Migration strategies and circannual patterns of habitat use of snowfinches (*Montifringilla nivalis nivalis*) in a patchy alpine landscape

Estrategias de migración y patrones circanuales de uso del espacio del gorrión alpino (*Montifringilla nivalis nivalis*) en un ambiente alpino parcheado

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RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

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RESUMEN (en español)

La biodiversidad está íntimamente conectada al funcionamiento del ecosistema, y por eso también con el bienestar humano. Cambios están ocurriendo a una velocidad preocupante, como consecuencia de sobreexplotación, contaminación, invasiones de especies, fragmentación y alteración del hábitat y cambio climático. Las respuestas de las especies no son siempre lineares o instantáneas, y tampoco son las mismas a todas las escalas espaciales. Es entonces necesario identificar señales precoces de alarma y para eso se propuso el monitoreo de las variables esenciales de la biodiversidad (EBVs) como herramienta para capturar los componentes constituyentes clave del cambio de biodiversidad.

Las montañas pertenecen a los ecosistemas más ricos en término de biodiversidad y más amenazados por el cambio global. Son ecosistemas complejos y heterogéneos, que pueden actuar como cunas, barreras, puentes y refugios para las especies, además de influenciar la biodiversidad a escala continental. La modificación antropogénica de los hábitats de montaña y el cambio climático están amenazando seriamente estos ecosistemas. Las especies que los habitan están respondiendo a través de cambios fenológicos o migratorios hacia altitudes mayores. Sin embargo, la velocidad a la que el clima está cambiando, junto con la alteración del hábitat, pueden desafiar sus capacidad de respuesta. Debido a la complejidad de la dinámica de las especies y de las comunidades, los efectos reales del cambio climático sobre la biodiversidad de montaña, especialmente cuando interactúa con otras fuentes de estrés, son extremadamente difíciles de prever. Además, la dureza del ambiente de montaña obstaculiza las actividades de investigación. Por eso a menudo falta el conocimiento sobre la ecología de las especies, que es esencial para un monitoreo y una conservación rigurosos. Falta también investigación sobre las relaciones entre los rasgos funcionales de las especies y el funcionamiento del ecosistema.

El objetivo de esta tesis doctoral es de ampliar el conocimiento sobre (i) el rango de distribución, (ii) la especificidad del hábitat, (iii) las estrategias de movimiento y (iv) las dinámicas de grupo de una de las especies de aves alpinas más emblemáticas, el gorrión alpino *Montifringilla nivalis nivalis*, a través del estudio de las poblaciones de los Alpes, Apeninos, Cordillera Cantábrica y Pirineo español.
Además, introducimos nuestro estudio con una exploración de la diversidad funcional de las comunidades de aves de montaña del Holártico, y de la rareza funcional de sus especies, en la cual encontramos que la rareza funcional de las especies de montaña es independiente de sus rangos de distribución, y aumenta a lo largo del gradiente altitudinal, siguiendo el incremento de especialización de las adaptaciones de las

especies de alta montaña.

La distribución actual del gorrión alpino es considerablemente mayor que la potencial, obtenida a través del modelaje de observaciones de individuos reproductores con variables climáticas, topográficas y de cobertura del suelo. Las discrepancias son particularmente evidentes en el este de Europa, donde el monitoreo es escaso. Las poblaciones sureñas están mas fragmentadas y aisladas y entonces tienen mayor riesgo debido al calentamiento global. A través del estudio del uso del hábitat circanual del gorrión alpino a diferentes escalas espaciales, encontramos que la especie depende de los hábitats de alta montaña durante todo el año, aunque con un mayor grado de plasticidad durante el invierno. Teniendo en cuenta las menores elevaciones de los macizos del sur de Europa, las poblaciones que viven en estas areas podrían experimentar una mayor contracción de sus rangos de distribución. Encontramos también que la especie puede desplazarse en latitud durante el invierno, a través de migración parcial, un movimiento que conecta la población de los Alpes con las de los macizos ibéricos y que podría potencialmente reducir la deriva genética, con consecuencias importantes para la resiliencia y persistencia de estas poblaciones. Sin embargo, estos movimientos parecen desencadenados por las condiciones climáticas, es decir los gorriones alpinos se mueven cuando las condiciones invernales en los Alpes son más duras. El calentamiento global podría así reducir la propensión a migrar, con efectos sobre la demografía, estructura y heterogeneidad de las poblaciones. Los resultados sugieren también que el cambio climático puede afectar las dinámicas sociales. Los gorriones alpinos parecen responder a condiciones más cálidas reduciendo el tamaño y la duración de las bandadas. Esto podría llevar a un desequilibrio entre el periodo de reproducción y el pico de disponibilidad y accesibilidad de recursos. Además, en el caso de que la migración parcial fuese determinada por diferencias entre sexos o edades, cambios en las dinámicas sociales podrían afectar también las estrategias migratorias.

Esta tesis doctoral aporta información novedosa de la ecología del gorrión alpino, que puede ayudar a la hora de implementar el monitoreo y los planes de conservación futuros. Representa también el punto de partida para futuras investigaciones para comprender mejor la dinámica y conectividad de las poblaciones, para identificar fenómenos de aislamiento y profundizar el conocimiento de las respuestas de la especie al cambio climático.

RESUMEN (en Inglés)

Biodiversity is intimately linked with ecosystem functioning, and thus with human well-being. Changes are occurring at a worrying rate, in response to overexploitation, pollution, species invasions, habitat fragmentation and alteration and climate change. Species responses are not always linear or instantaneous, nor they are equal at any spatial scale. Detection of early-warning signs of critical biodiversity changes is thus needed and the monitoring of essential biodiversity variables (EBVs) has been proposed as a tool to capture major dimensions of biodiversity change.

Mountain regions are among the richest terrestrial ecosystems in terms of biodiversity and most threatened by global change. They are complex and heterogeneous systems, which act as cradles, barriers or bridges and refuges for species and they can also influence biodiversity at a continental scale. Anthropogenic modification of mountain habitats and climate change are posing serious threats to these ecosystems. Species living in mountain regions are already responding through e.g. shifts in phenology or upslope migration. However, the speed at which climate is changing, together with the pressure of habitat alterations might challenge their response abilities. Due to the complexity of species and community dynamics, the actual effects of climate change on mountain biodiversity, especially when interacting with other stressors, are extremely difficult to predict. Moreover, the harshness of mountains hampers research activities. Thus, there is often a lack of understanding of species ecology, which is essential for accurate monitoring and conservation. There is also a general lack of research into the relationships between species' functional traits and ecosystem function. Identifying rare species which contribute disproportionately to ecosystem function is crucial for establishing conservation priorities.

The aim of this doctoral thesis is to broaden the knowledges about *(i)* the distribution range, *(ii)* the habitat specificity, *(iii)* the movement strategies and *(iv)* the group dynamics of one of the most emblematic alpine bird species, the snowfinch *Montifringilla nivalis nivalis*, specifically studying the populations of the Alps, the Apennines, the Cantabrian Mountains and the Spanish Pyrenees.

We also introduced our study with an insight into the Holarctic mountain bird communities, their functional diversity and the functional rarity of their species. Functional uniqueness is independent from the geographical distribution of mountain species and it increases along the elevational gradient, following increasing specialization in high-elevation taxa adaptations.

We found that the current breeding distribution of the snowfinch is considerably greater than the potential distribution obtained by modelling breeding records with climatic, topographic and land-cover variables. Discrepancies are particularly evident in eastern Europe, where there is a lack of monitoring. Southern populations are more fragmented and isolated and thus at major risk because of global warming. Through the study of circannual use of habitat of the snowfinch at different spatial scales, we found that the species depends on high-elevation habitats throughout the year, although with a higher plasticity during winter. Considering the lower elevation of southern Europe ranges, populations living in these areas could experience higher range contraction. We also found that the species is capable of latitudinal winter movements in form of partial migration, that connect the population of the Alps with those of the Iberian ranges (e.g. Pyrenees and Cantabrian Mountains) and that could potentially reduce genetic drift, with important implications for the resilience and persistence of these populations. Yet, these movements seem to be triggered by weather conditions, i.e. snowfinches move when winter conditions in the Alps are harsher. Global warming might thus reduce migration propensity, with effects on population demography, structure and heterogeneity. Our results suggest that climate change seems also to affect social dynamics. In fact, snowfinches seem to respond to warmer conditions through reduction of size and duration of flocks. This could increase asynchrony with the peak of resource availability and accessibility, with consequences on breeding performances. Moreover, if partial migration is sex or age conditioned, changes in social dynamics could also affect movement strategies.

This doctoral thesis brings novel insights into the ecology of the snowfinch which can help implementing future monitoring and conservation plans. It also represents the starting point for future research focused on better understanding population connectivity and dynamics, identifying isolation phenomena and deepening the knowledges about the responses of the species to climate change.

SR. PRESIDENTE DE LA COMISIÓN ACADÉMICA DEL PROGRAMA DE DOCTORADO EN BIOGEOCIENCIAS

To the memory of Bona

“Wherever we go in the mountains,
we find more than we seek”

(John Muir)

“A flock of birds
Hovering above
One minute they arrive,
next you know they’re gone.
They fly on, fly on”

(“O” Coldplay)

List of abbreviations

AEMET	Agencia Estatal de Meteorología
AIC	Akaike Information Criterion
AP	Italian central Apennines
a.s.l.	above sea level
AUC	Area Under the Curve
BLD	BirdLife Distribution
°C	Celsius degrees
CBS	Keratin standard EC1 - Caribou Hoof Standard
CHELSA	Climatologies at high resolution for the earth's land surface areas
CI	Confidence Interval
CM	Cantabrian Mountains
CO_2	Carbon dioxide
δ^2H	stable hydrogen isotopes
δ^2H_f	stable hydrogen isotopes of feathers
EBVs	Essential Biodiversity Variables
EDF	Effective Degrees of Freedom
ESG	European Snowfinch Group
GAM	General Additive Model
GAMMs	Generalized Additive Mixed Models
GEO BON	Group of Earth Observations Biodiversity Observation Network
GLM	Generalized Linear Model
GLMMs	Generalized Linear Mixed Models
gVIF	generalized Variance Inflation Factor
h	hours
HWI	Hand-Wing Index
IOC	International Community of Ornithologists

