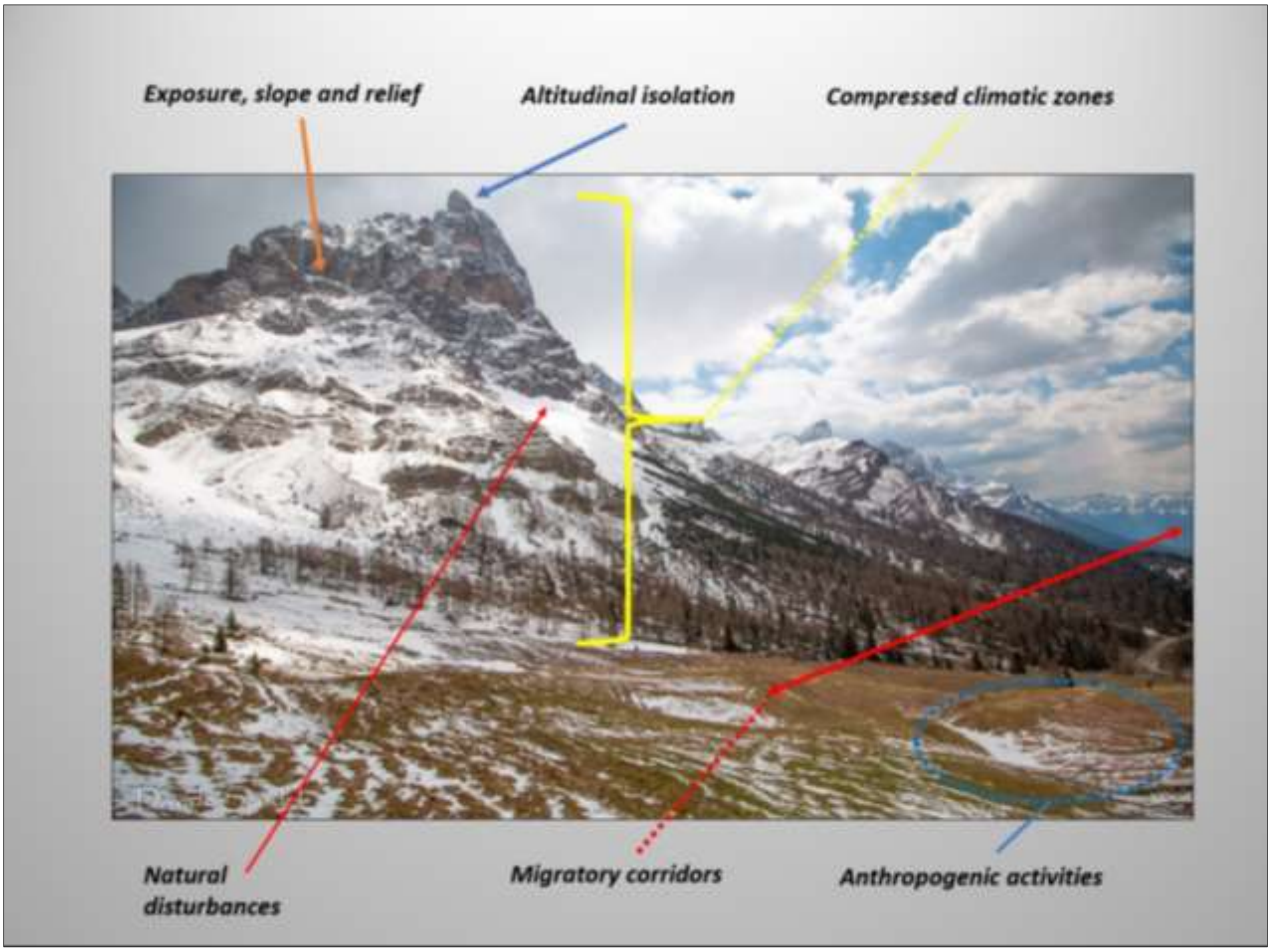

Figure 4 Visual representation of some ecological characteristic driving richness and diversity patterns in mountain systems. Foto D. Scridel – Parco Naturale Paneveggio-Pale di San Martino.

Mountains are also extremely important systems for humankind, providing a vast array of natural goods (e.g. timber, food and fibre) and services (e.g. pollination, carbon sequestration, watershed protection) to both people living within mountains and outside them (e.g. MA 2005, Figure 5 & 6). Freshwater supply is perhaps the most crucial resource with more than 50% of human population being dependent on mountains as the world's "water towers" (Viviroli *et al.* 2007, Vanham & Rauch 2009). Mountains are also important regulating system for climate, air quality, water flow and erosion. Much less is known on their influence in providing biological services such as pollination, seed dispersal, and the regulation of pests and diseases, but their contribution is believed to be fundamental worldwide (Egan & Price 2016). The preservation of mountain regions has also important socio-cultural implications. About 12% of the world's population lives in mountain regions and represent an important legacy of human adaptability, as living in these challenging environments has occurred over many centuries or even millennia (Huddleston *et al.* 2003). The remoteness and inaccessibility of these landscapes have allowed the conservation of unique populations, making mountain regions a true hotspot for cultural and ethno-linguistic diversity. For example, in the Hindu Kush Himalaya region, over 1000 different languages and dialects are spoken (Turin 2005). In spite of their small size, also the European mountains are the home of various ethnic minorities, with specific cultures, languages or dialects, and traditions which have been diluted in many areas by external influences and the loss of indigenous people, especially from younger generations (Schuler *et al.* 2004). In the European Alps, for example, the attractive "cultural landscapes" (World Heritage Committee), the high-quality food and the diverse recreational opportunities has led to an increase in the number of people visiting these otherwise remote areas (Debarbieux *et al.* 2014) to the point that tourism and recreation activities are recognized as fundamental drivers of local economies in Europe's mountains and around the world. It is estimated that mountain tourism accounts for 15-20% of the world's tourism industry, amounting up to an estimated USD 70 to 90 billion per year (FAO 2012).

Despite their importance, various authors have raised concerns on the vulnerability of mountain ecosystem services to changes in land use and climate (e.g. Palomo 2017, Tang *et al.* 2018). Global warming is influencing freshwater and biodiversity patterns, while changes in land use (especially in the form of urban development) has been shown to negatively impact biodiversity and to deteriorate these attractive cultural landscapes (Egan & Price 2016). The abandonment of pastoral practices in the Alps has also been associated with a loss of biodiversity, forage material and landscape aesthetics (MacDonald *et al.* 2000, Krauβ & Olwig 2018). On the other hand, climate change and the abandonments of pastoral activities have led to an increase in forest coverage, with beneficial effects on services such as carbon storage, timber production and soil erosion (Palomo 2017). True evaluations of cost and benefits of climate change and land use on ecosystem services remain still poorly understood and more work should be targeted to assess the sensitivity of mountain ecosystem services to the rapid global development (Körner 2000, Schröter *et al.* 2005).

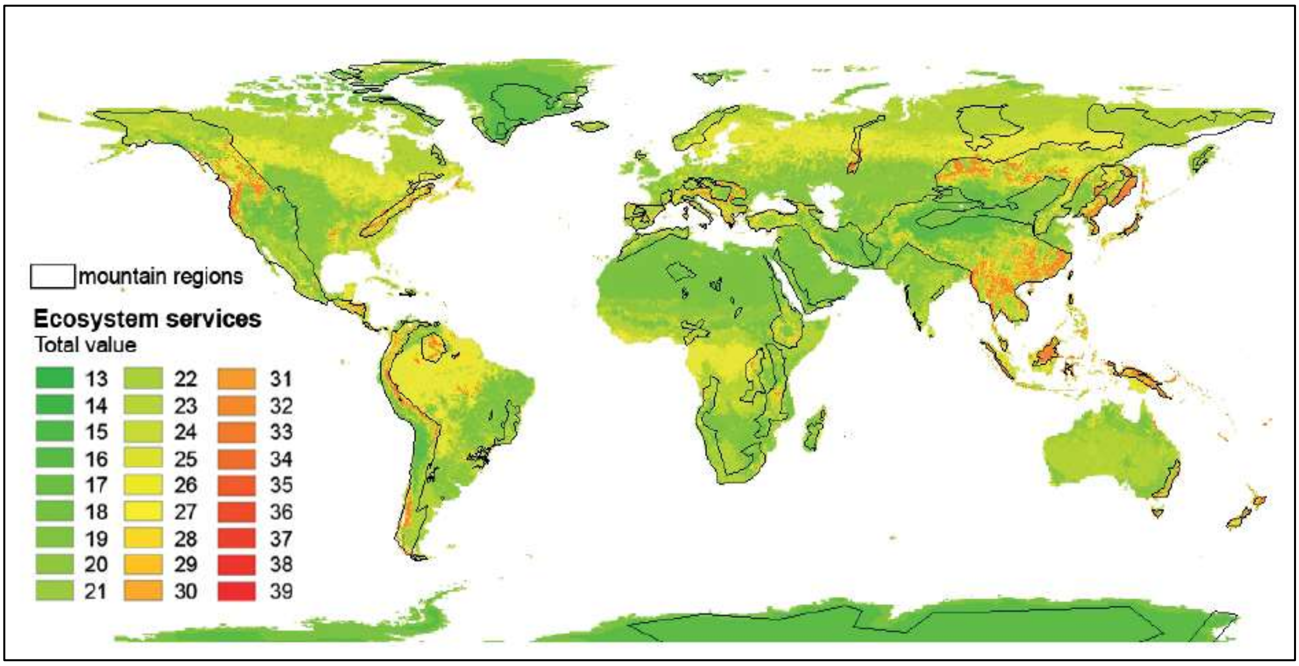

Figure 5 Mountains systems (highlighted by the bouldering line) provide the most numerous ecosystem services worldwide. Available from Egan & Price (2016) available at: http://unesdoc.unesco.org.

Figure 6 Visual representation of some of the goods and services present at Passo Gavia, Stelvio National Park (Italy). Photo: D. Scridel

I.c Climate and land use change in mountain regions

"All mountain landscapes hold stories: the ones we read, the ones we dream and the ones we create" George M. S. Kennedy

Mountain regions offer a unique opportunity to detect climatic alterations and to evaluate their impacts on biodiversity and ecosystem services. Apart from the peculiar features already highlighted in Table 1, a further reason for such uniqueness is the rate of warming that mountain are experiencing, faster than the global average and parallel to the rates experienced by the Arctic. For example, the European Alps have warmed about 2°C in the past 100 years, with the biggest jump in the last three decades (Böhm *et al.* 2001, Auer *et al.* 2007, Brunetti *et al.* 2009). Despite this, knowledge of the rate of warming in mountain regions requires further investigation. As Pepin *et al.* (2015) pointed out, out of the 7.297 meteorological stations available present in the GHCNv3 database, only 3% are located above 2000m and 0.7% above, 3.000m and long-term data is non-existent above 5.000m. Notwithstanding these limitations, an elevation-dependent warming relationship (EDW) has been shown for most studies (but see Rangwala & Miller 2012 and Pepin *et al.* 2015), with warming being more rapid at higher elevation. Reasons why mountains are subjected to faster warming are still under debate and include complex interacting feedback mechanisms ranging from snow-albedo effects to air pollution (Table 2, Figure 7).

Table 2 Description of the most studied mechanisms that strongly influence EDW in a mountain area. Such mechanisms may act independently or in combination depending on the sites considered.

Snow-albedo feedback mechanisms	In response to increasing surface air temperature, snow cover shrinks revealing land surface that is much less reflective of solar radiation. According to Pepin & Lundquist (2008) 20th century temperature trends are most rapid near the annual 0°C isotherm due to snow-ice feedback. For example, in the Swiss Alps, the daily mean temperature of a spring day without snow cover is 0.4 °C higher than one with snow cover (mean value for 1961–2012).
Cloud cover	Changes in cloud cover and cloud properties can influence condensation as well as shortwave and longwave radiation (Liu *et al.* 2009, Pepin *et al.* 2015)
Moisture levels	Water vapour can influence downward longwave radiation resulting in greater warming (Pepin *et al.* 2015).
Air pollution	Little is known about the effects of pollutants at high elevations (Pepin *et al.* 2015). Aerosols dusts deposited on snow decreases surface albedo leading to more warming (Lau *et al.* 2010, Gautman *et al.* 2013)
Topography	Topographic features (slope, aspect and exposure) typical of mountain systems can cause extreme variations in local climate. Stronger warming has been observed for flat and incised valley sites (Pepin *et al.* 2008).
Urbanisation	According to Pepin *et al.* (2008) some urban mountain locations showed enhanced warming rates than average.

Apart from changes in climate, mountain regions are also subjected to changes in land-use with effects that can act synergically or in contrast with climate change and vary in intensity and frequency, depending on the region considered (Lenoir *et al.* 2010, Bhatta *et al.* 2018, Bani et al. 2019 Figure 7). This is particularly true in the European Alps where milder temperatures are pushing the treeline towards higher elevations (Leonelli *et al.* 2011, Körner 2012). At the same time, shrub and tree encroachment of formerly open grasslands is also occurring as consequence of pastoral abandonment (Ameztegui *et al.* 2016, Braunisch *et al.* 2016; Figure 7). At lower elevations, climatic alterations are influencing patterns of tree composition and growth in forested zones (Rebetez & Dobbertin 2004). However, forests have been historically managed influencing cover, composition and natural stand dynamics (Bebi *et al.* 2017). The European mountains are also important sites for leisure activities including skiing, snowboarding, rock climbing, hiking, paragliding and hunting which in turn offer opportunities for tourism development and urbanisation. There is growing evidence that increases in such activities can negatively alter biodiversity (Laiolo & Rolando 2005, Arlettaz *et al.* 2007). Indeed, whilst the Alps are experiencing a loss in settled rural population and abandonment of traditional farmlands believed beneficial to biodiversity (Figure 8), changes in land use with the development of new artificial areas (ski pistes, dams, new roads, etc.) is occurring at a fast rate, with strong impacts on biodiversity (Figure 9; Alpine Convention 2018).

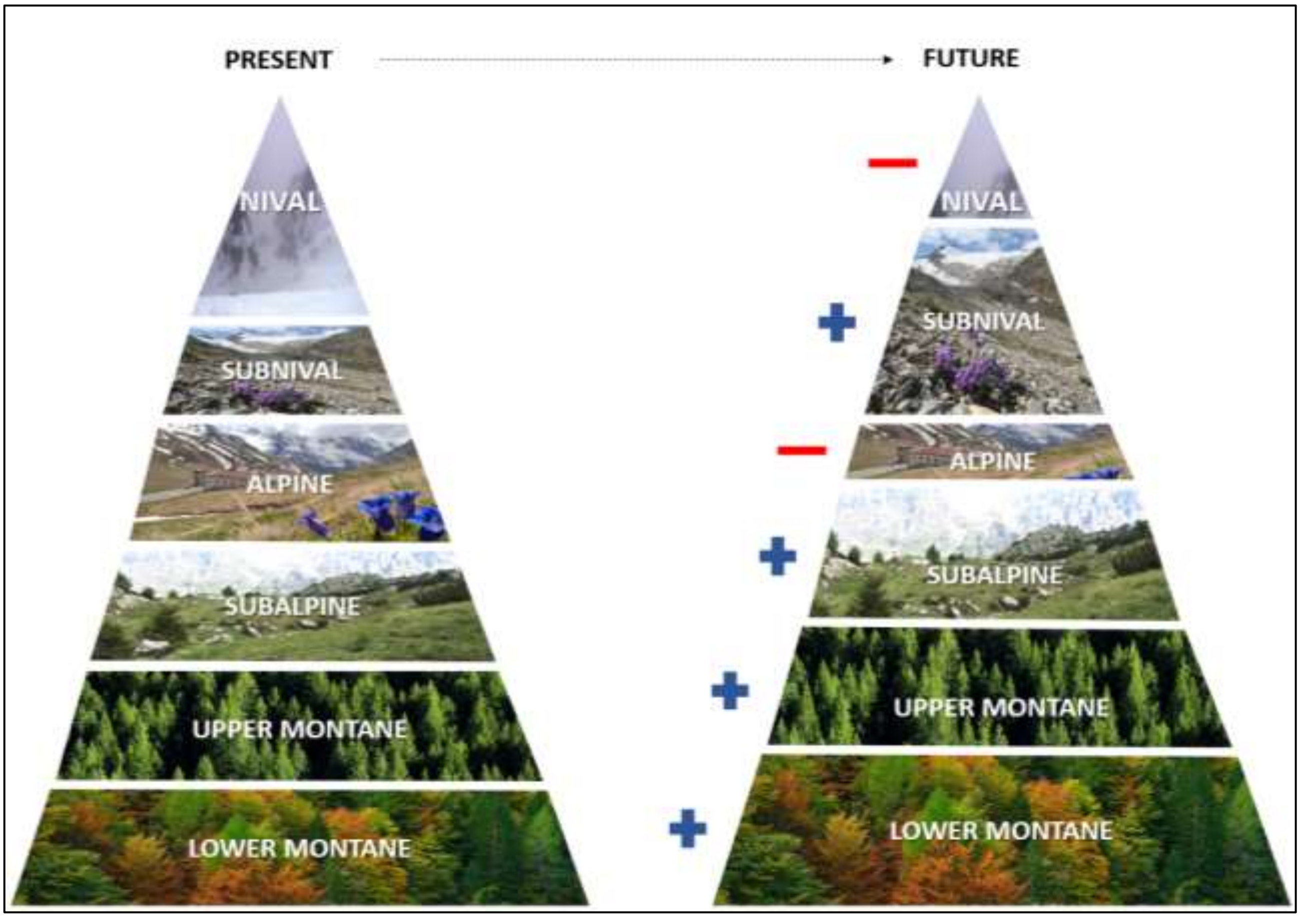

Figure 7 A generalisation of the observed changes in the European Alps across altitudinal zones. The symbol "-" indicates a reduction in size, whilst "+" expansions. Starting from the top, nival zones once covered by perennial snow and glaciers are now retreating because of increased temperatures revealing rock and screes expanding the sub-nival zone. Alpine grasslands are experiencing a reduction in size as shrubs colonize milder climates and abandoned by pastoral lands. Subalpine, upper montane and lower montane zones are undergoing an increase in forest cover mostly due to changes in land management. Here climatic effects and forest practices are influencing patterns of tree composition.

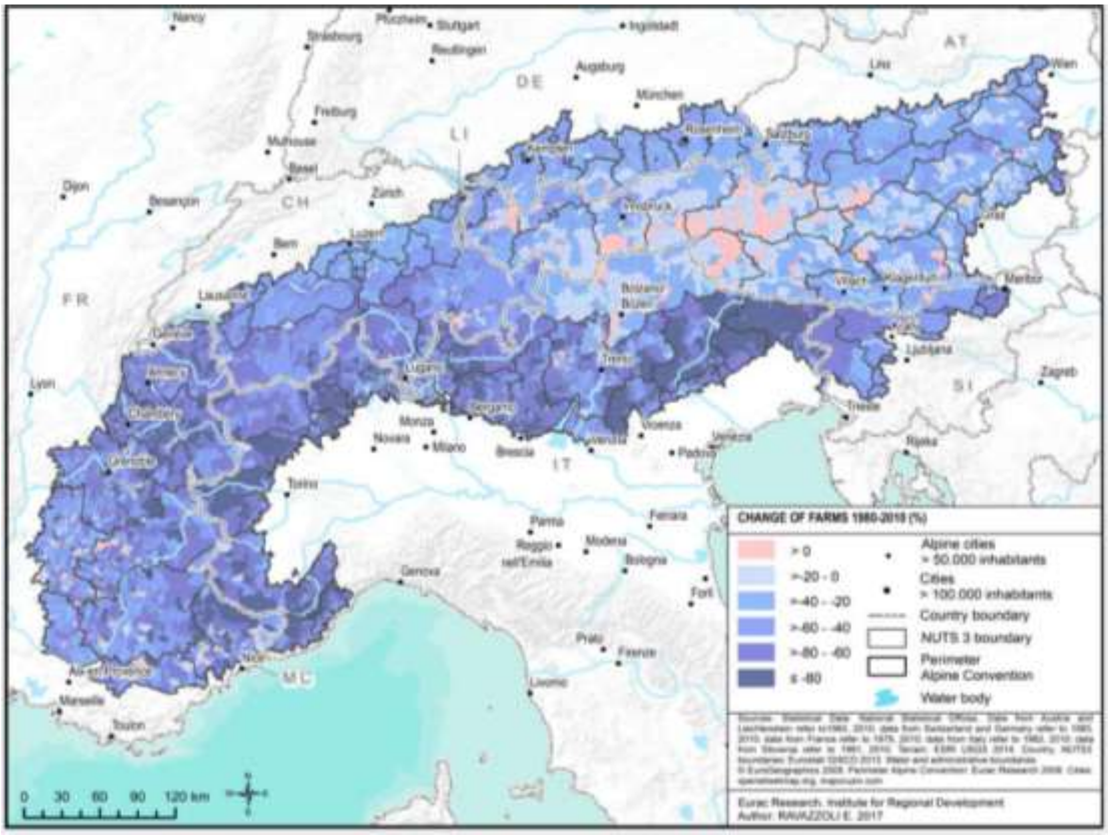

Figure 8 Changes in the number of farms from 1980 to 2010. Important to notice that strong declines have occurred mostly in Italy and it concerns mostly small farms with less than 10 hectares, while the number of farms with more than 20 hectares has increased (Alpine Convention 2018). Available from: http://www.alpconv.org/en/publications/alpine/default.html

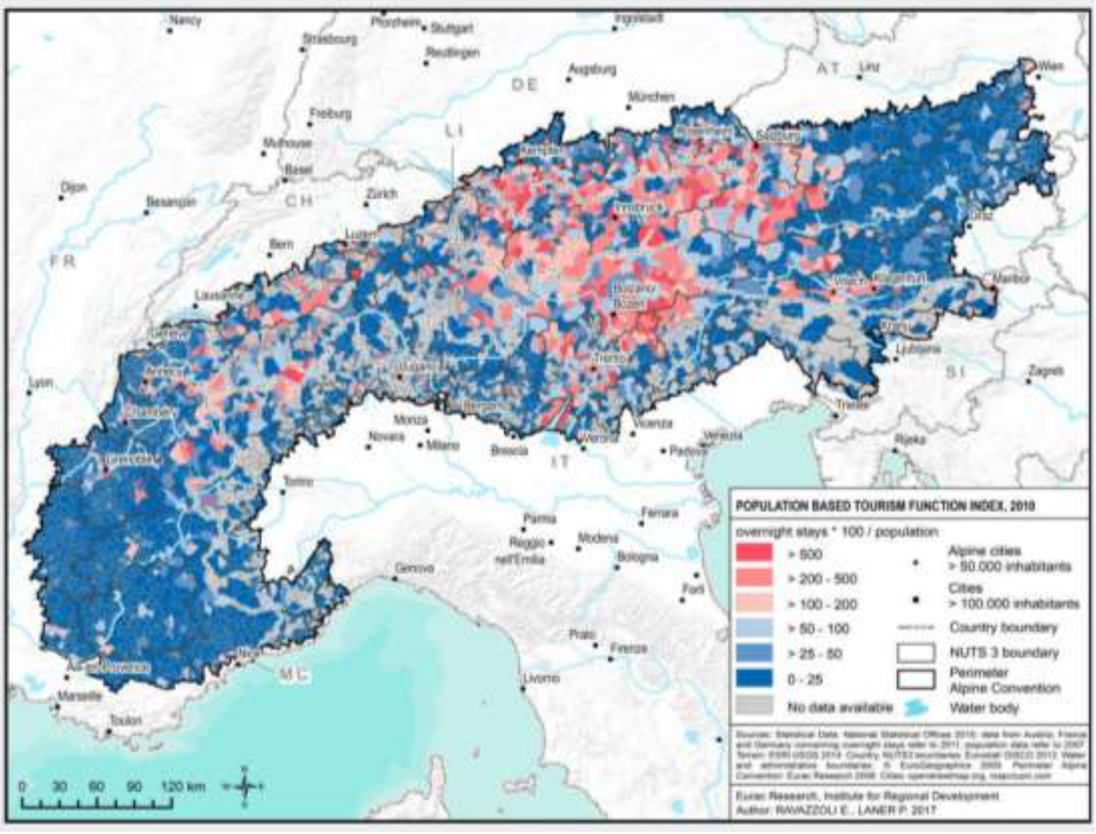

Figure 9 Tourism intensity map based on the ratio between data on overnight stays and population (Alpine convention 2018). Available from: http://www.alpconv.org/en/publications/alpine/default.html

I.d Mountain birds and climate change

"When a flock of snowfinch visits your doorstep, bad weather is on its way" Local proverb heard in various mountain refuges during this PhD.

Mountains are considered areas of high species richness for a variety of taxon including birds (Myers *et al.* 2000, Körner & Ohsawa 2006) and according to Orme *et al.* (2005), 89% of bird's biodiversity hotspots occur on the mountains of mainland continents. Despite this, even in the most developed countries, knowledge on birds inhabiting these topographically complex areas is vague, with little information on species' distribution and poor insights into their biological and ecological requirements (Chamberlain *et al.* 2012, Sato *et al.* 2013, Scridel 2014). Given the higher level of wilderness that mountains hold compared to other systems, these regions are unlikely to be important exclusively from mountain breeding birds. For example, it has been estimated that 35% of all North America species use mountain habitats during their life cycle and ¼ of these species are also listed as species of conservation concern (Boyle & Martin 2015). In Europe, mountains are also important refuge areas for many open habitat species which have lost their former habitats in the lowland areas due to agricultural intensification and urbanisation and are sheltering at higher elevation (Laiolo *et al.* 2004, Archaux 2007, Calledine & Bray 2012, Assandri et al. 2019). Indeed, birds are good indicators of changes in habitat quality, but they have been also investigated for their worrying response to anthropogenic climatic change (Walther *et al.* 2002, Crick *et al.* 2004, Pacifici *et al.* 2015). In this regard, mountain birds are considered to be particularly threatened as they exhibit a high degree of evolutionary adaptations that could become counterproductive in a changing climate (Table 3 & Figure 10) and the few evidence available suggests that species are suffering and shifting their distribution to track suitable climate (Tingley *et al.* 2009, Maggini *et al.* 2011, Auer & King 2014, Lehikoinen *et al.* 2014, Pernollet *et al.* 2015). According to climate envelope theories, species may be able to respond to climatic alterations by shifting their distribution latitudinally (i.e. polewards) or towards higher elevations (Grinnell 1917, Guisan & Zimmerman 2000, Morin & Lechowicz 2008). However, species tracking climate uphill are considered particularly at risk because typically less areas is available at higher elevation, leading to a loss of habitable land and to an increased isolation between populations (Colwell *et al.* 2008). This is particularly evident in studies modelling the future distribution of mountain birds in response to increases in temperatures where species are projected to disappear or to decline, resisting only at higher elevation or in topographically cool and complex sites (e.g. small nival valleys) where local temperature is colder than the average surrounding climate (Nagy *et al.* 2003, Avalos & Hernadez 2015, White & Bennet 2015, Brambilla *et al.* 2016). In addition to climate change effects, land use conversion is also a strong influencer of biodiversity, which may act in concert with climate potentially posing even more severe constraints on the persistence of mountain birds to current and future climate conditions. For example, while in Europe the abandonment of traditional farming practices has changed favouring forest species at the expense of open habitat ones (Laiolo *et al.* 2004, Brambilla *et al.* 2007, Rippa *et al.* 2011), milder temperatures are also pushing the treeline at higher elevation hence expanding forested habitats and reducing suitable land for open habitat species (Lamprecht *et al.* 2018). Overall assessment of the combined and independents effects of climate change and land use in mountain regions is complex, but according to Maggini *et al.* (2014) which combined climatic with land use scenarios, birds inhabiting coniferous woodlands, alpine habitats and wetlands are predicted to be significantly more vulnerable than species in other habitats. Other confounding factors might be linked to species-specific biological and ecological traits (Reif & Flousek 2012, Auer & King 2014, Lehikoinen & Virkkala 2016, Pacifici *et al.* 2017), the mountain range and the time frame considered (Rocchia *et al.* 2018). For all these reasons, it is in my hope with this thesis to advance our current understanding in identifying drivers of change for birds living in mountain regions.

Table 3 Summary of the main challenges and relative adaptations (morphological and physiological) that mountain birds face by living at high-elevations according to Martin & Weibe (2004) and Scott (2011).

CHALLEGE	DESCRIPTION	ADAPTATION
Hypothermia	Reduced body temperature occurring when a body dissipates more heat than it absorbs.	Morphological and physiological • Larger body size to retain heat. • Plumage (special insulation to trap warm air and coloration to retain/ attract heath). • Counter-current blood exchange keeping heat loss at minimum. • Facultative torpor. Behavioural • Migration. • Shivering. • Heat retention on an individual in a crowd situation. • Increased feeding "penguin effect". • Build snow burrows for shelter and warmth.
Hypobaric hypoxia	Decrease in barometric pressure and a consequential reduction in the partial pressure of oxygen (PO_2).	Morphological and physiological • Specially designed lungs with superior capacity for gas exchange. • Larger hearth and cardiac stoke volumes. • Muscle ultrastructure (muscle capillary per fibre higher for birds at high elevations). • Longer flight feathers (wings and tail) to cope with strong winds reduce metabolic costs. • Haemoglobin with a higher O2 affinity. Behavioural • Increases in ventilation (breathing). • Variable wingbeat frequency to adjust metabolic rate and conserve energy.
Extreme weather and seasonality	Extreme weather events and short seasonality (short food availability and breeding window) are typical challenges of birds living in mountain environments.	Morphological and physiological • Longer flight feathers (wings and tail) to cope with strong winds. • Stress hormone levels to allow breeding in conditions that would cause nest abandonment in low elevation birds. Behavioural • Life history variations and strategies (opting out breeding, delaying/anticipating breeding, maintain fecundity but sacrifice body condition, reduce number/quality of eggs, adjust migration phenology etc.).

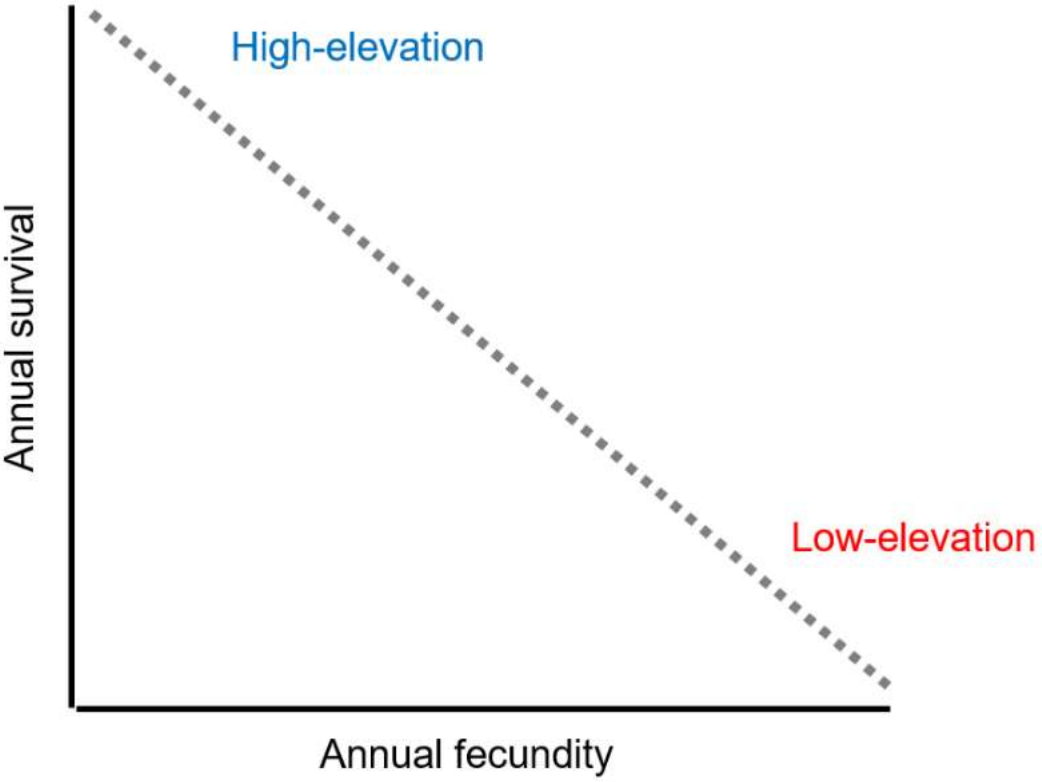

Figure 10 Generalisation of intra and inter specific patters of life history traits in mountain birds. Various scientific works (Sandercock *et al.* 2005, Bears *et al.* 2009, Martin *et al.* 2009; Wilson & Martin 2010, Camfield *et al.* 2010, Laiolo *et al.* 2015, 2017, Bastianelli *et al.* 2017) have shown that birds breeding at high-elevations have a higher-survival and low annual fecundity compared to conspecifics living at lower elevation. This pattern is most likely explained due to an increase in investment in self-maintenance by living in cold sites with a short breeding season. Image from (Martin, K. The conservation value of mountain habitats for birds and predicted impacts of climate change, International Ornithological Conference 2018, Vancouver, Canada).

I.e General aim of this thesis

The aforementioned research has left many unanswered and unexplored questions regarding the effects of climate change on mountain bird communities. A systematic review of the literature available on this topic is lacking and it may be a good starting point for understanding general patterns of change, identify current research gaps and set future objectives. A primary aim of this thesis is to elucidate if there is any evidence of change in distribution for mountain birds in response to climate change both at local, national and global scale. Indeed, impacts of climate change effects on mountain birds are rare or show mixed responses depending on the species and the mountain range considered. To tackle the various gaps in knowledge research activities should focus on comprehending how mountain birds may biologically and ecologically respond to such change. Therefore, an under-laying aim of this thesis is also to provide further insights on the ecology and biology of species breeding at high elevations. Via the identification of a candidate species sensitive to climate change (i.e. white-winged snowfinch *Montifringilla nivalis*), I intend to investigate biological, ecological and population dynamics aspects of such species as well as attempting to set a long-term study for this species. A further target of this thesis is to better evaluate the use and the value of microhabitats (Nelli *et al.* 2013, Visinoni *et al.* 2016, Jähnig *et al.* 2018) as they are considered fundamental refugia sites for many species threatened by climate change which would be worth identifying and protecting them. Future projections are also a fundamental tool when evaluating climate change impacts and part of this thesis is dedicated at modelling habitat suitability at various spatial scales according to future climatic scenarios (Figure 11).

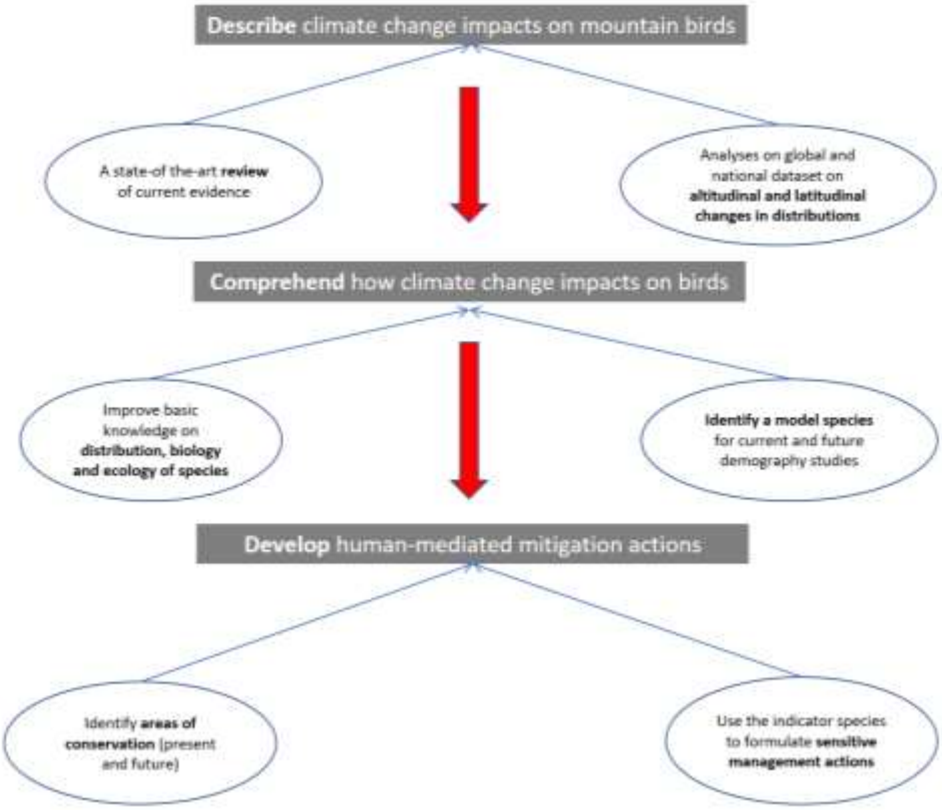

Figure 11 Diagram summarising general (grey bars) and specific aims (bubbles) of my PhD. This thesis attempts to describe and comprehend how climate change impacts on mountain birds in order to develop sensate human-mediated actions via a series of specific research projects.

I.f Thesis structure

Chapter I: By conducting a systemic literature survey, we reviewed evidences for impacts of climate change on Holarctic mountain bird populations in terms of physiology, phenology, trophic interactions, demography and observed and projected distribution shifts, including effects of other factors that interact with climate change. This was carried out by developing an objective classification of high-elevation mountain specialist and generalist species, defined by proportion of their breeding range occurring in mountain regions.

Chapter II: Evidences of the effects of climate change in Italy remain poorly demonstrated particularly for vertebrates. In this study, we related 30 years change in range size to species thermal index (average temperature at occurrence sites) and to other factors (birds' associated habitats, body mass, hunting status) potentially affecting bird populations/range size. We analysed trends of breeding bird range in Italy for a suite of poorly studied cold-adapted animals potentially sensitive to global warming, and for a related group of control species taxonomically similar and with comparable mass but mainly occurring at lower/warmer sites.

Chapter III: Key components of population persistence in face of climate change can be attributed to resistance (the capacity to remain unaffected) or resilience (capacity to absorb and recover) to climate change. *In situ* climatic refugia can act as resistant distribution units, and *ex situ* climatic refugia and the corridors to reach them may enhance resilience. Here, for a set of mountain species conservation priorities, we identified resistant units and resilient areas according to structural connectivity and future distribution, to formulate strategies that maximize the chances of species persistence in a changing climate.

Chapter IV: This chapter focuses on a model species highly threatened by climate change (white-winged snowfinch *Montifringilla nivalis*) and investigates microhabitat selection by that species in the most critical phase of its life cycle. We assessed the potential impact of climate change on habitat suitability for the model species and explored the potential benefits of a targeted (micro)habitat management considering the mechanistic responses to fine-grained, climate-induced modifications of habitat suitability.

Chapter V: Habitat characteristics may modulate extinction risk posed by climate change to animal species, by determining different degrees of reliance on climate-dependent resources, with important implications for conservation. We tested this hypothesis evaluating whether landscape composition may affect the use of microhabitats by snowfinches more or less subject to climate impacts: populations/individuals mostly relying on snow could be at higher risk (spring snow-cover is decreasing in the Alps), but the reliance on snow could be mediated by the presence of alternative habitats in the surrounding landscape.

Chapter VI: Dynamic microhabitat selection, adjusted to better match variations in prey availability in space and time, could be crucial for species living in harsh or extreme environments, where resources are limited and affected by climate change. We aimed at understanding drivers and adjustments of foraging microhabitat selection in snowfinches *Montifringilla nivalis*, a high-altitude species vulnerable to climatic changes, by analysing the availability of invertebrate preys across microhabitats exploited by the species.

Chapter VII: The mechanisms how global warming affects species population dynamics are largely unknown for mountain species. Using a 15 years mark-recapture data on snowfinches in the Apennines, we estimated apparent survival for adults (males and females) and juveniles and relate this to climatic data and weather variables (temperature and precipitation).

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SECTION II

- *Thesis chapters* –

Golden eagle, Stelvio National Park, Italy

SECTION II: *Chapter I*

A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations

SCRIDEL, D., BRAMBILLA, M., MARTIN, K., LEHIKOINEN, A., IEMMA, A., ANDERLE, M., JÄHNIG, S., CAPRIO, E., BOGLIANI, G., PEDRINI, P., ROLANDO, A., ARLETTAZ, R. & CHAMBERLAIN, D.

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Review article

A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations

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Mountain regions are globally important areas for biodiversity but are subject to multiple human-induced threats, including climate change, which has been more severe at higher elevations. We reviewed evidence for impacts of climate change on Holarctic mountain bird populations in terms of physiology, phenology, trophic interactions, demography and observed and projected distribution shifts, including effects of other factors that interact with climate change. We developed an objective classification of high-elevation, mountain specialist and generalist species, based on the proportion of their breeding range occurring in mountain regions. Our review found evidence of responses of mountain bird populations to climate (extreme weather events, temperature, rainfall and snow) and environmental (i.e. land use) change, but we know little about either the underlying mechanisms or the synergistic effects of climate and land use. Long-term studies assessing reproductive success or survival of mountain birds in relation to climate change were rare. Few studies have considered shifts in elevational distribution over time and a meta-analysis did not find a consistent direction in elevation change. A meta-analysis carried out on future projections of distribution shifts suggested that birds whose breeding distributions are largely restricted to mountains are likely to be more negatively impacted than other species. Adaptation responses to climate change rely mostly on managing and extending current protected areas for both

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species already present, and for expected colonizing species that are losing habitat and climate space at lower elevation. However, developing effective management actions requires an improvement in the current knowledge of mountain species ecology, in the quality of climate data and in understanding the role of interacting factors. Furthermore, the evidence was mostly based on widespread species rather than mountain specialists. Scientists should provide valuable tools to assess the status of mountain birds, for example through the development of a mountain bird population index, and policy-makers should influence legislation to develop efficient agri-environment schemes and forestry practices for mountain birds, as well as to regulate leisure activities at higher elevations.

Keywords: avian physiology, biotic interactions, conservation, elevation shift, global warming, high-elevation species, interspecific competition, phenology, population dynamics, projections, snow, trophic mismatch.