IUCN	International Union for Conservation of Nature
km	kilometres
km^2	squared kilometres
KSH	Keratin standard EC2 – Kudu Horn Standard
m	metres
mg	milligrams
mm	millimetres
OLS	Ordinary Least Squares
P1	innermost primary feather
PCA	Principal Component Analysis
R6	outermost rectrice feather
RIV	Relative Importance Values
ROC	Receiver Operating Characteristic
SA	Swiss Alps
SD	Standard Deviation
SE	Standard Errors
SP	Spanish Pyrenees
SPK	powdered keratin from Spectrum Chemical
TPD	Trait Probability Density
VSMOW-SLAP	Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation

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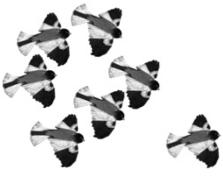
General Introduction

"*Nature is not only more complex than we think,*
but it is more complex than we can think"
(Frank Egler)

"*Nature considered 'rationally', that is to say, submitted to the process of thought, is a unity in diversity of phenomena; a harmony blending together all created things, however dissimilar in form and attributes; one great whole animated by the breath of life*"

(Alexander von Humboldt)

"*Das Ganze unterscheidet sich von der Summe seiner Teile*"
"*The whole is other than the sum of its parts*"
(The psicology of Gestalt)



Soulé's postulate that "*Diversity of organisms is good*", together with its corollaries and parallels that gave also birth to Conservation Biology in its modern sense (Soulé, 1985), were the result of decades of environmental and philosophical debate, stemming from the recognition of the impact humans were having on nature (Sessions, 1987). Nearly half a century before this postulate, Leopold's "*thinking like a mountain*" (Leopold, 1949) had already shed a light on the ecological cascade effect caused by the removal of a single species from an ecosystem, changing forever the way we see our ecological impact on nature. Thus, the twentieth century gave birth not only to the Age of Ecology, but also to the recognition that we live in a new geological era driven by humankind, the Anthropocene (Steffen et al., 2011). Over the years, the awareness of the effects of human footprint on the planet spread beyond the scientific and policy makers communities. In the 80s, the Deep Ecology movement was born, advocating people to cultivate an ecological consciousness and have a more spiritual approach to nature (Tresca, 2020). Recently, a paradigm shift developed even at a moral level: *"[…] global warming is a moral crisis and a moral challenge. The solution of the ecological problem is not only a matter of science, technology and politics but also […] a matter of radical change of mind, of new values, of a new ethos"* (Bartholomew, 2015). The perspective thus moved from considering humans as "lords of the universe" to "responsible administrators" (Francis, 2015), thus leading to an ecocentric approach where "everything has to be respected in its own right" (Sessions, 1987).

Therefore, today no one doubts that biodiversity is good. However, what is exactly biodiversity and how important is it?

What is biodiversity and how we measure it

With the term *biodiversity* we refer to the taxonomic, genetic and ecological diversity measured over all spatial and temporal scales, thus including the diversity within species, between species and of ecosystems (Harper and Hawksworth, 1994). Historically, ecologists puzzled to describe which factors – both biotic and abiotic - drive the diverse patterns of species abundances (Gamfeldt and Hillebrand, 2008). Mainly driven by the changes happening at global scale, from the early 90s the emphasis shifted towards the functional consequences of biodiversity, that is, the linkage between biological diversity and ecosystem functioning and the mechanisms that underpin the relationship (Gamfeldt and Hillebrand, 2008; Naeem et al., 2002). Ever since, a large body of research has indeed demonstrated that biodiversity enhances ecosystem process rates and can affect the stability of the natural systems (Balvanera et al., 2006; Hooper et al., 2005). At the same time, however, the strength and the direction of this relationship did not appear to be always defined, and above all, consistent across scales and systems (Thompson and Starzomski, 2007). This fact opened the debate on how the biodiversity, and the biodiversity-ecosystem functioning relationship, were being measured.

Early studies typically focused on species richness as a measure of biodiversity. Species richness refers to alpha (α) diversity, i.e. the number of species at a location in a certain moment. Biodiversity, however, may change across space (β diversity). Abundance and biomass are useful measures of biodiversity as well. Depending on the scale considered, changes in biodiversity can be considerably different, with local biodiversity increasing due to the contribution of non-native species, while decreasing at regional or global scales (Sax and Gaines, 2003). Thus, failing to address the scale and the type of measure when discussing biodiversity trends may lead to confusing remarks (McGill et al., 2015). When confronted with the complex changes in biodiversity and the need to investigate its trends and effects on ecosystem functioning, species richness alone proved to be an insufficient measure of biodiversity (Wilsey et al., 2005) and, in recent years, alternative metrics of biodiversity have emerged (Reiss et al., 2009), incorporating a measure of *quality* to the existing approaches based on *quantity*.

Research on biodiversity and ecosystem functioning has therefore moved from species richness – and thus taxonomic diversity – towards a trait-based approach, focusing on understanding the role of organisms in the ecosystem (by means of their functional traits) and how many and what types are needed to maintain ecosystem functioning (functional diversity). Functional traits are morphological, physiological, phenological or behavioral features of an organism that can be measured at the individual level and that have an effect on its fitness (Cadotte et al., 2011). The variety of traits in a community, i.e. its functional diversity, explains variation better than species richness because it contains a magnitude, expressed by the level of redundancy (Cadotte et al., 2011). In fact, although species richness and functional diversity are inherently linked, each species in the assemblage has a different "weight" and this has important implications when investigating the effects of species loss. For example, in communities with functionally redundant species, species loss will not affect functional diversity considerably, and in turn will have negligible effects on biodiversity-ecosystem functioning relationship (Cadotte et al., 2011; Violle et al., 2017).

Appropriate measuring of biodiversity is essential because biodiversity is changing at a rate and with patterns that urge accurate research and effective measures to counteract its dramatic decline.

Global biodiversity changes: patterns and drivers. The add-on of the climate change

Like many other organisms, humans have used and modified ecosystems for enhancing their fitness and decreasing competitors' success. However, the remarkable difference lies in the magnitude and the speed at which humans have been able to modify ecosystems (Figure 1). The impact of human activities can directly affect ecosystem processes – e.g. industrial nitrogen fixation – with indirect and direct effects on biodiversity, ultimately affecting ecosystem functioning.

Four classes of biodiversity change patterns can be identified (Pereira et al., 2010, 2012): *(i)* species extinctions; *(ii)* changes in species abundances and community structure; *(iii)* loss of genetic diversity; *(iv)* shifts in the distribution of species and biomes. Overexploitation, pollution, species invasions and habitat fragmentation and alteration are the main drivers of the changes in biodiversity. In particular, habitat degradation and loss currently represent the major threat to biodiversity (Pereira et al., 2012). It has both evolutionary and genetic consequences on populations, although species responses are not uniform. That is, while some species can be favoured by fragmentation, more specialist species can go locally extinct. Importantly, species responses to changes may delayed, leading to an "extinction debt" that most of the times is difficult to identify (Hanski, 2011; Kuussaari et al., 2009).

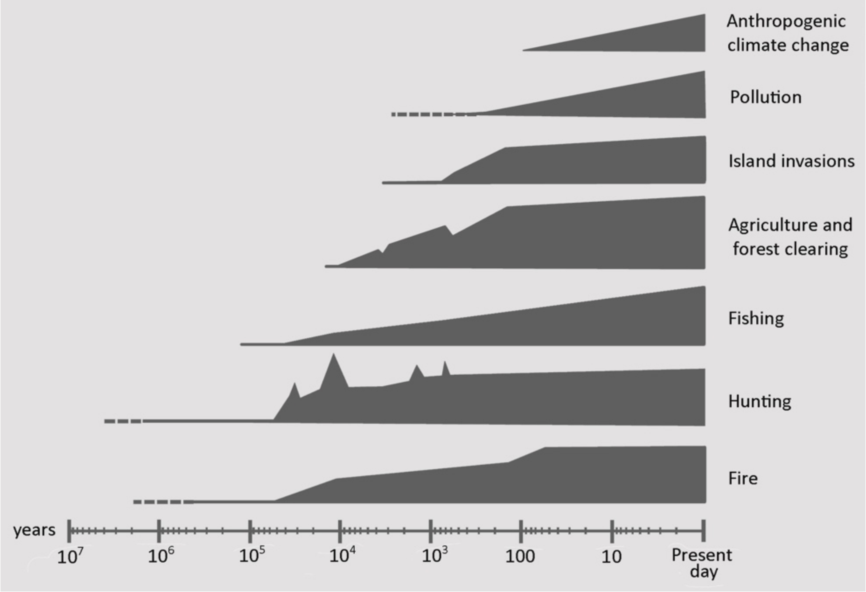


Figure 1. Temporal evolution of the main anthropogenic drivers of biodiversity change. Adapted from Pereira *et al.*, 2012.

Since the Industrial Revolution, human activities have acted as single or synergistic drivers of biodiversity change, causing the loss of many populations and species, and the damage of parts of the ecosystems and their services, creating a degraded baseline upon which climate warming is acting today. Species are not new to fluctuations, even abrupt, of global climate, and have responded to it over evolutionary timescales, proving natural resilience and adaptive responses capacity (Dawson et al., 2011). Although there is limited evidence of current extinctions driven by climate change, the fundamental question is whether species can cope with sucha a rapidly changing climate (Kannan and James, 2009).

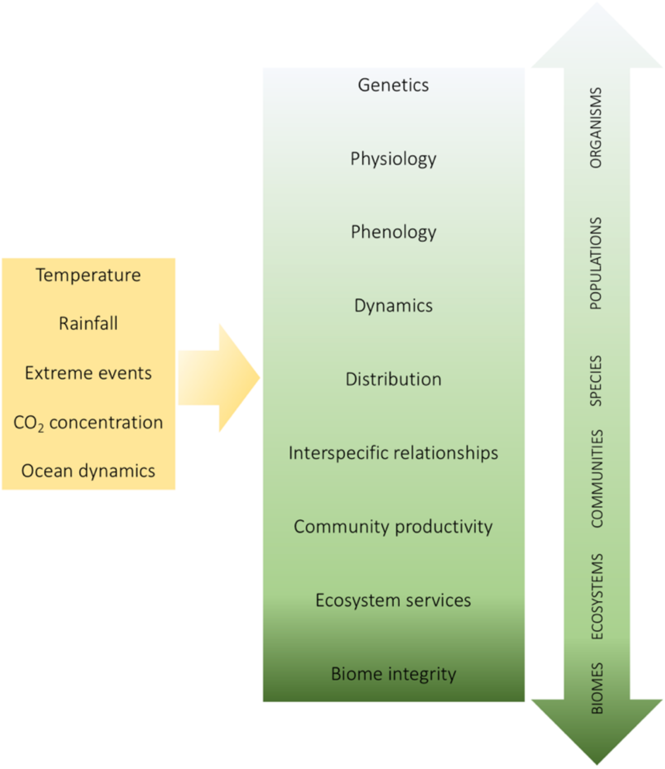


Figure 2. Climate change components (yellow box) and their expected effects (green box) on different levels of biodiversity (green arrow). Adapted from Bellard *et al.,* 2012.