Climate change has been recognized, alongside modifications in land use, as a key driver of global change in biological diversity (e.g. IPCC 2007, Ameztegui *et al.* 2016), and there is now a large body of evidence that animals and plants are responding to climate change through shifts in distribution (e.g. Chen *et al.* 2011), changes in population size (e.g. Stephens *et al.* 2016) and changes in phenology leading to inter-linked effects at different trophic levels (e.g. Both *et al.* 2006, Thackeray *et al.* 2016). Such effects vary geographically, and biodiversity in temperate, boreal and Arctic regions is considered particularly vulnerable, with greater warming at higher latitudes (e.g. Meehl *et al.* 2007). Furthermore, rates of warming and frequency of extreme cold events are more pronounced at higher elevations (Beniston & Rebetez 1996, Liu & Chen 2000, Pepin *et al.* 2015). As a result, high-elevation areas are particularly threatened, as they are more susceptible to changes in climate (Diaz *et al.* 2003, Böhning-Gaese & Lemoine 2004, La Sorte & Jetz 2010).

Mountain and high-latitude upland regions (henceforth 'mountains') cover around 25% of the Earth's surface (Kapos *et al.* 2000). They support one-quarter of terrestrial biodiversity (Körner & Ohsawa 2006) and contain nearly half the world's biodiversity hotspots (Myers *et al.* 2000). These are complex ecosystems of high conservation value, as they encapsulate a high diversity of small-scale habitats dictated by different topoclimates within narrow elevation gradients (Körner & Ohsawa 2006). As a result, mountains accommodate high levels of species diversity with heterogeneous communities adapted to specific environmental conditions that change along the elevation gradient, including climate and other abiotic factors such as slope, exposure, solar radiation, wind direction and substrate (Körner & Spehn 2002, Nagy & Grabherr 2009, Viterbi *et al.* 2013, Boyle & Martin 2015). For example, marked changes occur over short distances, with temperature varying in temperate regions on average by 0.6 °C every 100 m elevation (Dillon *et al.* 2006). Aspect can also influence temperature, with greater solar radiation on southern than northern slopes in the Northern Hemisphere (Nagy & Grabherr 2009). Global warming is causing changes to these environments, with documented responses including the upward advance of the treeline and a general increase in dominance of woody deciduous shrubs at high elevations (Gehrig-Fasel *et al.* 2007, Myers-Smith *et al.* 2011).

Many unique ecological features of temperate mountain systems also arise from the strong seasonality in temperatures which result in a very short growing and reproductive season, typically less than 3 months in alpine-arctic and boreal habitats (Nagy & Grabherr 2009). Strong inter-annual variations in temperature, precipitation and snow cover regimes are also observed in these systems (IPCC 2013, Klein *et al.* 2016) with changes in the timing, quantity and duration of precipitation likely to influence mountain habitats and biodiversity (Beniston *et al.* 2003, IPCC 2013, Martin *et al.* 2017). Snow cover has insulating properties, protecting plants and invertebrates from frost during the coldest months of the year and thereby influencing survival rates of many slow-growing high-elevation plants, insects and mammals (Hågvar 2010, Wipf & Rixen 2010, Berteaux *et al.* 2017). Snow cover in the Northern Hemisphere has declined since the 1920s, particularly in spring and summer (IPCC 2007).

Although often perceived as true wildlands, mountain ecosystems typically have a long history of human activity, especially in Europe and Asia (FAO 2015). Twenty per cent of the global human population inhabits mountain regions, with about 8% living above 2500 m (Körner & Ohsawa 2006). However, mountains provide essential ecosystem services, including nearly half of the human population's water supply, carbon storage and sequestration (forests and peatlands) and natural resources (timber, productive soils and medicinal plants; Körner & Ohsawa 2006). Mountains are also very important in terms of leisure and tourism activities (skiing, snowboarding, hiking, biking, wildlife watching and hunting). Mountain systems are thus continuously subject to landscape changes due to human activities, which might have even more severe consequences than climate change itself (Jetz *et al.* 2007) or which could potentially exacerbate climate effects (Mantyka-Pringle & Rhodes 2012).

Among birds, changes in climate have been reported to influence migration timing (Hüppop & Hüppop 2003, Knudsen *et al.* 2011), breeding output (Crick *et al.* 1997, Laaksonen *et al.* 2006), population size (Sæther *et al.* 2000, Townsend *et al.* 2016) and changes in elevational (Reif & Flousek 2012) and latitudinal (Hickling *et al.* 2006, Zuckerberg *et al.* 2009) distributions. Because the severity of climate change varies over the Earth's surface (e.g. Meehl *et al.* 2007), avian responses may also vary in intensity depending on their geographical distribution. Birds may exhibit rapid distributional responses to climate fluctuations, for example tracking changes in surface temperature latitudinally (Hickling *et al.* 2006, Zuckerberg *et al.* 2009). However, there is also evidence that range shifts in birds are lagging behind climate change (Devictor *et al.* 2008, Ralston *et al.* 2017), potentially due to asynchronous phenology of birds and their prey (e.g. Mayor *et al.* 2017). Species inhabiting high-elevation mountain systems often exhibit a high degree of habitat specialization and unique ecological traits within narrow thermal ranges (Reif & Flousek 2012, Reif *et al.* 2015, Mahon *et al.* 2016, Pacifici *et al.* 2017, Scridel *et al.* 2017a). Adapting to rapid climate change may be particularly challenging along the elevation gradients of many mountains, where temperatures and area decrease monotonically with elevation (Elsen & Tingley 2015). As a result, species tracking rising temperatures in these systems are predicted to decline according to the species–area relationship (Preston 1962) as populations become isolated and thus increasingly vulnerable to stochastic events (Lande 1993, Bech *et al.* 2009, Fjeldså *et al.* 2012). A successful shift into a new area by a species is possible only when abiotic as well biotic requirements are fulfilled (Martin 2001a, Heikkinen *et al.* 2007, Wilson & Martin 2012). Given the fast rate of warming, species might have to track temperatures in areas where their associated habitat and resources require longer to establish (e.g. mature trees, alpine and sub-nival plants; Engler *et al.* 2011, Reif & Flousek 2012, Brambilla & Gobbi 2014) or where suitable habitat formation cannot occur due to constraints of other factors such as soil processes or rock substrate (Freppaz *et al.* 2010) or by direct human activities (e.g. deforestation; Nogués-Bravo *et al.* 2008, Patthey *et al.* 2008, Kohler *et al.* 2014, disturbance via outdoor recreation; Arlettaz *et al.* 2007, 2015). Finally, climate effects coupled with negative synergistic changes in land use might pose even more severe constraints on adaptation of mountain birds to future climate conditions.

Due to the documented general responses of birds and the more extreme climate changes observed in mountains, it seems reasonable to expect that mountain birds may be particularly threatened by climate change. In this review, we assess the existing evidence for direct and indirect effects of climate change on mountain birds in the Holarctic region (Heilprin 1887) and we evaluate their future conservation prospects. We address six specific objectives: (1) to define mountain generalist and high-elevation specialist birds for the Holarctic region; (2) to review the impacts of climate change on mountain birds through a summary of the literature, and a quantification of general responses throughout the Holarctic, including a meta-analysis; (3) to review and quantify projected impacts from future climate change scenarios using a meta-analysis; (4) to assess stressors that are likely to interact with climate change in affecting birds living at high elevations; (5) to review proposed conservation actions; and (6) to identify current gaps and future priorities for research.

METHODS

Defining mountain birds

Mountain systems and species inhabiting them are difficult to describe geographically and ecologically, and definitions may not apply consistently across the globe (Strahler 1946, Gerrard 1990, Körner 2012, Scridel 2014). To assess the status of mountain birds, it was first necessary to define mountain areas and habitats. Using elevation thresholds to define these regions would immediately exclude older and lower mountain systems, such as the Urals, Scottish Highlands and Appalachians, and include areas with little topographic relief and few environmental gradients (e.g. large, high-elevation plateaux). Using slope as a criterion on its own or in combination with elevation may resolve the latter problem, but not the former. For these reasons, we adopted the definition of Kapos *et al.* (2000), who classified mountain systems in seven classes on the basis of elevation, slope and local elevation range (Fig. 1). The last criterion is particularly useful as it identifies lower elevation mountain ranges (300–1499 m) by defining a radius of interest (5 km) around each grid cell (30 arc-second) and measuring the maximum and minimum elevation within a particular neighbourhood and their difference. This allows the identification of areas that occur in regions with significant relief, even though elevations may not be especially high (Kapos *et al.* 2000). This is a broad definition which includes high-latitude 'upland' habitats at relatively lower elevations, as well as mountain forest, the alpine belt (the treeless region between the natural climatic forest limit and the snow line) and the nival belt (the terrain above the snowline). The last is defined as the lowest elevation where snow is commonly present all year round (Kapos *et al.* 2000, Körner & Ohsawa 2006). Hereafter, we refer to 'mountain regions' as those as defined by Kapos *et al.* (2000).

We developed a broad definition of Holarctic mountain birds based on the proportion of their Holarctic breeding range that was within the defined mountain regions in order to assess the evidence base for impacts of climate change on birds largely restricted to mountains as a breeding habitat. We stress that we are interested in all bird species occurring in Holarctic mountain regions, including species that also occur in a range of habitats, rather than only focusing on high-elevation specialist species. We used a geographical information system (GIS) software (GRASS, GRASS Development Team 2015; QGIS, Quantum GIS Development Team 2015) to restrict the map of Kapos *et al.* (2000) to the Holarctic realm and imposed over it the breeding range of global bird species (n = 10 280 species; BirdLife International & NatureServe 2015). We defined as 'high-elevation mountain specialist' a species for which at least 50% of its range was in the higher elevation classes 1–4 of Kapos *et al.* (2000). We further defined a 'mountain generalist' as a species for which at least 50% of its entire breeding range was

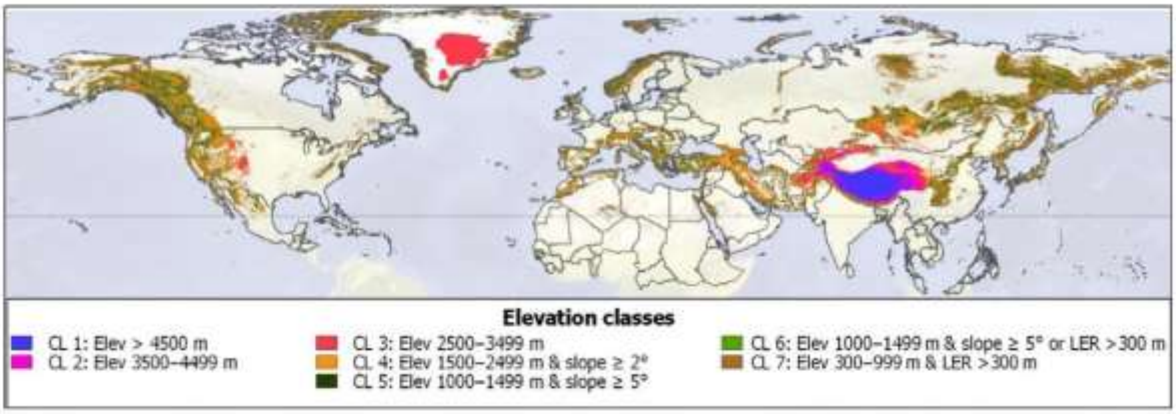

Figure 1. Mountain systems classified by Kapos *et al.* (2000) and adapted to the Holarctic region (above the Tropic of Cancer – grey line). The upper three classes ('CL') are delimited purely by elevation (≥ 2500 m). Areas below 2500 m were classified additionally in terms of slope, terrain roughness and local elevation range (LER).

within the defined Holarctic mountain region (i.e. classes 1–7 of Kapos *et al.* 2000) and which was not classed as a high-elevation mountain specialist. These definitions therefore identify which species are particularly associated with mountains over the whole Holarctic region. There are many species (e.g. Western Capercaillie *Tetrao urogallus*, Eurasian Pygmy Owl *Glaucidium passerinum*, Rock Ptarmigan *Lagopus muta*), termed boreo-alpine taxa, that occur in mountains at low latitudes (e.g. European Alps) but are also present at higher latitudes but lower elevations (e.g. northern Europe). The definition adopted here seeks to identify species linked more closely with mountains *per se* (for example due to topography or particular habitat types) across a broad region. We use the terms 'high-elevation mountain specialist' and 'mountain generalist' when specifically referring to our classification. We use the term 'mountain bird' to refer to any species occurring in our defined Holarctic mountain region, which also includes species that breed in other habitats and at a range of elevations across their geographical range.

Literature survey

We conducted the literature search using ISI Web of Knowledge (www.webofknowledge.com). To obtain relevant studies we used the following keywords: (bird* OR avian*) AND (mountain* OR montane* OR upland* OR alpine* OR moorland* OR arctic* OR polar* OR altitude* OR elevation*) AND (climate change* OR global warming*) NOT tropic*. The search period was from 1950 until 31 December 2016. Papers identified from this search were subsequently included if they concerned research wholly or partly carried out within the defined mountain regions or if the study species was/were defined as a high-elevation mountain specialist or mountain generalist (see Tables S1 and S4). The latter group of studies included some broad-scale analyses that were not focused specifically on mountains but which considered some high-elevation mountain specialists (typically analyses covering large regions, for example based on national atlases). In total, 764 studies were initially identified. We read the abstracts of each of these papers to determine whether it was relevant for the purposes of this review and eliminated 591 studies at this stage. We also checked the remaining 173 papers for other relevant references missed in the first search. This identified a further 61 relevant papers, giving a total of 234. We assigned these to eight broad topics: (1) climate change, physiological constraints and life history strategies; (2) links between climate and population dynamics; (3) changes in phenology; (4) trophic linkages; (5) observed evidence of elevation shift; (6) projected elevation shifts; (7) interactions between climate change and other drivers (agriculture, grazing and forestry, leisure and other threats, interspecific interactions); and (8) conservation and policy papers. We used the standardized literature search to summarize the main trends in the resulting database with respect to location and topic, and with respect to analysis of elevation shifts and future projections of species' geographical range and population size. We conducted two meta-analyses: one testing whether mountain birds have shifted in elevation to track suitable climate and a second to test whether climate changes will have greater effects on mountain than on non-mountain birds according to projected distribution range and population size. We also used the selected papers, in conjunction with the wider literature, as the basis of a qualitative review to highlight the key issues and findings.

Current and future elevation shifts in bird populations

We considered for meta-analyses papers that presented estimates for shifts in species distributions over time in relation to elevation if they focused, either wholly or mostly, on the defined mountain regions. Given that conditions may change rapidly over small distances in mountains due to the steep topography, smaller-scale studies are more appropriate than larger-scale atlas studies in tracking species distributions (Chamberlain *et al.* 2012). Thus we focused on studies with a maximum sampling unit area of 1 km^2. We collated additional data for each study on the period considered (in years), the elevation range (in metres) and the estimated mean annual rate of temperature change (°C/year) over the period considered. Similarly, we considered papers that predicted future effects of climate change on mountain birds if they were largely restricted to mountain areas, if they estimated a proportional change in geographical distribution or population size over time and if the sample size of the underlying dataset on which models were based was presented. We also recorded the period over which projections were made and the climate change scenarios considered, which were classed as either 'severe' (scenarios A2 and A1F1 or RCP8.5) or 'moderate' (all other scenarios and RCPs; IPCC 2007, 2013).

Statistical analysis

For elevation shifts, we included papers in the meta-analysis only if sample sizes and test statistics were presented or if parameter estimates (including mean shift) and standard errors, standard deviations or confidence limits were reported. In cases where only estimates of change in elevation and errors were presented (i.e. without any test statistics), we derived z-scores, testing against a hypothesis of zero change. In common with standard meta-analytical approaches (e.g. Koricheva *et al.* 2013), the goal was to estimate standardized responses of elevation shifts in bird distributions over time from studies that used a diversity of measurement methods. In most cases, the shift was measured as the change, in metres, of the distribution of a given species (sometimes a group of species) between two time periods. However, some papers also tested the effect of the interaction between elevation and time period on the probability of species presence, a significant interaction indicating a significant shift over time (e.g. Reif & Flousek 2012, Mizel *et al.* 2016).

Shifts in species distributions had been tested using a variety of methods in the above papers. The different test statistics (e.g. F, t, χ^2) presented in these papers were converted to Pearson's r using standard conversion formulae (Lajeunesse 2013) so that effect sizes (i.e. change in elevational distribution over time) could be compared across studies (further details are given in Table S2; meta-analysis methods). Positive values indicate an upslope shift in elevation over time. Pearson's r-values were not normally distributed, so prior to analysis, we transformed standardized Pearson's r-values from each study using Fisher's Z transformation to derive both normalized estimates and their variance (as per Musitelli *et al.* 2016).

We derived parameter estimates of standardized elevation shifts by analysing Z-transformed Pearson's r-values (henceforth 'standardized effects') and 95% confidence intervals based on linear mixed effects models using the nlme package in R (Pinheiro *et al.* 2017). The analytical unit was the estimate for a given species or group of species (some papers estimated shifts for the whole community). We therefore included 'study' as a random effect to account for multiple estimates derived from the same paper and 'family' as a random effect to account for the potential phylogenetic dependence of closely related species (or multiple observations from the same species). We weighted models according to the inverse of the variance of standardized effects and considered an effect as significant if confidence intervals on the parameter estimate did not overlap zero. To derive a single overall estimate of shift, no fixed effect was included (i.e. an intercept-only model). A significant effect of the intercept in this case would indicate a consistent standardized effect in terms of elevation shift across studies and species. We then tested study duration and rate of temperature change by including each as a fixed effect in the model.

Papers that made future projections of species distributions or abundances did not typically present significance tests, so we could not estimate standardized effect sizes. Instead, we analysed the mean percentage change in the response variable (either range size or a measure of population size). The response variable was approximately normally distributed. The model structure was similar to that for observed elevation shifts in that initially we specified an intercept-only model with 'study' and 'family' as random effects and then tested further fixed effects (high-elevation specialist or generalist species, period over which projections were made, climate change scenario). We specified the sample size of the initial input data as a weight in the model statement, the assumption being that models based on a larger sample size are likely to be more reliable than those based on small sample size. Confidence intervals of estimates that did not overlap zero were taken as evidence of consistent effects of future projections of elevation shifts.

RESULTS

The literature review considered 234 articles relevant to climate change across various mountain regions of the Holarctic (Table 1). In Europe, most studies occurred in the Alps and Pyrenees ($n = 45$), followed by Fennoscandia ($n = 25$) and the uplands of Britain and Ireland ($n = 24$). Many studies were also carried out in North America ($n = 75$), particularly in the Rocky ($n = 14$) and Appalachian ($n = 10$) Mountains, whereas only

Table 1. Frequency of studies of Holarctic mountain birds and climate change resulting from the systematic literature search across various regions and countries of the world. Reviews/commentaries and meta-analyses ($n = 25$) were excluded.

Geographical region	Frequency
Eastern European countries (Poland, Czech Republic, Russia)	6
Western European countries (France, Germany)	6
Spain	8
UK/Ireland uplands	24
Nordic countries (Denmark, Finland, Iceland, Norway, Sweden & Iceland)	27
Alps & Pyrenees (Switzerland, France, Italy, Spain, Germany, Austria, Slovenia)	44
Pan-European	12
Total European studies	127
Greenland	4
Pacific North West Coastal Mountains (Alaska, Yukon, British Columbia Coast Mountains, Hudson Bay Mountains, Cascades)	18
South-West Coastal ranges (California, Sierra Nevada, New Mexico)	7
Continental ranges (Rocky Mountains, Colorado, Arizona, Montana, Dakota, Wyoming)	23
Appalachian Mountains (including NY State)	11
North America wide region (Canada, USA also in combination)	12
Total North America studies	75
China	5
Asia	2
Total Asian studies	7
Global or nearly global	26
All studies	209

seven studies were carried out in Holarctic Asia. There were 26 papers included that investigated climate change impacts on bird communities at a global scale. The number of published studies according to our search criteria increased considerably over time, from one study in 1991 to 48 studies published in 2016 (Fig. 2).

The most commonly investigated climate change-related topic was the general ecology and physiology of mountain bird species ($n = 61$; Fig. 3), followed by papers that tested for effects of climate change on changes in population trends, elevation or latitude shifts or changes in community composition ($n = 57$). Papers investigating future prospects of species according to various climate scenarios were also frequent ($n = 47$). The least studied category involved studies that investigated interspecific or synergistic interactions between climate changes and other environmental or ecological factors ($n = 4$).

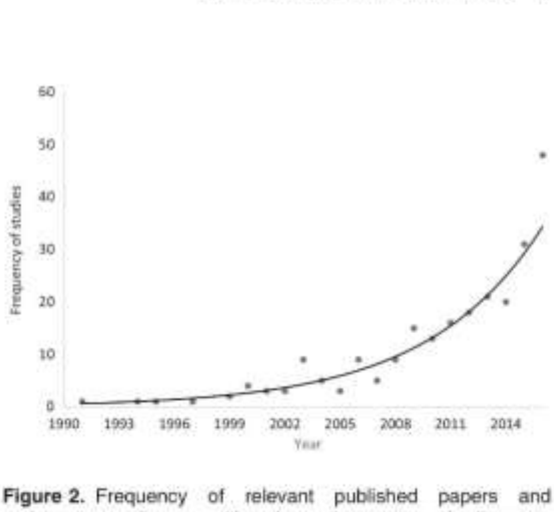

Figure 2. Frequency of relevant published papers and reviews over time resulting from the systematic literature search.

Mountain birds of the Holarctic region

We identified 2316 bird species breeding in the Holarctic realm, 818 (35.3%) of which were defined as either high-elevation mountain specialists ($n = 324$ species) or mountain generalists ($n = 494$ species). The most frequent Order of birds in both groups was Passeriformes (generalist $n = 333$ species; high-elevation specialist $n = 256$ species), followed by Piciformes for generalists ($n = 29$) and Galliformes for high-elevation specialists ($n = 27$; a complete list of the 2316 species is provided in Table S4). A great proportion of the high-elevation specialists breed almost exclusively on the Tibetan plateaux (i.e. Tibetan Babax *Garrulax koslowi*, Tibetan Rosefinch *Carpodacus roborowskii*) or have a large proportion of their breeding range confined to this region (i.e. Bearded Vulture *Gypaetus barbatus*, Wallcreeper *Tichodroma muraria*, Twite *Carduelis flavirostris*). Examples of non-Tibetan high-elevation specialists were few and generally displayed a restricted breeding distribution confined to the lowest class that defines high-elevation specialists (class 4; Fig. 1) and at the southern-most range of the Holarctic realm (i.e. Maroon-fronted Parrot *Rhynchopsitta terrisi*, White-naped Swift *Streptoprocne semicollaris*, Black Rose Finch *Leucosticte atrata*). Generalist mountain birds occur across various Holarctic mountain ranges, from the Tibetan Plateau and European Alps to the Pacific Mountain System in North America.

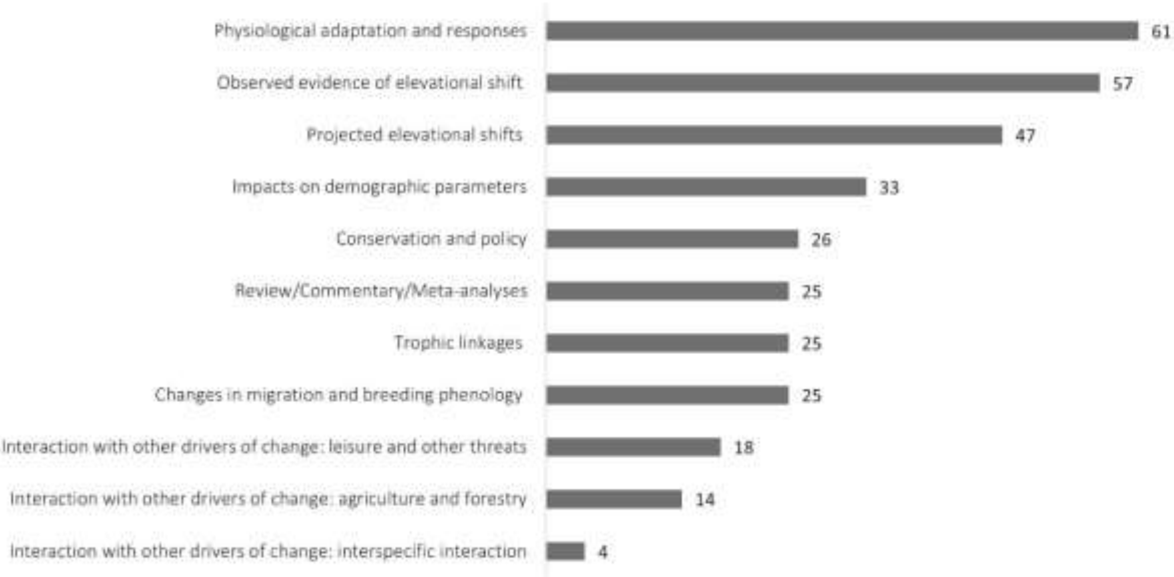

Figure 3. Frequency of climate-change related studies on Holarctic mountain birds (mutually inclusive) resulting from the systematic literature search, classified according to general subjects addressed.

Comparing the list of mountain birds across 232 relevant articles from the literature search (no information was available for two articles) revealed that almost all generalist (97%; n = 453/464) and high-elevation specialist species (96%; n = 311/324) have been investigated in the literature. The three generalist species most frequently studied are Black Redstart *Phoenicurus ochruros* (n = 32 studies), Water Pipit *Anthus spinoletta* and Ring Ouzel *Turdus torquatus* (n = 31 each). For high-elevation specialists, the most frequently studied species were White-winged Snowfinch *Montifringilla nivalis* (n = 22), Alpine Chough *Pyrrhocorax graculus* (n = 20) and Wallcreeper (n = 13). However, when excluding studies based solely on distributional data (e.g. species distribution models), meta-analysis and reviews, only 2% (n = 7/324) of high-elevation mountain specialists and only 14% (n = 67/494) of mountain generalist species had been investigated. This suggests that fine-scale studies on species ecology are scarce for these species.

Climate change, physiological constraints and life history strategies

Birds breeding in mountain systems have evolved complex physiological, behavioural and morphological adaptations (Dragon *et al.* 1999, Cheviron & Brumfield 2012). Adaptations to prevent heat loss rely particularly on insulation, for example by producing a denser coat of feathers (Broggi *et al.* 2011) and by exhibiting a greater body mass than lower-elevation conspecifics (Bergmann's rule; Ashton 2002). Physiological constraints are likely to be major determinants of how species respond to climate change. For example, Root *et al.* (2003) found that more than 80% of the species from various taxa and habitats that showed changes linked to global warming shifted geographically in the direction expected from known physiological constraints. Birds with physiological responses that are tightly coupled to specific environmental conditions (such as mountain species) are believed to be particularly sensitive to changes in climate, but little has been done to test whether these adaptations (especially morphological) are counterproductive in a warming climate. Anecdotal evidence and the limited literature available suggest there may be costs to higher temperatures for species such as Rock Ptarmigan, Ring Ouzel and White-winged Snowfinch, which have been observed panting and bathing in water or snow during hot sunny days in the Swiss Alps and Scottish Highlands (Glutz von Blotzheim *et al.* 1973, D. Scridel pers. obs.). Johnson (1968) found that White-tailed Ptarmigan *Lagopus leucurus* began panting at 21 °C. The above studies did not establish whether these behavioural changes were sufficient to prevent reduced survival or reproduction in warming conditions.

A species' life history strategy may be crucial in responding to climate alterations. Patterns along elevation gradients have highlighted that populations of the same species confined to higher elevations have slower life-history strategies (fewer nesting attempts, lower clutch size) compared with populations at lower elevation (Boyle *et al.* 2016). Higher nest survival has been found for higher elevation populations, which may partially compensate for the reduction in potential fecundity. Boyle *et al.* (2016) did not record a pattern of significant differences in body mass, egg or nestling size, or survival between paired populations of bird species breeding at high and low elevation. Tingley *et al.* (2012), however, found that species were more likely to shift their elevation range in the Sierra Nevada (USA) if they had smaller clutches, defended all-purpose territories and were residents or short-distance migrants, although these involved both upslope and downslope shifts. So it is possible that higher-elevation species may be more threatened by climate change than lower-elevation species due both to their morphological adaptations to cooler systems (e.g. insulation) and their life history strategies. However, future work is required to elucidate these ideas.

Links between climate and population dynamics

Although not specifically addressing climate change, several studies have indicated that fluctuations in climate influence demographic rates in mountain birds, thus implying potential climate change effects. In several cases, increasing temperatures may increase reproductive output. Sæther *et al.* (2000) demonstrated that increases in winter temperature (together with population density) positively affected White-throated Dipper *Cinclus cinclus* dynamics in the upland regions of southern Norway. Cold winters caused low recruitment and a decrease in population size associated with the amount of ice cover, which impaired foraging opportunities. Novoa *et al.* (2008) demonstrated that weather variables during both pre-laying and post-laying influenced reproductive success in Rock Ptarmigan in the French Pyrenees. Reproductive success was positively associated with early snow-free patches, but rainfall had negative effects, particularly after hatching. Novoa *et al.* (2016) also found positive effects of snowmelt on Rock Ptarmigan, but the intensity of the effect varied with respect to the geographical region considered (i.e. Alps vs. Pyrenees). Drier and cooler weather favoured nest survival of Mountain Plovers *Charadrius montanus* over a 7-year period (Dreitz *et al.* 2012).

There is also evidence for negative effects of climate on demographic parameters. Barnagaud *et al.* (2011) showed that winter and summer NAO (North Atlantic Oscillation) affects several indicators of breeding success of Black Grouse *Tetrao tetrix* in the French Alps, particularly during years of extreme weather. Interestingly, birds showed some acclimatization, being able to optimize their reproductive output in relation to the NAO index, but they performed particularly badly when extreme weather events occurred. Twenty-five years of prolonged spring warming was also associated with low breeding success in a Scottish population of Western Capercaillie (Moss *et al.* 2001).

In mountain systems, bird response to temperature may vary at both small and large scales. For example, Water Pipits select nest-sites with the particular species characteristics based on their accessibility to predators, snowfall and microclimate, with the latter two influencing nestling rearing periods and survival (Rauter *et al.* 2002). Because snowfall and predation pressure vary over time and space, it is possible that large-scale factors also influence species choices. The relative importance of small- and large-scale weather effects is still unclear, as these seem to vary between species, populations, seasons and time periods considered. Ptarmigan exemplify such complex responses: even though they have been considered indicators of temperature-induced effects on mountain biodiversity (Novoa *et al.* 2008, Wilson & Martin 2010, Imperio *et al.* 2013), some studies have shown little effect of climate change on their demography (Sandercock *et al.* 2005, Novoa *et al.* 2016). In one study by Wang *et al.* (2002), local minimum winter temperatures had a stronger effect on White-tailed Ptarmigan population dynamics than large-scale indices like NAO. On the other hand, Wann *et al.* (2014) found that the same species in the same study area responded to climate effects over a longer period when a 2-year lag time was considered. This nuanced evidence highlights the importance of testing both small- and large-scale weather predictors, and in particular focusing more studies on lagged effects of NAO on demographic parameters of mountain species.

Changes in phenology

Among birds, climate change has affected the phenology of many species, leading to changed timing of breeding and migration (e.g. Crick *et al.* 1997, Rubolini *et al.* 2007), which in some cases has led to population declines when phenological trends are mismatched with those of their key food resources (e.g. Both *et al.* 2006). Such mismatches are hypothesized to underpin the declines in many long-distance migrant species in the western Palaearctic (e.g. Møller *et al.* 2008). However, in the Fennoscandian mountains, Lehikoinen *et al.* (2014) found that long-distance migrants on average declined less than residents and short-distance migrants, suggesting the latter were more sensitive to climate change impacts.

Few studies have shown changes in mountain bird phenology explicitly linked to climate change. Timing of breeding in Mexican Jays *Aphelocoma wollweberi* has advanced in line with climate changes in the Chiricahua Mountains of Arizona (Brown *et al.* 1999). Inouye *et al.* (2000) found that American Robins *Turdus migratorius* in the Colorado Rocky Mountains arrived 14 days earlier over a 19-year period. However, local conditions (e.g. the average date of snowmelt) did not change at the study site, resulting in a 65-day gap between date of the first Robin sighting and date of snowmelt and suggesting that American Robins may have to cope with an extended pre-breeding period at higher elevation. Indeed, the extent, duration and timing of snow cover are likely to be important factors acting on the phenology of mountain birds in general. For birds in the European Alps and North American mountains, patterns in breeding season phenology are typically tied to the snowmelt (e.g. Novoa *et al.* 2008, Imperio *et al.* 2013, García-González *et al.* 2016). There is evidence that responses to changes in snowmelt phenology vary between species and populations. Martin and Wiebe (2004) compared White-tailed Ptarmigan and Willow Ptarmigan *Lagopus lagopus* breeding in alpine and Arctic environments, respectively, and found that extreme weather events greatly reduced breeding success in both species. In average years, breeding parameters of White-tailed Ptarmigan were not correlated with snowmelt phenology, suggesting a constraint in adjusting their reproductive phenology to a changing environment. Willow Ptarmigan, however, tracked local conditions, breeding earlier in years of early snow melt (Hannon *et al.* 1988, Martin & Wiebe 2004). Similarly Novoa *et al.* (2016) found that the median hatching date for Rock Ptarmigan was significantly correlated with the date of snowmelt in the French Alps but not in the Pyrenees. None of the above studies found trends over time linked to climate change, but it can be inferred that climate change acting on snow melt phenology could affect these species in the future, especially given that snow melt has occurred progressively earlier, and snow cover has declined in extent in the northern hemisphere (IPCC 2007).

Trophic linkages

Global warming may influence the distribution and abundance of invertebrate communities directly (Grigaltchik *et al.* 2012) or indirectly via the modification of suitable habitat conditions (e.g. soil desiccation, changes in vegetation communities; Carroll *et al.* 2015). However, little investigation of the links between such changes and bird populations has been done. Most of the evidence comes from the British uplands. Pearce-Higgins *et al.* (2010) demonstrated how abundance of adult craneflies (Diptera: Tipulidae), a keystone group in many mountain systems, was negatively correlated with August temperatures in the previous year and how, in turn, changes in the European Golden Plover *Pluvialis apricaria* populations were negatively correlated with August temperatures 2 years earlier. Fletcher *et al.* (2013) also concluded that low temperatures in May (a surrogate for late cranefly emergence; Pearce-Higgins *et al.* 2005) positively influenced Red Grouse *L. lagopus scotica* chick survival. These findings suggest that continued warming would have negative effects on these species.

We found only one study considering the role of climate change on plant food sources for mountain birds. Santisteban *et al.* (2012) correlated declines in adult survival of Cassia Crossbill *Loxia sinesciuris* with increasing temperatures in South

Hills and Albion Mountains (USA). The most supported explanation was that Lodgepole Pine *Pinus contorta* seed availability varied with temperature, where with increasing temperatures, trees prematurely shed their seeds, reducing the carrying capacity for Cassia Crossbill breeding later in the year. The warmer springs and increased precipitation in Europe will also influence food availability and the future geographical distribution for European Crossbill species (Common Crossbill *Loxia curvirostra*, Parrot Crossbill *Loxia pytyopsittacus*, Scottish Crossbill *Loxia scotica*) (Mezquida *et al.* 2017).

Snow patches can represent an important foraging habitat, providing both arthropod fallout and suitable sites at their margins for the collection of soil invertebrates, particularly during the nesting and rearing period of many mountain birds. These include White-winged Snowfinch, Snow Bunting *Plectrophenax nivalis*, Horned Lark *Eremophila alpestris* and Alpine Accentor *Prunella collaris* (Antor 1995, Camfield *et al.* 2010, Brambilla *et al.* 2016, 2017b, Rosvold 2016). In some extreme cases, birds may even choose to nest directly in glaciers (White-winged Diuca Finch *Diuca speculifera;* Hardy & Hardy 2008) or in very close proximity (Grey-crowned Rosy Finch *Leucosticte tephrocotis*, Johnson 1965, Rosvold 2016, Brandt's Rosefinch *Leucosticte brandti*, Potatov 2004) to capitalize on abundant supplies of insects. Changes in amount and duration of snow may therefore affect these species via food resources.

Where trees and shrubs have expanded their distribution upslope in response to increasing temperatures (Harsch *et al.* 2009, Myers-Smith *et al.* 2011), changes in invertebrate communities are expected. Ground- and canopy-dwelling arthropod communities have been assessed in the Arctic foothills of Alaska in relation to the presence of two passerine predators, Gambel's White-Crowned Sparrow *Zonotrichia leucophrys gambelii* and Lapland Longspur *Calcarius lapponicus*. Predicted changes in shrub dominance are likely to favour White-crowned Sparrow nesting habitat and food (canopy-dwelling arthropods), whereas declines of Lapland Longspurs have been projected as a consequence of shrub encroachment and consequent reduced availability of ground-dwelling arthropods (Boelman *et al.* 2015).

Climate change may also affect more complex linkages across different trophic levels. Martin and Maron (2012) conducted an experiment showing that climate change in the form of reduced snowfall in mountains and allowing increased ungulate herbivory in winter can negatively affect diverse species interactions. They experimentally tested the hypothesis that declining snowfall, which enables greater over-winter herbivory by Elk *Cervus canadensis*, indirectly influences plants and associated bird populations in montane forests. When they excluded Elk from one of two paired snowmelt drainages and replicated this paired experiment across three distant canyons over a 6-year period, there was a reversal in the multidecadal declines in plant and bird populations. These experimental results suggest that climate impacts can interact with other drivers of habitat change and strongly influence plant–animal and other ecological interactions.

Observed evidence of elevation shifts

Evidence exists, typically from broad-scale atlases of species distributions, that some species are shifting their geographical distributions to higher elevations in response to climate change, presumably tracking more suitable climate conditions (e.g. Auer & King 2014, Roth *et al.* 2014), although such effects are not universal (e.g. Zuckerberg *et al.* 2009, Tingley *et al.* 2012, Massimino *et al.* 2015). Furthermore, apparent elevation shifts may occur due to habitat deterioration or destruction at lower elevations (Archaux 2004, Bodin *et al.* 2013).

Few studies have considered elevation shifts in the distributions of Holarctic mountain birds. We found 10 relevant studies in our literature search that specifically considered elevation shifts in bird species distributions, partly or wholly in mountains (Table 2). Including papers that considered more than one study site ($n = 13$ sites from 10 papers), the mean period considered was 38 years ± 2.5 se (range 9–102) and the mean length of elevation gradients was 1970 m ± 76 se (range = 500–3400 m). There was little evidence of consistent patterns across the studies and a wide variation among species. In some cases, there were fairly consistent upward shifts in most species (e.g. Reif & Flousek 2012, Rocchia 2016) but other studies found that different species exhibited upward and downward shifts (Tingley *et al.* 2012, DeLuca & King 2017) or found shifts in only a small proportion of the species considered (Archaux 2004). Additionally, there was sometimes marked

Table 2. A summary of papers considering shifts in the elevation of bird species distributions in mountains over time. Papers were included if they were based on data carried out at relatively small scales (maximum 1-km^2) which were wholly or partly in mountainous regions (as per Kapos *et al.* 2000). MA indicates whether a given study was included in the meta-analysis (Y) or not (N).

Author	Location	Species	Sampling unit	Period	Temperature change (°C/year)	Elevation range (m)	MA	Key findings
Archaux (2004)	French Alps	All	Point count	1973–2002	0.05	350–3099	Y	41 site/species comparisons: 6 showed significant downwards shifts, 4 significant upwards shifts
DeLuca and King (2017)	Appalachian Mountains, USA	All	Point count	1993–2009	0.01[b]	740–1470	Y	9 of 16 low-elevation species shifted upwards; 9 of 11 high-elevation species shifted downwards
Maggini *et al.* (2011)	Switzerland[a]	All	1-km^2	1999/2002–2004/07	0.09[b]	210–2710	N	95 species: 33 species shifted upwards, 28 shifted downwards
Mizel *et al.* (2016)	Denali National Park, Alaska	Passerines	Point count	1995–2013	0.04	500–1200	Y	Upwards shifts associated with shrub/tundra-nesting species; weaker evidence of upward shifts in forest species
Pernollet *et al.* (2015)	Swiss Alps	Ptarmigan	1-km^2	1984–2012	0.1	1700–3100	Y	Mean elevation of Ptarmigan presence shifted upwards in 3 of 4 regions
Popy *et al.* (2010)	Italian Alps	All	1-km^2	1992/94–2003/05	0.08	550–2556	Y	Weak overall upwards community shift; wide variation in the response of individual species
Reif and Flousek (2012)	Giant Mountains, Czech Republic	All	Point count	1986/88–1996/98	0.12	400–1602	Y	Significant overall mean shifts to higher elevations; open-habitat shifted more than forest species
Rocchia (2016)	Italian Alps	All	Point count	1982–2012	NA	600–4000	N	Woodland species tended to show range expansion, higher-elevation grassland species range retraction; regional variation
Tingley *et al.* (2012)	Sierra Nevada, USA	All[c]	Point count	1911/28–2003/09	NA	61–3356	N	Shifts were heterogeneous within species and among regions; both temperature and precipitation likely to be important drivers
Tryjanowski *et al.* (2005)	Tatra Mountains, Poland	White Stork	Nest location	1974–2003	0.08	400–900	Y	White Storks nested at progressively higher elevations

[a] Included as the majority of the area of Switzerland is classed as mountainous by Kapos *et al.* (2000). [b] Annual temperature – others are spring temperatures. [c] Passerines and five other families (Odontrophoridae, Phasianidae, Columbidae, Trochilidae and Picidae).

variation in species' responses between geographical locations within the same study (Tingley *et al.* 2012, Pernollet *et al.* 2015).

Our meta-analysis supports the lack of consistent trends apparent in Table 2. There were 203 estimates of elevation shift from seven published studies analysed, five from Europe and two from North America. Pooling all estimates across the studies, there was no strong support for a general shift towards higher elevations (parameter estimate ± se = 0.083 ± 0.052, 95% CL −0.018 to 0.184). Shifts towards higher elevations were more positive when rates of temperature change were higher (estimate ± se = 0.543 ± 0.152, 95% CL 0.245–0.841). Duration of study had an unexpected negative effect on shifts, studies over longer time spans resulting in more downward shifts (estimate ± se = −0.026 ± 0.004, 95% CL −0.034 to −0.018). The above findings were robust to different model structures and different subgroups of species (Table S3).

Most studies in Table 2 also considered temperature variations over the same period, either modelling them in relation to bird distributions (Archaux 2004, Popy *et al.* 2010, Reif & Flousek 2012, Tingley *et al.* 2012, Pernollet *et al.* 2015, Rocchia 2016) or considering climate trends over the same periods (Maggini *et al.* 2011, Mizel *et al.* 2016). In most cases, trends in elevation shifts matched temperature trends over the same period, with a few exceptions (Pernollet *et al.* 2015, Mizel *et al.* 2016). Tingley *et al.* (2012) found a broad range of responses of bird species along elevation gradients in the Sierra Nevada, due in part to differential responses to increasing temperature (exerting a general positive upwards shift) and increasing precipitation (exerting a general downslope shift). However, few other studies considered potential effects of precipitation (only Archaux 2004, Popy *et al.* 2010, Pernollet *et al.* 2015).

Changes in bird population trends along elevation gradients over time are similarly inconsistent across studies. Some find positive changes in lower-elevation species and negative changes in higher-elevation species that are consistent with elevation shifts, as lower-elevation species colonize mountains and higher-elevation species lose suitable habitat (Flousek *et al.* 2015). However, others have reported opposite (Archaux 2007) or inconsistent patterns (Zamora & Barea-Azcón 2015, Furrer *et al.* 2016). Tingley and Beissinger (2013) found a decrease in total species richness and in species richness of high-elevation species over time in the Sierra Nevada, despite heterogeneous shifts in individual species in the same area (Tingley *et al.* 2012). At wider scales, there is evidence that bird communities are shifting towards warm-dwelling species (Switzerland; Roth *et al.* 2014), but also that communities at higher elevations have lower 'climate debt' (the spatio-temporal divergence between temperature changes and community changes) as elevation increases (France; Gaüzère *et al.* 2016).

Projected elevation shifts

Extinction risks are expected to increase following climate-induced elevation range shifts in the future (Sekercioglu *et al.* 2008, La Sorte & Jetz 2010). Shifting vegetation zones in mountains, in particular an advance of the treeline towards higher elevations, have been observed in many studies (e.g. Lenoir *et al.* 2008, Harsch *et al.* 2009). As a consequence, high-elevation specialists, in particular those of open, treeless habitats, are expected to be most threatened due to habitat loss or fragmentation (e.g. Chamberlain *et al.* 2013, Goodenough & Hart 2013, Siegel *et al.* 2014, Brambilla *et al.* 2016, 2017a). Nevertheless, some studies have also projected overall range loss in higher-elevation forest specialists (Braunisch *et al.* 2014, Brambilla *et al.* 2015). There were 95 estimates derived from 12 studies that satisfied the criteria to be included in the analysis (Table S2). There was a net prediction of negative impacts on species populations or distributions, although there was a degree of variability and confidence limits overlapped zero (estimate ± se = −28.9 ± 17.0%, 95% CL −62.4 to 4.6). High-elevation mountain specialists and generalists were projected to be more negatively impacted than other species (mountain specialists and generalists = −76.1 ± 27.1%, 95% CL −129.2 to −23.0; other = 29.8 ± 25.7%, 95% CL −20.6 to 80.2). There was a tendency for greater negative impacts in severe than moderate scenarios (moderate = −26.6 ± 17.1%, 95% CL −60.1 to 6.9; severe = −33.6 ± 17.5%, 95% CL −67.9 to 0.7). There was no evidence of an effect of the number of years over which projections were made (−0.01 ± 0.79, 95% CL −1.53 to 1.55). Re-running the models without weighting for sample size showed the same patterns, although results were less conservative (i.e. it was less likely that confidence intervals overlapped zero).

Interactions of climate change effects with other drivers of change

Land use

Disentangling the relative importance of climate effects and other drivers of environmental change that influence the persistence and maintenance of biodiversity has been a key issue across mountain regions (Mantyka-Pringle & Rhodes 2012, Cumming *et al.* 2014, Maggini *et al.* 2014, Elmhagen *et al.* 2015). It is also central to producing efficient, adaptive conservation frameworks for threatened species (Gehrig-Fasel *et al.* 2007, Gienapp *et al.* 2007, Eglington & Pearce-Higgins 2012, Titeux *et al.* 2016). For example, climate change and land use often interact in ways that influence biodiversity (Parmesan & Yohe 2003) and these interactions may amplify or reduce the magnitude of potential effects (Clavero & Brotons, 2010, Dreitz *et al.* 2012, Chamberlain *et al.* 2013, Oliver *et al.* 2017). Lehikoinen and Virkkala (2016) acknowledged a land use and species trait effect due to the high level of unexplained variation in models predicting the change in density of birds in relation to temperature change. Jetz *et al.* (2007) attempted to assess the relative importance of climate and land use changes using future scenarios. In that study, we identified 617 high-elevation mountain specialist or mountain generalist species. For these species, the predicted average percentage loss in geographical range due to land use change was 24.8 and 28.6% by the years 2050 and 2100, respectively. In comparison, the predicted loss due to climate change alone was 7.3 and 11.5%, respectively.

The interaction between climate and land use is particularly relevant to mountain habitats because they are experiencing a faster rate of climate change than the global average (Diaz *et al.* 2003, Nogués-Bravo *et al.* 2007) and are subjected to other landscape-scale anthropogenic changes (Arlettaz *et al.* 2007, 2015, Gellrich & Zimmermann 2007, Nogués-Bravo *et al.* 2008, Patthey *et al.* 2008, Braunisch *et al.* 2011, 2013, 2016, Douglas *et al.* 2015). However, land use change has only been rarely incorporated in analyses of distribution shifts; Reif and Flousek (2012) and Rocchia (2016) found that elevation shifts more closely matched temperature than habitat changes, Tryjanowski *et al.* (2005) found significant effects of both, whereas Popy *et al.* (2010) could not separate the effects of the two.

Agro-forestry and pastoral practices have shaped the landscape of Holarctic mountains in Europe and Asia, influencing the species composition and abundance of mountain birds (e.g. Gehrig-Fasel *et al.* 2007, Caprio *et al.* 2011, Douglas & Pearce-Higgins 2014, Wilson *et al.* 2014, Mollet *et al.* 2018). Over time, forest management has changed in intensity (e.g. clear-felling vs. single-tree selection), composition (planting of exotic conifers) and age dynamics (establishment of even-aged monocultures; Kirby & Watkins 2015). At the same time, climate change may be affecting forest bird assemblages either directly or indirectly by influencing cover, productivity and composition of forest systems. However, it is generally unclear which of these two pressures (climate change or forestry practices) is the most important driver in changes in bird distribution. Changes in forest composition could cause opposite shifts (i.e. downhill) to those forecast due to effects of climate warming (uphill). For example, Archaux (2004) suggested that changes in forest management that favoured coniferous at the expense of broadleaved trees might have caused forest birds to have shifted their mean elevation downwards. In other cases, there is evidence from boreal forests (including some mountain areas) that climate, in addition to vegetation type and management, is a crucial driver for determining passerine species distribution (Cumming *et al.* 2014, Frey *et al.* 2016). Virkkala (2016) found that forest management favoured passerine species benefitting from climate change, so that direct habitat alteration was connected to the indirect effects of climate change.

Climate variables can also be important for non-passerine species. Brambilla *et al.* (2015) found in the Italian Alps an important effect of climate in addition to habitat composition at the landscape scale in dictating the distribution of the cold-adapted Eurasian Pygmy Owl and Boreal Owl *Aegolius funereus*. Both of these forest species were predicted to undergo range contraction in the Alps as a consequence of climate change. Braunisch *et al.* (2014) evaluated the importance of climate, landscape and vegetation variables on the occurrence of indicator species (i.e. Western Capercaillie, Hazel Grouse *Tetrastes bonasia,* Three-toed Woodpecker *Picoides tridactylus* and Eurasian Pygmy Owl) in central European mountain forests and assessed future changes in habitat suitability of these species according to climate projections. Although climate variables were the most important factors for most species, the models predicted that *in situ* management actions could partially mitigate the detrimental impact of climate events and sustain bird populations. These included increasing the number of forest gaps (for Western Capercaillie), increasing bilberry *Vaccinium* spp. cover (for Hazel Grouse) and increasing the number of snags and/or the proportion of high (> 15 m) canopy forest (for Three-toed Woodpecker). However, such interventions may have to work against the natural forest dynamics and could be expensive.

Historically, agricultural expansion and changes in livestock management have had major impacts on mountain birds (Lundmark 2007, Elmhagen *et al.* 2015). In many mountain areas, traditional grazing practices are characterized by low stocking densities or transhumant pastoralism, the seasonal movement of livestock between high-elevation summer pastures and lowland winter pastures (Arnold & Greenfield 2006). These traditional grazing practices have been largely abandoned in some areas due to social and economic factors, especially in the European Alps. For example, in Italy, the number of farms has decreased drastically and many have changed to indoor production systems (Battaglini *et al.* 2014), which has led to substantial changes in mountain vegetation zones through encroachment of formerly open grasslands by trees and shrubs and a loss of structural heterogeneity (Braunisch *et al.* 2016). Elevation shifts in vegetation may therefore be due to both climate change and land abandonment (Gehrig-Fasel *et al.* 2007).

The reintroduction of grazing is an often recommended management solution to counteract tree and shrub encroachment in open areas (Gehrig-Fasel *et al.* 2007) and it has the potential to increase plant structural diversity and composition (Hoiss *et al.* 2013, Peringer *et al.* 2013), which is key to preserving emblematic birds of semi-open habitat (Patthey *et al.* 2012). However, the effects of grazing on mountain bird populations are still not well understood. Long-term grazing at high stocking densities is known to have negative impacts on soil fertility and consequently on the productivity of the whole system (McVean & Lockie 1969), although effects on mountain birds are not consistent and vary substantially among geographical regions, livestock types and stocking levels. Several studies have reported that grazing increases richness or densities of mountain grassland birds (Laiolo *et al.* 2004, Evans *et al.* 2006, Bazzi *et al.* 2015). Evans *et al.* (2006) found that mixed sheep and cattle grazing, at low intensity, improved the breeding abundance of Meadow Pipit *Anthus pratensis* compared with sites stocked with sheep only (at high or low density) or unstocked sites in the Scottish uplands, and Loe *et al.* (2007) reported the highest bird density on pastures with high sheep density in Norway. Other studies have shown no differences in bird abundance or species richness between grazed and ungrazed sites (Moser & Witmer 2000) or a negative influence of grazing animals on nesting success (Pavel 2004, Warren *et al.* 2008).

Climate change can also have direct impacts on grazing management, although this is less well studied. In Nepal, where transhumance is a common practice, herders perceived the impact of climate change through personal experience. In several studies where herders have been interviewed, they described a rise in temperature, a decline of rain- and snowfall, a scarcity of water resources (Aryal *et al.* 2014, Wu *et al.* 2015) and the presence of invasive weeds, which are replacing the valuable grasses on farmlands (Gentle & Thwaites 2016). These perceptions accorded with temperature and rainfall trends in the same region. As a result, herders sought to adjust their transhumance patterns to the changed conditions by altering the timing of seasonal livestock movements. The consequences of such management responses for mountain bird populations, however, remain unknown. Given the varied different effects of grazing on mountain birds and the lack of research on likely responses of grazing management practices to future climate change, further investigations are needed to examine potential effects of grazing regimes on mountain bird populations before we can apply them as potential conservation tools.

Leisure and other potential threats

Mountains are important ecosystems for biodiversity but are also multi-functional sites for various human activities, including leisure. People seek mountain landscapes to practise a range of different sports and hobbies such as skiing, snowboarding, hiking, biking, birdwatching, rock-climbing, paragliding and hunting. Local communities benefit economically from tourism. The leisure industry in mountain areas is growing (Debarbieux *et al.* 2014) and the potential effects of these activities on avian communities have received increasing attention from conservationists (e.g. Patthey *et al.* 2008, Arlettaz *et al.* 2013, DeLuca & King 2014). The impact of snowsports on biodiversity is a major topic studied in the European Alps, where there are c. 40 000 km of ski-runs served by c. 14 000 ski-lifts capable of transporting c. 1.5 million skiers per hour (Weed & Bull 2004). As a consequence of this and other activities, the Alps receive nearly 100 million visitors per year, spending $60 billion annually (Giuliano 1994). In contrast, snowsport activities, including skiing operations in North America and the Eastern Holarctic, remain at a relatively low density, probably with only local effects on biodiversity (Martin 2001b).

There are several lines of evidence showing that ski-pistes have deleterious effects on both grassland and forest birds via loss and degradation of habitat and a decrease in food availability (Laiolo & Rolando 2005, Rolando *et al.* 2007, Caprio *et al.* 2011, Rixen & Rolando 2013). In addition, there is evidence that hormonal stress in birds generated by intensive human activities can negatively impact already vulnerable populations of Western Capercaillie (Thiel *et al.* 2011) and Black Grouse (Arlettaz *et al.* 2007, 2013). Anthropogenic disturbance also entails extra energetic costs that may negatively affect population dynamics (Arlettaz *et al.* 2015). Effects may also operate through infrastructure associated with skiing, for example increased mortality due to collision with ski cables (Baines & Andrew 2003, Watson & Moss 2004), and reduced reproductive success of ground-nesting birds associated with development of tourist resorts (Watson & Moss 2004, Patthey *et al.* 2008, Tolvanen & Kangas 2016), although negative effects are not universal (Rimmer *et al.* 2004).

Interactive effects of climate change and outdoor sports could increase the above negative impacts on bird populations in the future. Global warming is having important economic consequences for the skiing industry due to reduced snow cover and persistence. Compensatory mechanisms are targeted at prolonging the ski season by direct spraying of artificial snow or by creating new ski-pistes at higher elevations where snow conditions are more reliable. Brambilla *et al.* (2016) modelled ski-pistes and mountain bird presence according to future climate scenarios. Strong overlaps between areas climatically and topographically suitable for the development of ski-pistes and areas suitable for breeding alpine birds were predicted to occur, suggesting that the conservation of mountain bird communities will require careful planning to reduce potential increased future conflicts between outdoor winter sports and birds. Global warming is also causing the abandonment of ski-runs at lower elevations. Natural grassland re-vegetation at some abandoned sites resulted in a partial recovery of important alpine birds, although never back to the state of the 'original' alpine grasslands (Caprio *et al.* 2016).

Novel interspecific interactions

Species may respond to climate change by shifting their distribution to track local climates (Tingley *et al.* 2009, Jackson *et al.* 2015), which may result in novel interactions as species colonize new areas.

Including such interactions has improved model predictions at different scales (Araújo & Luoto 2007). Heikkinen *et al.* (2007) and Brambilla *et al.* (2013) suggested that including the presence of woodpeckers that produce the cavities used by secondary cavity-nesting raptors improved model performance in predicting cavity-nesting forest owl distributions. We found only one relevant example that tested the importance of biotic interactions among birds along elevation gradients. Freeman and Montgomery (2015) assessed potential competition between Swainson's Thrush *Catharus ustulatus*, which generally inhabits lower elevations but which has shifted its distributions towards higher elevations, and the conspecific Bicknell's Thrush *Catharus bicknelli*, which is largely confined to mountaintops. Using playback techniques, the authors found that, where the species co-occurred, Swainson's Thrush responded aggressively to Bicknell's Thrush, but not vice versa.

Conservation and policy

Our literature review has clearly highlighted the need for more detailed studies of mountain birds, with several papers stating that a valuable conservation framework can be achieved only if such knowledge gaps are bridged (see Research gaps and conclusion; Fig. 4). Despite this, we found that most studies on this topic identified adaptation strategies for mountain and upland species threatened by climate change. Most of these studies (n = 21; Fig. 4) focused on the quality, quantity and geographical location of protected areas. Existing protected areas may have already

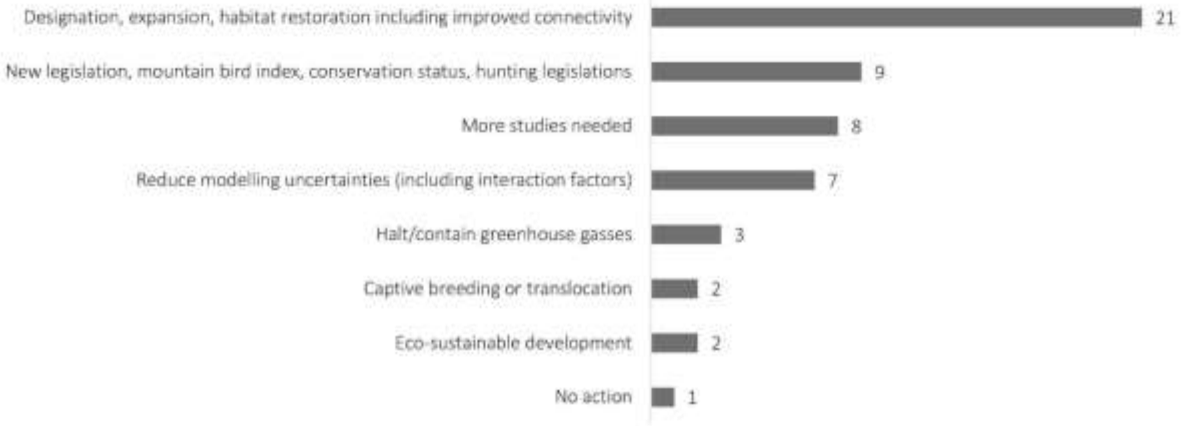

Figure 4. Number of conservation (mutually inclusive) actions suggested across all papers classified as 'conservation & policy' ($n = 26$) in the systematic literature search.

functioned as important compensatory systems, increasing species' resilience to climate change (Virkkala *et al.* 2014, Gaüzère *et al.* 2016, Santangeli *et al.* 2016) and in future scenarios of greenhouse gas emission, greater biodiversity losses have been predicted in unprotected than in protected areas (Virkkala *et al.* 2013). In Europe, nationally designed protected areas are likely to retain climate suitability better than unprotected areas in the future, as they tend to occur at high elevations and hence act as climatic refuges for species, although this was not found to be the case for the European Union-wide Natura 2000 network (Araújo *et al.* 2011). The same authors also predicted that 97.2% of alpine species and sub-species of vertebrates and plants of European concern will lose suitable habitat due to their small ranges, although that study did not consider species dispersal.

Some habitats may also be more prone to climate change than others. Montane forest species are predicted to be less impacted by climate change due to the stronger self-regulation of the forest microclimate compared with open habitats (Reif & Flousek 2012) and to native forest expansion that has already occurred and which is predicted to continue in many areas (European Alps; British uplands; Chamberlain *et al.* 2013, Scridel *et al.* 2017b). However, they could be prone to other climate change-related threats such as pests, disease and wild fires (Dale *et al.* 2001, Sturrock *et al.* 2011, Lesk *et al.* 2017). Furthermore, natural grasslands in the Alpine region may face serious challenges to elevation shift because they are being progressively colonized by trees at lower elevations following land abandonment or release of grazing pressure, while facing constraints at higher elevations, for example due to slow rates of soil formation (Freppaz *et al.* 2010, Chamberlain *et al.* 2013, Jackson *et al.* 2015).

Targeted habitat management should be considered as an adaptive conservation tool for various species threatened by climate change (Fig. 4). Improving habitat structure and offering greater prey availability has been reported to increase mountain species' resilience and resistance for forest, semi-open and open-habitat species (Carroll *et al.* 2011, Braunisch *et al.* 2014, Scridel *et al.* 2017b). This might be achieved by targeted grazing to maintain open habitats and enhance invertebrate populations (Signorell *et al.* 2010, Patthey *et al.* 2012, Braunisch *et al.* 2016). Such intensive actions can be very costly and in conflict with many economic goals, so management should projected over large areas to support viable wildlife populations. Increasing the quantity and quality of protected areas is important not just for mountain species *per se* but also because these areas are likely to become stopover refuges for many migrant species tracking climate change (Loarie *et al.* 2009, Boyle & Martin 2015) and management action should also accommodate these species' requirements. When intensive management *in situ* does not compensate for climate effects, then captive programmes ($n = 2$; Fig. 4), translocation of species to new suitable areas ($n = 2$;

Bech *et al.* 2009) or creation of corridors to favour dispersal and colonization of new areas (Huntley *et al.* 2008, Conroy *et al.* 2011, Lu *et al.* 2012, Virkkala *et al.* 2013) could be considered.

These adaptation responses for mountain species threatened by climate change can work only if scientists and policy-makers collaborate to influence current legislation. Our classification of high-elevation mountain specialists and mountain generalists indicates initial steps for a joint common Holarctic mountain bird index, which so far has only been developed for some regions in the world (Fennoscandia; Lehikoinen *et al.* 2014, North America and British Columbia, Canada; Boyle & Martin 2015). Such an index could be an essential element for scientists and policy-makers to measure progress in the conservation of mountain birds, especially if this index includes full life cycle avian use of mountain habitats. While in the long-term global measures to contain and reverse anthropogenic emissions are important ($n = 3$; Fig. 4), most authors admit that the persistence of mountain species also depends on immediate short-term national and local conservation actions and legislation ($n = 9$; Fig. 4).

DISCUSSION

Our literature review has shown that there is a growing body of evidence that climate change is affecting the reproduction, survival population trends and distribution of mountain birds. These changes may have been mediated by direct effects of climate on physiology, indirect effects of changes in habitat or via interactions with other biotic and abiotic changes. However, patterns are often highly variable (e.g. both increases and decreases in population size, range changes towards both higher and lower elevations) between species and between different study areas for the same species.

Defining a 'mountain bird' across a large region such as the Holarctic is difficult because many species that are mountain birds in warmer climates are lowland species in colder climates. Our goal was to derive an objective definition that could be applied over a large geographical area and which identified species associated with mountains *per se*, rather than occurring in mountains due to interactive effects of climate, elevation, latitude and land use. This is important when considering species distributions over large scales and in particular when projecting future distributions. For example, the Water Pipit was identified as a generalist mountain breeding bird across various mountain slopes, even in the northern, colder parts of its geographical range. Predictions based on climate alone may therefore be inaccurate for such species (e.g. Huntley *et al.* 2008). In general, the species identified as high-elevation specialists or mountain birds (Table S4) accorded with the authors' expectations, although there were some surprising results. For example, Rock Ptarmigan is considered an archetypal mountain bird in many parts of its range (the European Alps, the Pyrenees, British Columbia and Alberta) but not according to our definition. This may have been partly due to the coarse scale of the defined breeding range but also reflects the widespread populations of this species inhabiting lowland Arctic tundra. Because conservation policy is typically applied at national or regional level, a regional definition of mountain birds would also be useful, and could be achieved readily using our methods. Although this first classification of Holarctic high-elevation mountain specialist and generalist birds was not the primary aim of this review, we consider this exercise of considerable value for future work on this group of poorly studied species (e.g. baseline monitoring, development of a joint mountain bird index, and ecological and conservation research).

According to our meta-analysis, there was no evidence for consistent elevation shifts in mountain bird species. Although we failed to detect any direct and conclusive evidence that climate change has caused widespread distribution shifts in Holarctic mountain birds, it is likely that we lack sufficient data to generate robust conclusions. The meta-analysis included a range of species encompassing a great variation in life history strategies, demographic parameters and geographical regions. All of these factors are likely to influence potential responses to climate change and hence cause a wide variation in patterns of elevation shift among mountain birds across the mountain ecosystems and avian taxa considered (Martin & Wiebe 2004, Wilson & Martin 2010, Tingley *et al.* 2012, Novoa *et al.* 2016).

The consistency in climate projections across studies was somewhat at odds with the heterogeneity of responses of observed elevation shifts. This may in part have been due to more mountain high-elevation specialists being included in the projection papers. However, in many cases, there was a focus on climate (usually temperature and precipitation) as a driving factor and only half of the studies considered alternative scenarios of climate change in tandem with land use change or other anthropogenic pressures. In general, species distribution models only rarely include scenarios of changes in land use and human disturbance alongside those of climate change (Sirami *et al.* 2017). It is clear that many factors influence range shifts in mountain birds, including temperature, but also precipitation, habitat and topography, and that species may vary widely in their response. Assessments of elevation range shifts and predictions of future shifts in mountain birds should consider all these factors.

Adaptation responses for mountain species threatened by climate change rely on enhancing the quality and quantity of suitable habitat, in particular via protected areas, but also the conservation of suitable ecological conditions at regional and wider levels, including improving landscape connectivity. We have shown that human activities can be beneficial for climate-sensitive species (i.e. some pastoral activities) and yet mechanization, leisure and urbanization may impede potential benefits. Major changes can occur if scientists and legislators work closely together, for example through the development of efficient agri-environmental schemes, forestry practices, regulation of leisure activities and sustainable urban planning in mountain areas, with explicit recognition of the general ecological requisites for wildlife persistence such as connectivity across their full life cycle.

Research gaps and conclusions

From our literature review, it was evident that mountain species are little-studied relative to species in lowland habitats of the Holarctic such as farmland, forest and wetlands. For many common species in mountains even basic biological and ecological knowledge is lacking (e.g. Alpine Accentor, White-winged Snowfinch, Twite, Wallcreeper, North American Rosy Finches *Leucosticte* spp.). Although both high-elevation mountain specialists and mountain generalists are well represented in the literature in terms of large-scale distribution studies (e.g. species distribution models based on atlas data), they are very poorly represented when considering finer-scale, usually more intensive studies which address ecological mechanisms. In particular, there were very few studies of the ecology of high-elevation mountain specialists, yet these are the species that are most likely to be affected by climate change. Aside from broad-scale species distribution, the evidence base therefore largely concerns species that occur across a range of habitats and elevations, rather than species whose geographical range, at least in the Holarctic, is largely restricted to mountain areas.

Our understanding of physiological mechanisms underpinning bird responses to climate change is still limited, despite recent studies emphasizing the importance of specifying ecological traits, notably physiological tolerance, when predicting responses to climate change (Kearney & Porter 2009, Reif & Flousek 2012, Auer & King 2014, Pacifici *et al.* 2017). This is particularly important in terms of developing conservation strategies. If a species responds directly to climate through a physiological effect, then there might be limited conservation actions that could implemented beyond the need to reduce our dependence on non-renewable fossil energy sources. There is more potential for developing conservation actions for species that are affected indirectly by climate change, although for mountain birds, we still lack information about species' basic ecological requirements, such as key trophic resources for reproduction, that are required to develop management strategies. We therefore emphasize the need for more basic studies of both physiological tolerance and ecological requirements of mountain birds, and in particular high-elevation mountain specialists, as well as for all those lower-elevation species that are predicted to colonize mountain regions in the near future (Loarie *et al.* 2009).

The importance of considering cross-ecosystem linkages such as trophic structure when identifying climate change effects has been shown to be crucial for a clear understanding of the underlying mechanisms affecting species and populations (Pearce-Higgins *et al.* 2010, Santisteban *et al.* 2012, Fletcher *et al.* 2013). Furthermore, a better understanding of energetic values in food sources (prey) and how these influence demographics in species is particularly important for future climate-related adaptation responses. Relatively few studies had considered long-term trends over several years that could encompass a full range of climate variation and hence assess climate trends (rather than year-to-year changes in weather over shorter periods). In particular, the low number of studies assessing elevation shifts suggests that monitoring in high mountains is inadequate, probably due to a combination of complex terrain and lack of field surveyors available in these sparsely populated areas. Targeted monitoring in mountain areas, with a focus on high-elevation mountain specialists, is therefore essential if we are to improve our assessments of current and future climate effects on bird distributions.

Monitoring reproductive success and survival of mountain birds would be similarly useful. The demographic mechanisms that underpin species distributions and population changes are not well understood for mountain birds. There have been some short-term effects of climate demonstrated in several species, but longer-term studies are rare. More intensive, long-term studies would enhance understanding of the key factors that determine population trends and distributions and would therefore facilitate the predictions of future climate change impacts by elucidating more complex mechanisms, such as phenological effects. Many studies acknowledge that a valuable understanding of climate impacts can only be achieved if key interacting factors are considered, such as land use changes and biotic interactions, including interspecific competition. Given that projections of distributions of future mountain bird species may be quite sensitive to assumptions about how land use will change in the future (e.g. Chamberlain *et al.* 2013), we urge a greater consideration of land use change in species distribution modelling in mountain environments. Finally, we invite scientists and policy-makers further to develop studies and related frameworks efficiently to develop habitat restoration plans in mountain areas, particularly where climate change and changes in land use are likely to offer such opportunities in the near future (i.e. encroaching pastures after grazing/abandonment of ski-pistes, afforestation of native woodland on moorlands). Indeed, conservation and restoration frameworks have already been developed for various birds species inhabiting mountain regions considered susceptible to changes in climate and land use (e.g. Signorell *et al.* 2010, Carroll *et al.* 2011, Patthey *et al.* 2012, Braunisch *et al.* 2016, Caprio *et al.* 2016, Scridel *et al.* 2017b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Further details on methods used to produce the mountain bird list.

Appendix S2. Further details on the meta-analyses methods.

Table S1. List of relevant publications resulting from the systematic ISI Web of Knowledge search.

Table S2. Studies included in the meta-analysis of projected changes in geographical distribution or population size in mountain birds under scenarios of future climate change.

Table S3. Parameter estimates (± standard error), lower (LCL) and upper (UCL) 95% confidence limits estimating change in elevation of bird species distributions over time, and the effects of rates of temperature change (°C/year) and duration of study on different subsets of data.

Table S4. Mountain bird list.

SECTION II: *Chapter II*

Thermal niche predicts recent changes in range size for bird species

SCRIDEL, D., BOGLIANI, G., PEDRINI, P., IEMMA, A., VON HARDENBERG, A. & BRAMBILLA, M.

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Thermal niche predicts recent changes in range size for bird species

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ABSTRACT: Species' distributions are strongly affected by climate, and climate change is affecting species and populations. Thermal niches are widely used as proxies for estimating thermal sensitivity of species, and have been frequently related to community composition, population trends and latitudinal/elevational shifts in distribution. To our knowledge, no work has yet explored the relationship between thermal niche and change in range size (changes in the number of occupied spatial units over time) in birds. In this study, we related a 30 yr change in range size to species thermal index (STI: average temperature at occurrence sites) and to other factors (i.e. birds' associated habitats, body mass, hunting status) potentially affecting bird populations/range size. We analysed trends of breeding bird range in Italy for a suite of poorly studied cold-adapted animals potentially sensitive to global warming, and for a related group of control species taxonomically similar and with comparable mass but mainly occurring at lower/warmer sites. We found a strong positive correlation between change in range size and STI, confirming that recent climatic warming has favoured species of warmer climates and adversely affected species occupying colder areas. A model including STI and birds' associated habitats was not so strongly supported, with forest species performing better than alpine open habitat and agricultural ones. In line with previous works highlighting effects of recent climate change on community composition, species' population trends and poleward/upward distributional shifts, we found STI to be the most important predictor of change in range size variation in breeding birds.

KEY WORDS: Climate change · Mountain · Cold-dwelling · Warm-dwelling · Alps

1. INTRODUCTION

Climate is a major factor determining a species' distribution as this largely depends on species-specific physiological tolerance to temperature (Woodward 1987, Hoffman & Parsons 1997, Kreyling et al. 2015) and precipitation (Tingley et al. 2009, Toledo et al. 2012, Illán et al. 2014), and on climate-driven habitat characteristics (Deutsch et al. 2015). Recent changes in climate have induced range shifts of animal species towards higher latitudes and elevations (Thomas & Lennon 1999, Parmesan & Yohe 2003, Zuckerberg et al. 2009, Gillings et al. 2015), altered species' phenology (Roy & Sparks 2000, Fitter & Fitter 2002) and affected population dynamics (Thompson & Ollason 2001, Stephens et al. 2016). Direct and indirect effects of climate change are expected to aggravate the conservation status of many organisms in the current century, with numerous species predicted to become endangered (Parmesan et al. 1999, Thomas et al. 2004, Cahill et al. 2013).

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Many studies investigating climate change effects on animal populations focus on bird species as they are considered good indicators due to their ability to respond rapidly to environmental changes and spatially track suitable climatic conditions (Chen et al. 2011, Maggini et al. 2011). Studies investigating wide-scale effects of climate change on bird populations commonly use the species thermal index (STI; i.e. the average temperature across a given species' distribution) as a proxy for estimating the thermal sensitivity of a species (e.g. Gaüzère et al. 2015). These kinds of study typically model population trends (changes in population size over time) as a function of climate change (e.g. Jiguet et al. 2010). Other studies evaluate changes in the community thermal index (CTI; i.e. the average temperature for a community of species) over time (e.g. Gaüzère et al. 2015, Tayleur et al. 2016). Generally, those studies report that population trend varies according to species' STI, and that CTI increases coherently with increasing temperature (Tingley et al. 2009), displaying consistent latitudinal variation (Devictor et al. 2008). However, to the best of our knowledge, until now no study has considered the net change in species' range size in a given geographical area over time as a function of the mean temperature experienced by the species across their distributional range. Changes in range size (changes in the number of occupied spatial units over time in a geographical region) related to the climatic sensitivity of the species would signal a very important effect of climate, different from the reported change in population growth (e.g. Jiguet et al. 2010) and community structure (e.g. Gaüzère et al. 2015) in a given area, and even different from a range shift that does not affect range size. This is particularly relevant for cold-dwelling species like mountain birds, which are predicted to be affected by global warming more than warm-dwelling species (Araújo et al. 2011, Pearce-Higgins et al. 2015, Tayleur et al. 2016). Compared to birds in other habitats, mountain birds are relatively poorly studied, largely due to the logistical problems of surveying in such challenging climatic and topographic environments (Chamberlain et al. 2012, Scridel 2014), but are particularly at risk because of global warming, as species are often confined to discrete habitat isolates, and cannot track suitable climate latitudinally (Fjeldså et al. 2012, Bech et al. 2009).

Here we investigate the relationship between change in range size and STI for a set of cold-dwelling birds and for their closest (non cold-dwelling) relatives breeding in Italy, whilst accounting for other important factors known to potentially affect bird trends such as species' broad habitat association (e.g. Chamberlain et al. 2013), hunting status (e.g. Sandercock et al. 2011) and body mass (e.g. Brommer 2008). Moreover, various studies show that population trends (Thomas 2008) and extinction risks (Purvis 2008) are not randomly distributed with respect to phylogeny: species that share a long evolutionary history are more likely to exhibit similar responses than evolutionary distant ones. Therefore, to provide an unbiased assessment of climate change effects, we used a phylogenetic comparative approach, which accounts for evolutionary relatedness between species.

2. MATERIALS AND METHODS

2.1. Model system

We worked with the reported change in range size in the last 30 years for breeding bird species in Italy. Italy represents a good study model to investigate the relationship between birds' climatic niche and the variation of their range size trends because (1) it encompasses a wide latitudinal and elevational gradient, (2) it comprises different biogeographical regions with different assemblages of species (i.e. from Mediterranean islands to high mountains) and (3) it includes one-third of the Alps, a mountain chain for which strong impacts of climate change have been already observed (Sergio 2003, Maggini et al. 2011, Pernollet et al. 2015) and may act synergically with changes in land use (e.g. Laiolo et al. 2004). Europe has recently experienced a linear increase in average temperatures from the 1980s onwards by over 0.9°C (KNMI, 2007 Climate research unit, http://climexp.knmi.nl), but in the Alps the rate of warming has been double the global average (Brunetti et al. 2009), and rising temperatures, higher snow lines and lower snowfalls are predicted to continue (EEA 2010). Adverse effects are therefore expected for these regions hosting many geographically isolated species, often being glacial relicts occurring at the edge of their ecological and climatic niche (e.g. boreo-alpine species and other species found only in high mountains), and often predicted to undergo range contractions and/or population decline as a response to climate change (Maggini et al. 2011, Chamberlain et al. 2013, Viterbi et al. 2013, Braunisch et al. 2014, Brambilla et al. 2015, 2016, 2017a, Pernollet et al. 2015). To understand whether changes in range size differ according to different STI, we investigated changes in range for breeding bird species by considering a set of species comprising closely related taxa with largely different STI, in order to get an indirect measure of the species' sensitivity to climate change. Firstly, we chose bird species displaying in Italy a breeding distribution strictly related to the main mountains (i.e. Alps and Apennines; Nardelli et al. 2015). We included boreo-alpine species (rock ptarmigan *Lagopus muta*, pygmy owl *Glaucidium passerinum*, boreal owl *Aegolius funereus*), species occurring in southern European mountains (alpine accentor *Prunella collaris*, yellow-billed chough *Pyrrhocorax graculus*, white-winged snowfinch *Montifringilla nivalis*) and other species that in southern Europe and in the Alps occur only or predominantly on mountains or in relatively cold areas: hazel grouse *Bonasa bonasia*, black grouse *Lyrurus tetrix*, capercaillie *Tetrao urogallus*, nutcracker *Nucifraga caryocatactes*, water pipit *Anthus spinoletta*, citril finch *Carduelis citrinella*, common redpoll *Carduelis flammea*, ring ouzel *Turdus torquatus*, wallcreeper *Tichodroma muraria*, three-toed woodpecker *Picoides tridactylus*, black woodpecker *Dryocopus martius*, grey-headed woodpecker *Picus canus* and willow tit *Parus montanus* (although the latter 3 species occur broadly in lowland habitats in central-northern Europe, in the Alps and in southern Europe they are mostly associated with relatively cold areas). Secondly, for each of the above-mentioned taxa (n = 19), whenever possible a control species was chosen (n = 19), taking the one most closely related according to Roquet et al. (2014) and generally associated with lower elevation in order to have a balanced sample (Table 1). With such ad hoc selection, we ensured a phylogenetically balanced sample of species, the inclusion of cold-dwelling taxa and of others not specialized for cold environments, the focus on species with similar movement strategies (all species apart from tree pipit *Anthus trivialis* being resident or short-distance migrants), and the exclusion of species for which change in range size may be due mostly to improved knowledge or reintroduction/restocking projects carried out between the 2 reference periods (as actually occurred for some species; Nardelli et al. 2015).

2.2. STI and distribution trends

To quantify STI for each species, we gathered breeding distribution data available from the European Environment Information and Observation Network (EIONET) portal (www.eionet.europa.eu/), which provided presence/absence data at a 10 × 10 km resolution for 23 European countries (UK, France, Italy, Slovenia, Spain, Portugal, Austria, Denmark, Sweden, Finland, Greece, Belgium, Gibraltar, Slovakia, Malta, Lithuania, Latvia, Ireland, Hungary, Germany, Estonia, Romania and the Czech Republic). For each species, we merged all available data to create a large-scale breeding distribution map using geographic information system (GIS) software (QGIS, Quantum GIS Development Team 2016; GRASS, GRASS Development Team 2015). We then coupled the above-mentioned species' digitized breeding distribution with 30 arcsec resolution data describing the mean annual temperature (downloaded from Worldclim database version 1.4; www.worldclim.org/; Hijmans et al. 2005). STIs were consequently calculated by averaging mean, median, minimum and maximum temperature (in °C) experienced by each species during the breeding season across its distribution range. To date, many studies have used a variety of thermal indexes to evaluate potential responses of bird communities to climate change, such as thermal maximum and minimum (mean of hottest/coldest 5% cells; e.g. Jiguet et al. 2010), thermal range (difference between thermal maximum and minimum; e.g. Jiguet et al. 2010), seasonal thermal average (mean temperatures during breeding period; e.g. Devictor et al. 2008), coldest month mean temperature (e.g. Green et al. 2008), and annual temperature sum above 5°C (e.g. Green et al. 2008). To minimize collinearity, we used variance inflation factors (VIFs) on our 4 temperature predictors, and highly collinear variables (VIF > 5) were omitted following Zuur et al. (2009). There were high levels of collinearity between these variables, and only mean annual temperature was used, as it was considered to be the most representative estimate for the thermal niche of the study species, due to the largely non-migratory status of our target species (most species are resident, and only tree pipit *A. trivialis* is a long-distance migrant).

To estimate change in range size, we used long-term bird distribution trends from Nardelli et al. (2015), which compared occupied vs. unoccupied cells of breeding species in Italy between the 1980s (1983 to 1986, according to data available for each species) and 2012, therefore calculating a net change of range size (Table 1). Species ranges were estimated by collating all available data, such as regional and local atlases, published reports, papers, and monitoring schemes (Nardelli et al. 2015). Given that most of the sources used to define species' range were general and not species-specific, the potential effect of confounding factors such as an increase in knowledge should affect all the species in the same way, thus it is un-

Table 1. Selection of species considered for this study. The left column shows the cold-adapted species initially selected, while on the right their respective related species are listed. Broad habitat category and percentage variation of species distribution over the period 1983/1986 to 2012 in Italy (according to Nardelli et al. [2015]) are also shown

Cold-adapted species				Control species			
Scientific name	Common name	Habitat	Trend (%)	Scientific name	Common name	Habitat	Trend (%)
Tetraonidae							
Lagopus muta	Ptarmigan	Alpine open habitat	−7	*Alectoris rufa*	Red-legged partridge	Agricultural	+53
Bonasa bonansia	Hazel grouse	Forest	−6	*Phasianus colchicus*	Common pheasant	Agricultural	+8
Lyrurus tetrix	Black grouse	Alpine open habitat	−4	*Perdix perdix*	Grey partridge	Agricultural	−11
Tetrao urogallus	Capercaillie	Forest	−4				
Strigiformes							
Aegolius funereus	Boreal owl	Forest	−8	*Athene noctua*	Little owl	Agricultural	+7
Glaucidium passerinum	Pygmy owl	Forest	−4	*Strix aluco*	Tawny owl	Forest	+22
Picidae							
Picus canus	Grey-headed woodpecker	Forest	+16	*Picus viridis*	Green woodpecker	Forest	+20
Dryocopus martius	Black woodpecker	Forest	+36	*Dendrocopos major*	Great spotted woodpecker	Forest	+18
Picoides tridactylus	Three-toed woodpecker	Forest	+30	*Dendrocopos medius*	Middle-spotted woodpeker	Forest	+68
Motacillidae							
Anthus spinoletta	Water pipit	Alpine open habitat	−2	*Anthus trivialis*	Tree pipit	Alpine open habitat	+18
Prunellidae							
Prunella collaris	Alpine accentor	Alpine open habitat	−15	*Prunella modularis*	Dunnock	Alpine open habitat	−9
Turdidae							
Turdus torquatus	Ring ouzel	Alpine open habitat	−1	*Turdus merula*	Blackbird	Agricultural	+4
Paridae							
Parus montanus	Willow tit	Forest	−5	*Parus palustris*	Marsh tit	Forest	+21
				Parus cristatus	Crested tit	Forest	+8
Tichodromadidae, Certhiidae							
Tichodroma muraria	Wallcreeper	Alpine open habitat	−6	*Certhia familiaris*	Treecreeper	Forest	+23
Corvidae							
Nucifraga caryocatactes	Nutcracker	Forest	−8	*Corvus corone*	Carrion crow	Agricultural	0
Pyrrhocorax graculus	Alpine chough	Alpine open habitat	−9	*Pyrrhocorax pyrrhocorax*	Red-billed chough	Agricultural	+23
Passeridae							
Montifringilla nivalis	White-winged snowfinch	Alpine open habitat	−7	*Petronia petronia*	Rock sparrow	Agricultural	+42
Fringillidae							
Carduelis citrinella	Citril finch	Alpine open habitat	−2	*Serinus serinus*	Serin	Agricultural	+5
Carduelis flammea	Common redpoll	Alpine open habitat	−9	*Carduelis carduelis*	Goldfinch	Agricultural	−2

likely to produce any bias in our analyses. The only partial exception to this pattern is represented by an increased effort at high elevation in the common bird monitoring scheme (MITO 2000 project Pan-European Common Bird Monitoring Scheme, Fornasari et al. 2014). We stress that species' net changes in range size reported in Nardelli et al. (2015) are unlikely to be biased in respect of elevation as these are in line with various national (Fornasari et al. 2004, Gustin et al. 2010, Rete Rurale Nazionale & LIPU 2014) and international studies on population trends (i.e. Zbinden et al. 2005), which generally highlight a wide-scale decline for mountain birds, particularly marked for open habitat species.