Climate change can affect biodiversity at any level (Figure 2), causing e.g. a decrease of genetic diversity, changes in phenology and species interactions and shifts in species distributions (Bellard et al., 2012; Mooney et al., 2009). To persist, individuals, populations or species need short-term adaptive responses, which can be plastic or genetic, and involve adaptations in space (spatial shift to track suitable climatic conditions), in time (phenological shifts), or self adaptations to the new conditions *in situ* (Bellard et al., 2012).

Because of the complexity of both drivers and patterns of biodiversity change, it is crucial to detect early signals of critical perturbations, in order to establish effective management responses.

Detecting changes: the essential biodiversity variables

The Convention on Biological Diversity at the Rio Earth Summit in 1992 turned the spotlight on biodiversity and its global change. Ever since, and despite the renewal of the Strategic Plan for Biodiversity in 2011, biodiversity has continued declining (Tittensor et al., 2014). First, due to its inherent complexity, biodiversity change is often detected when effective responses are no longer achievable and ecosystem damage is irreversible. Second, a global, common system of collecting, organizing and delivering data was missing (Pereira et al., 2013). Furthermore, global indicators of biodiversity decline such as the IUCN Red List Index or the Living Planet Index are not proactive and function as a "late-warning" alarm (Schmeller et al., 2018). For those reasons, in 2013 the Group of Earth Observations Biodiversity Observation Network (GEO BON) proposed the concept of Essential Biodiversity Variables (EBVs) (Pereira et al., 2013).

EBVs represent a framework for organizing complex data on biodiversity from different ecosystems and species of different locations into a limited set of variables which capture major dimensions of biodiversity change. Pereira *et al.*, 2013 originally proposed the following classes of EBVs, with the idea that at least one EBV per class should be monitored: genetic composition, species populations, species traits, community composition, ecosystem structure and ecosystem function. From the original idea, the framework has evolved (and is currently still evolving), with the aim of developing and improving EBVs (Kissling et al., 2018; Schmeller et al., 2018). In this thesis, some of the EBVs spanning different levels of biodiversity organization are investigated (see Box 1), and the ecosystem considered is one of the most diverse and most threatened, that is mountains.

Box 1 | Essential biodiversity variables

In this thesis, 5 out of 21 EBVs identified by GEO BON (Figure 3) are considered in different chapters:

Species distribution (Chapter II)
Understanding the factors shaping species' ranges is a central topic in ecology and evolutionary biology. Recently, global warming, exotic invasions and habitat fragmentation are modifying the distributions of many species. Therefore, understanding and modelling species distribution has become essential to, e.g. identifying prioriting areas of habitats for conservation, forecasting range shifts or impact of habitat changes (Engler et al., 2017; Thuiller et al., 2013).

Morphological and reproduction traits (Chapter I)
In a broad context, morphology captures the essence of organisms' forms and functions and can thus influence performance and fitness. In avian species, morphological traits can be related to dispersal and foraging abilities, and may influence responses to habitat fragmentation and patterns of geographical range. Reproduction is a major component of fitness and life-history.

Movement (Chapter IV)

Individual movement strategies are essential to determine spatial population structure and the persistence of species and communities in fragmented landscapes (Schlägel *et al.*, 2020). Movement affects biodiversity by determining patterns in species distribution and species interactions as well as patterns of changes in species' traits and genetic diversity.

Moving individuals can be considered as "mobile links": by transporting resources, genetic material or processes, they connect communities and ecosystems that otherwise would remain separate (Jeltsch et al., 2013; Schlägel et al., 2020). Movement affects the degree of intra- and interspecific interactions and shapes the way in which these interactions affect populations and communities (Jeltsch *et al.*, 2013).

Taxonomic diversity (Chapter I)

Determining what species live together in a community is the basis of comunity classification and ecosystem health assessments. By coupling taxonomic diversity with trait-based analysis, it is also possible to study functional diversity and redundancy of communities, as well as functional rarity of a species within its community.

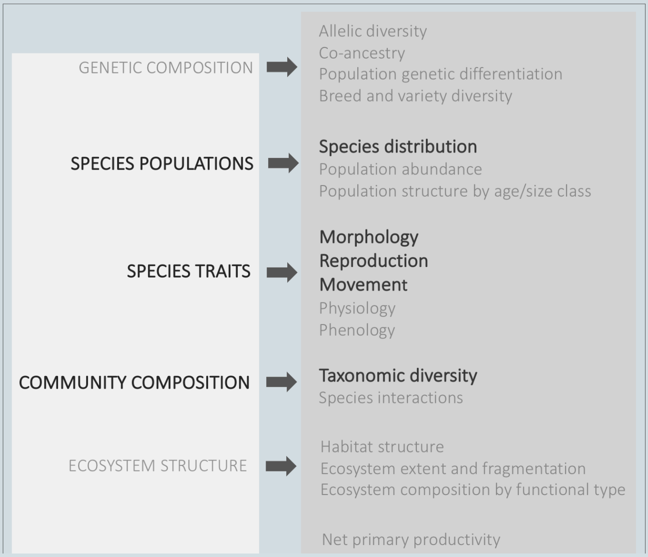


Figure 3. The 21 Essential Biodiversity Variables (grey panel) organized in 6 classes (light grey panel). Retrieved from https://geobon.org/. In bold, the EBVs considered in this thesis are highlighted.

To conclude, diversity of organisms is good, and not just because humans enjoy variety. Biodiversity is intimately linked with ecosystem functioning, and thus with human well-being. The recognition of how determinant is biodiversity for our future has been the driving force of a gradual, rising consciousness at all levels of society, of the impact that humans are exerting on the planet biota. This has motivated and enhanced scientific research as well, with the aim of improving the way we measure biodiversity and monitor its changes. Nevertheless, humans did not modify their habits, or at least not enough. Biodiversity kept changing at a worrying rate, and it still does, pushed by overexploitation, pollution, species invasions, habitat fragmentation and alteration and climate change. Responses are multifaceted and not always linear or instantaneous, nor they are equal at any spatial scale. Detection of early-warning signs of critical biodiversity changes is thus needed and the monitoring of essential biodiversity variables (EBVs) has been proposed as a tool to capture major dimensions of biodiversity change.

Mountains and biodiversity: relief conceives variety

Despite their relatively small area (25% of terrestrial land), mountain regions host an extraordinary proportion (~ 87%) of the Earth's vertebrate species (Figure 4) (Rahbek et al., 2019a), and are among the richest regions in terms of plant endemisms, with around four percent of the global flowering plant species occurring in the alpine belt (Spehn et al., 2010).

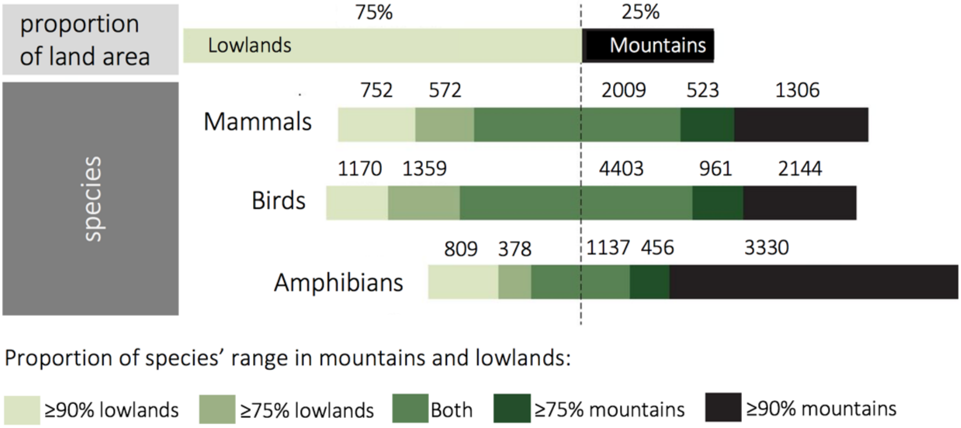


Figure 4. Proportion of species hosts by mountain regions, which represent the 25% of the world's land area (Antarctica excluded). The dashed line separates species that have most of their range in lowlands from mountain species. Adapted from Rahbek *et al.*, 2019a.

Complexity is what makes mountains unique as a reservoir of biodiversity and as a landscape feature. Early acknowledgement of the uniqueness of mountain regions lies in the words of Alexander von Humboldt: "*Thus the awful revolutions, during which […], great mountain chains have been elevated […], have served, after the establishment of repose, and on the revival of organic life, to furnish a richer and more beautiful variety of individual forms, and in a great measure to remove from the earth that aspect of dreary uniformity.*" (von Humboldt, 1877) and "*the arrangement of mountains […] individualizes and diversifies the climate as regards heat, humidity and the diaphaneity of the air, and, in these respects, the frequency of winds and storms.*" (von Humboldt, 1843). von Humboldt understood that what determines the complexity of mountain systems is a combination of different factors (Figure 5) (Rahbek et al., 2019b).

First, geological events of orogeny and erosion create a heterogeneous and dynamic topography. Second, orogeny processes determine mineral composition of rocks, which in turn affects the degree of soil heterogeneity, that can be further intensified by erosion. Third, elevation, orientation, topography and the interaction of mountains with the global climate system create peculiar climate types, characterized by strong seasonality, pronounced diurnal variations and the juxtaposition of different climatic zones (Rahbek et al., 2019b).

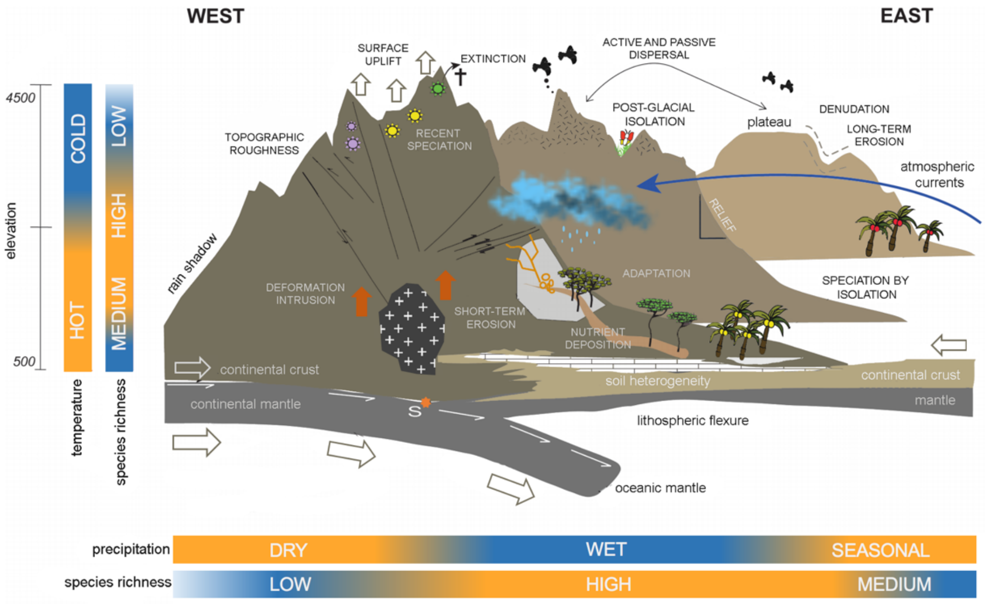


Figure 5. Graphical representation of the geological, climatic and biological processes occurring in mountains, which shape biodiversity. Adapted from Antonelli *et al.,* 2018

This unique combination of factors and the resulting highly dynamic environment, determine the multi-faceted role that mountains play in influencing biodiversity (Perrigo et al., 2020). First of all, mountains can be considered *cradles* of biodiversity, enhancing adaptive radiation in an "island-like" manner: the synergy of species diversification and the evolution of particular traits, allow the species to better exploit montane niches. Second, mountains act like *bridges* and *barriers*, connecting or isolating species and populations depending on their ecological and physiological requirements and dispersal ability. Third, mountains can be *refugia* for biodiversity, especially during periods of rapid climate change, when species need to move short distances along an elevation gradient to find their optimal niche.

Depending on their geographical position and spatial orientation, mountains can also influence biodiversity beyond their topographical limits (Rahbek et al., 2019b). For example, the east-west orientation of the European Alps enhanced the persistence of cold-adapted species, but did not provide corridors for their survival further north; by contrast, the north-south oriented American Rocky Mountains facilitated latitudinal connectivity.

The climatic peculiarity of mountains may be determinant to the level of species diversity and this is particularity true in the tropics, where mountains have more climatic zones than temperate mountains of similar height (Rahbek et al., 2019a). Similarly, topographic relief and soil heterogeneity exert a positive effect on species richness (Antonelli et al., 2018). In both temperate and tropical mountains, another factor that has been shaping biodiversity for centuries was human presence, especially through agriculture and grazing. Modest-intensity grazing and appropriate fire could actually increase biodiversity (Spehn et al., 2010). However, two opposite land use changes are recently threatening and decreasing mountain biodiversity. On the one hand, temperate mountain regions are suffering from the abandonment of steep terrains, resulting in invasion of shrubs and forest in formerly open areas, and from increasing fertilization of valley bottoms; on the other hand, tropical (and sub-tropical) mountains are experiencing increasing population pressure, with unsustainable land practices (Spehn et al., 2010). In the European Alps, the abandonment of traditional pastoral activities has been often accompanied by an intensification of outdoor activities, which have been proven to cause costly allostatic behavioural and energetic adjustements in wildlife (Arlettaz et al., 2015). Moreover, the spreading of ski-pistes also above the treeline has detrimental effects on the structure and composition of alpine vegetation, with cascade effects on richness, abundance and diversity of arthropods and bird species (Rolando et al., 2007).

In this scenario of anthropogenic modification of mountain habitats, climate change acts as a catalyst of biodiversity changes (Brambilla et al., 2016). In fact, mountain regions are particularly threatened by global warming (Brunetti et al., 2009), which is leading to the disappearance of local climates (Williams et al., 2007). For example, one consequence of global warming is the upslope migration of both animal and plant species with increasing temperatures: while lowland species are increasing their elevational distributions, high elevation species experience a range contraction, with disruption and restructuring of community relationships (Mooney et al., 2009). The magnitude of the effects of climate change on mountain biodiversity will depend on species' ability to cope with the different challenges. Mountain species often have high genetic diversity; also, they are well adapted to high seasonality and heterogeneity of the environment (Spehn et al., 2010). Thus, they could have higher capacity of morphological, physiological or behavioural responses to local changes in situ (Garcia et al., 2014). However, the responses might represent transient responses of populations with already reduced fitness, and fail to counter the speed and magnitude of current climate change.

The snowfinch as a biological model

The white-winged snowfinch *Montifringilla nivalis* is one of the most emblematic high-alpine passerine species. It is distributed from Iberia to the Tibetan plateau with different subspecies (del Hoyo et al., 2009). The European subspecies *M. nivalis nivalis* presents a patchy distribution (Figure 6), ranging from the Spanish Cantabrian Mountains eastwards through the Pyrenees, the Alps, Corsica and the Apennines, to the Dinaric Alps and Pindo Mountains in Greece (Cramp and Perrins, 1994). The snowfinch inhabits rocky habitats next to alpine grasslands and pastures above the treeline and thus strictly depends on alpine and subalpine habitats. It breeds in cliffs, buildings and skilift pylons mostly above 1900 m a.s.l. in the Alps (Knaus et al., 2019) and above 1700 m a.s.l. in the Spanish Cantabrian Mountains (Fernández-González, 2014). During the breeding season (May-August), it commonly forages on invertebrates next to snow patches or in grassland with low sward height (Brambilla et al., 2018a, 2017a). After fledging, family groups gather in large flocks, ascending above breeding grounds up to glaciers and they move to lower elevations with first snow falls (Cramp and Perrins, 1994).

Until few years ago, it had been little investigated and many aspects of its circannual biology and ecology are still unknown. Recently, the species has captured the attention of some research groups in Central and

Southern Europe, interested in understanding the effects of global change on alpine species. In 2016 they created the European Snowfinch Group (ESG, www.snowfinch.eu), aiming to coordinate research activities and promote and monitor the conservation of the species.

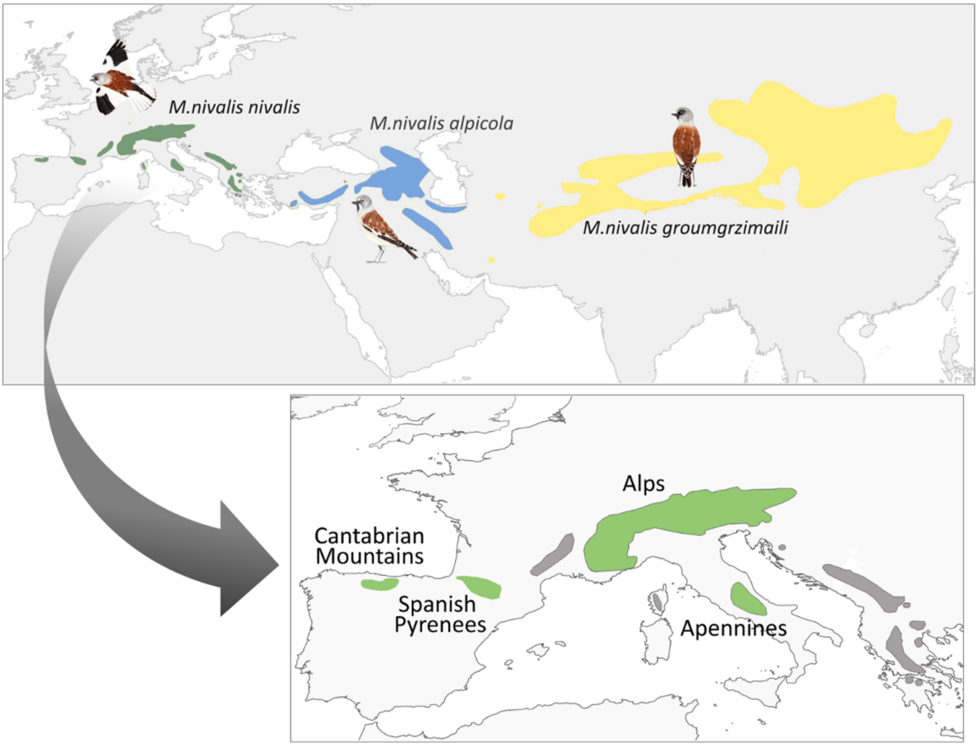


Figure 6. Distribution range of the species *Montifringilla nivalis* and its subspecies (upper map). On the lower map, a zoom into the distribution of the subspecies *M. nivalis nivalis* and, in green, the four populations object of this thesis (snowfinches drawings by G. Bombieri).

Given its extremely large range (from Europe to Asia) and a population trend considered as stable, the species is currently classified as 'Least Concern' in the last Red List of European birds (BirdLife International, 2015). However, accurate monitoring of the breeding population is hampered by the harshness of the environment the species lives in, and occurrence data are still scarce in several areas. Indeed, the first studies carried out by the ESG gave a worrying picture of the situation caused by the changes that are affecting mountain ecosystems: range contraction and connectivity decrease (Brambilla et al., 2017b; Scridel et al., 2017), human disturbance (Brambilla et al., 2016) and changes in foraging habitat (Brambilla et al., 2018a) are concerning threats for the species. Moreover, southern populations living in mountains of lower elevation, are more constrained when tracking suitable climatic conditions, and might thus face major risks of population decline and extinction due to current climate change.

The existence of the ESG as a network of cooperating research groups not only allows an improvement of the knowledges about different aspects of the species ecology, but also represents an integrated effort to assess the status of the European populations. Moreover, studying the snowfinch on a regional level could improve our understanding of connectivity among populations in fragmented habitats, detect possible isolation phenomena, and help develop effective conservation strategies. Importantly, the snowfinch could be considered as a “flagship” species for the benefit of the entire alpine community.

In this thesis, we focused on the European subspecies *M. nivalis nivalis*, specifically studying the populations of the Alps, the Apennines, the Cantabrian Mountains and the Spanish Pyrenees (Figure 6). Taking advantage of the collaboration with the ESG, we could share valuable data and thus investigate, under the perspective of the strong impact of global change on mountain systems, the species’ potential distribution, its circannual habitat requirements, the movement strategies and group dynamics.

Due to the complexity of species and community dynamics, the actual effects of climate change on mountain biodiversity, especially when interacting with other stressors, are extremely difficult to predict. Moreover, the harshness of mountains as open air laboratories hampers research activities (Chamberlain et al., 2012). Thus, there is a general lack of understanding and monitoring of most of the EBVs in mountain ecosystems. For avian alpine species, in particular, data on migration rates, habitat specificity and fine scale range limits are scarce, although they are prerequisites for accurate monitoring and conservation. There is also a general lack of research into the relationships between species' functional traits and ecosystem function. Identifying rare species which contribute disproportionately to ecosystem function is crucial for establishing conservation priorities. A call for more research focused on these EBVs is therefore imperative, to provide the basis for developing biodiversity forecasts under different policy and management scenarios.