2.3. Statistical analysis

To test the hypothesis that STI is associated with changes in range size (and thus that cold-adapted species have contracted their range size more than warm-dwelling species), we fitted phylogenetic generalized least squares (PGLS) models implemented in the package 'Caper' (Orme et al. 2013; ver.0.5.2) in the statistical environment R version 3.2.3 (R Core Team 2015). The response variable was the long-term trend (as percentage variation reported in Nardelli et al. 2015) in the national breeding range of the selected bird species. Explanatory variables were the STI of each species and the following 3 other factors potentially driving variation: (1) the broad habitats with which the species is mostly associated in Italy (forest [n = 16 species], alpine open [n = 12] and agricultural habitats [n = 10]; Cramp et al. 1977–1994); (2) a categorical variable defining the prevalent hunting status in Italy (i.e. hunted/non-hunted; Article 2, Law 157/92); and (3) the average body mass of each species as a proxy for demographic traits (Cramp et al. 1977–1994, Julliard et al. 2004, Brommer 2008). An interaction term between species' associated habitat and STI was also included to test the hypothesis that the relationship between STI and changes in range size differs across habitats. PGLS models were chosen to incorporate the covariance between related birds and therefore account for the non-independence of data points due to common ancestry (Paradis 2014). Firstly, we built a phylogenetic tree for our selected species, based on the supertree from Jetz et al. (2012), and trimmed it using the related website www.birdtree.org. A covariance matrix was then produced calculating the branch lengths of the phylogenetic tree and fitted in the PGLS model to estimate maximum likelihood of the parameter λ and for phylogenetic signal in the model residuals (Pagel's λ). A value of $\lambda = 0$ represents no phylogenetic signal, whilst $\lambda = 1$ means a high phylogenetic signal and therefore consistency with a Brownian motion model of trait evolution (Pagel 1999). Model selection for fixed terms was then performed by comparing Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002) using the dredge function in the R package 'MuMIn' (Barton 2015), which allows generation of mathematical models (PGLS in our case) using all combinations of variables.

3. RESULTS

Our sample of 38 species covered a wide range of thermal positions (STI = 7.6 ± 0.4°C [mean ± SE], range = 3.1 to 13°C), with the 'coldest' species being rock ptarmigan *Lagopus muta* and the 'warmest' being rock sparrow *Petronia petronia*. STI values were cooler for species of alpine open habitat (5.6 ± 0.4°C) than for species of forest (7.1 ± 0.6°C) and agricultural habitat (10.7 ± 0.4°C). Changes in range size were negative for alpine open habitat species (% trend = −4.4 ± 2.3), and positive for agricultural (12.9 ± 6.4) and, especially, forest species (14.2 ± 5.1). Based on AIC_c, the most supported model explaining change in range size only included STI as a fixed variable (Table 2) and explained a good proportion of the variance (adjusted $R^2 = 0.36$). All other models with similar support ($\Delta AIC_c < 2$) included the most supported as a nested model, thus all the other parameters may be considered uninformative. For the most supported model, Pagel's $\lambda = 0.48$.

We thus found a positive correlation between long-term changes in range size of Italian breeding birds and the respective thermal niche (STI) of a species (Fig. 1): species that experienced losses in their distribution were mostly associated with cold STI values. A poorly supported effect (uninformative parameters) was found for habitat and for the habitat × STI interaction, generally suggesting a more favourable change in range size for forest species than for those dwelling in open habitats and, especially, agricultural ones.

4. DISCUSSION

This work highlights for the first time the importance of thermal niche (described as the average temperature experienced by a species across its

Table 2. Most supported ($\Delta AIC_c < 2$) PGLS models for net range variation of selected breeding bird species in Italy, ranked according to the AIC_c value. Hunting status and habitat were factorial variables with the intercept representing 'agricultural habitat' and 'no hunting status', respectively. Beta coefficients (±SE) for each level are also shown

Intercept	Habitat	Hunting status	STI	Body mass	Habitat × STI	logLik	AIC_c	Delta	Weight
−19.38 ± 11.1			3.84 ± 0.8			−155.5	315.3	0	0.228
−103.9 ± 31.8	Open: 82.42 ± 34.2 Forest: 86.35 ± 31.9		11.25 ± 2.9		Open: STI: −7.48 ± 4.1 Forest: STI: −7.05 ± 3.1	−150.56	315.8	0.48	0.179
−40.84 ± 15.7	Open: 10.34 ± 9.1 Forest: 16.5 ± 7.9		5.27 ± 1.3			−153.38	316	0.63	0.166
−17.67 ± 11.4		Yes: −6.81 ± 8.5	3.91 ± 0.8			−155.16	317	1.67	0.099
−20.01 ± 11.6			3.87 ± 0.8	0.0013 ± 0.006		−155.48	317.7	2.31	0.072
−124.1 ± 38.3	Open: 95.8 ± 37.2 Forest: 102.4 ± 36.3	Yes: 9.41 ± 9.7	12.68		Open: STI: −8.15 ± 4.2 Forest: STI: −8.17 ± 3.3	−150	317.7	2.39	0.069
9.145 ± 8.4						−164.53	331.2	15.82	0

breeding range) as a predictor for the change in breeding range size for a suite of European birds with different thermal niches and habitats. Our work analysed changes in range size in Italy, which represents an optimal context for such an assessment, given its location at the southern boundary of Europe and the presence of wide latitudinal and elevational gradients.

Thermal niche is frequently reported as the most important component of the climatic niche of birds, and it is known to be a reliable tool to evaluate climate change effects on species' dynamics (Jiguet et al. 2007, Barnagaud et al. 2012, Howard et al. 2014, Stephens et al. 2016). Our findings are consistent with previous studies reporting the importance of thermal niche in predicting bird population trends

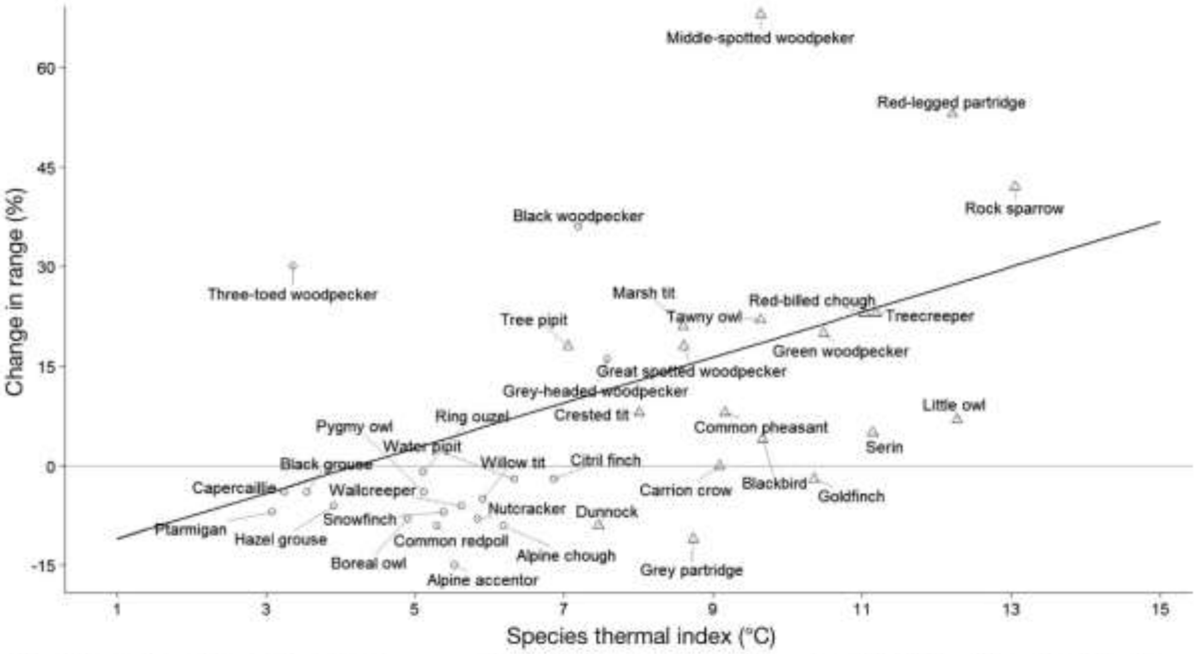

Fig. 1. Fitted line of the relationship between species distribution trends over the period 1983/1986 to 2012 and STI. Predictions are derived from the most supported PGLS model. Circular and triangular symbols: species associated with cold and warm environments, respectively

(Jiguet et al. 2010, Thaxter et al. 2010, Pearce-Higgins et al. 2015) and complement them by highlighting the relationship between thermal niche and range dynamics, in addition to the already reported link between thermal niche and population trends.

The overwhelming importance of STI in predicting changes in range size variation for breeding bird species in the last 30 yr provides additional support for the strong effect of climate change on the change in the size of their breeding range, even over a relatively short timeframe. Thousands of cases of species changing their distribution in relation to climate change are already reported (Bellard et al. 2012), mostly in the form of latitudinal and elevational shifts, which seem particularly frequent in species displaying good dispersal abilities (Parmesan 2006). Range contractions are indeed reported for species of polar and high-mountain regions (Forero-Medina 2011). Consistently, our results further confirmed how cold-adapted species inhabiting mountain regions are at particular high risk, as their range has already contracted most likely because of climate change effects. Indeed, it is likely easier for lowland species to track suitable climates by performing latitudinal shifts, whereas for mountain species, confined to discrete habitat isolates, tracking suitable climates almost invariably means contracting the relative range (Fjeldså et al. 2012, Bech et al. 2009). In fact, species showing no or positive changes in range size might also have shifted their range, but only in the case of cold-adapted species did range shifts result in definite range contraction.

The positive correlation between changes in range size bird distribution trends and STI supported our initial expectation, suggesting that recent climatic warming has favoured species adapted to warm areas while adversely affecting species occupying cool sites. Tayleur et al. (2016) found that changes in CTI were driven by warm-dwelling species colonizing new sites, whereas cold-dwelling species contracted. Pearce-Higgins et al. (2015) found that cold-adapted species experienced more negative effects of higher temperatures than species associated with warmer temperatures.

In addition to thermal niche, a minor effect of habitat (an 'uninformative parameter' according to Arnold [2010]) partly emerged from models, basically highlighting a positive change in size for forest species (as shown by position of e.g. woodpecker species in Fig. 1), coherent with the better conservation status shown by woodland birds at the national level, determined by an increase in both woodland cover and quality (see Brambilla et al. 2013 and references therein). The only cold-dwelling species showing a positive change in range size was three-toed woodpecker, and in general woodpeckers, tits and other typical forest-dwelling species showed positive variation of range size. Some forest species experienced more positive variation in range size than some farmland species with a higher STI (Fig. 1). However, consistent with the prominent effect of STI, even the forest species with the lowest STI values, such as boreal and pygmy owl, have experienced negative changes in their breeding distribution; these are species showing a cold STI (4.9 and 5.1°C, respectively) and they might be particularly sensitive to climate warming. This interpretation is in line with other studies, which predict boreal and pygmy owl distribution to contract furthest according to future global warming scenarios (Brambilla et al. 2015, 2017a). In contrast, the respective control species in the same habitat (i.e. tawny owl *Strix aluco*) has experienced a positive trend in the last 30 yr whilst having a higher STI (9.6°C). Tawny owl distribution is known to be limited by climate (Vrezec & Tome 2004), and recent increases in distribution and breeding success in Finnish populations are attributed to climate warming (Mikkola 1983, Solonen 2005).

Except for tree pipit, all other alpine open habitat species were associated with long-term losses in range and low STI. For some of those species (e.g. ptarmigan), strong contractions have also been observed in other alpine regions (Revermann et al. 2012, Pernollet et al. 2015), with global warming effects likely to influence not just the habitat but also the breeding mechanisms of species (Martin & Wiebe 2004). Furthermore, our results also agree with other studies, which forecast future losses in distribution of open habitat species (i.e. water pipit) due to climate and to the disappearance of alpine grassland as it becomes slowly colonized by shrub and trees (Chamberlain et al. 2013). Even if we cannot rule out the potential impact of land use change, and in particular of land abandonment (see e.g. Brambilla et al. 2010, 2017b), modelling results suggest an overwhelming importance of STI, and thus a major impact of climate change.

In conclusion, our work provided evidence for a direct link between species' thermal niche and the change in range size in the last 30 yr. Coherent with previous works highlighting an effect of recent climate change on community composition, species' population trend and poleward or upward distributional shift, we found climate warming to be the most likely factor explaining the change in range for breeding birds in Italy.

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SECTION II: *Chapter III*

A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate

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Pygmy owl, Stelvio National Park. Photo: M. Skodler

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A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate

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Abstract

Aim: Human-induced climate change requires conservation strategies incorporating its potential effects on species and communities. Key components of population persistence can be attributed to resistance (the capacity to remain unaffected) or resilience (capacity to absorb and recover) to climate change. In situ climatic refugia can act as resistant distribution units, and ex situ climatic refugia and the corridors to reach them may enhance resilience. We develop a novel approach selecting conservation priorities, resistant units and resilient areas according to structural connectivity and future distribution, to identify strategies that maximize the chances of species persistence in a changing climate.

Location: Italian Alps.

Methods: Conservation priorities were defined across species according to the regional conservation status and the level of threat from climate change, and across sites according to their suitability for target species and their related potential for population persistence (in situ climatic refugia, i.e., resistant units) or redistribution (ex situ climatic refugia and main corridors according to current and future connectivity, i.e., resilient units).

Results: Models suggested a marked loss of suitable area for all species by 2050 (ranging from ~50% for pygmy owl and water pipit, to 84% for snowfinch in the worst scenario), and a general loss of connectivity, which was particularly marked for pygmy owl and snowfinch. The approach applied to Alpine birds of different habitats led to a spatially explicit definition of conservation priorities.

Main conclusions: The spatial definition of conservation priorities according to species (regional importance and level of threat), resistance and resilience refines the definition of management/conservation priorities (including protected area definition), complementing the existing approaches to address climate change-induced threats in planning conservation and ecological networks.

KEYWORDS
Alps, birds, distribution, ecological connectivity, global warming, spatial planning

1 | INTRODUCTION

Human-induced climate change is one of the main threats to species and ecosystems (IPCC, 2013). Several species have shifted their distribution as a consequence (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), especially towards upper elevations and/or higher latitudes (Walther et al., 2002). Models that relate species distributions and climate to predict the future geographical range of species in response to forecast climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012) have shown that species living at high altitudes are expected to be particularly threatened (Brambilla, Pedrini, Rolando, & Chamberlain, 2016; Chamberlain, Negro, Caprio, & Rolando, 2013; Dirnböck, Essl, & Rabitsch, 2011; Sekercioglu, Schneider, Fay, & Loarie, 2008; Viterbi et al., 2013). This situation requires conservation strategies that incorporate the potential effects of climate change on species and communities; hence, conservation planning that takes into account climate change impacts is a priority (Groves et al., 2012; Hannah et al., 2007). A key point is clearly whether the losses determined by climate change could be compensated by the species' colonization of the so-called new climate space (Pearson, Dawson, Berry, & Harrison, 2002), which will be conditioned by both species and landscape characteristics (Vos et al., 2008). Only species with good dispersal abilities and relying on widespread habitats are expected to react to climate change by expanding their range (Warren et al., 2001), and habitat availability and fragmentation may affect the species' response to climate warming (Hill, Hughes, Dytham, & Searle, 2006; Hill, Thomas, & Huntley, 1999; Opdam & Wascher, 2004). In this context, the maintenance of ecological connectivity has a crucial role for biodiversity conservation (Hannah, 2011) and for species persistence (Alagador, Cerdeira, & Araújo, 2016), and thus, it is particularly important to integrate connectivity and ecological network concepts in studies considering the potential effects of climate change (Mazaris et al., 2013; Verboom et al., 2010; Vos et al., 2008).

A common objective of strategies of adaptation to climate change is resilience (Morecroft, Crick, Duffield, & Macgregor, 2012), defined as "the ability of a social or ecological system to absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organization, and the capacity to adapt to stress and change" (IPCC, 2007). In ecology, resilient systems are those able to absorb disturbance and recover from its effects, by reorganizing so as to retain essentially the same characteristics (Walker, Holling, Carpenter, & Kinzig, 2004), and resilient populations are those able to recover when favourable conditions are re-established (Harrison, 1979). Resistant systems are those that can remain essentially unchanged despite disturbance (Grimm & Wissel, 1997), a definition which implies rather limited responses promoting the stability of an ecological system when facing a severe disturbance (e.g., Sternberg et al., 2015). Ideally, we can also apply the concepts of resistance and resilience to populations in relation to their regional distribution and use them for conservation planning, aiming to maximize their persistence in an era of climate change.

Identifying the sites that are and will remain suitable in future for a given species (resistant distribution units) would allow the most important areas for the conservation of a species to be identified. In those areas, the species populations could remain largely unchanged in spite of the influence of climate change, at least from a distributional point of view (Ficetola et al., 2016).

Modelling potential connections among suitable habitat patches in current and future climatic conditions is of pivotal importance for identifying key corridors and connections which will promote the resilience of species to climate change (Hannah, 2011). Favouring colonization, dispersal and exchange of individuals across populations would promote the potential for species (and communities) to re-establish themselves under future conditions, especially by tracking suitable climates (Vos et al., 2008). Sites potentially suitable in future and connected with those currently occupied could be considered as resilient distribution units.

Several approaches have been proposed that link current and future distribution and potential connectivity to develop conservation planning considering the effects of climate change. Such studies are generally based on species-specific assessments, consider connectivity mostly in terms of dispersal distance (e.g., Mazaris et al., 2013) or rely on climate alone as a predictor of species distribution and connectivity (e.g., Alagador et al., 2016). Here, we use fine-scaled (see Seo, Thorne, Hannah, & Thuiller, 2009) species distribution models in conjunction with spatially explicit connectivity mapping (e.g., Phillips, Williams, Midgley, & Archer, 2008), considering the effect of both climate traits and habitat features (Virkkala, Heikkinen, Fronzek, Kujala, & Leikola, 2013). Our approach thus integrates distribution and connectivity models to identify spatial conservation priorities (considering both population resistance and resilience) among species potentially affected by climate change. We considered a set of species occupying different habitats to assign conservation and management priority to each spatial unit, and evaluated species distribution and connectivity among populations on the basis of both climate and land cover. To the best of our knowledge, this is the first time that future climate-induced variations in distribution and structural connectivity (based on landscape characteristics) have been considered together for conservation of a set of species dwelling in different habitats and hence requiring potentially different management options. To define conservation priorities among taxa in the face of climate change, we attributed a priority level to each target species, considering both the regional responsibility for the conservation of a given species, and the level of threat to which the species is subject due to climate change. We also assigned a priority value to areas according to their suitability for the target species and their related potential role for population persistence or connectivity.

We used Alpine bird species as biological models to illustrate our approach (see also Figure 1). We predicted the impact of climate change on the potential distribution and ecological connectivity for Alpine species inhabiting different habitats. Identifying areas where species can occur in current and future conditions can be used to define key sites to maximize resistance, whereas mapping (and conserving) key areas for connectivity among populations (both in current and in future conditions) is needed for the preservation of areas and habitats that will facilitate movement across sites, thus promoting resilience to climate change.

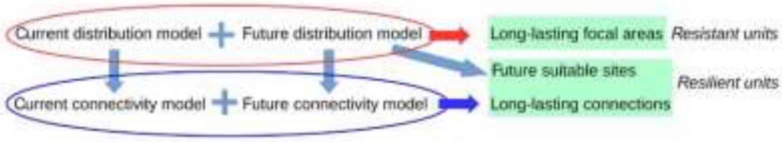

FIGURE 1 Flow chart summarizing our approach to the definition of spatial priorities for species conservation under a changing climate. [Colour figure can be viewed at wileyonlinelibrary.com]

Conservation planning that incorporates effects induced by climate change (e.g., Williams et al., 2005) is particularly relevant in mountain regions such as the Alps (Brambilla et al., 2016; Walzer et al., 2013). The higher recent and projected increase in global temperature (Böhm et al., 2001), the impact of human activities (Chamberlain, Pedrini, Brambilla, Rolando, & Girardello, 2016) on species and ecosystems and the synergic interaction of human impacts and climate change (Mantyka-Pringle, Martin, & Rhodes, 2012) are posing severe threats to biodiversity in this and other mountain areas, and developing the most effective conservation strategies coherent with regional priorities is therefore an urgent task for the Alpine region.

2 | METHODS

2.1 | Study area and fieldwork

The study area encompassed a large portion of the Alps (c. 44,000 km^2), located in northern Italy (Figure 2). Within this area, bird occurrence data were collected between 2000 and 2015 (Supporting Information), mostly by means of point count surveys of 10-min duration (1,196 points throughout the area, distributed across the three main sectors, i.e., Piemonte and Valle d'Aosta, Lombardia, Trento Province, broadly in proportion to their relative extent) performed during the breeding season (Bibby, Burgess, Hill, & Mustoe, 2000). Owl data were collected using nocturnal and crepuscular playback techniques (broadcast male song) during the breeding season (Brambilla, Bergero, Bassi, & Falco, 2015). Full details of these datasets are given in the relevant references (Chamberlain et al., 2013; Chamberlain, Brambilla, Caprio, Pedrini, & Rolando, 2016; Brambilla et al., 2015; Brambilla et al., 2016) and in Appendix S1. The majority of survey points were carried out in locations selected so as to be broadly representative of at least one (e.g., Brambilla et al., 2015) or both (e.g., Brambilla & Pedrini, 2016; Chamberlain, Brambilla et al., 2016) montane and Alpine and vegetation belts (sensu Körner, 2003), and there was no focus on, for example, protected areas or habitats subject to specific environmental pressures (e.g., skiing activities, urbanization, changes in livestock management). Further points were carried out in all parts of the study area at lower elevations, both in forest and in open habitats. In summary, considering diurnal surveys, in the western (and largest) part of the study area (Piemonte and Valle d'Aosta), 570 points were carried out, within the framework of different projects, sampling all main habitats along a wide altitudinal range (c. 100–2,900 m asl); in Lombardy (the central part of the study area), 248 point counts were surveyed within four different projects/areas (c. 220–2,800 m asl); in the Trento Province (the eastern part of the study area), 207 point counts were surveyed along altitudinal transects (c. 1,350–2,750 m asl) representative of the main mountain systems of the province, whereas 142 points were made in six areas at lower elevations (c. 350–1,400 m asl, Assandri, Bogliani, Pedrini, & Brambilla, 2016); a further 29 points were surveyed between c. 1000 and 1900 m asl within another project. The dataset so obtained was then integrated with further occurrence records collected by means

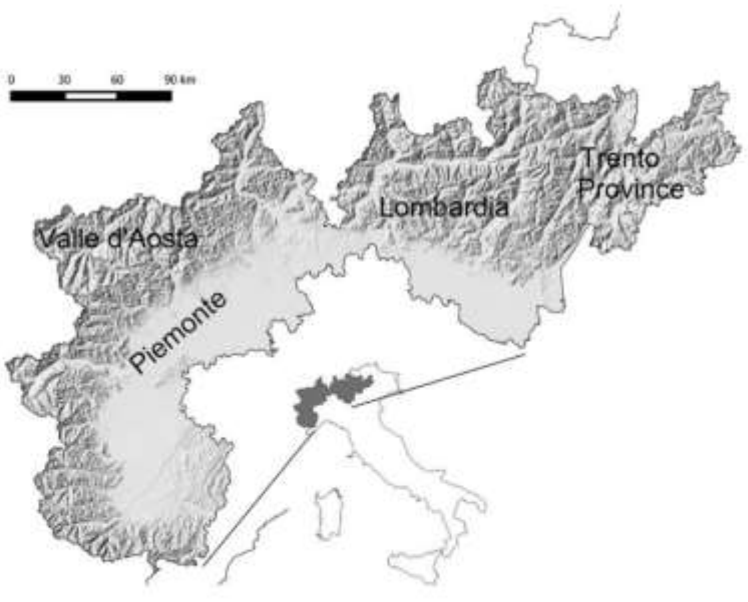

FIGURE 2 Study area and mountain relief. The inset shows its location within Italy

of other surveys (e.g., ptarmigan- or grouse-specific counts) and occasional observations of target species.

2.2 | Selecting model species

We chose species representative of the main types of landscapes at medium-high elevation in the Alps: (1) subalpine coniferous forest, (2) high-altitude open habitats (i.e., alpine grassland and rocky habitats), and (3) transitional belt habitats, which connect the former two. Model species were chosen from those which show a distribution potentially affected by climatic variables (northerly distributed species that in the Alps are close to their lower latitudinal range limits, and/or are high-altitude specialists strictly tied to mountain habitats). For (subalpine) forest habitats, we chose pygmy owl (*Glaucidium passerinum*) and boreal owl (*Aegolius funereus*), two nocturnal raptors known to be affected by climate, for which the Alps represent a relict portion of their former range in a colder past (Brambilla et al., 2015). For open habitats, we selected rock ptarmigan (*Lagopus muta*), water pipit (*Anthus spinoletta*) and white-winged snowfinch (henceforth snowfinch; *Montifringilla nivalis*), all species likely to be impacted by climate change (Brambilla et al., 2016; Brambilla, Cortesi et al., 2017; Chamberlain et al., 2013; Pernollet, Korner-Nievergelt, & Jenni, 2015; Revermann, Schmid, Zbinden, Spaar, & Schröder, 2012) and occupying high-elevation habitats. For transitional habitats (around the tree line, where forest and grassland intergrade), black grouse (*Tetrao tetrix*) was chosen according to its preference for edge habitats and cold climates (Braunisch, Patthey, & Arlettaz, 2016; Loneux & Lindsey, 2003; Ludwig et al., 2006; Spidsø, Hjeljord, & Dokk, 1997). All those species are largely resident species, with the exception of water pipit, which is mostly a short-range migrant, commonly wintering in lowland sites within the study area. Sample sizes are reported in Table 1.

2.3 | Modelling species distributions

We used Maxent (release 3.3.3k; Phillips, Anderson, & Schapire, 2006) to model species distributions (Braunisch et al., 2013), which is routinely adopted for distribution modelling with data collected under different field protocols (Elith et al., 2011; Engler, Rödder, Stiels, & Förschler, 2014). We used bird occurrence data with a spatial resolution ≤100 m for Passeriformes and <1 km for other species to build models at a relatively fine spatial scale (1 km). As environmental variables, we considered land cover, topographical and bioclimatic factors.

All variables were calculated for 1 km × 1 km cells, within which we measured the total cover of 11 land cover types derived from CORINE Land Cover (CLC2006; EEA, 2007): arable land, pastures, broadleaved forest, coniferous forest, mixed forest, natural grassland, transitional woodland–shrub, bare rocks, sparsely vegetated areas, lakes, built-up areas (urban and productive areas, large infrastructures; several different categories summed together; Supporting Information). Average slope for each cell was derived from a 20-m resolution Digital Terrain Model, but was considered for non-Passeriformes only (see Supporting Information). For the same 1 km × 1 km cells, we calculated six climate variables (downloaded from WorldClim v.1.4; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; http://www.worldclim.org; resolution: 30 arc-seconds) that we a priori believed could be important determinants of species distributions: annual average temperature (BIO 1), maximum temperature of the warmest month (BIO5), mean temperature of warmest quarter (BIO10), annual precipitation (BIO12), precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19). However, variance inflation factors (VIFs) calculated for these variables showed a high degree of collinearity and, in particular, a strong correlation with annual temperature. Given the degree of collinearity, and that average annual temperature has a major importance in dictating the distribution of our model species in the Alps (Brambilla et al., 2015; Brambilla et al., 2016) and is likely to be particularly important for our largely resident species, it was decided to use annual temperature as the only climatic variable in the model. Annual temperature therefore acted as a surrogate for general climatic conditions in order to reduce the risk of overfitting the effects of climate change on species distribution.

To further minimize the risk of overfitting species–habitat or species–climate relationships, we fitted all distribution models by means of linear and quadratic terms only. The continuous output of Maxent models was transformed into a presence/absence value, selecting the most appropriate threshold for each single species by comparing the output of the reclassification with the current distribution of the species in Italy (Nardelli et al., 2015). To produce as general and robust models as possible, we applied a masked geographically structured evaluation of models for most species (Radosavljevic & Anderson, 2014). We partitioned the study area into four different longitudinal belts (Brambilla et al., 2016), and built models using records and 10,000

TABLE 1 Basic statistics of distribution models for the target species. N: sample size (number of presence points comprising 1,196 points surveyed and additional records); AUC: area under the curve. Training values refer to data used to build the models and to their performances, testing values to data used to test the models (and to their relative performance on the independent dataset used for validation). For owl species, AUC and standard errors were calculated using cross-validation, due to the relatively small sample sizes

	Rock ptarmigan *Lagopus muta*	Water pipit *Anthus spinoletta*	Snowfinch *Montifringilla nivalis*	Black grouse *Tetrao tetrix*	Pygmy owl *Glaucidium passerinum*	Boreal owl *Aegolius funereus*
N training	132	179	26	257	42	49
N testing	53	577	71	66	5	6
AUC training	0.95	0.96	0.97	0.95	0.94 ± 0.00	0.91 ± 0.01
AUC testing	0.94	0.96	0.97	0.95	0.91 ± 0.08	0.89 ± 0.04

background points from two belts. We then evaluated models using the occurrence records from the other two belts as test data. Values of the area under the curve (AUC) of the receiver-operator plot were very similar between training and test data for all species, thus suggesting model stability (Table 1). Given the reduced sample size, we preferred not to divide the sample into training and test sets for the owl species. Instead, we carried out a 10-fold cross-replication of models, and calculated test and training AUC over the different subsets produced for each replicate. As for the other models, the close values between testing and training subsets suggested model stability (Table 1).

Although we used mean temperature as the sole predictor of distribution, due to the high level of collinearity among the climatic variables, this is an infrequent practice in species distribution modelling. Furthermore, there is a risk of overestimating the effect of climate change on a given species when its whole range is not considered (Barbet-Massin, Thuiller, & Jiguet, 2010). Therefore, we tested whether mean temperature produced good distribution models at a broader scale. We followed a previously adopted approach (Brambilla, 2015; Brambilla et al., 2016), where we assessed the reliability of the modelled climatic niche (specifically, thermal niche) for a species by modelling distribution as a function of annual temperature across a large part of Europe, and validating it with the known species range at larger national and European scales derived from independent data sources (BirdLife International, 2015; Nardelli et al., 2015; Brambilla et al., 2016; see Supporting Information). We obtained a reliable prediction of species distribution in relation to temperature for all species (Supporting Information), thus confirming that the use of a single measure representing thermal niche (i.e., annual temperature) provides a good general surrogate of climatic niche that can be used to predict species distributions.

We re-projected distribution models over future conditions, by varying mean annual temperature according to two different scenarios characterized by increasing values of representative concentration pathways (RCPs; Moss et al., 2010; van Vuuren et al., 2011; Diffenbaugh & Field, 2013). Following previous work (Brambilla et al., 2015; McQuillan & Rice, 2015), we chose the two RCP values of +4.5 and +8.5 W/m^2, respectively, representing a rather optimistic and pessimistic future (Meinshausen, 2011). The two scenarios correspond to an average increase of +1.4 and 2.0°C in global temperature by c. 2050 (IPCC, 2013), respectively. We obtained the annual temperature values for 2050, according to the Hadley Global Environment Model 2 (HadGEM2-ES), at the finest available resolution (30 arc-seconds). In developing the method, we treated land cover as constant over the time period considered (up to 2050; see Supporting Information). Our approach is therefore fairly conservative in that potential habitat losses that may occur as a result of climate change (especially of open habitats; Chamberlain et al., 2013) are not incorporated (but see Discussion).

2.4 | Modelling connectivity

For each species, we modelled connectivity as a function of habitat suitability and of the spatial arrangement of habitat patches with different levels of suitability. We used our target species as exemplars for particular macrohabitat types in order to evaluate (structural) landscape connectivity, and thus to have wider relevance for other species inhabiting the same habitats. We modelled structural connectivity for the selected species using Circuitscape (ver. 4.0.5; http://www.circuitscape.org; Araújo & Townsend Peterson, 2008; McRae, Shah, & Mohapatra, 2013). Circuitscape adopts an approach that combines circuit and graph theories and fits connections following a random walk and evaluates the contributions of multiple dispersal pathways (Araújo & Townsend Peterson, 2008; see Supporting Information for details). This approach needs a map of conductance (or its opposite, resistance) of the study landscape, and a set of focal areas, which are habitat patches where the current is injected or is tied to ground, representing source areas or areas where individuals may settle after dispersing (Araújo & Townsend Peterson, 2008). The procedure considers all focal areas and uses the conductance/resistance map to estimate the current flow among patches, and sums up all the obtained current maps to produce a final map, representing the total current in each cell of the landscape (Araújo & Townsend Peterson, 2008). This final value can be taken as the probability of a random walker passing through an individual cell (Doyle & Snell, 2000), and is thus used to weight the importance of individual cells and of pathways in connectivity models (Araújo & Townsend Peterson, 2008). It therefore provides a suitable measure of the structural landscape connectivity we aimed to evaluate. As conductance maps, we used the continuous value of environmental suitability calculated by the output of Maxent models (Rödder, Nekum, Cord, & Engler, 2016).

Focal areas are suitable habitat patches from which animals can start or finish a dispersal event. In our approach, they are equivalent to "key patches" (Verboom, Foppen, Chardon, Opdam, & Luttikhuizen, 2001), which are relatively large areas with a preeminent role in habitat networks. We defined focal areas as continuous blocks (considering patches as contiguous according to a rook connection scheme) of potentially suitable habitats with a minimum extent of 500 ha (large enough to permit regular occurrence and breeding for all the model species). Patches smaller than this extent were excluded from focal areas, but they still contributed to connectivity estimation within models.

Circuitscape was run under the pairwise mode, which iterates across all pairs of focal areas, using the four-neighbour-connection scheme (Engler, Balkenhol, Filz, Habel, & Rödder, 2014).

For all species, connectivity models were built for current and future (RCP +8.5) conditions. To identify areas potentially suitable for species-specific connectivity, we considered as suitable for species movement all the sites with a predicted electric current higher than the 10th percentile of the current values for species locations in the present scenario (Supporting Information; Engler, Rödder et al., 2014; Liu, Berry, Dawson, & Person, 2005; Peterson, Raxworthy, Nakamura, & Peterson, 2007).

The whole modelling approach is summarized in Fig. 3.

2.5 | Defining priorities for species conservation

To define conservation priorities among species, we considered both the relative importance (and hence the "responsibility") that the Alps

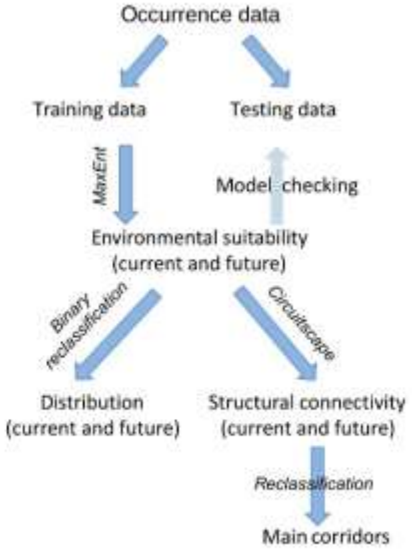

FIGURE 3 Graphical summary of the modelling approach adopted to estimate species distribution and connectivity across sites. [Colour figure can be viewed at wileyonlinelibrary.com]

have for the conservation of each species at a European scale, and the estimated decrease in potential modelled distribution. By incorporating the two concepts, we combined relative importance and level of threat into one single estimate of conservation priority. To estimate the relative importance of the Alpine region, we calculated the proportion of the European population that occurs in the Alps. This proportion was then multiplied by the estimated range contraction for each species. The resulting value was used as a conservation priority index for each species (Table 2). We also repeated this process at the subspecies level, in order to assess whether conservation priority rankings changed when prioritizing at a finer taxonomic level (see Supporting Information).

2.6 | Ranking areas for conservation to maximize resistance and resilience

We identified two types of priorities for sites (i.e., cells in our approach) in order to carry out a spatially explicit definition of priority conservation targets which considered the need to maximize both resistance and resilience (Figure 1). Resistant distribution units are current focal areas for threatened species which will remain so in future. Such areas are putative in situ refugia ("areas where negatively impacted biota can persist as anthropogenic climate change progresses with the potential to expand if suitable regional climate conditions return," Keppel et al., 2012) and are crucial for population resistance in the face of climate change. They could also contribute to population resilience (Selwood, Thomson, Clarke, McGeoch, & Mac Nally, 2015).

Resilient distribution units include two functionally different kinds of sites: key areas for connectivity (i.e., areas suitable for movement both currently and in future) and sites that are currently unsuitable for threatened species, but will become so in future (ex situ refugia, Keppel et al., 2012). These types of priority sites are key areas for resilience to climate change, as their conservation would allow populations to move towards, or colonize, new suitable areas.

Some sites may be resistant or resilient distribution units for more than one species and may include different habitats and thus require different management and conservation strategies. The main nesting macrohabitat (subalpine forest, open habitat, transitional belt) was identified for each species. All species of each of these habitats were considered together. Given that we have analysed three species for high-elevation habitats, but only two for subalpine forests and one for

TABLE 2 Species (and subspecies) conservation priority in the study area according to percentage of the European population harboured by the Alps and to the predicted decline by 2050 in the worst climatic scenario

Taxon	Approximate % of European population in the Alps	Predicted % decline (2050, RCP +8.5 W/m^2)	Priority index	Priority rank
Species				
Rock ptarmigan *Lagopus muta*	13.02	58.56	7.63	3
Black grouse *Tetrao tetrix*	4.77	55.78	2.66	6
Pygmy owl *Glaucidium passerinum*	7.57	49.98	3.78	5
Boreal owl *Aegolius funereus*	8.06	66.74	5.38	4
Water pipit *Anthus spinoletta*	19.02	51.95	9.88	2
Snowfinch *Montrifringilla nivalis*	12.28	84.09	10.33	1
Subspecies				
Rock ptarmigan *Lagopus muta helvetica*	100	58.56	58.56	2
Black grouse *Tetrao tetrix tetrix*	4.79	55.78	2.67	6
Pygmy owl *Glaucidium p. passerinum*	7.57	49.98	3.78	5
Boreal owl *Aegolius f. funereus*	8.06	66.74	5.38	4
Water pipit *Anthus s. spinoletta*	19.02	51.95	9.88	3
Snowfinch *Montrifringilla n. nivalis*	73.67	84.09	61.95	1

transitional habitats, we considered only the first two (sub)species (in order of priority index) for the high-elevation habitats. We gave priority to resistant distribution units (long-lasting focal areas, which could also promote resilience; Mackey et al., 2012) rather than to resilient units (sites suitable in future and key sites for connectivity). Within the resilient distribution units, priority was given to key connectivity areas rather than to sites suitable in future. In the case of overlapping resistant units for different species, we selected focal areas according to the species hierarchy obtained by the priority index (as described above; see also Results). The same was carried out in the case of overlapping resilient units.

3 | RESULTS

3.1 | Current and future distribution of model species and ecological connectivity

All models performed equally or nearly so over the training and testing datasets, thus confirming a good level of model stability and validity over all the area (Table 1), which was supported by a critical comparison with the reported species occurrence (Appendix S2). Model details are reported in Table S1. All the model species were predicted to undergo range contractions (Table 2 and Figures 4–6, Appendix S3), with a progressive shrinkage towards upper elevations as a result of the temperature increase. Forecast range contraction was most pronounced for snowfinch, but the other species were also predicted to lose at least half of their current potential range under the pessimistic climatic scenario (RCP +8.5) considered here (Table 2).

Ecological connectivity across focal areas was predicted to decrease for all species and within all habitats (Appendix S4). Snowfinch and pygmy owl were predicted to be particularly subjected to loss of connectivity, but significant reductions were found for all species.

3.2 | Priority for species conservation

Combining responsibility and predicted contraction led to the following prioritization hierarchy (according to the priority index for species): snowfinch, water pipit, rock ptarmigan, boreal owl, pygmy owl and black grouse. When considering the subspecies inhabiting the Alps, the order was almost the same, with only a change between rock ptarmigan (which ranked second) and water pipit (now third; Table 2). Therefore, open-habitat species had consistently the highest priority index, followed by subalpine forest species and finally by black grouse, our model species for transitional habitats. Considering the value of the endemic rock ptarmigan subspecies, we took the ranking at the subspecific value and thus considered snowfinch and rock ptarmigan as target species for open habitats.

3.3 | Prioritizing areas for conservation and management

Given the results of the priority index for species/subspecies, the ranking relative to habitat type was the following: open habitat, subalpine forest, transitional belt. This order was followed to select the priority group at sites where there was overlap for resistant or resilient units for species inhabiting different habitats. Therefore, the hierarchy adopted to select priorities was the following: long-lasting focal areas for open-habitat species, long-lasting focal areas for subalpine forest species, long-lasting focal areas for transitional belt species, key connectivity areas for open-habitat species, key connectivity areas for subalpine forest species, key connectivity areas for transitional belt species, future suitable sites for open-habitat species, future suitable

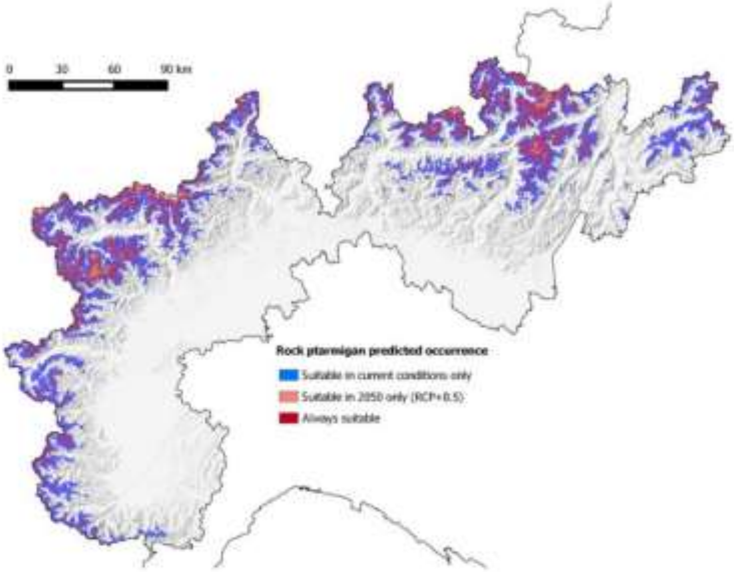

FIGURE 4 Current and future distribution for rock ptarmigan (*Lagopus muta helvetica*), an open-habitat species living at high elevation. [Colour figure can be viewed at wileyonlinelibrary.com]

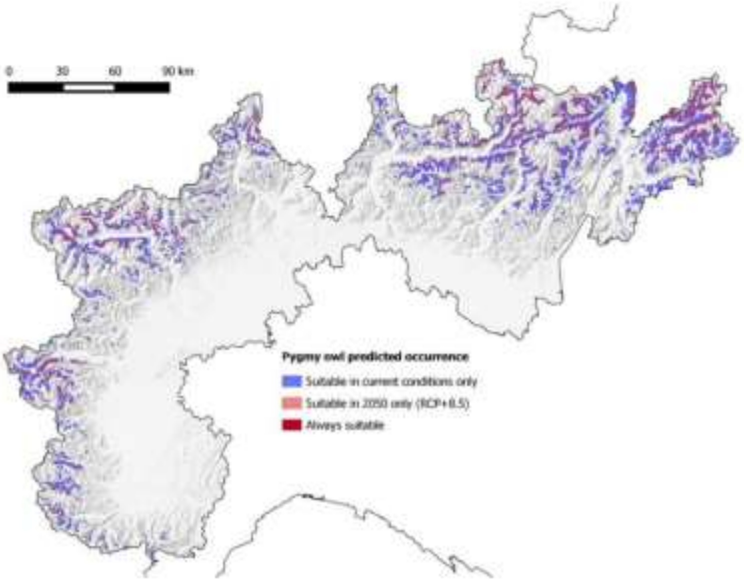

FIGURE 5 Current and future distribution for pygmy owl (*Glaucidium passerinum*), a nocturnal raptor occupying coniferous forests. [Colour figure can be viewed at wileyonlinelibrary.com]

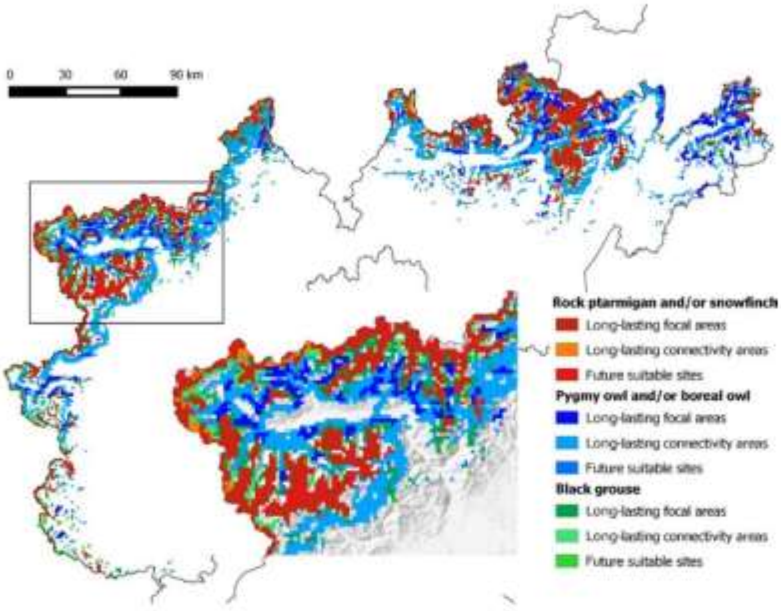

FIGURE 6 Spatial priorities for conservation and management according to the current and future suitability of sites as focal areas or corridors and according to the species hierarchy (see text). The inset shows a detailed view of Valle d'Aosta region, to show the spatial relationship among the three different types of management/conservation priorities (high-elevation open habitats, forests, transitional belt). [Colour figure can be viewed at wileyonlinelibrary.com]

sites for subalpine forest species and future suitable sites for transitional belt species.

This procedure for the selection of priority areas led to the map shown in Figure 6: in large parts of the "true" Alps, priority areas were rather continuous for all the three main habitats, and mirror the typical altitudinal stratification forest–transitional belt–open habitats. However, in most prealpine areas (the southern portions of the Lombardy and Trento mountains) and in the south-western Alps, the dramatic reduction in distribution and connectivity forecast for most species led to a fragmented and discontinuous distribution of priority areas.

4 | DISCUSSION

4.1 | Resistance, resilience and distribution: implications for conservation planning in the face of climate change

Species survival in a warming climate depends on several factors, such as physiological and phenological adaptation, dispersal ability, behavioural traits, interspecific interactions, habitat stability (Bellard et al., 2012), and on the availability of in situ and ex situ refugia (Keppel et al., 2012). All or nearly all of those key components of population persistence can be attributed to resistance or resilience to climate change. In this study, we considered populations to be potentially resistant to climate change when they occupied suitable habitats, likely to remain suitable in a warmer future (in situ climatic refugia-resistant distribution units; see also Ficetola et al., 2016). In our approach, resilience to climate change was considered in terms of potential range shifts to track suitable conditions (e.g., to reach ex situ climatic refugia), at a spatial scale where the dispersal ability of all the bird species we considered should enable such shifts (resilient distribution units).

Integrating these two issues allowed a more informed and thorough identification of sites of strategic importance for species conservation (see also Alagador et al., 2016). Resistance-only approaches ignore the potential effect of increasing isolation, and the associated risk of identifying areas too small and isolated to allow long-term persistence (Verboom et al., 2001), while resilience-only strategies may miss the overwhelmingly important resistant refugia (Ficetola et al., 2016; Keppel et al., 2012). We believe that an integrated strategy may maximize the chance of species persistence and should therefore be encouraged for conservation planning.

Modelling connectivity has been accomplished by considering dispersal distance in relation to distribution changes (e.g., Mazaris et al. (2013), using network flows (e.g., Alagador et al., 2016; Phillips et al., 2008) or according to graph-theoretical approaches (e.g., Kang, Minor, Lee, & Park, 2016). Our approach could provide a significant improvement in our ability to develop sound conservation policies, thanks to the continuous evaluation of structural connectivity in current and future scenarios, based on both climate conditions and habitat cover, calculated according to a circuit theory approach. For the owl and passerine species we considered, a limited decrease in landscape connectivity could be a minor issue (Spina & Volponi, 2008), thanks to good dispersal abilities. On the other hand, black grouse is a low- and female-biased dispersal species, for which connectivity could be a key issue, especially in marginal or contracting populations (Warren & Baines, 2002). Contrasting evidence has been reported for rock ptarmigan, suggesting isolation in the Pyrenean populations (Bech, Boissier, Drovetski, & Novoa, 2009), but not in the Alps (Collini, 2011). More importantly, our model species may be used as "umbrella" species for the respective Alpine communities which include those with similar ecological (climate, main habitat) requirements, but with much more restricted dispersal capabilities (e.g., small terrestrial vertebrates and arthropods, and plants). The use of structural landscape connectivity metrics was indeed selected to offer the broadest possible evaluation of connectivity for living organisms, as such a connectivity estimate is less dependent on species-specific dispersal distance or abilities.

4.2 | Prioritization of species and areas

Predicted distributions and connectivity among suitable areas for all Alpine bird species are both predicted to decrease as a consequence of rising temperatures. Our results thus confirmed the findings of previous work on distributional changes from largely overlapping areas of the Alps (Chamberlain et al., 2013; Brambilla et al., 2015; Brambilla et al., 2016) and further highlighted a negative effect on landscape connectivity.

Our approach combined the relative importance of Alpine populations and climate change-induced threats, and allowed us to rank species in terms of priority for development of conservation strategies in the Alps. Using species or subspecies resulted in only minor changes, but in other geographical contexts, changing the reference taxonomic level could result in substantial re-ordering of ranks.

The prioritization of areas for conservation and management was based on both the species hierarchy and the attribution of a higher-priority level to resistant distribution units than to resilient ones. Resistant units are more important because they offer suitable conditions to the target species irrespective of climate change, their identification is less subject to the uncertainties in future climatic scenarios (such sites would be suitable under current conditions as well as under the worst possible scenario), and they could also promote resilience.

4.3 | Modelling issues

All models appeared fairly robust, in line with the consistent species–habitat relationships found for bird species in the Italian Alps (Chamberlain, Brambilla et al., 2016). Moreover, the output they provided matched fairly well the current distribution for all species except the owls, although the apparent overestimation predicted in parts of their range was most likely due to the lack of dedicated surveys in those sites (Beraudo, Caula, & Pettavino, 2012; Nardelli et al., 2015), rather than problems with the modelling approach (Supporting Information). The underlying species–environment relationships and the resulting predicted distribution seemed therefore highly reliable, even if we did not consider other potentially meaningful climatic variables in addition to annual temperature. It is important to note that annual temperature had been repeatedly reported to be by far the most important climatic driver of avian species' occurrence in the Alps (see, e.g., Brambilla et al., 2016; Chamberlain et al., 2013).

Although we used the same spatial scale to build all models, our target species have fairly different spatial requirements. For the non-Passeriformes, the landscape grain we adopted for distribution models was roughly equivalent to their territory or home-range size (Brambilla et al., 2015), whereas for the smaller species, the 1 km × 1 km cells are clearly larger than the extent actually used by a breeding pair of those species (and which should ideally be taken as the grain size for modelling, e.g., Brambilla et al., 2016). Despite this limitation, good results (in terms of the models' statistical performance and consistency with the reported distribution) were also obtained for the two passerine species we considered, suggesting that this grain is still adequate to evaluate the effect of land cover and temperature on species occurrence at this scale. Nevertheless, the increasing availability of fine-scale data on land cover and other environmental predictors of species occurrence would allow deeper insights into species–habitat relationships and consequently into species distribution modelling.

We did not consider land use/land cover changes. Although we considered a rather limited timeframe, such changes are possible, and even likely around the tree line (Harsch et al., 2009), and in sites where land abandonment is driving encroachment over open habitats. The approach adopted here is therefore conservative in estimating potential decreases in species distributions and in connectivity for most of the model species considered. This is because habitat losses caused by upward shifts in vegetation zones, and in particular the tree line, are likely to reduce more open habitats. The lack of consideration of habitat changes in our approach means that predictions could be even more dramatic than suggested by our models (Brambilla et al., 2016). Further developments of our method could incorporate scenarios of future habitat change (see, e.g., Ficetola et al., 2010; Wisz et al., 2008), although modelling such changes is a considerable challenge.

Connectivity models are based on the continuous environmental suitability calculated by Maxent models. However, the identification of the main connectivity areas was based on the application of specific threshold values. We chose the 10th percentile of the current values of connectivity for species locations as the threshold to identify strong priorities for connectivity; when translating such areas into landscape planning, an expert-based enlargement or buffering around the main connectivity areas should be considered.

5 | CONCLUSIONS

Incorporating species prioritization and future variation in structural connectivity, our work provides a novel framework for the definition of conservation priorities potentially relevant for management under a changing climate. Knowing what guild of species (high-elevation, forest, transitional habitat) should be considered as a priority in a given site is key information for conservation planning, enabling management strategies to focus on certain habitat(s) and habitat traits. Considering both sites that will maintain suitable climate in future for the species they already harbour (in situ refugia), and sites crucial for connecting habitat patches, the potential resistance and resilience of species populations to climate change can be maximized through appropriate conservation planning.

This kind of approach may be replicated over different areas, sets of species/habitats and scenarios of environmental changes, including different climate predictions, land cover change or human exploitation (Brambilla et al., 2016; Chamberlain et al., 2013).

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AUTHOR CONTRIBUTIONS

M.B. conceived the idea and developed the main parts along with D.C., D.S., C.C., G.B., P.P., R.F. and A.R.; all authors contributed to data collection; M.B. led the analyses helped by D.C., D.S. and E.C.; G.A., E.B., R.B., M.B., D.S. and P.P. critically assessed models' outcomes; M.B., D.C. and D.S. led the writing; all authors contributed to the final version of the manuscript.

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BIOSKETCH

Our research group conducts studies on animal ecology and conservation in the Alps, with a particular focus on the effects of environmental change and human-related impacts on alpine species and habitats.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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SECTION II: *Chapter IV*

Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: management options to buffer against global warming effect

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Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects

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ABSTRACT

The majority of predictions about the impacts of climate change on wildlife have relied either on the study of species' physiological tolerance or on broad-scale distribution models. In comparison, little attention has been paid to species' mechanistic responses to fine-grained, climate-induced modifications of habitat suitability. However, such studies would be pivotal to the understanding of species' ecological requirements (and hence their adaptive potential to environmental change) and the design of management strategies. We investigated foraging microhabitat selection in a potentially climate-change sensitive species, the white-winged snowfinch *Montifringilla nivalis*, during the breeding season in the Alps. Our microhabitat selection model considered topography, ground-cover variables and sward height within a 5-m radius at foraging and control locations. Habitat selection was positively affected by grassland cover, negatively by sward height and quadratically by snow cover (optimum around 40%); birds avoided anthropized (urban areas, roads) sites. We estimated past (1976) and future (2066) climate-driven changes in foraging microhabitat suitability, assuming a progressively earlier date of snowmelt due to increasing temperatures over this entire time span. We then modelled the potential impact of snowmelt (and related sward height) on habitat suitability under two scenarios: maintaining the current situation (i.e. irregular seasonal grazing) and implementing targeted management in an attempt to mitigate impacts of earlier snowmelt. Predicted foraging habitat suitability (estimated as the fraction of suitable plots) significantly declined over time (−23% between 1976 and 2016, further 32% loss by 2066). However, model outputs demonstrated that maintaining sward height below 6 cm on breeding grounds (e.g. by regular grazing) would significantly decrease the predicted loss of suitable foraging habitat. Detailed information about patterns of resource exploitation allows the identification of mechanistic, functional responses of species to environmental change, and enables an evaluation of habitat management options that can buffer against the detrimental effects of global warming.

1. Introduction

Anthropogenic climate change is increasingly threatening ecosystems and species worldwide (IPCC, 2013; Rosenzweig et al., 2008). Evidence from a wide range of taxa and ecological systems suggests that climate change has already started to affect biodiversity at a global scale (e.g. Carnaval and Moritz, 2008), for instance by modifying species distributions, altering their habitats or increasing extinction risk

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due to rapid shifts in abiotic conditions (Chen et al., 2011; Parmesan and Yohe, 2003). Based on forecast climatic scenarios, several studies have furthermore attempted to predict future climatic impacts on biodiversity (e.g. Bellard et al., 2012; Thomas et al., 2004).

The potential effects of climate, and hence of climate change, on animal species have been mostly assessed either by experimental approaches evaluating physiological tolerance to climate variations (e.g. temperature) at the individual level (Johnson, 1968) and under controlled environments (Chapin et al., 1995), or via large-scale distribution models, the latter representing one of the commonest ways to explore potential changes in species distributions owing to climate change (Fitzpatrick and Hargrove, 2009; Hijmans and Graham, 2006). Ecophysiological investigations usually include field observations and laboratory measurements that aim to detect how alterations of environmental constraints influence species' physiological responses and hence population processes (Arlettaz et al., 2000; Pörtner and Knust, 2007). In contrast, correlative models of species distribution (Guisan and Thuiller, 2005) rely on environmental factors such as climate, landcover and topographic variables, which are usually linked with species occurrence at a broad scale, and thus can help to identify those species that are most likely to be affected by climate or environmental change in a given area. They can, to some extent, be downscaled to the territory/home-range size of a target species (Brambilla et al., 2015; Braunisch et al., 2013), but often remain fairly limited in their predictive power as they may miss essential mechanistic components (Williams and Jackson, 2007) linked to patterns of resource exploitation, such as food acquisition. Hence, species distribution models may not embrace species' niche complexity as a whole (Braunisch et al., 2013) and may both over- and underestimate extinction risk due to climate change (Bellard et al., 2012). Although species distribution models are indeed the most widely used (and scalable) approach to assess species' spatio-temporal responses to climate change (Engler et al., 2017; Moritz and Agudo, 2013), there is a need for complementary approaches that integrate finer-scale ecological information for, on the one hand, improving our mechanistic understanding of the tolerance and resilience, i.e. the adaptive potential of target organisms to shifting environmental conditions (e.g. Baudier et al., 2015; Bennett et al., 2015), and, on the other hand, modelling appropriately the consequences of environmental changes upon population dynamics (Fedy and Martin, 2011; Fordham et al., 2017). This could be addressed by considering the impacts of climate change upon fine-scale habitat structure and availability (henceforth, microhabitat), which eventually drives habitat suitability. However, this aspect has received comparatively little attention so far, despite its crucial importance in understanding mechanistic responses of species to environmental change (Fordham et al., 2017; Kearney and Porter, 2009). Fine-grained species-habitat associations are essential to understand how changes in microhabitat due to climate change will affect species' habitat suitability at local and broader scales, which will ultimately influence a species' ability to respond to climate-induced environmental changes (Scheffers et al., 2014).

Studies of the effects of microhabitat alteration due to changing climatic conditions have mostly focused on small-sized organisms (e.g. invertebrates) that are highly sensitive to local climatic/habitat variation, especially due to their strong temperature-dependent life-cycles (Davies et al., 2006). Pincebourde et al. (2016) have shown that microhabitat properties shape species responses to climate change. Research has generally focused on species with limited mobility (e.g. plants (Pradervand et al., 2014), benthic invertebrates (Schiel et al., 2004)). In contrast, studies on the distribution of terrestrial and highly-mobile species usually deal with broad spatial scales, despite the fact that habitat selection in these species operates at multiple scales. In birds for instance, this concerns the selection of breeding sites (Jedlikowski et al., 2016; Rauter et al., 2002), foraging grounds (Brambilla et al., 2017b; Martínez-Miranzo et al., 2016; Schaub et al., 2010), and even shelters to avoid unsuitable climate (Visinoni et al., 2015). An absence of information about microhabitat preferences can lead to serious biases in predictions of climate change effects on species' distributions (cf. Bellard et al., 2012). As a matter of fact, microhabitat characteristics may allow species persistence when the general climate of the region appears to have become unsuitable, and vice versa. Studies of microhabitat suitability are thus pivotal to our basic understanding of species' ecological requirements and to devise efficient conservation management of climate-sensitive biodiversity. Several such studies have emerged recently (Suggitt et al., 2011; Turlure et al., 2010), which have established the importance of both microhabitat and microclimate to understand the sensitivity of species to environmental shifts and, ultimately, their population dynamics and distribution patterns (Fedy and Martin, 2011; Frey et al., 2016). The basic question here can thus be formulated as follows: to which extent can microhabitat characteristics, and their potential management, buffer against any detrimental effects of overall climate change (e.g. Braunisch et al., 2014)?

Among terrestrial organisms, high-elevation cold-adapted species seem to be particularly vulnerable to climate change (Dirnböck et al., 2011; Lagerholm et al., 2017; Scridel et al., 2018), with their future distribution being either expected to contract towards higher elevations due to ambient temperature warming (Braunisch et al., 2013; Chamberlain et al., 2013; La Sorte and Jetz, 2010; Pernollet et al., 2015; Sekercioglu et al., 2008), or to vary in a complex way in response to shifts in precipitation regimes that remain difficult to forecast (e.g. Tingley et al., 2012). Mountain areas are indeed subject to higher rates of warming compared to the global average (e.g. Böhm et al., 2001; Brunetti et al., 2009), yet at the same time, they are also experiencing strong changes in landscape and land use (e.g. forest encroachment in abandoned pastures, upward treeline shift or loss of areas permanently covered by snow). High-elevation ecosystems thus represent an ideal setting to investigate the fine-grained impact of environmental change on habitat and biocenoses, especially due to the complex topography, including steep elevational gradients, that generates a large range of microhabitats and microclimates (hereafter topoclimates) and offers numerous refugia opportunities (Körner and Ohsawa, 2006). Such heterogeneity may per se represent a chance to maintain biodiversity, either naturally (Brambilla et al., 2016) or through informed conservation management (Braunisch et al., 2014). However, to the best of our knowledge, mitigation strategies to maintain niche opportunities for high-alpine biodiversity facing climatic risks have not been investigated so far (Shoo et al., 2011; Turlure et al., 2010).

In this study, we investigated the foraging microhabitat selection in a high-elevation, cold-adapted and snow-exploiting passerine bird, the white-winged snowfinch *Montifringilla nivalis* (Aves: Passeridae; henceforth: snowfinch), during the nestling rearing period, a crucial phase of the life-cycle. The snowfinch is a mountain specialist species breeding at high elevations above the treeline (in the European Alps mostly between 1800 and 3000 m asl; Cramp and Perrins, 1994). Nests are usually located in rock crevices or human-built infrastructure such as mountain buildings or ski-lift pylons (Cramp and Perrins, 1994). Females lay the first clutches of 4–5 eggs during the second half of May to early June, and nestlings fledge at ca.18–22 days of age (del Hoyo et al., 2009). During the nestling rearing period, adults collect invertebrate prey in the surroundings of nest sites, usually within 300 m of the nest, frequently on or at the margin of melting snow patches and in alpine grasslands (Antor, 1995; Brambilla et al., 2017b; Catzeflis, 1975; Cramp and Perrins, 1994; Strinella et al., 2007).

A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower values favoured, especially late in the season, indicating avoidance of warmer sites). This previous study was based on 314 m^2 plots (i.e. at a meso-scale) and did not explicitly address the key question of climate change effects on habitat suitability (Brambilla et al., 2017b). Based on the outcome of correlative distribution models which accounted for climatic, topographic and land-cover variables, both at the landscape (Maggini et al., 2014) and the territory level (Brambilla et al., 2016), the snowfinch is expected to undergo a marked range contraction in the Alps because of climate change, especially due to increases in ambient temperature and habitat loss, snow cover being a key component in the species' ecology (Brambilla et al., 2017b). In this study, we focus on assessing the magnitude of climate change effects on the suitability of foraging habitats, and identifying habitat management measures at the territory-level scale that might help mitigate some detrimental effects of climate change. More specifically, our aims were: 1) to identify key habitat factors driving foraging microhabitat selection during food provisioning to nestlings by parents in a wide area of the Central Alps; 2) to evaluate past and forecast future changes in foraging microhabitat suitability by building models of microhabitat suitability, based on longitudinal data (both historical and projected) on changing snowmelt date, which has become progressively earlier in recent decades (by c. 6 days per decade; Klein et al., 2016); and, 3) to assess whether habitat management operations could maintain microhabitat suitability in the face of climate change. To the best of our knowledge, this is the first study to explicitly model the potential impact of climate change on foraging microhabitat suitability in a terrestrial vertebrate. Our study paves the way for better forecasts of wildlife responses to climate-induced alterations of habitat, and provides targeted conservation guidance for maintaining suitable foraging grounds in the face of climate change.

2. Methods

2.1. Study area and data collection

We investigated foraging microhabitat selection by 22 snowfinch breeding pairs from 8 different study sites (Sorebois, Zermatt, Furka Pass, Valle Spluga, Stelvio, Gavia, Passo Sella, Rosetta) of the Swiss and Italian Alps (Fig. 1). The elevation of the study sites ranged from 1880 to 2840 m a.s.l., adequately covering the elevational and macroclimatic gradient of snowfinch distribution in the Alps. All surveys were carried out between 14th June and 26th July 2016, focusing exclusively on snowfinches collecting food for nestlings (nestling-rearing period). First, by means of direct observations, we located snowfinch breeding pairs and active nests. Once an occupied nest was located, we adopted the following field protocols in order to record foraging and random points (hereafter, foraging and control plots).

In Switzerland, we mist-netted at least one parent from each monitored breeding pair to attach a radio-transmitter (Holohil Systems Ldt., model BD-2, weight: 1.4 g – corresponding to 3.2–3.9% of our birds' body mass, life span: 9 weeks) to its back using a leg-loop harness (Naef-Daenzer et al., 2001; Rappole and Tipton, 1991). As soon as tagged birds were provisioning food to the nestlings, foraging events were monitored over 2–6 days (spread along the nestling rearing period) with the aid of a hand-held three-element foldable Yagi antenna wired to a radio-receiver (Australis 26 k, Lawnton, Australia). Radio-tagged birds were first located from a distance from the radio signal and, once visual contact was made with the foraging bird, the exact site of a successful prey capture was identified with the aid of binoculars and marked with a labelled stick. Then, a control plot was generated by selecting a random angle (0–359°) and a random distance (between 26 and 100 m) from the actual foraging plot.

In Italy, breeding individuals were visually tracked when flying from the nest to foraging sites, with the aid of binoculars (Brambilla et al., 2017b). Once a foraging event was encountered, the exact location was recorded with a GPS device or by mapping the point on a detailed aerial photograph. The foraging location was established as the first position where a food item was collected (or as the last location of the bird before returning to the nest, when we could not directly assess prey capture, since snowfinches usually provision food to the nest immediately after prey capture; Brambilla et al., 2017a). After the collection of 10 foraging locations per study pair, an equal number of control plots (with the only constraint that they should not overlap with foraging plots) were randomly selected within a radius of 300 m around the nest (Brambilla et al., 2017b; Grangé, 2008; Strinella et al., 2007) so as to map habitat characteristics.

The difference in the methods used for the selection of control plots between Switzerland and Italy did not affect the results, as control plots showed similar suitability values across the two approaches (as revealed by a mixed model analysing habitat suitability of control plots including site identity as a random factor and methods of control plot selection as fixed effect, where the AIC value was larger than the null model; Table A3).

Habitat cover and structure were recorded within a 5 m-radius around each foraging location and control plot. Habitat variables described vegetation and other ground cover, as well as sward height and the occurrence of grazing (Table 1). In addition, topographical features (slope, solar radiation) were calculated in a geographic information system (GRASS 7.04) using detailed Digital Elevation Models (resolution between 1 and 5 m) made publicly available by regional/provincial authorities in Italy and by SwissTopo maps for 2013 (Swiss Federal Office of Topography). Solar radiation was calculated as global radiation on 21st June, taking into account the shadowing effect of the relief.

Sward height could not be recorded where grass was absent ($n = 16$ locations out of a total of 470). Because of this, in exploratory analyses we compared the modelled relationships between foraging occurrence and sward height by setting sward height to zero at these 16 locations or by omitting these locations from the analysis. Given that the coefficients for sward height were very similar between models with or without 'filled gaps' (-1.02 and -1.03, respectively), we decided to apply the former option.

2.2. Statistical analyses

2.2.1. Foraging habitat selection

Habitat variables were recorded at 470 locations (235 foraging and 235 control plots) obtained from 22 breeding pairs (see Table A1 for summary statistics). All variables were standardized (i.e. centred on their mean value and scaled by their standard deviation) before analyses. After checking for outliers and zero-inflated variables, sand and mud cover were discarded, and human-altered habitats (two types of roads and urbanized areas) were joined into a single variable (anthropized areas).

We modelled foraging habitat selection by means of conditional logistic regression (Hosmer and Lemeshow, 1989), which accounts for the intrinsically paired nature of the sampling protocol and resulting dataset. According to this approach, each set of foraging plots of a given breeding pair was matched to the respective control plots, henceforth taking into account the pair-based sampling design. Pair identity was thus specified as a so-called "stratum" variable. Conditional logistic regressions were run by using the 'clogit' function of the 'survival' package in R (R Development Core Team, 2016).

Model selection was performed using an information-theoretic approach, based on the Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). First, to reduce the risk of model overfitting and to limit the potential effects of multicollinearity, the explanatory variables were divided in two groups (Assandri et al., 2018). These groups were "vegetation" and "other variables" (Table 1). We tested for within-group collinearity by calculating the variance inflation factor (VIF) using the package *car* in R (R Development Core Team, 2016). For all variables within a given group, there were no collinearity issues ($VIF < 3$ for all variables in both groups). Within each group, models with all possible variable combinations were constructed, and models were ranked according to their AICc value using the MuMIn package (Bartoń, 2016). The difference in AICc between each model and the top-ranking model (ΔAICc) was

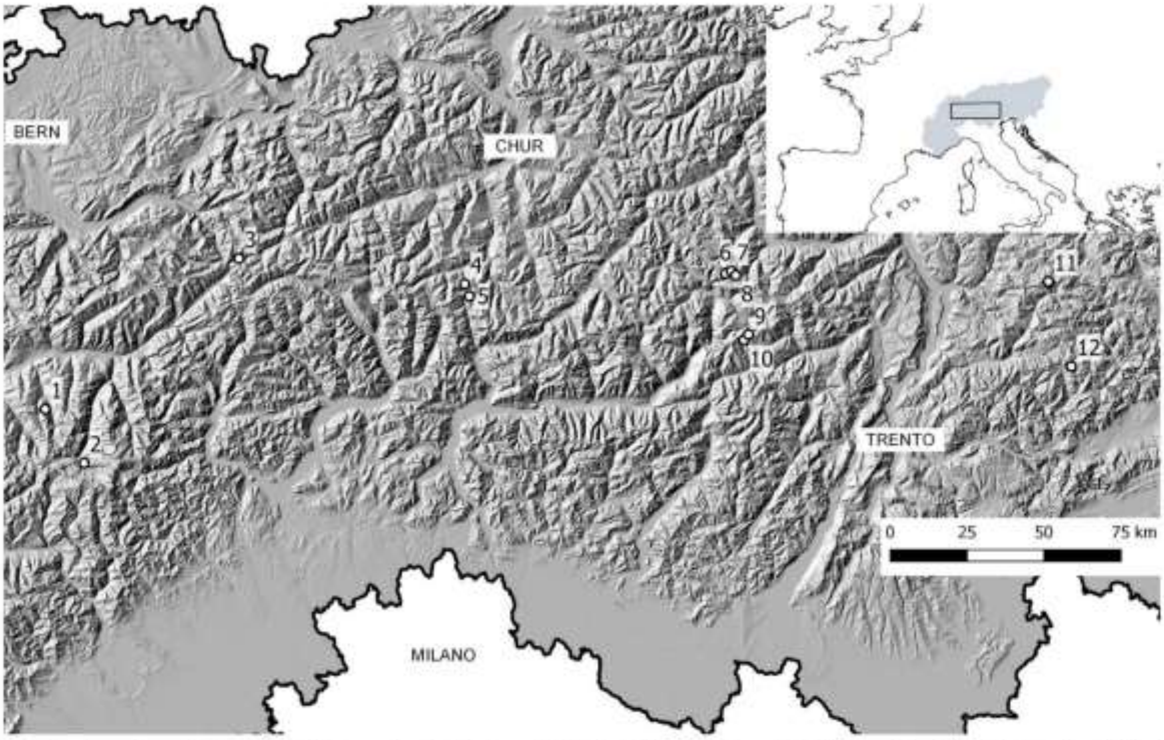

Fig. 1. Map of the study area showing the 12 study sites monitored in the Swiss and Italian Alps (1: Sorebois; 2: Zermatt; 3: Furka Pass; 4: Passo Spluga; 5: Montespluga; 6: Valle del Braulio; 7: Passo Umbrail; 8: Passo dello Stelvio; 9: Rifugio Gavia; 10: Passo Gavia; 11: Passo Sella; 12: Rosetta). The location of some major towns (Bern, Chur, Milano and Trento) is also given for a better interpretation of the geographical extent of the study area. The inset shows the location of the study area (rectangle) within the European Alps (grey).

calculated. Based on a previous study, we hypothesised that snowfinches would preferentially forage in sites with high grass cover but low sward height (Brambilla et al., 2017b). Therefore, we added a potential interaction term to the "vegetation" group (grassland cover × sward height). Moreover, in order to test for selection of melting snow patch margins (see e.g. Antor, 1995) and according to preliminary data exploration (which suggested a potential curvilinear relationship for snow cover), we also included a quadratic term for snow cover (in the "other variables" group). Then, for each group we selected all the variables (and interactions) included in the most supported models ($\Delta AICc < 2$) after the exclusion of 'uninformative parameters' (i.e. variables for which inclusion resulted in a higher AICc value of the model, but with an increase in $AICc < 2$; Arnold, 2010; Jedlikowski et al., 2016). We finally combined the retained variables of both groups and carried out a further model selection using the same procedure (see e.g. Assandri et al., 2016; Brambilla et al., 2017c). In the latter process, given that snowfinches could preferentially forage in fine-scaled mosaics of snow and grass (Brambilla et al., 2017b), we added the interaction term snow × grassland cover.

2.2.2. *Past, current and future habitat suitability*

To predict climate-driven changes in foraging habitat suitability, we modelled snow cover and sward height as a function of season progression and environmental characteristics, selected on the basis of a potential effect of climate on those two variables according to the literature and expert opinion. We built models based on the control plots, which were randomly selected and thus ensured unbiased sampling (snowfinches may select patches where micro-topography or other local conditions can result in values of snow cover or sward height deviating from the average values of each territory). First, we built a model relating snow cover to Julian date, solar radiation, elevation and slope. Then, we modelled sward height as a function of solar radiation, elevation, slope, snow cover and grazing occurrence, excluding the few sites without grass cover. In both cases, we used linear mixed models (LMM) considering breeding pair as a random factor to take into account the spatial dependency of control plots within areas frequented by the same breeding pair. Effect size for variables in the mixed models was calculated according to the semi-partial R^2 statistic proposed by Jaeger et al. (2017) using the r2glmm package in R.

We estimated past and simulated future conditions based on the observed rate of change in the date of snow melt: research from the Swiss Alps reported a linear pattern of advance in snow melt timing by c. 6 days per decade (5.8 days/decade; Klein et al., 2016). To hindcast past conditions (40 years ago), we therefore decreased the sampling date by 24 days. To model conditions 50 years into the future (at year 2066), we added 30 days, assuming the trend in melting pattern will remain unaltered. We then recalculated predicted snow cover and grassland height for each of the three time steps (in the following termed 'past', 'current' and 'future').

Finally, we calculated for each plot (foraging or control, $n = 470$) the potential suitability under past, current and future conditions, by means of the final habitat selection model obtained in the previous analysis, and averaged predicted habitat suitability for all plots related to each breeding pair. We used modelled snow cover and sward height (i.e. predicted values from snow cover and sward height models), instead of the values actually recorded in the field, including model predictions for the current period in order to eliminate the effect of the site- and time- specific conditions associated with the sampling period and to obtain habitat suitability estimates that were comparable with past and future conditions. In this estimation of habitat suitability in

Table 1
List of habitat variables measured within a 5-m radius at foraging and control plots, with information about methods, metrics and descriptor category. Ground cover variables sum up to 100%. For the statistical analyses, sward height, grassland cover, shrubs cover were assigned to the "vegetation" group, whereas all the others were assigned to the "other variables" group.

Variable type/ variable name	Description	Unit
Vegetation structure		
Sward height	5 measurements of grass height at the plot centre and at 2.5 m along each of the four cardinal directions (or at the closest point with grassland cover, respectively)	cm
Ground cover		
Grassland	Cover of grassy vegetation	%
Shrubs	Dwarf-woody vegetation (e.g. *Rhododendron*, *Juniperus*, *Salix*…)	%
Snow	Snow-covered areas	%
Boulders	Rocks detached from the substrate	%
Bare ground	Bare soil (compact soil)	%
Rocks	Emerging rocky substrate (bedrock)	%
Scree	Small rocky material (a few cm in diameter)	%
Gravel roads	Unpaved roads, large footpaths	%
Paved roads	Roads, paved parking	%
Sand	Sandy soil (not compact)	%
Urbanized	Buildings, walls, pylons	%
Water	Lakes, ponds, watercourses	%
Other	Other uncovered categories	%
Grazing occurrence	Dung of current or previous year or active grazing	Yes/no
Topography		
Slope	Angle in degrees (°) calculated at the plot center using a digital elevation model (resolution: 1–5 m)	Degree
Solar radiation	Calculated as global radiation for 21st June based on a digital elevation model, incorporating the shadowing effect of the surrounding relief	kWh/m^2

different periods, we used the original values for the two other variables (cover of grassland and of anthropized areas) included in the habitat selection model.

2.2.3. Mitigation scenarios

To simulate and evaluate any potential benefits of targeted management actions to maintain foraging microhabitat suitability, we also modelled current and future suitability under two scenarios, with and without mitigation management. The 'non-mitigation' scenarios (without management) corresponded to the modelled habitat suitability as described above. For the mitigation scenarios (via habitat management), we assumed that sward height would be managed according to optimal snowfinch requirements by keeping grass height below 6 cm (see Fig. 2 and Brambilla et al., 2017b). We assumed that such optimal sward height could be achieved by mowing or controlled grazing. We therefore used the predicted sward height under current and future climate conditions, respectively, both adjusted by truncating the highest values at 6 cm. Finally, to evaluate whether habitat suitability significantly changed from past to current and from current to future conditions under both scenarios (with vs without management), we performed a Wilcoxon matched-pairs test on the mean plot suitability for each pair. For descriptive purposes, we also counted the number of plots with average plot suitability above 0.5 (suitable plots) for each time step (past, current, and future).

3. Results

3.1. Foraging habitat selection

We obtained a single most supported synthetic model, as all other candidate models (after the exclusion of uninformative parameters) had a ΔAICc > 2 (Table A2). According to this model ($R^2 = 0.35$), the most suitable foraging habitats were characterized by low sward height and cover of anthropized areas, intermediate snow cover and high grassland cover (Table 2). Effect sizes for these variables ranged between 0.17 and 0.34, with snow cover and sward height having the largest effects (Table 2). The influence of these predictors on the probability of occurrence of foraging snowfinches is shown graphically in Fig. 2.

3.2. Past, current and future habitat suitability

The model for snow cover (intercept: -0.19 ± 0.10) suggested, as expected, a positive effect of elevation (0.24 ± 0.11, effect size: $r = 0.28$) and negative effects of Julian date (-0.13 ± 0.07, $r = 0.17$), slope (-0.05 ± 0.09, $r = 0.04$) and solar radiation (-0.08 ± 0.09, $r = 0.07$), and had a conditional R^2 equal to 0.23. The model for sward height revealed a positive effect of solar radiation (0.26 ± 0.09, $r = 0.23$) and slope (0.47 ± 0.09, $r = 0.41$): well exposed steep slopes are likely those where snow disappears earlier and where the plant growing season may start earlier, leading to higher swards. As expected, a negative effect on sward height was found for grazing (grazing occurrence: -0.08 ± 0.15, $r = 0.05$), elevation (-0.60 ± 0.14, $r = 0.61$) and snow cover (-0.14 ± 0.08, $r = 0.15$), likely due to both different grass species at different elevations and to the delay in growing season caused by elevation and snow cover. The model for sward height had a conditional R^2 equal to 0.53.

Foraging habitat suitability was predicted to have declined from 1976 to 2016, and to continue declining from 2016 to 2066 at all breeding sites (Fig. 3). The predicted average site-level plot suitability had strongly declined from 1976 to 2016 (Wilcoxon matched pairs test, $Z = -4.11$, effect size: $r = 0.71$, $n = 22$ breeding sites), and is expected to greatly decline further by 2066 ($Z = -4.11$, $r = 0.71$). The overall number of suitable plots (plots with habitat suitability higher than 0.5; $n = 470$) declined from 364 (77%) to 281 (60%) from 1976 to 2016 (−23% in the number of suitable plots), and was predicted to further decline to 191 (41%) by 2066 (i.e. a further change of −32% in the number of suitable plots relative to the current situation).

3.3. Mitigation scenarios

The mitigation scenarios yielded higher current and future habitat suitability values than the estimates obtained without any intervention targeted at limiting sward height, especially for sites with most or some plots located at the lower end of the elevational range exploited by the species (Fig. 3). Under current conditions, if appropriate management actions were implemented, the number of suitable plots would be 359 (76%; which roughly corresponds to the figure back-projected to 1976 without management), while the average territory-level plot suitability would be significantly higher (+0.07; Wilcoxon matched pairs test; $Z = -3.52$, effect size: $r = 0.62$, $n = 22$ breeding sites) compared to a scenario without management. The future number of suitable plots under an active mitigation scenario would be 268 (57%; very close to the number of currently suitable plots). Compared to a scenario with no management implemented in the future, average habitat suitability could thus be increased by 0.07 (Wilcoxon matched pairs test; $Z = -3.52$, $r = 0.62$, $n = 22$ breeding sites) via mitigation measures.