Objectives

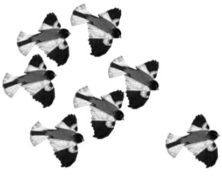
As an answer to the "call for research" that mountain regions need, and by moving within the EBVs framework, the ultimate scope of this doctoral thesis is to broaden the knowledge about the distribution range, habitat specificity, movement strategies and group dynamics of one of the most emblematic alpine bird species, the snowfinch. For each variable, we will also try to address the possible consequences of global change, pointing to possible directions for future research. We will introduce our study with a broad insight into the mountain bird community, its functional diversity and the functional rarity of its species, moving afterwards to the species and population levels.

With the increasing body of studies based on functional traits, the way that rarity – and commonness – are considered has changed and depends on the function that species fulfil in the community. For example, a species can be common with respect to its habitat requirements, but have rare traits and therefore a rare function in its community. Because of the strong seasonality of mountain environments, high-elevation organisms exhibit complex life-history strategies and a high degree of habitat specialization, and thus they may be considered rare. However, are they really rare? By taking into account the bird communities of the Holarctic mountain ranges, in **Chapter I** we explore species functional uniqueness (or rarity) with respect to their morphological and vital rates traits. Specifically, we investigate whether the degree of functional uniqueness could be related to the latitudinal distribution and/or the elevation gradient.

In the next chapters (**II-V**) we focus on the snowfinch (*M. nivalis nivalis*). By comparing suitable breeding areas with the current distribution range of the species, we first address the importance of a detailed knowledge of the distribution range of high mountain species, in order to highlight possible discrepancies and detect "hotspot" areas for planning conservation measures (**Chapter II**). An exhaustive knowledge of the ecology of a species, especially when living in a heterogeneous environment where resources change spatially and seasonally, cannot disregard its requirements over the entire annual cycle. Thus, in **Chapter III** we investigate the spatio-temporal variations of the ecological niche, through a circannual analysis of the habitat used at different spatial scales. Snowfinches respond to resource seasonality by adopting a migratory movement strategy. The degree of mobility of a species or a population might also determine its ability to respond to a changing environment. In high elevation ecosystems, animal migration strategies may take the form of both obligate and irruptive migration, as well as elevational movements. However, the information is still scarce and little is known about how weather might influence movements of high mountain species. Through the analysis of stable hydrogen isotope of feathers, in **Chapter IV** we try to disentangle the winter movement patterns of different European populations of snowfinches and their possible relationships with climate. Movement is not the only behavioural response to harsh weather conditions. Animals may as well gather in large groups for e.g. enhancing food tracking. The snowfinch shows a marked gregarious behaviour outside the breeding season, and in **Chapter V** we quantify large-scale patterns in wintering association in relation to abiotic gradients, trying to identify possible variations driven by changes in weather conditions.

Chapter I

Variation in geographical and elevational gradients of functionally rare bird species in the Holarctic mountain systems



Summary

Rarity constitutes an important aspect of community diversity and the study of functional rare species is especially important in mountain ecosystems, where climate change is particularly acting as a catalyst of biodiversity changes. Here, by considering morphological and vital rates traits of mountain bird species, we explored the functional diversity of Holarctic communities and study the variation in elevational and geographical gradients of the species' functional uniqueness. Communities at lower latitudes have higher species and functional richness, compared to high latitude communities, despite showing lower redundancy, meaning that they could suffer severe consequences from the loss of species. Species uniqueness is independent from the geographical distribution, but linked to the pool of species of each community. Moreover, functional uniqueness increases along the elevational gradient, following increasing specialization in high-elevation taxa adaptations. However, the role played by rare species in the functioning and processes of mountain ecosystems is unknown and calls for more studies.

Introduction

In the quest to understand species coexistence and community assembly, and in order to address the ecological consequences of global warming, ecologists have recognised the importance of shifting from simply counting species to also accounting for species functions (Carmona et al. 2016). This shift explicitly recognises the need to identify and understand functional traits as the main drivers of the responses of species to environmental conditions, disturbance, and biotic interactions, as well as their effects on ecosystem processes (Pereira et al. 2013). This includes the role of functional rare species (Violle et al. 2017; Loiseau et al. 2020). Recent studies have suggested that identifying the rarity of functional traits (e.g., morphological, physiological and phenological traits; Carmona et al. 2016; Violle et al. 2017) is a promising avenue to answer questions related to the role of rare species for the resilience and functioning of natural communities under the ongoing global warming (Lyons et al. 2005; Bracken and Low 2012; Loiseau et al. 2020). Since high trait diversity usually enhance ecosystem functioning, functional rare species thus support unique traits or functions that might be irreplaceable (Winter et al. 2013; Thuiller et al. 2015).

The recognition that rarity constitutes an important aspect of community diversity has emerged only recently (Violle et al. 2017; Loiseau et al. 2020). Students of community and population ecology are interested in rarity since they have become aware of the importance of redundancies and complementarities of phenotypes for the adaption of organisms and for species interactions (Knapp 2011). It has also fascinated evolutionary biologists, for whom it is unrealistic to say that an organism is adapted to be rare, and for whom it is difficult to explain, under the umbrella of natural selection, that rarity is an adaptive strategy (Hughes et al. 2013; McKinnon and Servedio 2013). Further, rarity is of the interest for conservation managements because some aspects of rarity are tightly linked to population extinction (Hartley and Kunin 2003; Harnik et al. 2012). Historically, species have been considered to be rare when they had small geographic ranges, a high level of habitat specificity, small populations or any combination thereof (Rabinowitz 1981). However, the ecology of functional rare species goes beyond those features (Violle et al. 2017).

Some studies have showed that, on the one hand, if rare species are not redundant with other species but hold unique combinations of traits, they will likely increase the functional diversity of natural communities, thereby increasing its complementarity and functionality (Oliver et al. 2015; Dee et al. 2019). In this sense, functional rare species may be considered as the analogous of mutations occurring at the population level which, by increasing population genetic diversity, allow them to cope with variations stochastically occurring in the abiotic and biotic environments. On the other, a reduction of functional rare species may increase the redundancy, allowing natural communities to be able to adapt to the varying conditions, and thus persist even though some species may disappear (Bascompte and Stouffer 2009). Therefore, functional rare species may be important for natural communities facing climatic perturbations.

The study of functional rare species is particularly important in mountain ecosystems, where climate change is particularly acting as a catalyst of biodiversity changes (Williams et al. 2007; Brunetti et al. 2009; Brambilla et al. 2016). The combination of diverse geological and orogeny processes, together with the global climate system that create peculiar climate types, make mountain ecoystems unique reservoirs of biodiversity (Spehn et al. 2010; Mccain and Colwell 2011; Antonelli et al. 2018; Rahbek et al. 2019a). However, as most alpine species are geographically restricted, they are of particular concern because they might have a high extinction risk (Gaston 1998; Loiseau et al. 2020). The magnitude of the effects of climate change on mountain biodiversity will depend on species' ability to cope with the different challenges. Therefore, in the context of the ever-increasing biodiversity crisis we are facing in the Anthropocene (Johnson et al. 2017), it is essential to understand the functional characteristics of rare species in mountain ecosystems.

Elevational clines have received far less attention than latitude in studies of functional diversity and structure, thus generally hampering our understanding of the potential ecosystem-level consequences, also beyond their topographical limits, of biodiversity loss in mountainous systems due to global change. Global studies have suggested a decline in functional and phylogenetic diversity along single elevational gradients (Dehling et al. 2014; Vollstädt et al. 2017; Hanz et al. 2019), with phylogenetic and functional structure changing from overdispersed assemblages at lower elevations towards clustered assemblages at higher elevations (Graham et al. 2009; Xu et al. 2017; Hanz et al. 2019). Recently, two studies have provided a comprehensive evaluation of global variation in both functional and phylogenetic diversity in elevational gradients along the world's most defining geographic gradients. They showed dissimilar patterns, from no consistent elevational patterns in functional and phylogenetic diversity in montane avifaunas on the one hand (Montaño-Centellas et al. 2020) to a strong latitudinal variation in elevation gradients in functional diversity and structure on the other (Jarzyna et al. 2020). This discrepancy has been mainly attributed to the differences in the spatial and taxonomic scales considered (Jarzyna et al. 2020). Despite these findings, most studies on alpine community assembly still evaluate functional diversity with single indexes of functional diversity (Montaño-Centellas et al. 2020), largely ignoring that rare species may contribute disproportionately to the functional structure of the community assembly (Mouillot et al. 2013; Leitão et al. 2016; Jarzyna et al. 2020). Therefore, we still lack of a general assessment of the functional rarity in mountain systems.

Here, by considering a pool of functional traits related to vital rates and morphology of mountain birds (817 species), we first projected species into a functional space of the different communities throughout the Holarctic. Second, we assessed the distinctiveness of species functional traits within these communities to study the variation in elevational gradients of ecological rarity in mountain bird communities.

Methods

Data collection

For a complete list of the Holarctic mountain bird species, we referred to the database published by Scridel et al. (2018). The authors identified Holarctic mountain bird species based on the classification of mountain systems by Kapos et.al (2000). For our purposes, we only considered from this dataset those species categorised as "high-elevation mountain specialist" (i.e., species for which at least 50% of the breeding range falls in the classes 1-4 of Kapos et al. (2000)) and as "mountain generalist" (i.e., species for which at least 50% of the range falls in the classes 1-7 of Kapos et al. (2000) but was not classified as specialist). We thus retained a total number of 817 species belonging to 92 families and 21 orders (Supplementary Table S1.1). 494 out of 817 were classified as "generalist" and 323 as "specialist" mountain bird species. For each species we completed the taxonomy by adding the Family and Order and, when needed, by updating the scientific name, following the IOC World Bird List (Gill and Donsker 2016). We grouped the Holarctic mountain systems in eight different bird communities (Figure 1.1) and assigned each species to the corresponding community or communities, depending on their breeding range.