4. Discussion

Our retrospective and prospective modelling showed that a climate-sensitive species of high-alpine ecosystems, the white-winged snowfinch, is at risk from microhabitat loss induced by climate warming, confirming at a fine-scale level previous suggestions derived by large-scale modelling (Brambilla et al., 2016, 2017a). Not only has it seemingly already lost a substantial fraction (−17% of plots, or −23% of suitable plots, from 1976) of its structurally suitable foraging habitat in

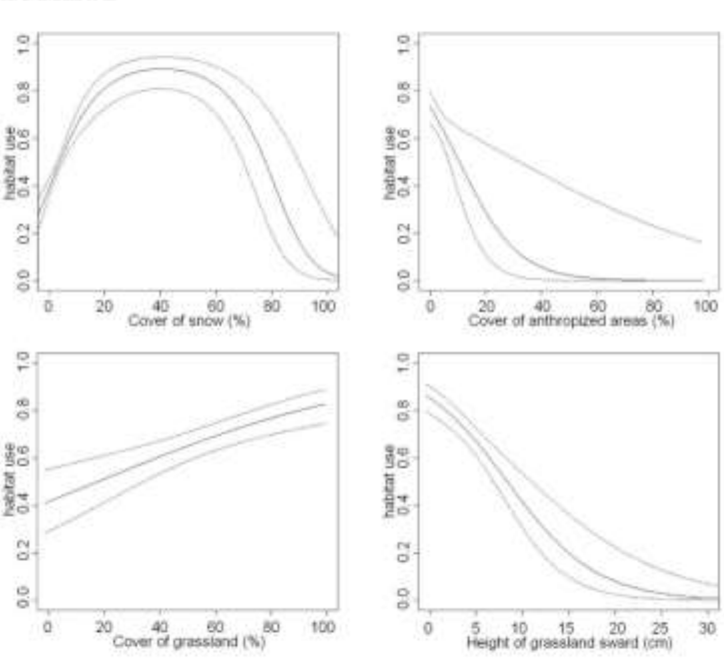

Fig. 2. Effects of habitat variables affecting the probability that a bird foraged in a given habitat patch according to the best-fitting conditional logistic regression model reported in Table 2. In each panel, the variable's effect on predicted probability of habitat use (mean and 95% confidence interval) are shown while all other predictors included in the models are kept at their mean value.

Table 2
Best-fitting conditional logistic regression model for foraging habitat selection by breeding snowfinches during the nestling rearing period. Effect size (Pearson's r) was computed considering a sample size equal to 235 dyads.

Variable	Estimate (SE)	Z	P	r
Grassland cover	0.57 (0.14)	4.14	< 0.001	0.26
Sward height	−0.85 (0.16)	5.37	< 0.001	0.34
Snow cover	2.00 (0.32)	6.18	< 0.001	–
Snow cover^2	−0.72 (0.13)	5.32	0.003	0.34
Anthropized	−1.21 (0.45)	2.65	0.008	0.17

the Central European Alps over the past decades, but the unabated habitat alterations induced by climate change would also continue to reduce habitat suitability in the decades to come (−19%, or −32% of suitable plots, by 2066). To the best of our knowledge, this is the first study that has quantified fine-grained microhabitat requirements for reconstructing past, and predicting future, foraging habitat suitability in a high-elevation species, i.e. a species occurring in an ecosystem that is more affected by climate change than the global average (see Moritz and Agudo, 2013 and references therein). Indeed, most research on the impact of climate change on biodiversity has so far dealt with modelling macro-ecological relationships between climate and species' biological attributes (Bellard et al., 2012). Even if such broad-scale correlative models could identify the pool of species in a given area that are likely to be mostly impacted by climate change, more detailed approaches (like the one we have adopted here) are required to produce accurate projections of changes in fine-scale habitat suitability and to assess the potential effectiveness of habitat management as a mitigation measure. This study is also one of the first to illustrate that mitigation measures (targeted sward management by grazing) could be implemented to maintain habitat suitability and thus buffer against the detrimental effects of climate change, in line with what Braunisch et al. (2014) have proposed for montane and subalpine forest bird species, and with what Regos et al. (2017) suggested for birds in wildfire-prone ecosystems. This lack of fine-grained mechanistic studies of habitat selection is surprising as understanding species' ecological requirements is a prerequisite both for sound modelling of species-habitat relationships and for designing adequate mitigation strategies for conservation. In particular, microhabitat selection studies carried out during the main bottlenecks of a species' life cycle, notably the critical and intense phase of food provisioning to offspring (nestlings), are key as breeding output depends on parental investment into progeny. The mechanical links evidenced in our field surveys between environmental characteristics favouring foraging activity (snow cover and sward height) and the alterations of these characteristics induced by climate warming exemplify how meaningful forecasting of future species distributions via spatial modelling should operate to gain predictive power. The general lack of fine-grained studies is probably linked to the intensive and time-consuming data collection required, and such studies are unlikely to be feasible for a large number of species at the same time. Additionally, the high-precision information required for the study we carried out prevented similar modelling over broad scales (e.g. at the regional or continental level), even if the increasing availability of high-resolution data will likely allow new steps in that direction in the near future.

4.1. Microhabitat suitability for foraging snowfinches is affected by climate-related habitat variables and anthropization

Breeding snowfinches collected food for nestlings in microhabitats characterized by intermediate snow cover intermixed with short grassland, while avoiding human-altered areas, notably roads and buildings. These results are in line with previous findings obtained at a much coarser scale in a largely overlapping study area, where snowfinches were also found to primarily select short grassland and snow-covered areas (Brambilla et al., 2017b). In addition, at a coarser scale, snowfinches were found to be associated with sites with lower solar radiation (especially later in the season, when those sites are the ones most likely to be still covered by snow and with short vegetation), bare ground and some boulders (Brambilla et al., 2017b), which were no longer important at the fine scale we considered. The preference for an intermediate snow cover (optimum at c. 40%) reflects the species' foraging tactics: snowfinches either collect invertebrate fallout on the snow surface (Antor, 1995), or exploit the melting margins of snow fields where they can find abundant tipulid larvae, one of their

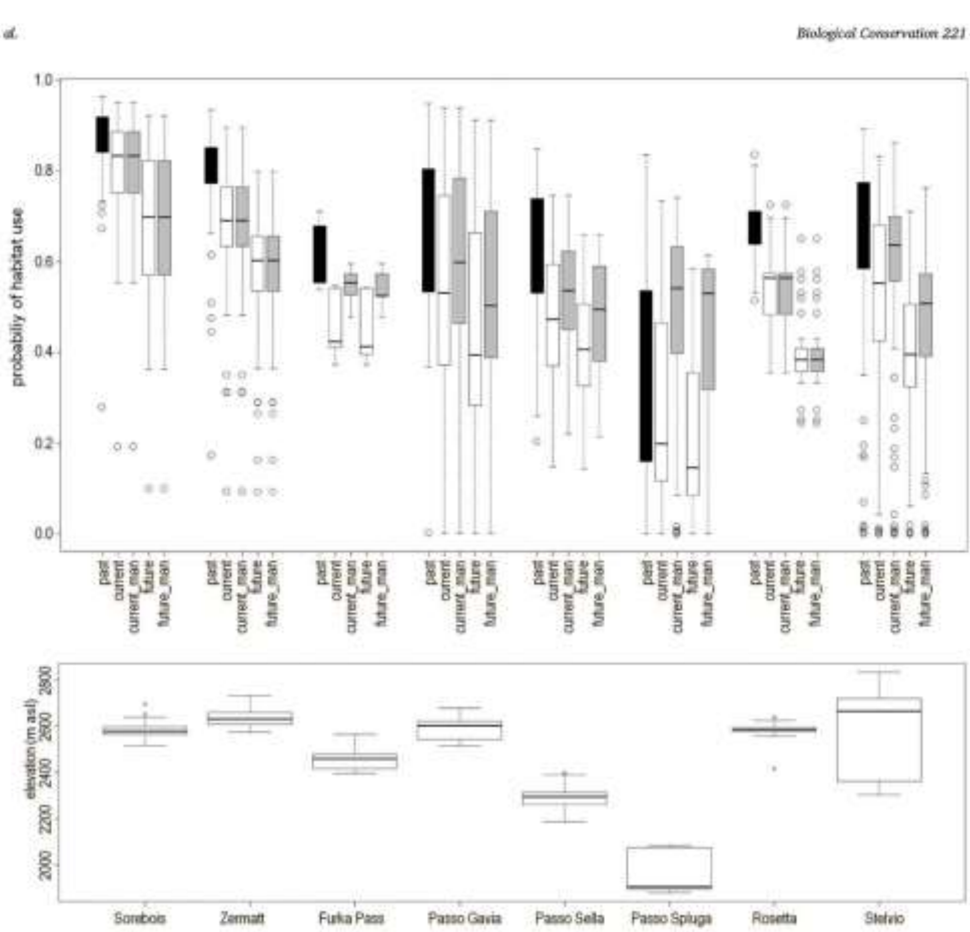

Fig. 3. Upper half: boxplots of past, current and future habitat suitability of all sampled plots (n = 470) within each study site (n = 8 sites), according to the best-fitting model of microhabitat selection and the simulated scenarios of managed vs. unmanaged grassland sward height (in the managed scenario, grassland sward was kept at a maximum height of 6 cm; see Methods section for details of the procedure). For each site, boxes show from left to right habitat suitability for different time steps and scenarios: past (black), current – unmanaged (white), current – management scenario (grey), future – unmanaged (white), future – management (grey). Plots show median, upper quartile, lower quartile, maximum and minimum values excluding outliers, i.e. value above 1.5 the upper quartile or below 1.5 the lower quartile. Lower half: boxplot of plot (foraging and control) elevation within each study site.

favourite and most profitable prey items (Cramp and Perrins, 1994). Sward height constrains foraging opportunities: short grass is likely to boost prey availability, which is prey abundance modified by its accessibility (Schaub et al., 2010). Yet, to further refine our mechanistic understanding of microhabitat-species associations, future work should also investigate how prey abundance varies with respect to snow cover and the melting front of the snow field in particular, and throughout the breeding season in relation to the different habitat types in general.

Overall, our findings confirm that properly predicting mountain birds' responses to global change necessitates the consideration of both climate and habitat factors simultaneously (Chamberlain et al., 2016a), as habitat traits could be extremely important and interact with climate change itself (Sirami et al., 2017; Titeux et al., 2017, 2016). High-elevation species spend a large part of their life-cycle in extreme habitats. They have thus evolved specific adaptations to cope with harsh environmental conditions (Cheviron and Brumfield, 2012; Gobbi et al., 2017; Scridel et al., 2018). However, climate change is accompanied by increased weather variability and an acceleration of extreme events, which represents a new evolutionary challenge for biodiversity in general (Di Marco and Santini, 2015) and high-alpine biodiversity in particular (Lu et al., 2009). The effects of the increased weather variability and frequency of extreme events on the suitability of foraging habitats also deserve further investigation. Moreover, direct anthropogenic impacts on Alpine ecosystems are increasing: the tourism industry modifies high-elevation landscapes and biodiversity via the creation of new infrastructures (e.g. Rolando et al., 2007), recreational disturbance (e.g. Arlettaz et al., 2015, 2013, 2007) and other anthropogenic stressors (Chamberlain et al., 2016b; Scridel et al., 2018). Although the snowfinch is considered a synanthropic species benefiting from human infrastructures both for nesting (mountain buildings, ski-lift pylons and even nest-boxes) and winter foraging (seed-feeding stations at ski resorts or mountain chalets) (Cramp and Perrins, 1994), our results show that roads, paths, buildings and other man-made structures decrease foraging microhabitat quality during the reproductive period. It would thus be particularly interesting to estimate the year-round costs and benefits of breeding in anthropized in contrast to natural habitats.

Climate change can threaten alpine species to such an extent that the large-scale distribution of species like the snowfinch could shrink considerably (Brambilla et al., 2017a; Maggini et al., 2014). Our study demonstrates a high sensitivity of snowfinch towards climate-induced alteration of microhabitat conditions, notably in snow cover and sward, shedding light on the possible mechanistic causes behind the ongoing range contraction of this and other cold-adapted species (Scridel et al., 2017). Warming climate induces both an anticipation of the seasonal timing of snowmelt (Klein et al., 2016) and an earlier and faster grass growth at high elevations (Theurillat and Guisan, 2001), which affects the snowfinch as well as other elements of alpine biocenoses (Pettorelli et al., 2007).

A note of caution should be made about our models for snow cover and sward height. On the one hand, the snow cover model had a rather low explanatory power, suggesting that local conditions may be very important in driving seasonal patterns of snow cover changes. In particular, winter precipitation and spring temperature are crucial in determining how long snowfields can last during the snowfinch breeding season. Therefore, improving the modelling of snow melting patterns at a high spatial resolution would be an important future task for a better assessment of changes in foraging habitat suitability for alpine birds. On the other hand, sward height may also depend on the pool of locally occurring grassland species. Despite this, the sward height model performed very well, suggesting that common patterns in the study area can be detected even without considering grassland species' composition. Hence, our results can be considered as representative of the general patterns of snow cover and sward height variation experienced by snowfinches in the Alps.

4.2. *Buffering climate change impacts via habitat management*

While slowing down climate warming requires long-term global measures to drastically reduce society's reliance on fossil energy sources, sward management through targeted grazing is amenable to local action. Our model outcomes suggest that the management of sward height might offer some room to buffer the negative impacts of climate warming on foraging microhabitat configuration, especially for sites located at relatively low elevation, where grassland cover and sward height play a crucial role in determining habitat suitability for snowfinches (for sites located at higher elevation or with low grassland cover, this would hardly provide any tangible benefit – see e.g. the first plots on the left side of Fig. 3). According to our proposed scenario, a systematic implementation of sward height management at our study sites would have compensated for the decline in structural microhabitat suitability that has occurred from the 1970s and could also strongly reduce the predicted reduction of foraging habitat suitability over the next 50 years. However, it remains to be seen whether: 1) other effects of climate change may turn into unsuitable also the sites where foraging habitat can be kept structurally suitable by means of management, and 2) implementing this measure would be sufficient to compensate for the effect of the snowpack reduction and earlier snowmelt, which may directly or indirectly impact on the invertebrate community upon which alpine birds feed. If the dependence on accessible foraging grounds is the main factor, then management might effectively increase habitat suitability. However, if the conditions prevailing along the melting snow front dictate not only prey accessibility, but also prey abundance and phenology, this measure will likely not suffice, unless the snowfinches can alter their breeding phenology towards earlier nesting. This emphasizes the need to better understand, first, how invertebrate prey availability (which is, again, abundance modified by accessibility) drives foraging microhabitat selection (Vickery and Arlettaz, 2012); and, second, what is the adaptive potential of the species to environmental change, notably in terms of plasticity in reproductive phenology. From this point of view, the results of our retrospective habitat suitability model suggest that the snowfinch might have a limited capacity to cope with environmental change, notably with the ongoing major alterations in snow cover conditions. Investigations of its long-term breeding phenology are also needed to further appraise its adaptive potential. Finally, preventing the construction of new infrastructures at high elevation, converting disused tracks at construction sites into grassland, as well as ski-piste revegetation (Caprio et al., 2016), may limit or reduce further losses of suitable habitats due to human activities.

Future studies should evaluate whether a generalization of our recommendations is possible, both from a spatial and a taxonomic point of view. Indeed, keeping a low sward height could also favour prey capture by breeding snowfinches in the other parts of the species' breeding range. Similarly, this management regime could favour other insectivorous birds requiring low swards (Vickery and Arlettaz, 2012) that dwell in alpine grassland, such as water pipit *Anthus spinoletta*, ring ouzel *Turdus torquatus*, alpine accentor *Prunella collaris* or northern wheatear *Oenanthe oenanthe*. More generally, the potential consequences of grassland management on plant species (for which grazing or mowing could be both beneficial or counter-indicated, Pierce et al., 2007) and habitats should also be evaluated locally.

The present study highlights the importance of considering microhabitat selection for revealing fine-scale, functional and interacting effects of climate and land-use changes on climate-sensitive species and for identifying compensatory habitat management strategies that could to some extent allow buffering the negative effects of climate warming on high-elevation biodiversity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.03.008.

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SECTION II: *Chapter V*

Landscape-associated differences in fine-scale habitat selection modulate the potential impact of climate change on White-winged Snowfinch Montifringilla nivalis

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The rocky plateau of the Altopiano delle Pale (top, D.Scridel) in contrast with grassy slopes at the bottom of Piz Umbrail (photo B. Sudolska)

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BIRD STUDY
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Landscape-associated differences in fine-scale habitat selection modulate the potential impact of climate change on White-winged Snowfinch *Montifringilla nivalis*

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ABSTRACT

Capsule: Fine-scale use of climate-sensitive habitats by White-winged Snowfinches *Montifringilla nivalis* is affected by landscape composition, which thus modulates the potential impact of climate change.

Aims: To explore the fine-scale habitat use for foraging by breeding White-winged Snowfinches, with the aim of identifying the potential impacts of climate change on their dependence on habitat characteristics in the wider landscape, which could shape the species' response to climate change. Pairs mostly relying on snow could be at higher risk due to a decrease in spring snow-cover, but the reliance on snow may be mediated by the presence of alternative habitats in the landscape.

Methods: The White-winged Snowfinch uses alpine grassland, snowfields and melting snow margins for capturing prey during nestling rearing and is threatened by earlier snowmelt induced by climate change. We investigated habitat use in 17 Snowfinch pairs in relation to landscape composition within a 300 m buffer around their nests.

Results: The use of snowfields and snow-bare margins was positively associated with wind intensity (probably due to greater wind-borne arthropod fallout with wind), and negatively associated with grassland cover (i.e. the main alternative habitat) and date within the season.

Conclusions: Fine-scale habitat selection was affected by landscape composition: the availability of patches of alternative habitats decreased the reliance on more climate-sensitive resources, modulating the potential impact of climate change. Coupling assessments of fine-scale resource selection with broader habitat descriptors, which are easier to assess over broader scales, may help understand and predict climate change impacts.

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Climatic changes are impacting species of every taxonomic group across all continents, but their impacts are largely modulated by habitat characteristics (Otto *et al.* 2014, Bowden *et al.* 2015, Selwood *et al.* 2015). Local habitat may actually buffer the effects of climate change (Scherrer & Körner 2011, Nieto-Sánchez *et al.* 2015), although habitat management is unlikely to compensate for losses due to climatic alterations (Wessely *et al.* 2017; but see Braunisch *et al.* 2014, Brambilla *et al.* 2018). Microhabitat selection and, more generally, fine-scale habitat use, plays a fundamental role in a species' capacity to buffer changes due to climate variation (Higgins *et al.* 2010, Suggitt *et al.* 2011, Frey *et al.* 2016, Brambilla *et al.* 2017b), and the investigation of fine-scale ecological patterns may increase our mechanistic understanding of how extensively organisms might adapt to environmental change (Baudier *et al.* 2015, Bennett *et al.* 2015, Brambilla *et al.* 2018). This may be crucial for accurate predictions of species' responses to environmental or climatic impacts, and hence for the identification of conservation priorities. Studies on fine-scale habitat use by animal species are therefore required to better understand how species respond to climate change impacts (Scheffers *et al.* 2014, Pincebourde *et al.* 2016). However, so far only a few studies have investigated responses regulated by microhabitat/microclimate and their relative modifications, despite growing evidence highlighting their fundamental role (Turlure *et al.* 2010, Fedy & Martin 2011, Suggitt *et al.* 2011, Frey *et al.* 2016).

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Fine-scale habitat selection and microhabitat use may indeed buffer against climate change impacts, but at the same time it can vary according to various biological and environmental factors (Valdez *et al.* 2017), to seasonality (Lunghi *et al.* 2015) or according to individual traits (Whiteman & Côté 2004, Morales *et al.* 2008), eventually resulting in different impacts of climate change according to different microhabitat use (Bowden *et al.* 2015). Hence, an understanding of fine-scale habitat selection is often essential to predict the potential impact of climate change on a species, and it can vary according to habitat composition on a broader scale (i.e. landscape). Therefore, assessing variations in the use of fine-scale habitats (with different sensitivity to climate change) according to landscape may also help to identify landscape-dependent vulnerability to climate change. This would greatly facilitate the identification of areas where species are more likely to be threatened or, vice-versa, to persist, on the basis of the landscape characteristics, which are easier to assess on a large-scale. Fine-scale habitat assessment requires in-depth investigation which is not always feasible over broad areas.

Mountain regions are particularly sensitive to climate change (Gobiet *et al.* 2014), and mountain bird species are considered to be at higher risk compared to birds from other habitats (Chamberlain *et al.* 2016, Scridel *et al.* 2017, 2018, Brambilla *et al.* 2017a). Earlier snowmelt, due to global warming, is one of the main threats for several species inhabiting areas at high-elevation or latitude, including plants (Kudo & Hirao 2006) and animals (Rosvold 2016). One of the species most threatened by climate change in the European Alps is the White-winged Snowfinch (hereafter Snowfinch) *Montifringilla nivalis*; according to correlative distribution models, it is projected to lose large portions of its current range due to climate warming (Brambilla *et al.* 2016, 2017a). Snowfinches make abundant use of snowfields and of their melting margins for prey collection: during the critical phase of nestling rearing, Snowfinches often forage on snow margins and snowfields (Strinella *et al.* 2007, Brambilla *et al.* 2017b, 2018). Snow margins provide abundant and accessible insect prey (Muscio *et al.* 2005), whereas on snowfields invertebrate detectability is highest, and Snowfinches forage on wind-blown arthropod fallout (Antor 1995). Snow cover and its duration are decreasing in mountain systems, including the Alps (Klein *et al.* 2016) and particularly in springtime (IPCC 2007, Brown & Robinson 2011, Derksen & Brown 2012). This implies that fine-scale habitats linked to snow cover (and the species relying on these) are particularly vulnerable. In addition, Snowfinches frequently forage on alpine grassland, especially on sites with short grass sward (Brambilla *et al.* 2017b), and correct grassland management is a key feature for preserving foraging habitat suitability for Snowfinches (Brambilla *et al.* 2018). The importance of snow for the species represents one of the potential mechanistic links with climate and the increasingly earlier snow-melt date in the Alps (Klein *et al.* 2016; see also Brown & Robinson 2011), suggests that climate-induced modifications of foraging habitats may be one of the most critical impacts of climate change on this species. Snowfinch populations or individuals relying mostly on snowfields and their margins could thus be at greater risk than those relying on other fine-scale habitats (e.g. grassland). With this study, we investigated whether landscape composition surrounding Snowfinch nests affected their fine-scale habitat selection during the capture of prey items when provisioning their nestlings. We hypothesized that the availability of alternative suitable habitats may determine a lower reliance on snow-related habitats, and thus that landscape composition may modulate extinction risk posed by habitat modifications induced by climate change.

Based on previous knowledge (Brambilla *et al.* 2017b), we identified five main foraging fine-scale habitats for Snowfinches: snow, grassland, bare substrate, snow-grassland margin, snow-bare substrate margin. These fine-scale habitats are likely subjected to different intensities of threat imposed by climate change. The availability of snow cover and margins is clearly affected by climate and impacted by rising temperatures and changes in precipitation regimes. Indeed, snow cover in the Alps has reduced over time, including its duration, with an approximately 6-day advance in snowmelt date per decade (Klein *et al.* 2016). These fine-scale habitats are most likely to decrease or disappear in future decades. On the other hand, grassland and bare substrate are likely to be less subject to the potential impact of climate change; nevertheless, climate change will affect grassland structure and composition (Theurillat & Guisan 2001; but see Cannone *et al.* 2007, Harsch *et al.* 2009). In this study, we focused on the use of snowfields and their margins in relation to landscape composition.

Methods

Study area and fieldwork

The study was carried out in the Italian Alps, in the provinces of Sondrio, Brescia, Trento and Bolzano, across five study sites located at different altitudes

(1900–3200 m above sea level) and within different landscape characteristics. The average cover of habitats and snow (2–21%) varied greatly across study sites: grassland was dominant in two sites, bare substrates at another two, whereas the remaining one was characterized by a mixture of different habitats (Table 1).

We investigated foraging habitat selection by breeding Snowfinches between the 7th June and the 19th July 2017. Seventeen breeding pairs were included within this study, 8 of which were followed for one day and 9 pairs for two days, with the interval between subsequent visits ranging between 2 and 10 days. During each survey, we monitored breeding Snowfinches, visually tracking adults when moving from the nest to a foraging location. We recorded habitat exploited at approximately 20 foraging events per pair/day (Table 1); for each pair we included a mean (± sd) of 28 ± 13 foraging events. Each foraging event was attributed to one of the following fine-scale habitat types: grassland, bare substrate, snowfield, margin snow-grassland, margin snow-bare substrate. Bare substrate included rocks, sand, gravel, scree, mud or bare soil.

For each breeding pair/date we estimated the proportional cover of different habitat types (i.e. grassland, snow, bare substrate, other – mostly man-made areas and waterbodies) within a 300 m radius around the nest, as available studies indicate that adults largely forage within this distance from the nest (Strinella *et al.* 2007, Brambilla *et al.* 2017b, 2018). A 300 m fixed radius was used for all pairs to get daily and comparable data on landscape composition around the nests. Habitat coverage was estimated visually in the field with the help of aerial photographs. We adopted this approach as available databases did not provide enough details to distinguish key habitat features at such a fine scale, such as small areas of grass or snow patches. Further to this, snow cover had to be assessed periodically and in some cases on a daily basis. To verify the accuracy of these visual estimates, we performed checks of coverage estimates using a GIS software (Geographical Information System; QGIS Development Team 2018) by redrawing habitat plots, and the results were similar to the visual estimates. For each foraging event, we also recorded meteorological conditions (sky cover: 0: clear, 1: partly overcasted, 2: overcasted (cover > 95%); wind: 0: absent, 1: weak, 2: moderate or strong), as weather conditions may affect invertebrate activity and availability to Snowfinches (Losapio *et al.* 2016).

Data analysis

We built generalized linear mixed models (GLMMs) to evaluate whether landscape composition, meteorological conditions and season progression affected fine-scale habitat selection for foraging Snowfinches. We built models to quantify the effects of the above factors on the use of snowfields and of snow-bare substrate margins versus all other habitats. We selected snowfields and snow-bare substrate margins as they are the most sensitive to climate change, being directly dependent only on spring snow cover, which is steadily decreasing in the Alps (Klein *et al.* 2016). Snowfinch pair identity was entered as random factor to take into account the non-independence of records. Factors entered in the model were: date (as Julian date), sky cover (factorial), wind (factorial), percentage cover in the 300 m radius of grassland, snow, bare substrate and other habitats. All variables were standardized before analysis. To avoid overfitting and possible biases due to multicollinearity, we first built three models, one for meteorological factors and date, and two for habitat cover variables. Given that some pairs of land-cover variables were correlated (snow and grass: $r = -0.67$, grass and bare substrate: $r = -0.54$), we tested their effect by means of two separate models, the first including snow and bare ground cover ($r = -0.11$), and the second grassland and other habitats ($r = -0.41$). For each one of the three groups, we performed a model selection procedure based on an information-theoretic approach (Burnham & Anderson 2002), ranking all possible models within a group according to the Akaike Information Criterion corrected for small sample sizes (AICc). Then, from each of the three procedures of model selection, we selected the variables comprised in the most parsimonious (ΔAICc < 2) models (excluding the 'uninformative parameters' *sensu* Arnold 2010), as done

Table 1. Number of surveyed pairs, foraging locations and surveys (number of days-per-pair at a given site) and average landscape composition (300 m radius around the nests) for the different study areas; mean values are shown because within-study variations occurred because of snowmelt progression. The category 'other' includes man-made areas and water bodies.

Area	No. of pairs surveyed	No. of foraging locations	No. of surveys	Grassland cover	Snow cover	Bare substrate	Other
Passo Gavia	1	39	2	28.6	6.4	55	10
Passo Pordoi	2	80	4	71	4	20	5
Passo Sella	2	80	4	71.5	2	8.5	18
Passo Stelvio	10	216	15	15.3	21.1	33.8	29.8
Rosetta	2	40	2	14	5	81	0
Overall	17	455	27	36.0	12.1	32.9	19.0

in other studies (Jedlikowski *et al.* 2016). With these variables we built a single GLMM relating the use of a given fine-scale habitat (snowfields or margins snow-bare) to the selected meteorological and landscape factors (Assandri *et al.* 2016). All possible models were again ranked according to AICc. We then calculated marginal (variance explained by fixed effects only) and conditional R^2 (variance explained also by the random factor). All analyses were performed in R (R Development Core Team 2016) with packages lme4 (Bates *et al.* 2015) and MuMIn (Bartoń 2016). Variable effects according to the GLMM model were plotted with the package Visreg (Breheny & Burchett 2018).

Results

Data on 455 foraging locations were collected (Table 1) of which 130 (28.6%) occurred on snowfields or snow-bare substrate margins (68 and 62, respectively). Most of the other records occurred in grassland habitat (36.5%) or at snow-grassland margins (30.5%).

The use of different fine-scale habitats was related to the landscape composition. A single most supported model was identified at the final step (all other models ΔAICc > 2; Table 2). The use of snowfields and snow-bare margins decreased as the season progressed (Figure 1) and with grassland cover (Figure 2), while it was positively affected by wind (proportionally to wind intensity; Figure 3). Marginal R^2 of the model was equal to 0.29 (conditional $R^2 = 0.67$) and there was no overdispersion.

Discussion

Climate change is one of the main threats to biodiversity and represents a major pressure on several ecosystems and species over the coming decades (Scheffers *et al.* 2016). However, even for the species most likely to be negatively affected by climate change (such as mountain birds, Scridel *et al.* 2018), the impact is potentially multi-faceted and affected by abiotic or biotic factors, such as habitat/microhabitat characteristics, or the availability of key resources largely not dependent on climate conditions (Scheffers *et al.* 2014, Bowden *et al.* 2015, Brambilla *et al.* 2018). Species, populations or individuals that mostly rely on climate-dependent resources are the ones most at risk because of the direct impact of climate change. However, this topic has so far received little investigation, and we are not aware of studies focusing on the use of climate-dependent resources by animal species at a fine scale in relation to the broader environment they inhabit. Nevertheless, different degrees of reliance on such resources would result in different levels of resilience and vulnerability: species or individuals using a larger amount of other resources, which are not strictly dependent on climate, would display a higher resilience and a lower vulnerability to climate change.

In several Arctic and alpine environments, earlier snowmelt is a major driver of ecological change and could affect several species and ecosystems. Animal species relying on snowfields are thus particularly at risk (Rosvold 2016); they include the Snowfinch, which typically forages on or at the margin of snowfields, especially during the critical phase of nestling rearing (Brambilla *et al.* 2017b). The shorter duration of snow cover (Klein *et al.* 2016) and the lower availability of snowfields will dramatically reduce the availability of three of the fine-scale habitats exploited by Snowfinches during the crucial phase of its life cycle (Brambilla *et al.* 2018). Snowfields and the two types of snow margins hosted more than half of the foraging events recorded in our study. The negative effect of date on the probability of foraging on snowfields/snow-substrate margins could be due to changes in prey abundance or availability, or to a decrease in snow patches and/or an increase in grassland, with consequent increased use of the latter at the expense of snowfields. Other passerine species are known to use upland grassland at increasing elevation as the breeding season progresses, likely because of an increase in invertebrate availability in those habitats (Brambilla & Rubolini 2009).

According to our results, this impact of climate change will not affect all pairs/populations homogeneously, but the effects will be particularly important for those inhabiting areas dominated by bare substrates. In Snowfinches, the probability of foraging on snowfields or on snow-bare substrate

Table 2. Most supported (ΔAICc < 2) models for the use of snowfields and snow-bare substrate margins by breeding Snowfinches during the nestling rearing phase. For the categorical variables sky cover and wind, + indicates the inclusion in the model.

Intercept	Bare substrate	Date	Sky cover	Wind	Grassland	df	logLik	AICc	Delta
−2.56		−1.25		+	−1.96	6	−194.62	401.40	0.00
−2.56	0.10	−1.26		+	−1.92	7	−194.60	403.40	2.03
−2.30		−1.13	+	+	−1.96	8	−193.58	403.50	2.06
−2.31	0.25	−1.12	+	+	−1.84	9	−193.50	405.40	3.98
−2.76			+	+	−1.33	7	−195.62	405.50	4.07
−2.57				+	−1.29	5	−198.43	407.00	5.58

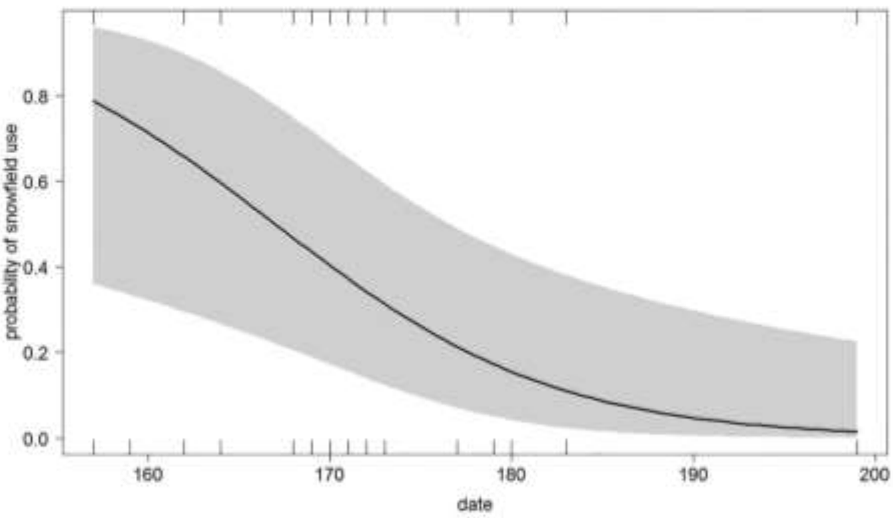

Figure 1. The probability of use of snowfields and snow-bare margins by breeding Snowfinches during the nestling rearing period in relation to season progression.

margins rather than in other fine-scale habitats decreased with increasing grassland cover. Grassland occurrence reduces the dependency on snow, being a high-suitability alternative foraging habitat (Brambilla *et al.* 2017b, 2018), but in rocky landscapes, where grassland is scarcer or even absent, Snowfinches have to rely on snow-related fine-scale habitats. In fact, snowfields are likely to be suitable for foraging Snowfinches even in rocky environments, as they 'trap' invertebrate fallout. The importance of wind-carried invertebrates on snowfields (Antor 1995) is confirmed by the higher use Snowfinches make of snowfields with weak and, especially, moderate or strong wind (Table 2), when invertebrates are more likely to be blown by wind and deposited on snow. Data from the site dominated by bare substrate investigated in our study (Rosetta area) confirmed the importance of grassland and snow for Snowfinches. Thirty-eight out of 40 (95%) foraging events recorded for the two pairs breeding there were in grassland, snow or margin snow-grassland, even though the average cover of grassland and snow totalled only 19%. Only two foraging events occurred on bare substrates, despite an 81% cover of the landscape. Even grassland could be subjected to climate change impacts, for example, because of treeline upshift (Harsch *et al.* 2009), potentially affecting Snowfinch pairs breeding at the lowest parts of the species' elevational range, or

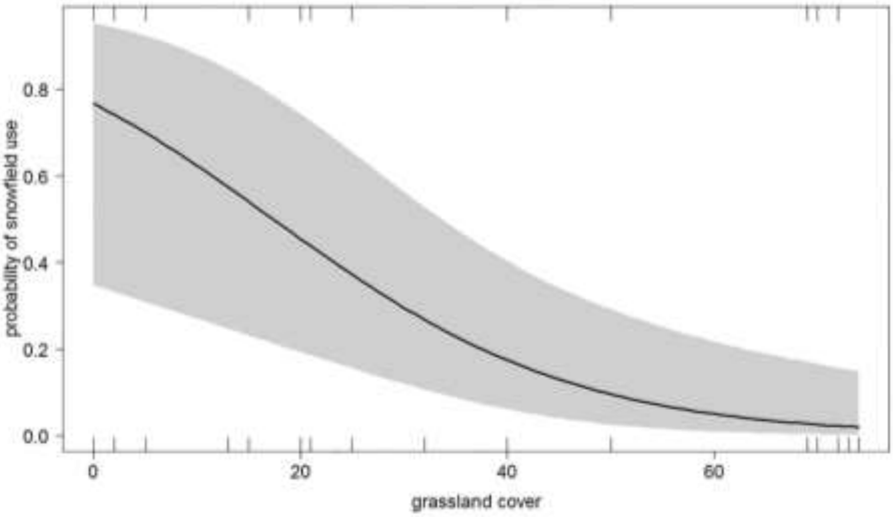

Figure 2. The probability of use of snowfields and snow-bare margins by breeding Snowfinches during the nestling rearing period in relation to grassland cover.

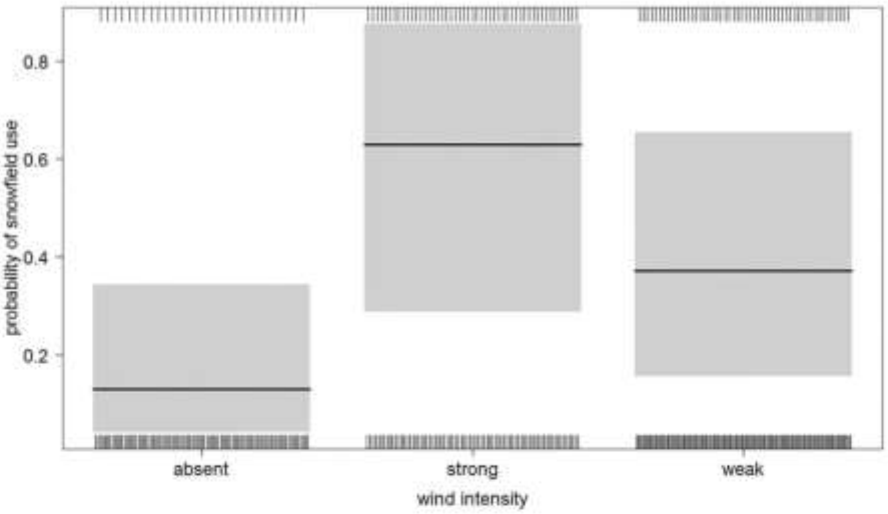

Figure 3. The probability of use of snowfields and snow-bare margins by breeding Snowfinches during the nestling rearing period in relation to wind intensity (moderate and strong wind considered together; see text).

because of change in structural parameters, in particular sward height (Brambilla *et al.* 2018). Nevertheless, grassland is clearly less likely to be affected than snowfields by the direct impacts of climate change.

Pair identity explained a substantial portion of deviance in the model (conditional R^2 definitely higher than marginal one; see Results): also local characteristics, social factors and/or individual traits are likely to contribute to the process of foraging habitat selection (Aplin *et al.* 2014), and hence may contribute to further modulate the potential response to environmental changes. Local characteristics may include height of the grassland sward (Brambilla *et al.* 2018), invertebrate abundance/availability in different habitats, habitat-specific disturbance or individual habituation to some specific patches (pers. obs.).

In conclusion, rock-dwelling Snowfinches will pay a higher cost to climate change, as the shortening of snow cover duration will result in the loss of most or all the suitable foraging fine-scale habitats during the most critical part of their life cycle. The conservation (and correct management, Brambilla *et al.* 2018) of alpine grassland, including the scarce grassland patches within sites dominated by bare substrates, is pivotal for the preservation of suitable foraging habitat for Snowfinches, under scenarios of predicted reduction in snow cover (Brown & Robinson 2011, Derksen & Brown 2012, Klein *et al.* 2016). However, if the overarching changes imposed by climate change in the long-term will disrupt ecological and food networks, even these small-scale habitats will lose suitability. Nevertheless, fine-scale environmental variations are essential for species' responses to climate change and should be included in adaptation strategies (Bradbury *et al.* 2011), exactly as local and landscape traits must be considered in management plans (Buchanan *et al.* 2017).

We highlight how coupling patterns of resource selection at fine scales with broader scale habitat descriptors may help understand and predict the potential impact of climate change on wild species, by combining a mechanistic assessment of species-habitat relationships with landscape characteristics. This approach could be used to define and evaluate the potential effectiveness of planned conservation strategies, such as the identification of priority sites for conservation or useful measures to increase species resilience to climate change.

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SECTION II: *Chapter VI*

Dynamic habitat selection in a high-elevation species: fine-tuning microhabitat use to match prey availability

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White-winged snowfinch, Passo Sella.

In preparation

Dynamic habitat selection in a high-elevation species: fine-tuning microhabitat use to match prey availability

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ABSTRACT

Microhabitat selection is a key driver of species ecology and their conservation, but it has been little investigated and mostly considered a static process where different microhabitats are preferred over others. Dynamic microhabitat selection, adjusted to better match spatio-temporal variations in prey availability, could be crucial for species living in harsh or extreme environments, where resources are limited and highly affected by climate change. We aimed at understanding drivers and adjustments of foraging microhabitat selection in snowfinches *Montifringilla nivalis*, a high-altitude species vulnerable to climatic changes, by analysing the availability of invertebrate preys across microhabitats exploited by the species during the breeding period. We assessed this by calculating the proportional use of each microhabitat and relating this to various measures of invertebrate abundance and diversity at the same spatio-temporal scale. We found that snowfinches selected in order of importance, alpine grassland, margin snow-grassland, margin snow-bare substrate, snow and bare substrate microhabitats. In addition, they were able to adjust the proportional use of different microhabitats in relation to local and temporal insect availability (positive effect). We also found a weak negative effect of arachnids, with snowfinches selecting areas with lower availability of spiders, mites and harvestmen. Arachnids are common predators in high-elevation mountain systems and may potentially act as indirect competitors of snowfinches. Our study provides a first demonstration of dynamic microhabitat selection in extreme terrestrial environments; further works should investigate how species can cope at the microhabitat scale with variation in resources also in other systems and in relation to ongoing environmental changes.

Keywords: snow, mountain, *Montifringilla nivalis*, climate change, birds

1. INTRODUCTION

Central to the study of animal ecology is the understanding of processes underpinning species distribution and the use that species make of the environment (Cody 1985, Levin 1992). This implies investigating what factors drive the use of certain habitats instead of others, according to a process generally referred to as habitat selection, which should allow a species to choose habitats where it can meet its ecological needs (Johnson 1980, Hutto 1985). Habitat selection has been investigated over very different spatial and temporal scales (e.g. foraging, nesting, migration), and studies suggested that for many species habitat selection is a hierarchical process encompassing different ecological scales and stimuli (Wiens 1989, Boyce et al. 2003, Jedlikowski et al. 2016, Schwemmer et al. 2016). For instance, habitat selection has been shown to govern macroecological patterns (e.g. species' geographical limits; Peterson 2003, Elith and Leathwick 2009), home range composition (Dickson and Beier 2002, Santangeli et al. 2012), migratory routes (Rettie and Messier 2000, Boone et al. 2006) and small-scale selections choices like nest location sites or sites holding key prey items (Martin 1996, Clark and Shutler 1999, Johnson and Sherry 2001).

A crucial aspect of habitat selection in animal species is to elucidate the use of microhabitats in spatio-temporally discrete areas that offer fundamental resources for life history functions (Barbosa et al. 2010). Indeed, the selection of the correct microhabitat is regarded as critically important for many animal species as it influences fitness (Partridge 1978), for example by improving foraging efficiency (Biscardi et al. 2007), reducing costs of thermoregulation (Du Plessis et al. 2012), providing shelter from predators (Skelhorn and Ruxton 2013) and it has even effects on species' survival and reproductive success (Wilson 1998, Jedlikowski and Brambilla 2017). Furthermore, studies investigating microhabitat selection are becoming increasingly important in the context of climate change, as small-scale habitats can maximise the resilience and resistance of populations (i.e. *refugia* sites; Barbosa et al. 2010, Suggit et al. 2011, Keppel et al. 2012, Frey et al. 2016, Betts et al. 2017, Brambilla et al. 2017). This may be pivotal in terms of biodiversity conservation, for example when the preservation of a species' entire geographic range in unfeasible, but the conservation of its habitats and microhabitats may be achievable.

In birds, microhabitat selection has been largely investigated as a function of habitat characteristics (Davis 2005, Watanuki et al. 2008, Visinoni et al. 2015, Winiarski et al. 2017, Swaisgood et al. 2018) and/or of prey availability and accessibility (Colwell and Landrum 1993, Whelan 2001). When both the effects of these two main drivers have been assessed, they have been often evaluated over different spatial or temporal extents (Guillemette et al. 1992, Johnson and Sherry 2001, Barbaro et al. 2008). Moreover, these have often been modelled separately leading to a potential spatial, temporal and conceptual mismatch between the observation of predators and environmental data such as prey-predator distribution. Modelling their combined effects at the same spatio-temporal scale is rare in the literature (but see Schwemmer et al. 2016), even if this could lead to a more precise inference of whether a species is able to adjust its microhabitat selection according to the presence of its prey items.

Although it is generally assumed that a forager distribution will occur at the highest prey densities to maximize their rate intake (Holling 1959a,b, Stephens and Krebs 1986, Zwarts and Wanink 1993, Wallace et al. 2015), there is some evidence that match between species presence and their food may be imperfect (Wiens 1976, 1977, 1989, Rotenberry and Wiens 1980, Martinez et al. 2010), because of different constraints including habitat complexity, presence of predators, density-dependent effects (Brown 1988, Heithaus et al. 2002, Piersma 2012). In birds, the relationship between predator-prey distribution at microhabitat level is still little studied. Theoretically, bird species target their foraging habitat according to a hierarchy of spatial and temporal scales, for example by selecting foraging microhabitats within their mesohabitat (Winiarski et al. 2017, Swainsgood et al. 2018,) and at landscape level (Schlacher et al. 2014). In addition, the search for prey-rich sites could correspond to well-defined habitat characteristics or to sites where preys are predictably found at accessible locations (Boyd et al. 2015). However, other factors can affect habitat selection, such as predation risk (Lindstrom 1990), density-dependent effects and distance to roost site (Gadenne et al. 2014) or scale- and/or time-dependent resource quantity and/or quality (Beerens et al. 2011). Interestingly, within the same area, foraging habitat selection may be predicted by food abundance for species exploiting easily assessable resources (i.e. fruits), and by proximate cues, such as vegetation structure, in species relying on less assessable resources like insects (Martin 1998, Wolfe et al. 2014), but drivers may be species-specific (Blendinger et al. 2012) and even individual-specific (i.e. conspecific attraction, site familiarity, age, sex; Piper 2011, Spiegel et al. 2017). Conversely, local variations on a common pattern of microhabitat selection could be expected if the environment they exploit is unpredictable, as for species living in dynamic (i.e. aquatic, costal) or extreme environments (i.e. high elevation/latitude systems, deserts), which should have developed strategies to cope with resource scarcity and highly variable in space and time (Beerens et al. 2015, Couribin et al. 2018); as an example, in desert mice, foraging microhabitat choice seasonally mirrors the pattern of resource availability (Vonshak et al. 2009), but similar variations could be expected also across space. Birds living in high-mountain systems (above the tree-line) are also similarly subjected to dynamic trophic changes in space and time. In these habitats, where local primary production is generally low, inputs from dispersing wind-borne arthropod fallout is a fundamental (yet unpredictable) resource for various breeding birds who collect invertebrates directly from snow patches (Antor 1994, Brambilla et al. 2017, Brambilla et al. 2018, Brambilla et al. 2019). Similarly, snow-melting margins and alpine grasslands are fundamental microhabitats to capture key invertebrates (i.e Coleoptera, Diptera, Lepidoptera), but their availability, accessibility and distribution may change on a daily basis as strictly dependent on the rate of snowmelt (Muscio et al. 2005, Gobbi et al. 2006, 2011, Brambilla et al. 2019).

With this study, we explicitly evaluate the potential adjustment of microhabitat selection during crucial phase of the nestling rearing period on the white-winged snowfinch *Montifringilla nivalis* (hereafter snowfinch) a high-elevation mountain species. By living in this highly-dynamic environment where resources change daily particularly in relation to abiotic factors (i.e. wind, temperature) we hypothesis that this species is highly adapted to track food availability in space and time. We assess whether birds may perform a dynamic habitat selection according to local prey availability across different types of microhabitats, which means modulating at a local scale the more general pattern of microhabitat use, in relation to the food resources available to individuals at a given site. We hypothesized that foraging individuals may increase or decrease (i.e. tuning) the use they make of a specific microhabitat, in relation to the prey availability offered by that microhabitat in a given site, therefore showing a dynamic microhabitat selection, which could be expected in species living in extreme environments where resources vary in space and time in an unpredictable manner.

2. MATERIAL AND METHODS

2.1 Model species

Our model species was white-winged snowfinch *Montifringilla nivalis* (L.), hereafter "snowfinch", a high-elevation Passeridae breeding across the Palearctic mountain ranges, from Iberia to the Tibetan plateau (del Hoyo et al. 2016). In Europe, the subspecies *Montifringilla nivalis nivalis* is confined to alpine nival and sub-nival habitats across the Cantabrian, Pyrenees, Corsica, Alps, Apennines and Balkans mountain ranges. This species lays one or, more rarely, two clutches per season, in a nest build with dry grass, moss and lined with feathers, located in either natural or artificial cavities such as rock crevices, ski-pilons, crags in building (i.e. mountain huts, ski resorts) and nestboxes (Cramp and Perrins 1994). Females lay between 4-5 eggs which are incubated for 12-14 days. Nestling fledge at 18-22 days and are fed by both parents for 12-15 days after leaving the nest (del Hoyo et al. 2016). During the nestling-rearing period, the adults feed their youngsters with a variety of food items, mostly arthropods collected for from the ground. According to the few references available, snowfinches diet during the nestling-rearing period is likely to vary depending on site but also according to snow availability. Invertebrates most commonly associated with snow patches are Diptera (particularly Tupilidae), Lepidoptera, Hymenoptera, Hemiptera, whilst in snow-free conditions diet seems to be primarily composed by Arachnida, Coleoptera, Orthoptera, but also Lumbricidae and Dermaptera (Cramp and Perrins 1994, Glutz von Blotzheim and Bauer 1997).

2.2 Study area

Pairs of snowfinches were studied in the Central and Eastern Italian Alps in the provinces of Sondrio, Brescia, Trento and Bolzano. Study sites were located between 2.200 and 3.020m asl, hence encompassing typical breeding snowfinch habitat above the treeline. Study areas were six in total and located around ski-pistes (Passo Sella, Passo Pordoi), mountain passes (Passo Stelvio, Passo Umbrail, Passo Gavia) and nival plateaux (Pale di San Martino), hence including a wide range of habitats from 'anthropized' mountain environments to alpine grasslands and rocky plateaux.

2.3 Foraging habitat selection

We monitored a total of 15 breeding pairs of snowfinches from the beginning of June to the end of July 2017. Breeding pairs were followed for one day during their provision from the foraging microhabitat to the nest, until reaching an ideal number of 20 consecutive foraging events per pair. However, due to the complexity in working in such extreme environments (adverse weather and terrain), we were not always able to achieve this objective. Indeed, the mean number of daily observations per pair was 17.7 (SE 0.9). For 9 out of 15 pairs we were also able to perform a second round of visits, 3-4 days after the first one. For each foraging event, we collected data on its exact geographical location and attributed it to a microhabitat type using a 1x1m quadrat according to 5 pre-identified categories, which represent the most important foraging habitats for the species (see e.g. Brambilla et al. 2017): i) snow patch (snow cover ≥90%); ii) grassland (grass cover ≥90%); iii) bare substrate (cover of bare ground, sand, rock, scree and/or boulders ≥90%); iv) margin snow-grassland; v) margin snow-bare substrate. Study sites contained all classes of microhabitats but at different proportions within 300m radius from the nest and all observations of foraging snowfinches occurred within the pre-defined microhabitats.

2.4 Invertebrate sampling

We collected data on invertebrate abundance, diversity and body size for each breeding pair and for each type of microhabitat to investigate if selection of foraging microhabitats by snowfinch can be adjusted according to local prey availability. To avoid the potential effect of predation by snowfinches on invertebrate availability, we specifically selected arthropod sampling sites just beyond the area most exploited by snowfinches for prey collection during the nestling rearing period. As snowfinches during this life stage mostly forage within 300m from the nest (Strinella et al. 2007, Brambilla et al. 2017), we sampled invertebrates at a slightly higher distance from each nest (mean distance of sampling sites from nest = 423.15, SE=46.4). In order to obtain a balanced sample of invertebrate measures across all microhabitats, for each nest and visit we randomly identified five transects that included a transition of all types of snowfinch foraging microhabitats (snow patch, margin snow patch-grassland, margin snow patch-bare substrate, bare substrate and/or grassland; Fig.1). Once transects were identified, we performed visual counts of 2 minutes long, stratified by microhabitat type. During this time, all arthropods present (dead or alive) within a 1x1m quadrat were broadly identified as either insects or arachnids and estimated for their body size (mm) as follow: arachnids from base of chelicera to the posterior end of opisthosoma; insects from the head to the last tergum; insect larvae from the head to the last urite. The appendages and legs were not taken into consideration. We established to base invertebrate assessment on visual counts, because we aimed at measuring invertebrate availability, which is the combined result of invertebrate abundance and detectability. Given that snowfinches perform a visual search of their preys, such counts should approximate well the availability of preys as perceived by our study species. Visual counts are a commonly used method in the literature, particularly for estimating abundances of butterflies (e.g. Pollard and Yates 1993), grasshoppers (e.g. Wettstein and Schmid 1999), Hymenoptera (e.g. Gunnarsson and Federsel 2014), spiders (e.g. Costello and Daane 1997). Other commonly used methods such as pitfall traps, sweep nets, sticky boards, suction sampler may screen invertebrates in a manner that can be considered unrepresentative of birds foraging behavior (Hutto 1990). This is particularly true for snowfinch which forages by picking conspicuous ground-dwelling invertebrates which stand out particularly well on typical high-elevation substrates such as snow, boulders, scree, short grass and bare ground (Brambilla et al. 2017, 2018). In order to minimize factors known to influence invertebrate variability (time of the day, temperature, cloud cover, wind), all surveys of foraging snowfinches and invertebrate sampling occurred either simultaneously or almost simultaneously (30 minutes after the foraging events) and in fine weather conditions (no rain, max. 5.5 m/s).

2.5 Statistical analysis

To test for a relationship between microhabitat selection and the relative invertebrate availability at the same spatial and temporal scale, we calculated the "proportional use" of each microhabitat as the proportion of foraging events occurred within a given microhabitat for each nest and visit. The proportional use was fitted as a response variable in Generalised Linear Mixed Models GLMM in R ("lmer" package; Bates et al. 2015) with a binomial conditional distribution of the response, weighted by number of foraging observations per nest and visit (Zuur et al. 2009). GLMM were choose in order to account for the non-independence of data points (foraging observations) across nest and visit by fitting a grouping variable named "nest ID" as a random factor. We applied multivariate descriptive statistics to understand which predictors (fixed effect) best explained the proportional use of microhabitats excluding models with combination of highly correlated predictors ($r>0.5$). Fixed effects included a categorical variable identifying each type of microhabitat and various measures of invertebrate availability, relative to each nest and visit: abundance (mean number of invertebrates summed up by quadrat and microhabitat), diversity (mean number of insects and spiders summed up by quadrat and microhabitat per each breeding pair) and body size (mean length of all invertebrates, insects and spiders summed up by quadrat and microhabitat). To account for overdispersion, an observation-level random effect was also included in all models (Bolker et al. 2009, Harrison 2014). We ranked all models according to second-order Akaike's information criterion (AICc; Burnham and Anderson 2002). We considered all models with ΔAICc < 2 to have received substantial support (Burnham and Anderson 2002). In addition to model comparison, we also calculated R2 values to estimate the variance explained by fixed factors only (marginal R2: R2m) or by both fixed factors and random factors together (conditional R2: R2c) (Nakagawa and Schielzeth 2013).

3. RESULTS

We obtained a total of 452 foraging observations of breeding snowinch, 267 (15 pairs) on the first visit and 185 (9 pairs) on the second visit. The most frequent foraging microhabitat selected by snowfinch was grassland (n=151; mean per session = 7.2, SE=1.4), followed by margin snow patch-grassland (n=132; mean per session = 6.3, SE=1.4, range), margin snow patch-bare substrate (n=58; mean per session=3.2, SE=0.6), snow (n=55; mean per session=2.4, SE 0.7), bare substrate (n= 15; mean per session = 1.3, SE=0.2). A total of 449 quadrats (grassland=145, snow=114, margin snow patch-grassland = 85, margin snow patch-bare substrate =61, bare substrate= 44) were used to sample the invertebrate community and resulted in total of 2891 arthropods recorded across all sites and microhabitats. The mean number of all invertebrates detected per quadrat varied greatly, but they were most commonly found on snow (mean=3.5, SE=0.5, n=114), margin snow patch-bare substrate (mean=2.8, SE=0.4, n=61), grassland (mean=2.5, SE 0.1, n=145), margin snow patch-grassland (mean=2.2, SE= 0.3, n=85), bare substrate (mean = 0.8, SE 0.1, n=61).

The model selection procedure, based on the AICc scores of GLMM models, identified two most supported models (Table 1). Predictors of the proportional use of microhabitats included in both models habitat type (with use of grassland, margin snow-grassland, margin snow-bare substrate, snow, bare substrate, in order of importance) and the insect abundance (with a positive effect). The most supported model (AICc=439.07; table 1) also included arachnid abundance (with a negative effect) and explained an appreciable proportion of the variance (R2m=0.20, R2c=0.20). The model therefore suggested a greater probability of microhabitat use by snowfinches with higher levels of insects across all habitats and also highlighted a negative (yet weaker) relationship with higher frequencies of arachnids across various habitats (Fig.1, table 2). The other partially supported model (ΔAICc < 2), which did not include arachnid abundance, explained a slightly lower proportion of model deviance (R2m=0.17, R2c=0.17; AICc= 440.92).

4. DISCUSSION

Dynamic habitat selection in animal species is essential to cope with varying resource distribution, especially in extreme habitats where resources vary in space and time. The main finding of our work is that, even if snowfinches select foraging microhabitats according to a well-established general pattern, they modify the proportional use of different microhabitats according to prey availability. Coherently with previous findings, breeding snowfinches forage mostly on grassland and retreating snowmargins, but they are able to spatially and temporally tune their foraging microhabitat selection to match greater availability of insects, and, more weakly, to lower densities of arachnids.

To our knowledge, this is the first study that models the combined effects of microhabitat selection with local prey availability at the same spatial and temporal scale for a high-elevation species. Dynamic habitat selection allowing to vary the relative frequencies of use of different microhabitats can be expected in species inhabiting harsh environments like high elevation systems. It is thus possible that other species, especially those living in environments with scarce and variable resources, could fine-tune microhabitat use in a similar way, to better cope with variation in food or other key resources. This knowledge could be very valuable also to evaluate and predict the impacts of climate change on those species.

4.1 Drivers of adaptive microhabitat selection in snowfinches

Our study confirms previous patterns on general foraging habitat selection by breeding snowfinches, which prefer microhabitats as grassland, snow margins and snow patches (Antor 1995, Strinella et al. 2007, Brambilla et al. 2017, 2018). The selection for these microhabitats is likely to be influenced by two important factors: prey abundance and accessibility. Previous studies carried out at broader scales highlighted how snowfinches make particular use of grassland and of the interface between grassland and snow; grassland is used almost exclusively when sward height is low, a condition which most likely improves prey detectability (Brambilla et al. 2017) and that is crucial for habitat suitability also in relation to climate change (Brambilla et al. 2018). Our invertebrate sampling revealed that invertebrate abundance was highest in snow patches (most likely due to a greater change of detecting prey; Antor 1995), still high on grassland and on snow-margins microhabitats, but low on bare substrates with no snow where prey detectability may be considered particularly high. Alpine grassland, which are recognized as biodiversity hotspots for phyto- and entomodiversity (Nagy and Grabherr 2009, Collins and Thomas 1991), can harbour some of the highest densities of arthropods, but prey detectability may be much lower than in snow habitats (Antor 1995); nevertheless, grassland was the most exploited microhabitat by snowfinches, followed by snow-grassland margins and by snow-bare margins and snow patches, the latter two being used with similar frequency. Bare substrate was the least exploited habitat, coherently with the lowest invertebrate availability. Therefore, snowfinches are likely to select foraging sites according to both prey abundance and detectability. In addition, also prey quality may be a key factor driving microhabitat selection: if considering the ranking of microhabitat based on prey abundance, snow patches should be the most profitable microhabitat to visit, but this was actually less exploited by snowfinches than grassland and snow-grassland margins. Snow patches harboured the highest availability of invertebrates, with most of them being fallout brought by upper air currents. For instance, one of the most common invertebrates found was the greater black spruce aphid *Cinaria piceae*, whose host is Norway spruce *Picea abies*, a tree species common at lower elevations, and lowland species such as the Colorado potato beetle *Leptinotarsa decemlineata*, a major pest of potato crops grown in the lowlands was also found. This dynamic pattern of wind-blown invertebrate influxes from the lowlands has been long known in the literature for its importance in sustaining life at high elevation and can found across mountain tops all over the world (Mani 1968, Antor 1994, Rosvold 2016). In our study areas, fallout found on snow patches was mostly composed by light and small insects, such as aphids (Hemiptera: Aphididae), flies (Diptera), midges (Diptera: Culicoides), ants (Hymenoptera), which might be not as suitable for snowfinch nestlings as the larvae present in grassland and melting snow margins. Retreating snow margins held accessible prey items as the weight of the snowpack kept previous year’s vegetation low, whilst new growth had still to emerge. Snow cover has fundamental insulating properties, influencing survival rates of many slow-growing high-elevation plants, insects and mammals (Hågvar 2010, Wipf and Rixen 2010, Berteaux et al. 2016). In addition, as the snow melts, it reveals moist microhabitats particularly suitable for hygrophiles and hygrobions invertebrates (i.e. Diptera, Coleoptera), typical insects of these high-elevation mountain environments (Mani 1968). Snowmargins appear to be particularly suitable for pupating craneflies (Diptera: Tupilidae), a keystone invertebrate prey for many mountain and upland birds across various latitudes including snowfinch (Cramp and Perrins 1994, Glutz von Blotzheim and Bauer 1997), Lapland longspurs *Calcarius lapponicus* (Tyron and Mclean 1980), Eurasian dotterel *Charadrius morinellus* (Galbraith et al. 1993), golden plover *Pluvialis apicaria* (Pearce-Higgins and Yalden 2004), ring ouzel *Turudus torquatus* (Cramp and Perrins 1994) and red grouse *Lagopus lagopus* (Park et al. 2001).

Rather surprisingly, we found a weak but negative effect of arachnid estimates on microhabitat use, with snowfinches selecting areas with lower availability of spiders, mites and harvestmen. Spiders have been acknowledged among snowfinch preys (Cramp and Perrins 1994, Glutz von Blotzheim and Bauer 1997), but on the other side they are among the most common high-elevation predators (Gobbi et al. 2011), feeding on a variety of invertebrates, including Diptera (Mani 1968). We can therefore suppose that arachnids may be indirect competitors of snowfinches, by preying upon the same insects, however more studies are required to better assess this possible effect.

4.2 Dynamic habitat selection: tuning responses to changing conditions

Species living in harsh and dynamic environments (i.e. where resources change at a relatively fast rate) may be expected to be able to track resources along their temporally and spatially variation. In such cases, species occurrence is potentially disconnected to static measures of habitat quality (Van Horne 1983). As far as we know, such behavioural adjustment has been only limitedly observed in animals in general and in birds in particular, with examples reporting waders feeding in accordance to changing water levels and prey availability (Beerens et al. 2011, 2015a,b, Schwemmer et al. 2016). Snowfinches and other high-elevation mountain birds must as well adjust to food resources that change quickly in relation to changes in snow cover and to unpredictable influxes of invertebrate fallout. Snowfinches showed good tuning in response to availability of their insect preys, particularly for grassland and snow-grassland microhabitats, the ones which were most exploited foraging microhabitats. Indeed, mountain regions and species are generally poorly studied (Scridel et al. 2018) but are valuable and novel model systems to investigate how species have adapted to live in extreme environments and to their changes, including by performing dynamic habitat selection allowing them to tune the use of foraging microhabitats to prey availability.

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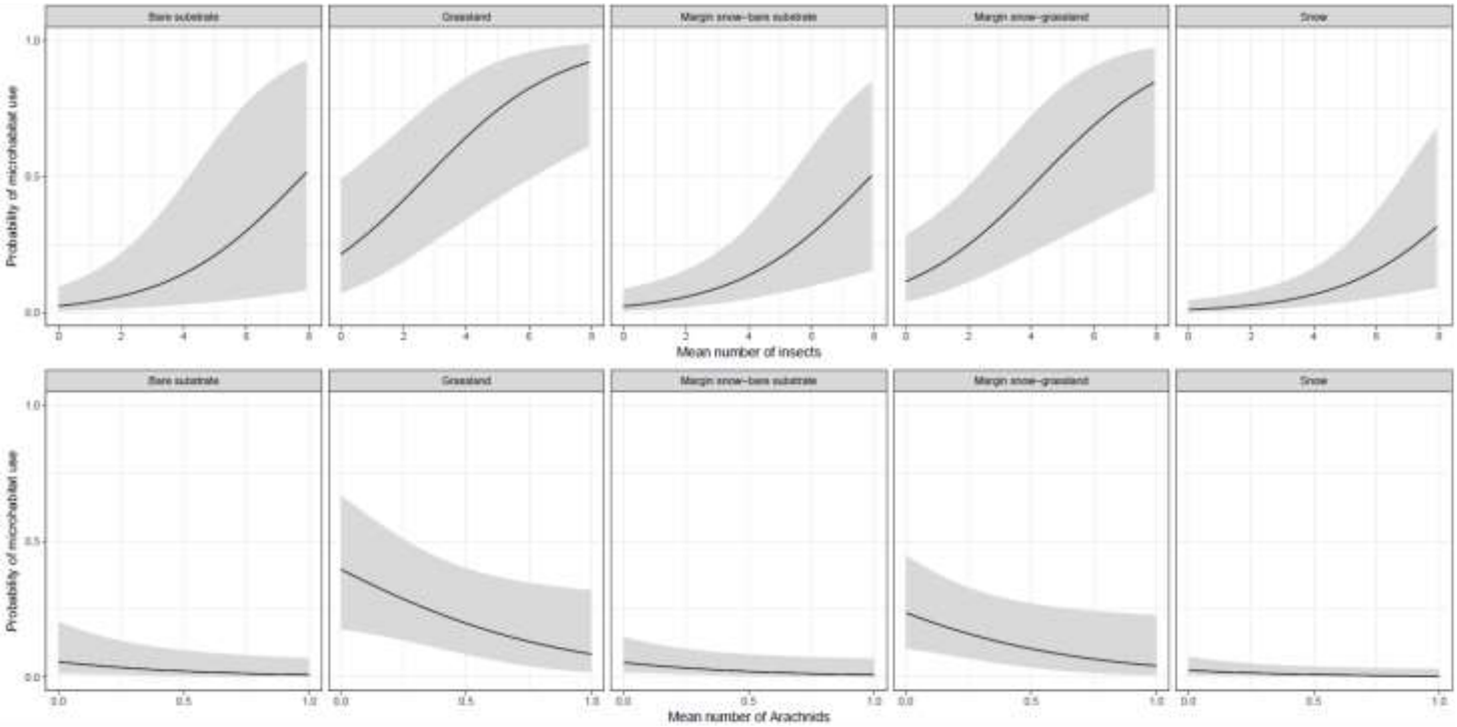
Table 1 Summary of all generalised mixed effects models performed to assess a relationship between the probability of microhabitat use with various measures of invertebrate frequency, diversity and size. Models are ranked according to Akaike's Information Criterion (AICc) and their difference between models (ΔAICc). *k* indicates the number of parameters estimated in each model.

Model	*k*	**AICc**	**ΔAICc**
Mean number of insects + mean number of arachnids + habitat	8	439.07	-
Mean number of insects + habitat	7	440.92	1.85
Mean number of all invertebrates + habitat	7	442.56	3.49
Mean length insects + habitat	7	447.74	8.67
Mean length all invertebrates + habitat	7	447.80	8.73
Mean number of arachnids + habitat	7	448.02	8.95
Habitat	6	448.56	9.49
Mean length insects + arachnids + habitat	8	449.18	10.11
Mean length arachnids + habitat	7	449.98	10.91
Null model	5	454.97	15.90

Table 2 Model output from the most supported GLMM model showing coefficients and relative standard errors for fixed effects. In experimental design models, the intercept coefficient includes bare substrate.

	Estimate	Std. error	z value	Pr(>|z|)
(Intercept)	-3.685	0.731	-5.04	<0.001
Arachnida	-1.962	1.002	-1.96	0.050
Insects	0.474	0.144	3.28	0.001
Habitat (grassland)	2.391	0.886	2.70	0.007
Habitat (margin snow-bare substrate)	-0.050	0.950	-0.05	0.958
Habitat (margin snow-grassland)	1.641	0.865	1.90	0.058
Habitat (snow)	-0.841	0.970	-0.87	0.386

Figure 1 Fitted probabilities (±CI) of microhabitat use according to mean number of insects and arachnids. across each class of microhabitat.



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SECTION II: *Chapter VII*

Sex-dependent effects of weather on the survival of a high-elevation bird species

ELISEO STRINELLA, DAVIDE SCRIDEL, MATTIA BRAMBILLA, CHRISTIAN SCHANO, FRÄNZI KORNER-NIEVERGELT

Nestling of white-winged snowfinch, Stelvio National Park. Photo: A. Forti.

In preparation

Sex-dependent effects of weather on the survival of a high-elevation bird species

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Abstract

Mountain ecosystems are recognized as world's biodiversity hotspots, hosting highly specialized and endemic species which are particularly susceptible to climatic changes. Though, the mechanisms how climate change affects species population dynamics are still largely unknown, particularly so for mountain birds. We investigate how weather variables correlate with survival of the White-winged Snowfinch *Montifringilla nivalis* a high-elevation species confined to the alpine and nival zone. We analyzed a 15 year (2003-2007) mark-recapture dataset of 671 individuals from the Apennines (Italy) using mark-recapture models. We estimated annual apparent survival to be similar between males and females (average □ = 0.46), but varied greatly (0.17-0.81) between years and sexes. Monthly apparent survival was lower in winter compared to summer. Female annual apparent survival was negatively correlated with warm and dry summers and with cold, snow-rich winters, whereas these weather variables had the opposite or no effect on male apparent survival.

Remarkably, the average apparent survival measured in this study was lower than in the Eastern European Alps 1973-1990. Recent survival of Snowfinches in the Apennines may be lower than they naturally have been because of changes in their environment that have been caused by global warming. Indeed, our results indicate that weather strongly influences the demography of the Snowfinch affecting differently male and female survival. Possible, non-exclusive mechanisms may include sex-dependent physiological limits to higher temperatures, weather-dependent food availability, and weather-dependent trade-off between reproduction and self-maintenance. This results not only contribute to the understanding of the mechanisms driving Snowfinch population dynamics but improve our current and limited understanding of the decline of mountain birds in general. Further high-quality data on all aspects of demography of different high-elevation species and populations are urgently needed in order to fully comprehend and counteract negative effects of climate change on the population trends of cold-adapted species.

Introduction

Mountain ecosystems are recognised as world's biodiversity hotspots, hosting highly specialized and endemic species (Körner & Ohsawa 2006; Myers *et al.* 2000; Dirnböck, Essl & Rabitsch 2011;) which are threatened by human-induced causes including climate change (Böhm *et al.* 2001; Auer *et al.* 2007; Brunetti *et al.* 2009; Pepin *et al.* 2015; Scridel *et al.* 2018). Mountain regions are particularly susceptible to climatic alterations and are experiencing a faster rate of warming compared to global average. Indeed, the European Alps have warmed about 2°C in the past 100 years, with the biggest increase being in the last three decades (Böhm *et al.* 2001; Auer *et al.* 2007; Brunetti *et al.* 2009). In parallel to changes in temperature, the frequency of extreme weather events is also increasing (Dieffenbaugh *et al.* 2017) and effects of this increase have so far been poorly investigated (Chapin and Körner 1994).

Organisms living in the most extreme mountain environments, such as the alpine and nival belts, may be vulnerable to changes in their environment and climate because of several reasons. Firstly, they may already live at the edge of their physiological niche, and even small shifts in one environmental or climatic factor may render an area unsuitable (Tingley, Monahan, Beissinger & Moritz 2009). Secondly, extreme environments are often inhabited by highly specialized species that are adapted to local conditions and, therefore, they may not be flexible enough to adapt their behavior, ecology or life-history traits rapidly enough to cope with changes in the environment and climate (Martin & Wiebe 2004; Cheviron & Brumfield 2012; Barve, Dhondt, Mathur & Cheviron 2016), but see below. Thirdly, many alpine species have a limited distributional range, or are even endemic: the loss of a few populations increases extinction risk of the species and consequently represents a threat to global biodiversity (La Sorte & Jetz 2010). On the other hand, high-elevation environments are highly variable in space and time due to unpredictable weather conditions. As solar radiation increases with increasing elevation (Blumthaler *et al.* 1999), species at high elevations can experience under direct sunlight extremely warm temperatures (>25° C in the European Alps) which can be unpredictably followed by opposite weather patterns with cold temperature and even snow storms. Inhabitants of these variable environments must show a high physiological and behavioral flexibility to cope with sudden abiotic changes within short periods of time.

In birds, the adaptations for living in alpine zones may be as manifold as there are species (Potapov 2004). Nevertheless, meta-analyses showed that populations at higher elevations have lower fecundity (number of breeding attempts and clutch size) but slightly heavier nestlings and higher juveniles survival compared to their conspecifics at low elevations (Badyaev & Ghalambor 2001; Boyle, Sandercock & Martin 2016). With regard to adult survival, we would expect that alpine species, compensate the risk of unpredictable conditions during the reproductive season with a longer life span (Tavecchia *et al.* 2002; Martin & White 2009). This seems to be the case in some alpine bird species (e.g. White-tailed Ptarmigan *Lagopus leucurus* in the alpine zone of the Rocky mountains compared to populations in the sub-alpine zone and Arctic, Sandercock, Martin & Hannon 2005a; an alpine subspecies of Horned Lark *Eremophila alpestris* compared to a lowland subspecies, Camfield, Pearson & Martin 2010). However, this does not seem to be universal Badyaev &

Ghalambor 2001; Sandercock, Martin & Hannon 2005b; Hille & Cooper 2015) and various calls have been made to improve basic knowledge on demographic parameters for the mountain bird community (Hille & Cooper 2015). This would be a crucial step for understanding how life-history traits of mountain birds are shaped by their extreme environment, and consequently understand the needs and vulnerability of their populations.

We studied the survival of a high-elevation bird species, the European subspecies of the White-winged Snowfinch *Montifringilla nivalis nivalis* (hereafter Snowfinch). It breeds exclusively above the treeline in southern European mountains. In the Alps, the species has lost part of its former distribution and population density decreased during the last decades (Willi & Kilzer 2011; Issa & Muller 2015; Kilzer, Nardelli *et al.* 2015; Knaus *et al.* 2018). There is evidence that global warming may be an important cause of this population decline: a comparison across species showed a correlation between thermal niche and changes in distribution ranges in Italy. The distribution of cold-adapted species, mostly restricted to the Alps, like the Snowfinch, generally shrunk during the last 30 year, whereas species of warm habitats expanded their distribution (Scridel *et al.* 2017). Further, both distribution models (Brambilla, Pedrini, Rolando & Chamberlain 2016; Brambilla *et al.* 2017) and fine-scaled habitat selection studies (Brambilla *et al.* 2017b; Brambilla *et al.* 2018) suggested that the Snowfinch is highly dependent on climate sensitive habitats (i.e. snow patches and short alpine grassland) and therefore it is potentially threatened by global warming.

The specific aims of this study are threefold. Firstly, we estimate annual survival for adult males, adult females and juveniles in order to fill in the knowledge gap in the life-history of this high-elevation specialist. Secondly, we describe how survival changes over the annual cycle in order to identify periods with higher mortality, a key information to better understand the factors driving annual survival. Thirdly, we assess the role of summer and winter temperatures as well as precipitation on males' and females' annual survival. The findings of this study will improve our current understanding of mechanisms underlying demographic trends and life history traits for a poorly studied group of species adapted to extreme and dynamic environment and potentially threatened by climate change and will also help predicting future population developments under climate change.

Methods

Study site and the capture-recapture data set

From June 2003 to June 2017, 671 Snowfinches were caught with mist nets and net traps in the Italian Apennine mountains within Gran Sasso National Park, specifically in the areas of Campo Imperatore and Monti della Laga" (42°27 N, 13°34 E, altitude 2000m, see Strinella, Cantoni, Faveri & Artese 2011). Captures took place all year round but more intensively during the summer (Table 1).

Table 1. Seasonal distribution of the captures (total 671 individuals) and recaptures.

month	1	2	3	4	5	6	7	8	9	10	11	12
first captures	21	13	14	14	67	165	141	184	24	18	7	10
recaptures	15	12	11	15	14	61	35	34	6	4	0	4

The Snowfinches were marked with individual metal rings and, if possible, their age and sex were identified according to (Strinella, Catoni, Faveri & Artese 2013). Of the 671 individuals, 101 were marked as nestlings and 570 as fully grown. Almost a quarter of the individuals, 157, were identified as males, 104 as females and for 410 individuals sex could not be identified. Of the 671 marked individuals, 138 were later recaptured between 1 and 6 times.

Weather data

We obtained data on daily minimum/ maximum temperatures (°C), precipitation (mm per day) from two local weather stations Assergi and Castel del Monte (Ufficio Idrografico e Mareografico Regione Abruzzo) for the year 2003 to 2017. Daily minimum and maximum were highly correlated (Pearson's correlation r=0.93). We used the average between the minimum and maximum temperature of both stations in order to measure average daily temperature. Precipitation was summed over the two stations for obtaining a measure of precipitation in the study area. We then averaged temperature and precipitation over the summer months (June to September) and over the winter months (November to March) for each year. These four weather variables were used to predict annual apparent survival (from summer to summer of the following year).

Survival models

General model structure

We used mark-recapture models (Lebreton, Burnham, Clobert & Anderson 1992; Cormack 1964; Jolly 1965; Seber 1965) that we applied to two different temporal aggregations of the mark-recapture data set. The first analysis aimed at assessing correlations between weather variables and annual apparent survival. In the second analysis, we described seasonal patterns of monthly apparent survival probabilities. The general model structures in both analyses were equal but they differed in the length of the time periods (years vs. months) and the predictors for survival (see below). For the first analysis, we aggregated the data in annual time intervals (1st January – 31st December; mean capture date within this interval is 30th June), and for the second in monthly time intervals. For the annual data, time period t was one year (of 15 years in total), and for the monthly data, time period t was one month (of 169 months in total).

The observations y_{it}, an indicator of whether individual i was recaptured during time period t, were modelled conditional on the latent true state of the individual birds z_{it} (0 = dead or permanently emigrated, 1 = alive and at the study site) as a Bernoulli variable. The probability $P(y_{it} = 1)$ is the product of the probability that an alive individual is recaptured, p_{it}, and the state of the bird z_{it} (alive = 1, dead = 0). Thus, a dead bird cannot be recaptured, whereas for a bird alive during time period t, the recapture probability equals p_{it}:

$y_{it} \sim \text{Bernoulli}(z_{it}p_{it})$

The latent state variable z_{it} is a Markovian variable with the state at time t being dependent on the state at time t-1 and the apparent survival probability Φ_{it}:

$z_{it} \sim \text{Bernoulli}(z_{it-1}\Phi_{it})$

We use the term "apparent survival" in order to indicate that the parameter Φ is a product of site fidelity and survival. Thus, individuals that permanently emigrated from the study area cannot be distinguished from dead individuals.

In both models, the parameters Φ and p were modelled as sex-specific. However, for 61% of the individuals, sex could not be identified, i.e. sex was missing. Ignoring these missing values would most likely lead to a bias because they were not missing at random. The probability that sex can be identified is increasing with age and most likely differs between sexes. Therefore, we included a mixture model for the sex:

$\text{Sex}_i \sim \text{Categorical}(\mathbf{q})$

where **q** is a vector of length 2, containing the probability of being a male and a female, respectively. In this way, the sex of the non-identified individuals was assumed to be male or female with probability q[1] and q[2]=1-q[1], respectively. This model corresponds to the finite mixture model introduced by Pledger et al. (2003) in order to account for unknown classes of birds (heterogeneity). However, in our case, for parts of the individuals the class (sex) was known.

Annual survival models

We used two different models for annual apparent survival. In the first model, we estimated independent annual survival for each year, age and sex class (3 levels: juveniles, adult males and adult females):

Model 1: $\Phi_{it} = a_{t,\text{age.sex}[it]}$

In the second model, we constrained annual apparent survival to linearly depend on average summer and average winter temperature (summertemp, wintertemp) and precipitation (summerprec, winterprec), and on age and sex class. We estimated different effects of temperature and precipitation on apparent survival for juveniles, adult males and adult females:

Model 2: $\text{logit}(\Phi_{it}) = a0_{\text{age.sex}[it]} + a1_{\text{age.sex}[it]}\,\text{summertemp}_{[t]} + a2_{\text{age.sex}[it]}\,\text{wintertemp}_{[t]} + a3_{\text{age.sex}[it]}\,\text{summerprec}_{[t]} + a4_{\text{age.sex}[it]}\,\text{winterprec}_{[t]}$

Annual recapture probability was modelled for each year and age and sex class independently:

$p_{it} = \text{b0}_{t,\text{age.sex}[it]}$

Uniform prior distributions were used for all parameters with a parameter space limited to values between 0 and 1 (probabilities), and a normal distribution with a mean of 0 and a standard deviation of 1.5 for the intercept *a0*, whereas for *a1, a2, a3,* and *a4* a standard deviation of 5 was used.

Monthly survival model

We assumed that monthly survival differed between age and sex classes (first year, adult male, adult female), and seasons (Nov-March, April – June, July – Oct), $\Phi_{it} = a_{\text{sex.age}[i],\text{season}[t]}$. Independent, and slightly informative prior distributions $a_{\text{sex.age}[i],\text{season}[t]}$ ~ Beta(2,0.35) were used. This prior gives 95% of the mass to values between 0.3 and 1 and has a median of 0.938. An average monthly survival of 0.938 corresponds to an annual survival of 0.46. By choosing a prior distribution with a mean corresponding to the overall mean of the data we make sure that estimates for specific months deviating from the overall mean show information that is inherent to the data. Using a uniform prior, Beta(1,1), with a mean of 0.5 would result in estimates close to 0.5 for those months with a small sample size, i.e. during winter. This would bias the conclusion on seasonal differences in monthly survival.

Recapture probability was assumed to be different between each month and sex, leading to 36 independent estimates for recapture probability:

$p_{it} = \text{b0}_{\text{month}[t],\text{sex[i]}}$

Independent uniform prior distributions were specified for each of the recapture probability parameters.

$\text{b0}_{\text{month}[t],\text{sex[i]}} \sim \text{Beta}(1,1)$

We used Hamiltonian Monte Carlo as implemented in Stan (Carpenter et al. 2017; mc-stan.org) to fit the monthly survival model to the data. We simulated 4 Markov chains of length 2000 and used the second half of each chain for the description of the posterior distributions of the model parameters.

Convergence, stationary and mixing of the Markov chains were assessed by the metrics and diagnostic plots provided by the rstan and shinystan packages (Stan Development Team 2017), i.e. no divergent transition, number of effective samples above 1000, Monte Carlo errors below 10%, and R-hat value below 1.01.

Results

Annual recapture probability and apparent survival

Both models (1: independent survival for each year, 2: survival constrained to linearly depend on summer and winter temperature and precipitation) gave similar estimates for the probability of recapturing an individual during one year (Figure S1). The estimates varied between 0.05 and 0.81 dependent on year and sex. Average recapture probability of the males was 0.31 and for females 0.35.

When estimating survival independent for each year (model 1), uncertainty of the estimated apparent survival probabilities were very high (Figure 1). Nevertheless, a large between-year variance was also evident. Adult apparent annual survival varied from 0.17 to 0.81 between the years and sexes. No temporal trend was visible (Figure 1). The posterior distributions for juvenile apparent survival stretched between 0 and 1 in most years, indicating that there is virtually no information on juvenile survival in the data (Figure S2).