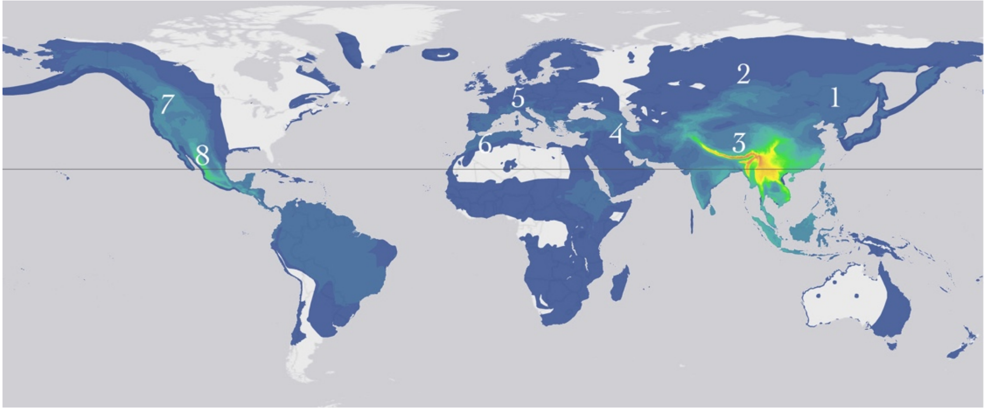


Figure 1.1. Heatmap of the 818 Holarctic (above the grey line) bird species, built using their distribution ranges retrieved from BirdLife International 2018. Colours from blue (1 to 7 species) to dark orange (295 to 313 species) represent increasing species concentration. The white numbers represent the zonation of the main Holarctic mountaineous regions: (1) North-East Asia, (2) Central Asia (3) Himalaya-China, (4) Middle East-Caucasus, (5) Europe, (6) Atlas, (7) Northern America and (8) Central America. For a detailed list of the mountain ranges included in each community see Supplementary Material, Data S1.1.

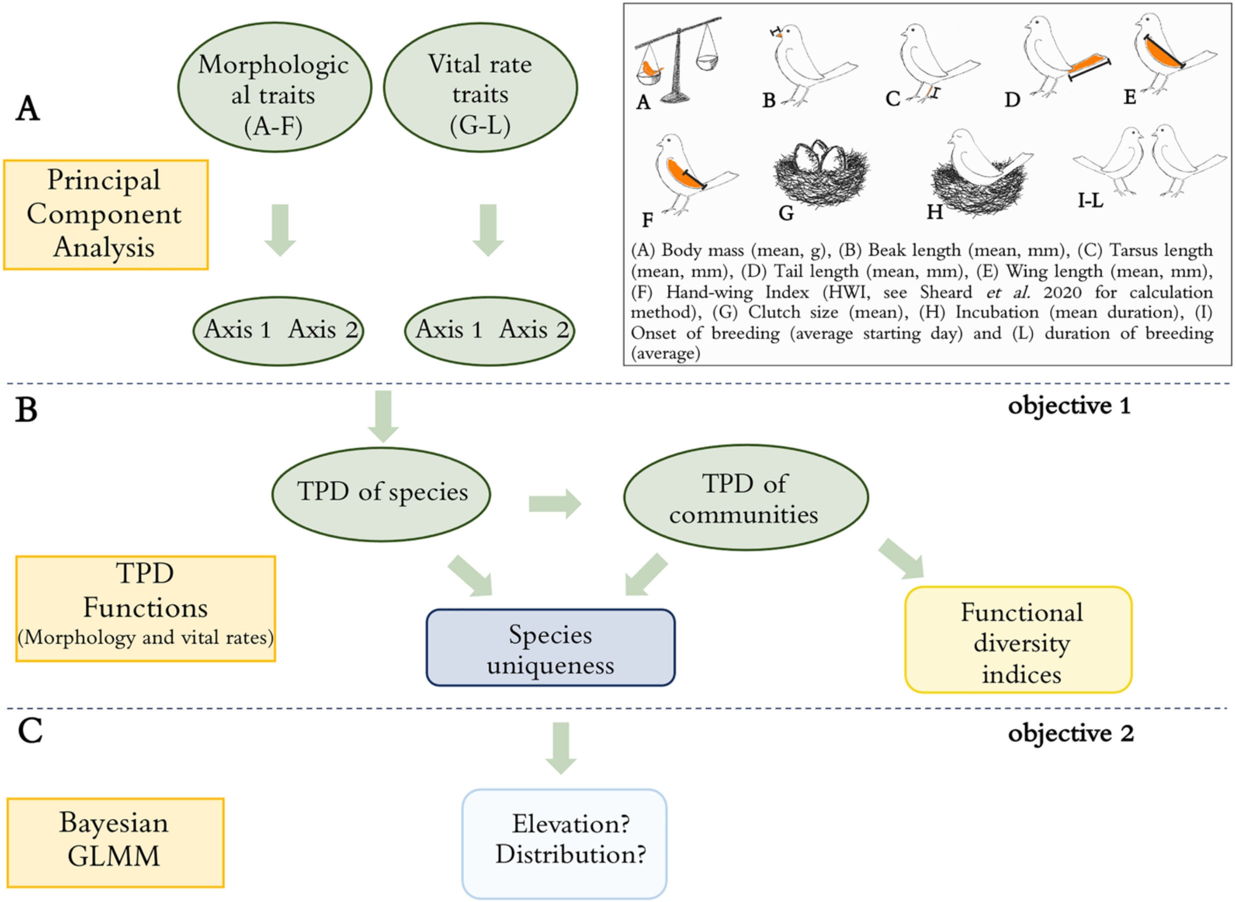
For each species, we collected information on 22 functional traits, classified into two main categories (Supplementary Table S1.1): (1) morphological traits; and (2) vital rate traits. Information about vital rate traits were generally scarce (Supplementary Table S1.1). For the analysis we could therefore retain only the following ones: clutch size, incubation, onset of breeding and breeding duration (see Figure 1.2 and Supplementary Text 1.1 for detailed information about the datasets used in the analysis). In addition, we collected information about the elevational breeding limits (maximum and minimum elevation, expressed in metres a.s.l., Supplementary Table S1.1), and about species' breeding range in mountain regions (expressed in km^2) contained in the database of Scridel et al. (2018).

Statistical Analysis

Prior to all analysis, in order to reduce the influence of extreme values, we log-transformed the variables body mass, beak length, tarsus length, hand-wing index (HWI), wing length and tail length, as well as clutch size and incubation. Since morphological traits were all related to the species size, we estimated species body condition from the residuals of OLS regressions of log-body mass on log-beak length, tarsus length, hand-wing index (HWI), wing length and tail length (Supplementary Table S1.2).

First, for both trait groups we used principal component analysis (PCA) to reduce trait dimensionality (Figure 1.2A). Following Kaiser's criterion (Kaiser 1958), only components with eigenvalues >1 were retained, which corresponded to the first two axes (accounting for 58.0% for morphological and 65.2% for vital rates traits out the total variance respectively, Supplementary Table S1.3). In order to facilitate the interpretation of the PCA, a varimax rotation with Kaiser normalisation was applied to the retained components (McGarigal et al. 2000). For morphological traits, the first axis was related to the residuals of tarsus length and HWI, while the second axis was related to the residuals of beak and tail lengths (Supplementary Table S1.3a). For vital rates, (Supplementary Table S1.3b) the first axis was related to measures of fitness (i.e. clutch size and incubation), while the second axis was related to the breeding cycle (i.e. the onset and duration of the breeding season).

Figure 1.2. Summary of the framework used to explore community functional diversity and the relationship between species uniqueness and elevational and distributional limits.



Second, to describe the communities of Holarctic mountain birds in terms of their functional diversity, and to obtain a measure of the functional rarity (hereafter "uniqueness") of each species within its community, we used the trait probability density (TPD) framework (Carmona et al. 2016, 2019) by means of the package TPD (Carmona 2018). We treated the two PCA axes as "traits" and used species' PCA scores as "trait values" (Figure 1.2B). A detailed description of the method used to calculate community functional indices and species uniqueness is reported in Supplementary Text 1.2.

Third, to investigate the relation between species uniqueness, elevational limits and breeding range of the species in the different communities (Figure 1.2C), we fitted two Bayesian equivalent of a generalised linear mixed models (GLMM) with a beta distribution, since our response variables (vital rates and morphology uniqueness) were an index ranging from 0 to 1. As the values of uniqueness were always > 0.5, we thus transformed them by $2*(x-0.5)$. Breeding range, maximum and minimum elevation and community were added as predictor variables. Possible collinearity among the explanatory numerical variables was tested using the variance inflation factor (VIF). For all variables there were no collinearity issues (VIF < 3). Quantitative variables were scaled to a mean of 0 and a standard deviation of 1. To control for the potential effect of phylogenetic relatedness, we included the taxonomic order as random effect. The models were fitted with Hamiltonian Monte Carlo using the function stan_glmer of the package rstanarm (Goodrich et al. 2020). We used the default weakly informative priors on coefficients ($\mathcal{N}(0, 2.5)$) and on intercept ($\mathcal{N}(0, 10)$). We further used the default prior for the covariance structure, which is developed to perform well for the majority of regression analysis (Muth et al. 2018).

We simulated four Markov chains of length 2000 and used the second half of each chain for the description of the posterior distributions of the model parameters. Model convergence, mixing of the Markov chains and posterior predictive checks were assessed using the package shinystan (Gabry 2018). All predictors had R-hat below 1.01, Monte Carlo standard error below 10% and number of effective samples above 1000. The means of the simulated values from the joint posterior distributions of the model parameters were used as estimates, and the 2.5% and 97.5% quantiles as lower and upper limits of the 95% credible intervals. We considered an effect to be significant if the posterior probability of being positive (or negative) was larger than 0.97 (limit of the 95% credible interval), while an effect signifies a trend if the posterior probability of being positive (or negative) was larger than 0.75 (limit of the 50% credible interval). All analysis were performed in R 3.4.4 (R 2018).

Results

Functional dissimilarity among communities was generally not high (values always <0.5, Supplementary Figure S1.3). However, we could identify some clusters of communities more similar among them, regardless of the group of traits considered: the communities Himalaya-China, Central and Northern America (Supplementary Figure S1.3 and the graphical representation of TPDc showed in Supplementary Figure S1.2); the communities of North-East and Central Asia, Middle East-Caucasus, Europe and Atlas.

Within the first cluster, the communities of Himalaya-China and, to a lesser extent, the communities of Central and Northern America are particularly singular in terms of their functional diversity. By presenting the highest number of different species (Figure 1.3A), they occupy the largest proportion of the overall mountain functional space observed (Figure 1.3B and Supplementary Table S1.4). Further, the community of Himalaya-China has the lowest functional evenness (Figure 1.3C and Supplementary Table S1.4) and the lowest functional divergence of morphological traits (Figure 1.3D and Supplementary Table S1.4). That is, species inhabiting there present a low degree of niche differentiation (and thus high resource competition), yet some part of the occupied niche space of this mountain bird community is under-utilised. In term of their morphological traits, most species of these communities are functionally unique, thus confering to the system a general low ability to lose species without a great reduction in ecosystem function (Figure 1.3E and Supplementary Table S1.4). Within the second cluster, the community of Europe has the lowest values of species richness (Figure 1.3A and Supplementary Table S1.4) and, based on vital rate traits, the lowest functional richness (Figure 1.3B and Supplementary Table S1.4) and high resource differentiation (Figure 1.3D and Supplementary Table S1.4). With respect to morphological traits, the European mountain bird community showed the highest values of redundancy.

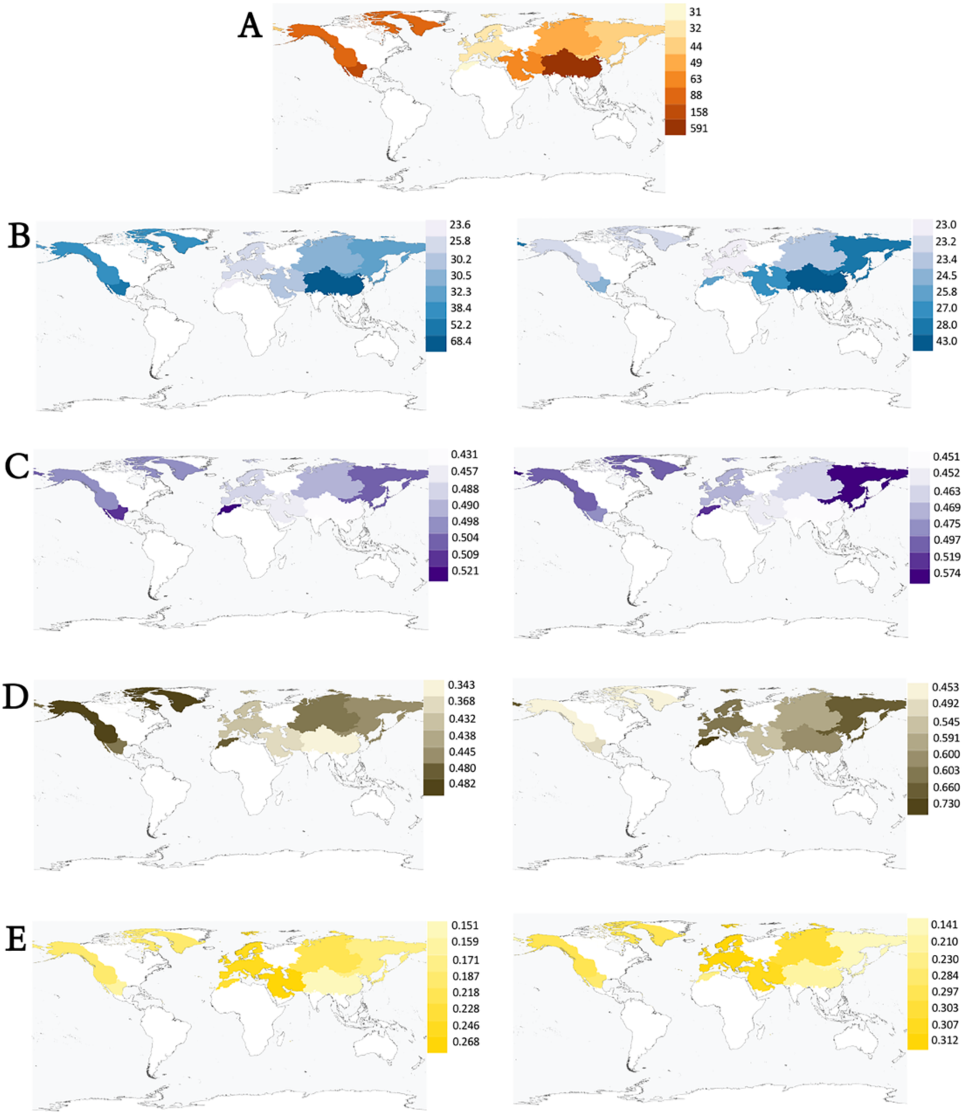


Figure 1.3. Maps showing the three primary components of community functional diversity: (B) functional richness, (C) functional evenness and (D) functional divergence, as well as (E) functional redundancy, based on morphology (left panels) and vital rates traits (right panels). Species richness (A) refers to the total number of species per community.

Interestingly, out of the 817 species considered, 655 (representing the 80.2%) were species that are present in only one community, and this was especially the case for those species inhabiting the communities of Himalaya-China and of Central America (Supplementary Figure S1.1). The communities of Asia contained high numbers of species with the highest values of uniqueness compared to the American communities, like for example the rock bunting *Emberiza cia*, the mountain hawk-eagle *Nisaetus nipalensis*, the wallcreeper *Tichodroma muraria*, the blue rock-thrush *Monticola solitarius*, the black-throated accentor *Prunella atrogularis* and the white-tailed nuthatch *Sitta himalayensis* with respect to morphological traits; the alpine accentor *Prunella collaris*, the fire-fronted serin *Serinus pusillus*, the twite *Carduelis flavirostris* and the bar-headed goose *Anser indicus* with respect to vital rate traits (Figure 1.4). With the exception of the Himalaya-China community, where the majority of the most unique species belong only to that community, the most unique species have generally a wider distribution, i.e. they are present in more than one community, even though they are not necessarily the most unique everywhere.

Species that were more unique in terms of their vital rates traits occupied larger breeding ranges in mountain regions at a higher minimum elevation (Supplementary Table S1.5A and Figure 1.5). Yet, the most unique species in terms of morphological traits had smaller breeding range at a higher maximum elevation, although these effects were weak (Supplementary Table S1.5B and Figure 1.5). Further, the mountain community partially explained the distribution of uniqueness values of morhological traits, being the species inhabiting the communities of Himalaya-China, Middle East-Caucasus and Central and Northern America functionally common (Supplementary Table S1.5B and Supplementary Figure S1.4). In both cases, Bayesian models performed reasonably well, although the model related to the uniqueness of vital rates traits fitted better (see Supplementary Text 1.3 for the posterior predictive checks) than the model related to the unquiness of morphological traits.

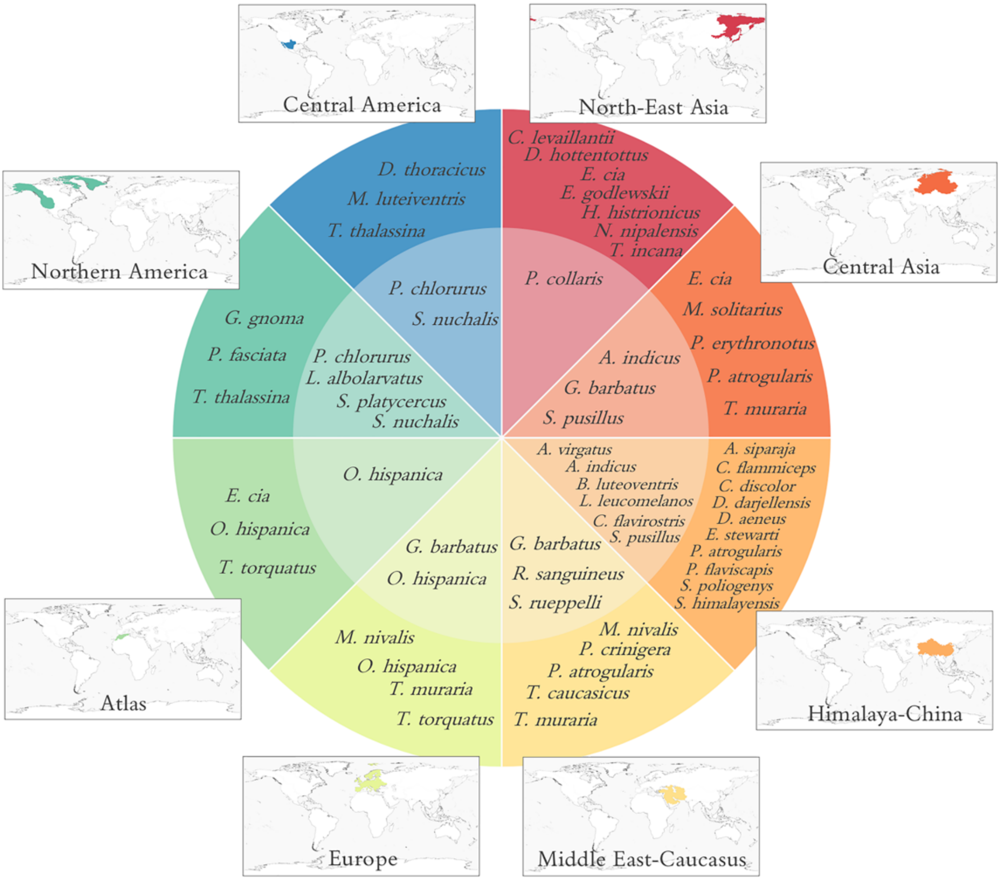


Figure 1.4. The species with the highest values of uniqueness related to morphology (outer ring) and vital rates (inner ring) traits for each community.