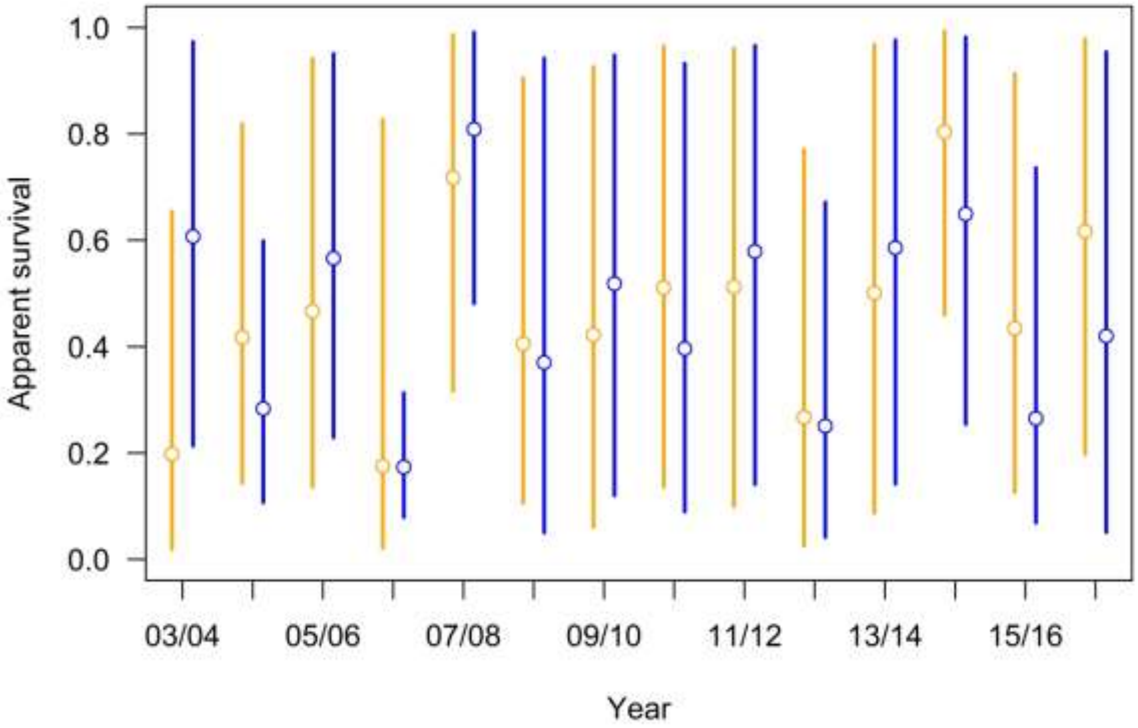

Figure 1. Annual apparent survival estimates for adult males (blue) and adult females (orange) estimated from the model with independent survival estimates for each year, age and sex class. Circles are means of posterior distributions, vertical bars are 95% credible intervals.

When constraining the annual survival to be linearly dependent on summer and winter temperature and rain, summer temperature was negatively (posterior probability, hereafter pp, = 0.92) and summer precipitation positively (pp = 0.90) correlated with adult female survival, whereas no correlations could be seen in males (Figure 2; pp of the hypothesis that female apparent survival correlated more strongly negative with summer temperature than male apparent survival: 0.87). Winter temperature and precipitation had the opposite effects compared to summer temperature and rain. In warmer winters, adult females survived better compared to colder winters (pp = 0.75), and winter precipitation were negatively correlated with female survival (pp = 0.78). Correlations between weather and survival were less clear for males, but they seem to survive slightly better in cold and snow-rich winters (Figure 2). Apparent survival estimates for juveniles were so uncertain (broad credible intervals, Figure 2) that we refrain from interpreting any correlations with weather variables.

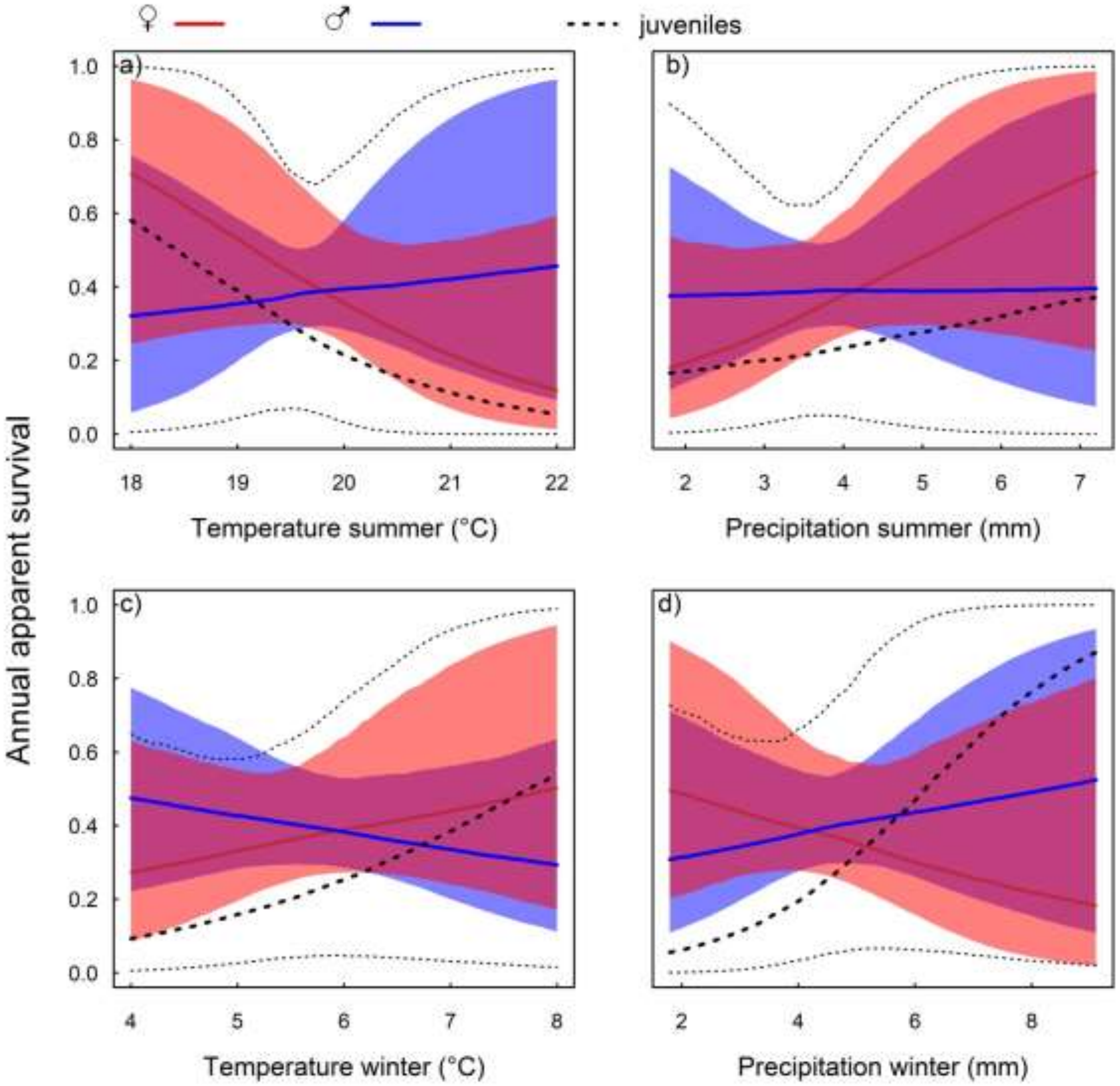

Figure 2. Annual apparent survival estimates for adult males (blue) and adult females (orange) against a) mean summer temperature (months June to September), b) mean summer precipitation, c) mean winter temperature, c) mean winter precipitation. Shaded areas = 95% uncertainty intervals. Dotted regression line with 95% uncertainty interval = juveniles.

Averaged over all years, apparent survival of female and males were very similar. Estimates varied between 0.36 and 0.46 depending on the model assumptions (Table 1).

Table 1. Annual apparent survival estimates for adult males, adult females and juveniles estimated from the two models. Model 1: independent survival between years; Model 2: survival constrained to be linearly dependent on summer and winter temperature and rain. In model 2, survival estimates are calculated for average temperature and precipitation values.

	Model 1: unconstrained survival		**Model 2: weather dependent survival**	
	Males	**Females**	**Males**	**Females**
Juveniles	0.38 (0.25 – 0.51)		0.16 (0.11 – 0.39)	
Adults	0.46 (0.38 – 0.54)	0.46 (0.38 – 0.55)	0.36 (0.28 – 0.44)	0.41 (0.11 – 0.72)

Monthly recapture probability and monthly apparent survival

Monthly recapture probability of juveniles could be estimated only with very large uncertainty (grey bars in Figure 3). Adult recapture probability varied between 0.01 and 0.15 (Figure 3). Highest recapture probabilities were in autumn, lowest in winter. There is no clear difference in recapture probability between the sexes.

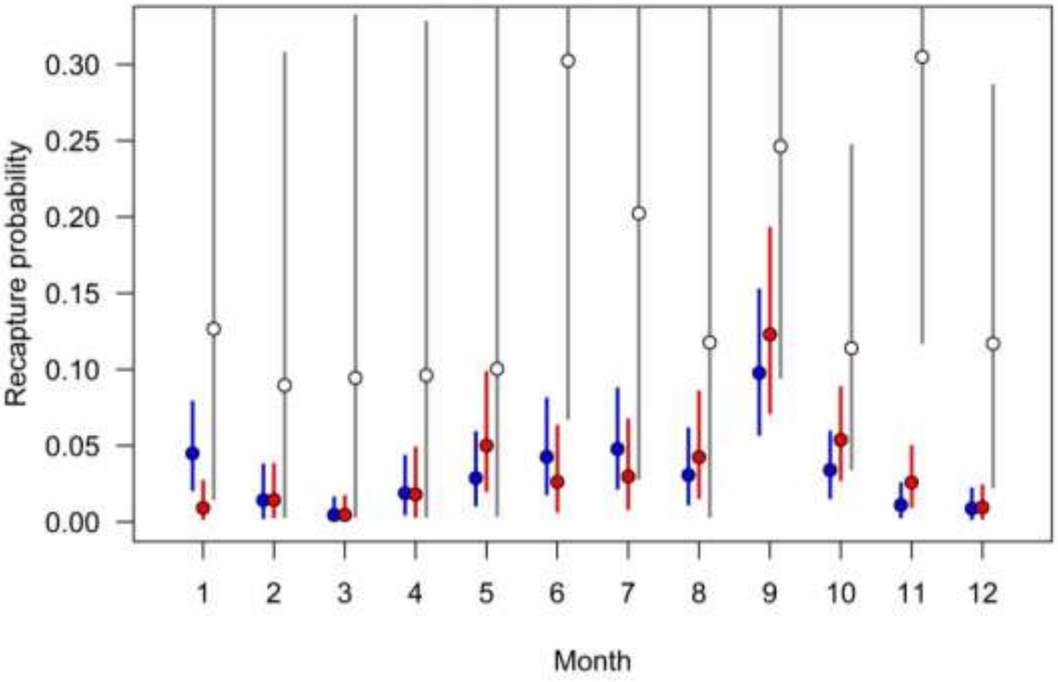

Figure 3. Posterior distributions of the recapture probability per month and sex. Blue = males, red= females, white/grey = juveniles. Filled circles = mean of posterior distribution, vertical bars = 95% uncertainty interval.

Apparent monthly survival during the winter months (November – March) was clearly lower compared to during the summer months (July – October; **Figure 4**) in both sexes.

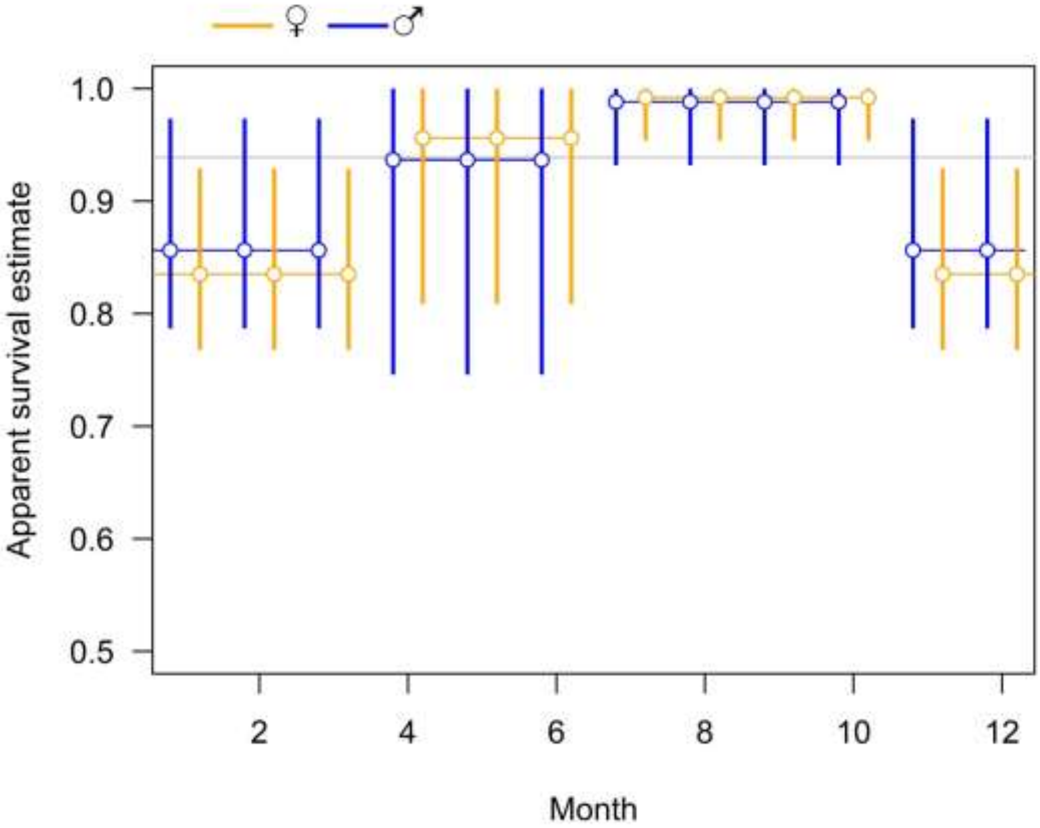

Figure 4. Monthly apparent survival of adult males and females. Circles = mean of the posterior distribution, vertical bars = 95% uncertainty intervals. Monthly survival estimates assumed to be equal are connected by horizontal lines. Grey horizontal line indicates the median of the prior distribution Beta (2, 0.35). Deviations of the estimates from this median is due to information in the data.

Juvenile monthly survival estimates showed high uncertainty: November – March: 0.75 (0.55-0.97), April-June 0.96 (0.83 – 0.99), and July- October 0.63 (0.45 – 0.99).

Discussion

Absolute annual survival estimates

The average annual adult apparent survival estimated in this study for Snowfinches based on mark-recapture data from 671 individuals in the central Apennines was around 0.46, a value similar for males and females. This estimate seems to be lower compared to earlier survival measures for Snowfinches in the Eastern Alps. Lindner (2002) reported that, out of 24 breeding birds, 14 returned at the next breeding season. This gives an apparent survival of 0.58 (95% uncertainty interval: 0.39-0.76). From 482 birds ringed in the Austrian Alps during the years 1973-1995 by Prof. A. Aichhorn, 52 were recaptured later (Markl 1995). The median age of these recaptured birds was 4 years (oldest bird was 14 years). These data indicate that annual survival must have been around 0.7 or even higher for those birds that survived their first year and stayed in the study area.

Thus, our estimate for annual adult apparent survival of 0.46 is substantially lower than the one obtained with a comparable method in the Austrian Alps 30 years earlier.

Adult annual apparent survival of the phylogenetically closely related House sparrow *Passer domesticus* in Norway was between 0.6 and 0.7 (Holand et al. 2014). Because body mass of Snowfinch is 1.5 times larger than the one of the House sparrow, according to allometric relationships we would expect that the Snowfinch has a higher survival compared to its smaller relative (Blueweiss *et al.* 1978).

Our estimate of 0.46 may be lower than expected or measured elsewhere because of several reasons. First, we might not have accounted for all capture heterogeneity in our analysis. Not accounting for capture heterogeneity in a mark-recapture model can lead to an underestimation of survival (Fletcher et al. 2012). Second, our sample of individuals may contain a high proportion of dispersing and transient birds. Third, the life span of Snowfinches in the Central Apennines during the years 2003 to 2017 may indeed have been shorter than expected due to unfavorable environmental conditions, or local adaptations of life-history characteristics.

Our models accounted for differences in capture probability and survival between three age and sex classes, juveniles, adult males and adult females, and between years and months respectively. We did not account for potential differences between different age classes among adults, because exact age was only known for a few individuals ringed as nestlings. However, bias in survival estimates caused by unaccounted heterogeneity in capture probability, normally is small and, therefore, we do not think that the difference between our estimate of apparent annual adult survival (0.46) and the one expected (around 0.6 or higher) can be explained by unaccounted heterogeneity in capture probability alone.

A predictive model checking revealed that our data contained slightly more individuals never recaptured after marking than the model would predict (598 observed vs. 548-599 predicted), whereas the number of individuals recaptured exactly once was slightly lower in our data compared to the model prediction (55 observed vs. 62-104 predicted). The number of individuals recaptured more than once matched the model predictions well (18 observed vs 6-27 predicted). This very slight lack of fit suggests that a small proportion of the individuals in our sample may have been so-called transients (Pradel, Hines, Lebreton & Nichols 1997). For the Alpine population, there is evidence that Snowfinches disperse also over larger distances, i.e. between the Alps and the Pyrenees, but the proportion of dispersers among the population is unknown (Resano-Mayor *et al.* 2017). Therefore, further investigations are needed to quantify dispersal which then would allow obtaining more reliable information on survival. Because in birds dispersal is generally higher in females compared to males (Schaub & Hirschheydt 2009; Forero, Donázar, Blas & Hiraldo 1999), we would expect a lower apparent female survival compared to male survival, if dispersal markedly affected our apparent survival estimate. However, we found similar apparent survival estimates for males and females. Further, the higher survival estimates from the Eastern Alps (Markl 1995) is potentially affected in a similar way by dispersal because this estimate was also based on mark-recapture data. Therefore, we believe that the unexpectedly low survival of Apennines Snowfinches estimated in this study is unlikely caused by dispersal.

Therefore, we infer that survival of Snowfinches in the Apennines is indeed lower than expected. This could be due to local adaptations of the life-history traits in Snowfinch populations of the Apennines (e.g., Bears, H., Martin & White 2009), or due to currently unfavorable environmental factors. Disentangling the two causes is topic of ongoing research. For the moment, we have more indications that unfavorable environmental factors caused the low survival: we found clear correlations of weather variables with survival estimates. Further, climatic factors have changed remarkably during the last 50 years in the Alps, and even more pronounced on the Apennines (Rogora *et al.* 2018), and it has been shown several times that many populations of mountain birds decreased due to climate change (Tingley *et al.* 2012; Lehikoinen *et al.* 2014; Scridel *et al.* 2018). The low adult survival found in this study from recent years may indicate that, for Snowfinches, climate-induced population declines may act via survival of adults.

Between-year and between month variance and weather influence

The strong between-year variance in apparent survival suggests that the latter is strongly dependent on weather. Indeed, both temperature and precipitation had a strong effect on female apparent survival, but less so on male apparent survival. We further showed that apparent survival is lower during the winter months compared to the summer months. This indicates that weather conditions that influence annual apparent survival may act during winter. Warm and dry summers and cold and wet winters were associated with low female apparent survival. In contrast, male apparent survival seemed rather independent of temperature and precipitation or might even be affected in the opposite directions than female survival.

We can think of three non-exclusive potential mechanisms by which weather conditions could affect adult survival in Snowfinches: 1) weather affects the physiology of the birds, 2) weather affects food availability and accessibility, and 3) weather conditions affect the trade-off between reproduction and self-maintenance.

Physiology is affected by cold and wet weather through an increase in energy demand. If the expended energy cannot be replaced, e.g. because food is scarce or not accessible (see below), mortality can increase. On the other extreme, hot and dry weather conditions can cause physiological problems due to dehydration or hyperthermia. Mountain birds seem to be particularly at risk to hyperthermia because of the intensive solar radiation at higher elevations. In ptarmigans (*Lagopus muta* and *L. leucurus*), body temperature and evaporative water loss increased at temperatures above 30°C (Johnson 1968; West 1972). However, in direct sunlight ptarmigans actively seek shelter from sun already at much lower temperatures (i.e., above 21°C, Visinoni *et al.* 2015). These observations indicate that birds at high elevations have to actively reduce the solar heat gain through radiation through hiding in the shadow. Thus, high temperatures can cause direct mortality through hyperthermia and dehydration or reduce the time for foraging and maintenance because of the need for seeking shelter and therefore indirectly increase mortality. Though, Snowfinch males are slightly larger than females (1% in body mass, 5% in wing length, Strinella, Catoni, Faveri & Artese 2013) it is little probable that physiological difference may explain the different correlations of weather and survival between the sexes found in this study.

The main food of adult Snowfinches are wildflower seeds, particularly in winter (Wehrle 1989; Heiniger 1991). During warm and dry summers the seed production of wild flowers can be lower compared to cool and wet summers (e.g. *Campanula thyrsoides*; Scheepens & Stöcklin 2013). Therefore, summer conditions may affect survival during the winter months via an effect on the abundance of food resources. During the winter, Snowfinches usually forage in flocks; when food is scarce, this may result in competition for food between individuals within the flock. In case of competition, males may dominate over females because of their slightly larger body size, and therefore food shortage may affect females more severely than males. A larger body size may similarly advantage males when access to food is more difficult because of the snow layer preventing or impeding access to seeds. Therefore, dry summers and harsh winters (and the combination of both) may impact more on female survival rather than on males' one. The null or slightly positive effect of cold and snowy winters on male survival might be due to better foraging conditions later in spring: more snow and colder temperature mean more snow patches and snow margins in spring-early summer, and probably also a shorter grassland sward, thus providing highly suitable conditions for foraging adults (Brambilla et al., 2017, 2018). The advantage provided in terms of foraging habitats may be offset for females by the more difficult access to food items in harsh winters.

At last, warm summers may allow for second broods. The number of broods in one season strongly depends on how early the snow is melting. When spring is late, Snowfinches can skip breeding (Heiniger 1988). During years with medium to early springs, a largely unknown proportion of the breeding pairs do a second clutch (Grangé 2008; Aichhorn 1966; Strinella, Vianale, Pirrello & Artese 2011). Early springs may allow for more breeding pairs raising two broods and, therefore, during warm summers Snowfinches may spend more energy in reproduction at the cost of allocating energy to self-maintenance (Stearns 1992; Ardia 2005). This may affect females more pronouncedly than males, because the energy invested in the brood may be higher for females compared to males, and/or because the proportion of non-breeders may be higher among males compared to females. To summarize, our results indicate that weather affects survival of males and females differently which may be either via food resources or via the balance of energy allocation to reproduction and self-maintenance.

Conclusion

Based on a 15-years (2003 – 2917) long mark-recapture data set from Abruzzo, we found evidence that the Snowfinch population inhabiting the central Apennines has a lower annual apparent adult survival than expected from its body size and phylogenetic relation, and from survival measures from the Austrian Alps (500 km to the north of the central Apennines we considered in this study) 30 years earlier. Thus, we showed that different Snowfinch populations may have different demographic characteristics that may be due to evolution under different environmental conditions or due to recent changes in environmental conditions caused by global warming. During the last 42 years, the thermophilic and nutrient-demanding plants species became more abundant, whereas cold tolerant plant species declined in the Apennines (Evangelista *et al.* 2016). Consequently, quantity and quality of the Snowfinch winter food has presumably changed during the last decades. This may be a potential reason why apparent survival of Snowfinches in the Apennines measured in this study is lower than that of Snowfinches in the Alps in the 70 and 80ies. However, this is speculation and further investigations are needed in order to identify causes of mortality in Snowfinches in different areas and periods.

We further showed that hot and dry summers are associated with low female apparent survival, whereas male apparent survival was substantially unaffected by summer weather. The mechanisms producing this pattern are not clear yet. However, because of global warming, it is expected that we will get more hot and dry summers. Therefore, we have to expect a decrease in female survival of the Snowfinch in future. This decrease in survival might be perhaps compensated by a higher reproductive output when breeding seasons become longer (due to global warming), allowing more pairs to raise two broods. However, it remains uncertain whether reproductive output can be increased to the level needed for a stable population and, even more important, conditions for rearing young change substantially after the completion of snow melt (Resano et al. in prep.), thus a longer breeding season may not necessarily result in a higher breeding success. Further, extreme weather events are predicted to become more frequently due to climatic change (Dieffenbaugh *et al.* 2017), and therefore, the risk of losing a brood may also increase.

If the expected decrease in female survival cannot be compensated by reproduction, the future of the species looks critically as already suggested based on species distribution models (Brambilla, Pedrini, Rolando & Chamberlain 2016) and its foraging habitat use (Brambilla *et al.* 2018). There is general evidence that negative population trends of cold adapted species is caused by global warming (Beniston 2003; Maggini *et al.* 2011). The different response in survival to climatic variables between the sexes shown in our results (and the differences with previous findings for the same species) indicates that a generalization to other high-elevation species of the mechanisms by which climate change impacts on species demography may be limited. High quality data on demographic parameters from different populations of different species living at high elevations are urgently needed in order to take effective measures for counteracting the expected negative population trends (Scridel *et al.* 2018; Chamberlain *et al.* 2016).

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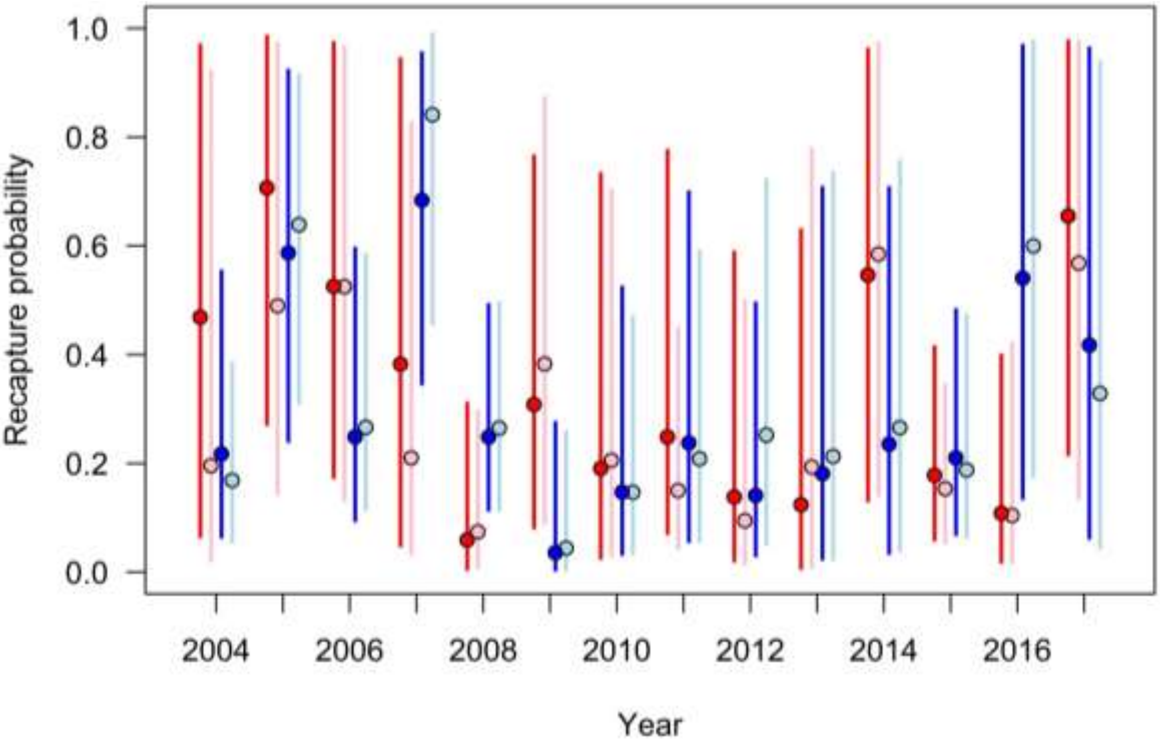

Figure S1. Recapture probability estimates for each year depicted for the sexes (blue=male, red=female) from the model with independent survival estimates per year (dark colours) and from the model with survival constrained to be dependent on summer and winter temperature and rain (light colours). Filled circles = median of the posterior distribution, vertical bars = 95% uncertainty interval.

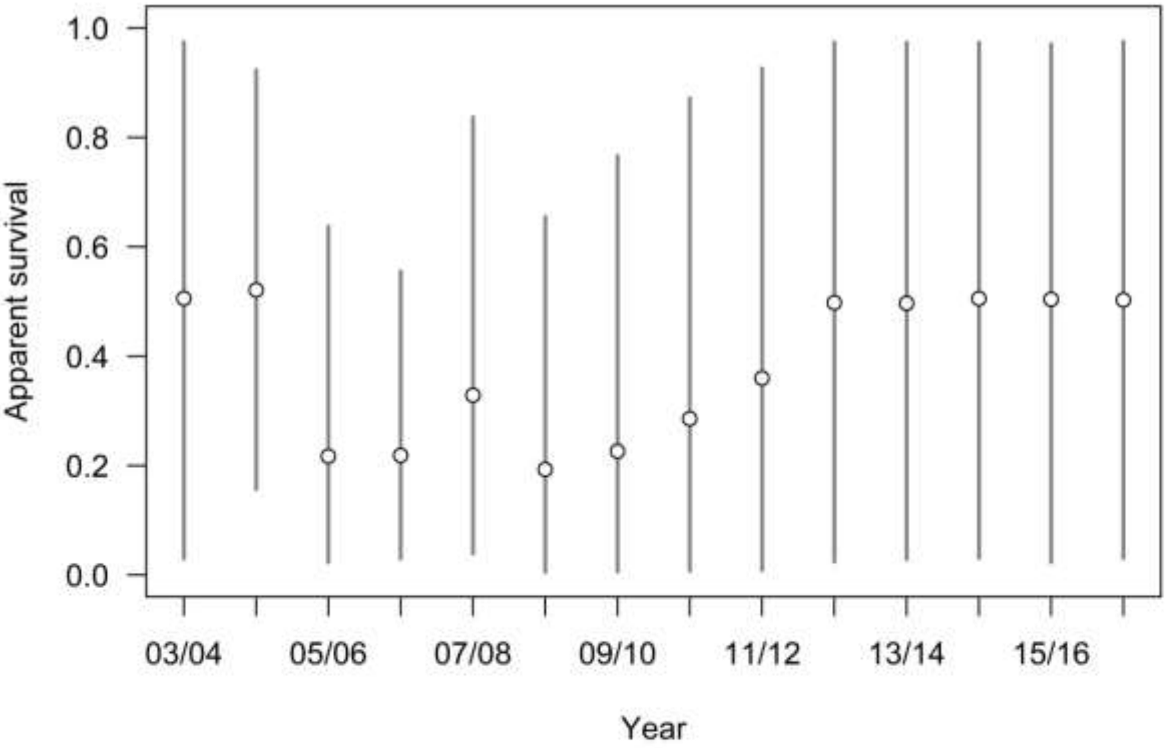

Figure S2. Annual apparent survival estimates for juvenile from the model with independent survival estimates for each year, age and sex class. Circles are medians of posterior distributions, vertical bars are 95% uncertainty intervals.

SECTION III

- *Conclusions and Perspectives* –

Rock ptarmigan, Cairn Gorm, Scotland.

III.a General conclusions

The findings of this thesis improved current knowledge on the ecology and biology of mountain birds and provided novel evidences of the impacts of climate change for this bird community, known to be difficult to study. Further to this, we identified climate-proof areas for conservation, based on the resilience and resistance of mountain birds' population in a changing climate, and developed human-mediated adaptation actions beneficial for climate-sensitive species and for the wider biodiversity related to mountain environments.

According to our systematic research of literature available, *Chapter I* demonstrated responses of mountain bird populations to both climate (i.e. changes in temperature and precipitations, extreme weather events) and environmental (i.e. land conversion) changes and highlighted how they remain a poorly studied group of species even in the most developed countries. In Italy, where evidences on climate change effects on mountain birds were lacking, we found a strong positive correlation between changes in range size and species thermal index (STI) for the last 30 years, inferring that recent climatic warming has favoured species of milder climates and adversely affected species occupying colder areas (*Chapter II*). Interestingly, we found STI to be the most important predictor of change in range size variation, more than other variables such as species' associated habitat, body mass or hunting status. Despite this does not fully disentangle the effects of climate change from land use, our findings support more the importance of the former in the 30-year variation at the broad spatial scale we considered. The importance of climatic variables is particularly evident for species confined to the highest elevations. In *Chapter III* we modelled the distribution under current and future scenarios for six high-elevation birds in the Alps to estimate future changes in distribution and identify areas of resilience and resistance. Climatic variables predicted particularly well the current distribution, giving credibility to future projections too, and model suggested a marked loss of suitable area and population connectivity for most species in the next-decades - many species will likely persist only at higher elevation and in topographically complex sites. These results are in line with our findings in the meta-analysis (*Chapter I*) which confirmed that in the future mountain birds are likely to be strongly impacted by climate changes, even more negatively than non-mountain species. However, most of these studies examining future projections in topographically complex areas are likely to overestimate the rapidity of climate change due to the coarse scale used, which does not always account for the fundamental value of microhabitats/microclimates as refugia areas for climate sensitive species (Loarie *et al.* 2009, Keppel *et al.* 2012, Mackey *et al.* 2012, Frey *et al.* 2016, Pincebourde *et al.* 2016). We selected the snowfinch as an indicator species of climate change due to its peculiar distribution confined to highest elevation sites in Europe and away from the confounding effects of land conversion and dedicated three chapters to investigate the role of microhabitats for this species. *Chapter IV* highlighted that snowfinches select specific and peculiar microhabitats during the chick rearing period: cool sites with short grass cover, melting snow margins with grassland and pure snow patches, whilst avoiding anthropized areas (i.e. roads, building). Such microhabitats harboured high quality and quantities of invertebrates and snowfinches seemed to efficiently tune their microhabitat selection in relation to prey abundance and type, suggesting a high adaptability to resource variability in specie and time, a typical characteristic of high elevation sites (Antor 1995; *Chapter VI*). When hindcasting and forecasting the suitability of such microhabitats to observed changes associated with climate change (i.e. earlier snowmelt and increased sward height) their suitability was better in the past and projected to decline in the future (*Chapter IV*). For sites composed by extensive alpine grasslands, their suitability may be improved in the present and in the future by grazing (or even mowing, where feasible) activities which keep the grass sward at a suitable height for snowfinches. However, for populations confined to more rocky habitats (i.e. subnival and nival), where grassland cover is generally low or even absent, this mitigation may not be applicable and snowfinches confined to these habitats could be more at risk from climate change (*Chapter V*). Indeed, climate change is unlikely to impact mountain species and population homogeneously and habitat characteristics may modulate its impacts. This has important implications for setting conservation priorities in the landscape, for example in identifying sites for the creation of new protected areas. A further problem highlighted in *Chapter I,* is the lack of long-term studies assessing reproductive success or survival of mountain birds in relation to climate change which could provide further insights on the mechanisms driving species and population declines. Whilst I attempted to bring this gap during my PhD by installing approximately 50 snowfinch nest boxes across mountain passes of the Central Italian Alps, I was also able to collaborate on an analysis based on a 14-years long mark-recapture dataset from the Italian Apennines. For this population, we found lower annual apparent adult survival than expected from its body size and phylogenetic relation and compared to survival measures of snowfinches from the Austrian Alps 30 years earlier. We also understood that this species might be particularly sensitive to extremes weather events (i.e. high/low precipitations and to cold/warm temperatures) with responses that vary depending on the season and the sex considered. In particular, hot and dry summers were associated with low female survival. Given that mountain regions are predicted to get warmer and drier with increasing extreme weather events as a result of climate change (Gobiet *et al.* 2014), snowfinches and wider mountain bird community are considered particularly at risk (La Sorte & Jetz 2010, Brambilla *et al.* 2017).

Despite being one of the classic concepts in applied conservation, the finding that protected areas and their management offers hopes in buffering the effects climate change effects, is one the most important messaged gathered by this this thesis and one that we should not underestimate or consider unfeasible. Climate change effects are usually perceived as an abstract topic, where direct adaptational responses are difficult to identify and deliver. Give the urgency to act against climatic alteration (IPCC 2018) and the evidences collected so far on this topic, scientist and policy-makers should already engage in influencing current legislations to manage and extend current protected areas for the benefit not only of mountain birds, but for biodiversity in general. Indeed, there are strong associations between preserving biodiversity and preventing climate change, and actions to achieve one are very likely to support the other (IPCC 2002, Dawson *et al.* 2011, Gaüzère *et al.* 2016). However, we should also avoid potential conflicts between climate change adaptation and biodiversity conservation. For example, allowing the treeline to expand at higher elevation could increase carbon absorption from the atmosphere, but at the cost of losing suitable habitat for unique flora and fauna assemblages present in the alpine grasslands that exists thanks to a low-input human-landscape relationship that has evolved over millennia. In this case the implementation of human-mediated management actions (i.e. grazing activities, see *Chapter IV*) might be desirable within protected areas and to the wider landscape via agri-environmental schemes that favour, for example, microclimate/microhabitat conservation/formation and the reduction of sward height and shrub cover, should be implemented in the European Common Agricultural Policy (CAP) schemes. Indeed, current agri-environmental schemes partially support sustainable habitat management for climate sensitive resources and habitats, but lack a joint approach specifically supporting actions for species sensitive to climate change. Despite not being a specific target of this thesis, the expansion of leisure activities and related land conversion (i.e. development of urban areas, roads and increased public access to otherwise remote areas) requires to be carefully regulated to avoid further deterioration of mountain habitats.

III.b Future perspectives

As for every scientific study, while this thesis has helped bridging some knowledge gaps, new questions have arisen that require careful investigation. The management of the mountain environment and its species, especially in Europe, will be a major challenge over the coming decades and here below I highlight some future research directions:

- Ecology and biology: Although both high-elevation mountain specialists and mountain generalists (*sensu Chapter I*) are well represented in the literature in terms of large-scale distribution studies (e.g. species distribution models based on atlas data), they remain very poorly represented when considering finer-scale, usually more intensive studies which address ecological mechanisms. In this thesis, we investigated in detail the biology and ecology of the snowfinch, but there are other high-elevation specialist and generalist (i.e. alpine cough *Pyrrhocorax graculus* wallcreeper *Tichodroma muraria*, rock ptarmigan *Lagopus muta*, alpine accentor *Prunella collaris*, water pipit *Anthus spinoletta*, red-billed cough *Pyrrhocorax pyrrhocorax*, wheatear *Oenanthe oenanthe*, tree pipit *Anthus trivialis*, rock thrush *Monticola saxatilis* etc.) which life history traits are almost unknown in mountain systems. At the same time, generalist species also common at lower elevation (i.e. white wagtail *Motacilla alba*, black redstart *Phoenicurus ochruros*) seem to be coping well also at these elevations (*pers. obs*). Studies comparing demographic parameters and life history traits between these two groups of species may be desirable to unveil mechanisms beyond these opposite trends, whilst offering novel information on their ecological requirements and relative dependence to climate sensitive resources (i.e. snow, alpine tundra).

- Physiology: Our understanding of physiological mechanisms underpinning bird responses to climate change is still very limited and could be particularly important also in terms of developing conservation strategies. If a species responds directly to climate through a physiological effect, then there might be limited conservation actions that could be implemented beyond the need to reduce our dependence on non-renewable fossil energy sources, whilst there might be more potential for developing conservation actions for species that are affected indirectly by climate change. We therefore emphasize the need for more basic studies of both physiological tolerance of mountain birds for example by relating various measure of fitness to measures of bird's thermal preferences (*as per* du Plessis *et al.* 2012).

- Altitudinal shifts: Given the limited number of studies attempting to assess if mountain birds are tracking suitable climate at higher elevation, we encourage to elucidate better this pattern by analysing data that might be already available with more recent surveys (*as per* Freeman *et al.* 2018) and setting new long-term monitoring schemes across elevation gradients.

- Climate change vs land use: Many studies acknowledge that a valuable understanding of climate impacts can only be achieved if key interacting factors are considered including changes in land use. This thesis is mostly focused on high-elevation species where land conversion has been historically quite limited. However, for lower elevation species land use conversion should be implemented in the models, for example via the comparison of changes in habitat type via old and more recent aerial photographs.

- Climate change effects on population dynamics: During this PhD we investigated the population dynamics of a high-elevation bird in relation to weather variables, whilst setting up our own study scheme with next boxes in the Central Italian Alps in collaboration with the European Snowfinch Group. More research should be carried out on this topic to clarify mechanisms behind observed changes in population trends in relation to climate change (*as per* Pearce-Higgins *et al.* 2010).

- Conservation - habitat management: Specific frameworks for habitat management adaptation for climate sensitive species are almost non-existent in the literature. To our knowledge, some adaptation actions have been developed in the British uplands for golden plover *Pluvialis apricaria* and red grouse *Lagopus lagopus scotica* (Pearce-Higgins *et al.* 2010, Fletcher *et al.* 2013) and they have been successfully implemented in various protected areas as management actions. In this thesis, we proposed mitigation actions to halt detrimental effects of climate change on snowfinches foraging habitats via grazing activities (*Chapter IV*). However, we lack definitive trail tests on the ground to check the effectiveness of this approach. We hope to test in the future this approach on snowfinches and on other alpine species.

- Conservation – policy support and application: This thesis highlighted that mountain birds are not only biologically and ecologically poorly investigated, but they are also poorly considered in terms of conservation policies. For example, some climate sensitive species are still hunted even in the lack of knowledge about basic demographic parameters such as population size and trends. Our classification of high-elevation mountain specialists and mountain generalists (*Chapter I*) offers initial steps for a joint common mountain bird index which so far has only been developed for some regions in the world and might be fundamental to raise the attention of policy-makers and governments (but see Leikohinen *et al.* 2019). In this regard, future works should thus further develop this mountain bird index as an important tool for delivering conservation actions (as it works for the Farmland Bird Index). Finally, in this thesis we provided a spatially explicit definition of areas of conservation priority for mountain species, therefore offering clear directions to policy-makers to deliver conservation actions on ground. However, scientific information on climate change and biodiversity rarely become applicative for intellectual, financial, or social impediments. A future policy-based research project could evaluate the relative importance of those obstacles, specifically focusing on mountain bird species threatened by climate change.

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Female snowfinch ringed at Furkapass in January 2018 (F. Korner-Nievergelt, J. Resano-Mayor), breeding in one of our nestboxes at Passo Gavia (obs. D. Scridel).