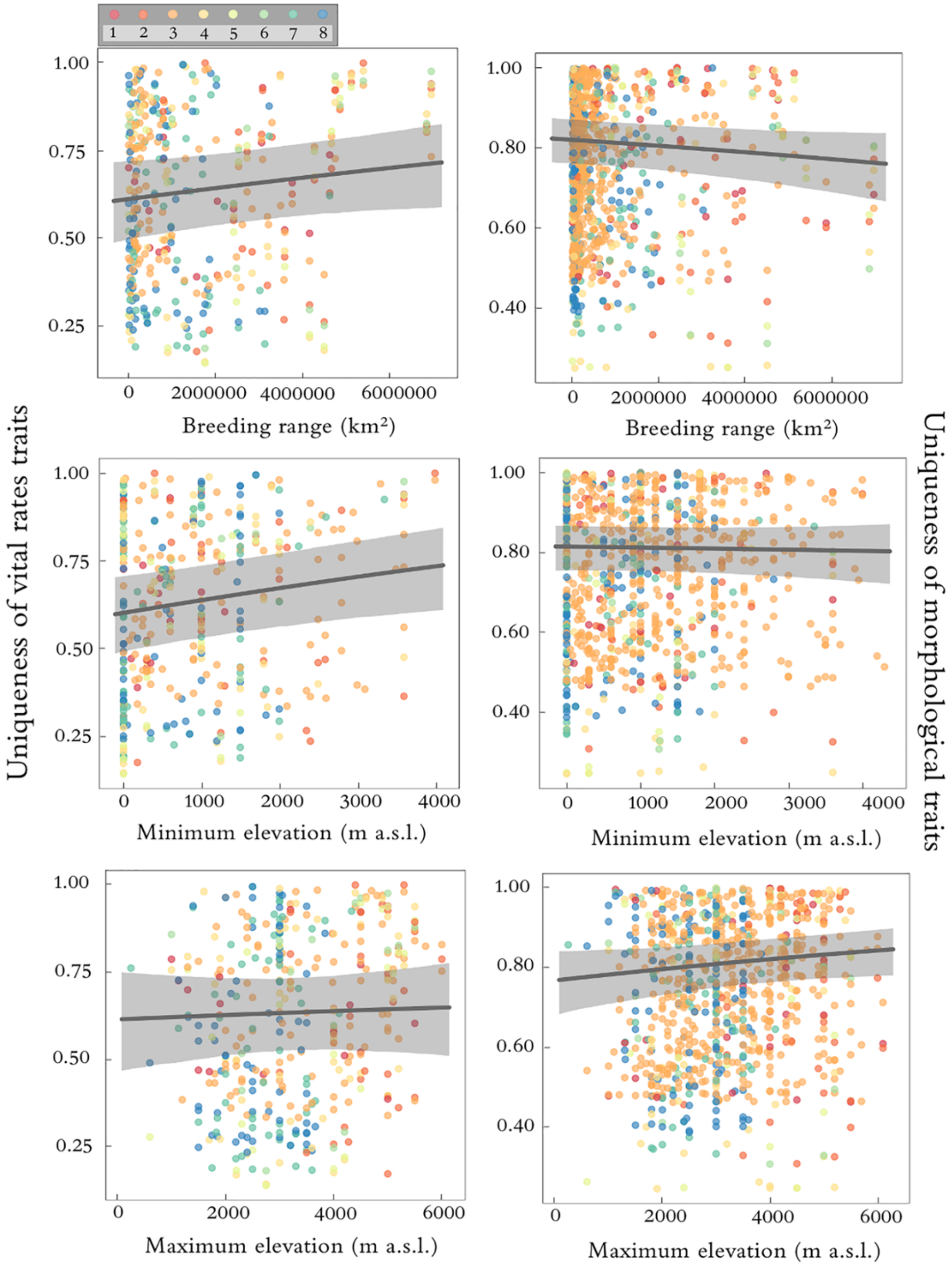


Figure 1.5. Uniqueness of vital rates (left panels) and morphology traits (right panels) against scaled breeding range, minimum and maximum elevation. The dots refer to the species, with colors indicating the community to which each species belongs. Thick grey lines represent the regression lines and shaded areas indicate their 95% credible intervals.

Discussion

We found that in Holartic mountain systems functional uniqueness increases along an elevational gradient. On the one hand, high functional uniqueness of vital rate traits seems to characterize those species living at high elevations and with a large breeding range. This result is consistent with the pattern described by Hille and Cooper (2015), who suggested a unique pace-of-life in species living at high elevations in temperate regions, with life-history trade-offs showing similarities to both the slow and fast pace occurring along latitudinal gradients. Under this unique pace-of-life, birds at high elevations show higher survival due to great investment in both self-maintenance and offspring quality, as well as high levels of mobility to allocate resources (Bastianelli et al. 2017). On the other, morphological characteristics are related to diet, foraging, habitat utilization (Ricklefs 2012), as well as to dispersal abilities (Sheard et al. 2020). In turn, morphology can be considered as a surrogate of the functional role of a species in key ecosystem processes such as predation, pollination or seed dispersal, and it has been demonstrated that the degree of specialization of functional roles increases with morphological uniqueness (Dehling et al. 2016). We found that high elevation species are unique also in terms of their morphology, with functional uniqueness increasing with maximum elevation. In such more open habitats, where resources are patchily distributed and the environment highly stochastic, birds need to move across large areas and thus manoeuvrability in flight is important (Reif et al. 2016). Jarzyna et al. 2020 attribute the increasing functional uniqueness with elevation to nestedness (Baselga 2010), i.e. the loss of species along the elevational gradient, so that higher sites with smaller numbers of species are subsets of the richer sites at lower elevations. However, a second mechanism that could be influencing functional uniqueness, which does not necessarily exclude the other, is species turnover, i.e. the replacement of some species by others, which in the case of higher elevations would present extreme, unique traits (Baselga 2010; Montaño-Centellas et al. 2020). Indeed, the treeline represents a sort of inflection line, above which low species-rich bird communities show a higher degree of functional turnover and habitat specialization compared to lower elevation communties (Altamirano et al. 2020).

The asynchrony of species' responses to environmental fluctuations is an important mechanism through which biodiversity can stabilize ecosystem properties (Loreau and de Mazancourt 2013). In this sense, rare species, which often hold irreplaceable functions and contribute to the diversity of ecological niches within assemblages, may provide resistance and resilience to a variety of disturbances (Mouillot et al. 2013; Leitão et al. 2016). Moreover, consistent effects of rare species can act not only from the top-down, as widely demonstrated for keystone species, but also from the bottom-up, with cascading effects on the richness and the abundance of other organisms in a community (Bracken and Low 2012). As such, they are likely to insure against future uncertainty arising from climate change and the increasing anthropogenic alterations on mountain ecosystems. Rare species may thus deliver more unusual and important functions than their local abundance or regional occupancy may suggest (Mouillot et al. 2013). Indeed, species rarity does not necessarily relate to the mere abundance, geographic range or habitat breadth, characteristics that have been traditionally used to define the potential vulnerability of species to global change (Grenié et al. 2018). Since functional traits reflect species' adaptations to the environment they live in, as well as their ecological role and function, functional distinctiveness adds a complementary dimension to biodiversity independent from the geographical range (Violle et al. 2017). Thus, although species that are considered threatened may be indeed both functionally unique and geographically restricted (Grenié et al. 2018; Cooke et al. 2020; Loiseau et al. 2020), many functionally unique species have wide geographical ranges and thus are not considered threatened, or have an unknown status (Grenié et al. 2018; Cooke et al. 2020).

Global scale assessments of ecological rarity, defined by the combination of functional uniqueness and geographical restrictiveness, identified tropical mountainous regions as hotspots of rare species (Loiseau et al. 2020). However, we showed that when reducing the spatial scale to a regional scale (i.e. Holarctic mountain communities) and considering only the pool of mountain bird species, the relationship between functional uniqueness and geographical range weakens. Functionally unique species of low latitudes have indeed a limited distribution. Yet, we found that species that are more ubiquitous in mountainous ranges may be functionally unique in some parts of their geographical range, depending on the regional species pool. For example, the rock bunting is distributed in all the communities except for the Americas', but it is among the most unique in terms of morphological traits only in the communities of North-East and Central Asia and of the Atlas, as well as the twite has unique vital rates traits inside the community of Himalaya-China, even though it is present also in Central Asia, Middle East-Caucasus and Europe. Thus, the ecological meaning of species uniqueness is scale-dependent (Kondratyeva et al. 2020): while a species can be functionally redundant at a broad scale, the same species can have a high functional uniqueness at the local scale, and viceversa.

Among the forecasted effects of climate change is the severe reduction of the distribution range of ecologically rare birds, driving some of them towards global extinction (Loiseau et al. 2020). This threat concerns in particular mountain ecosystems, which are classified as highly vulnerable to climate change impacts, mainly because of the narrow distribution and environmental niche of many taxa, but also because of the morphological and life-history adaptations to live in such specific environments, that makes high-elevation species functionally unique. This might be specially the case in those mountain communities at low latitudes that showed a higher species and functional richness compared to communities at higher latitudes, but a lower functional redundancy. That means that the loss of species in these mountain communities might have particularly severe consequences on the ecosystem function. Under this perspective, the independence of species functional rarity from their geographic distribution may have important implications for mountain systems. On the one side, while a species might become locally extinct, its presence elsewhere may prevent definitive extinction. Yet, given the differential functional role of a species with respect to the species pool, local extinction may result in the loss of rare functions within that community.

Overall, our results bring insights to the uniqueness of high-elevation bird species, which not only are highly ecologically specialized, but are equipped with functionally unique traits. However, the role of species with unique traits and their potential contribution to the functioning and processes of mountain ecosystems are unknown. This in turn hinders our understanding of the effects of their possible disappearance as a consequence of global change and thus opens a promising avenue for future research.

Supplementary Material

Given the length of the supplementary material, and the dimension of the tables contained, the material can be viewed at the following link:

https://drive.google.com/file/d/1Zv2fU9EotVhmd53FTaAsPV4HEVqpbMhO/view?usp=sharing

Chapter II

Potential distribution of a climate sensitive species, the white-winged snowfinch *Montifringilla nivalis* in Europe

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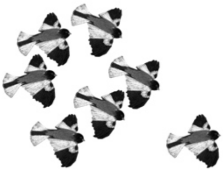


Summary

The white-winged snowfinch *Montifringilla nivalis nivalis* is assumed to be highly threatened by climate change, but this high elevation species has been little studied and the current breeding distribution is accurately known only for a minor portion of its range. Here, we provide a detailed and spatially explicit identification of the potentially suitable breeding areas for the snowfinch. We modelled suitable areas in Europe and compared them with the currently known distribution. We built a distribution model using 14574 records obtained during the breeding period that integrated climatic, topographic and land-cover variables, working at a 2 km spatial resolution with MaxEnt. The model performed well and was very robust; average annual temperature was the most important occurrence predictor (optimum between c.-3°C and 0°; unsuitable conditions below -10° and above 5°). The current European breeding range estimated by BirdLife International was almost three times greater than that classified as potentially suitable by our model. Discrepancies between our model and the distribution estimated by BirdLife International were particularly evident in eastern Europe, where the species is poorly monitored. Southern populations are likely more isolated and at major risk because of global warming. These differences have important implications for the supposed national responsibility for conservation of the species and highlight the need for new investigations on the species in the eastern part of its European range.

Introduction

Detailed knowledge of the occurrence and spatial arrangement of animal species and their preferred habitats is a basic, key requirement for most research applications and for species and habitat conservation. In this climate change era, climate-sensitive species (and environments) are of particular concern, as they are highly threatened by ongoing modifications in climatic parameters and by changes in the habitat prompted by such modifications.

The white-winged snowfinch *Montifringilla nivalis* (hereafter, snowfinch) in Europe (which includes the whole range of the nominate subspecies *M. n. nivalis*) inhabits a range restricted to higher elevations of central and southern mountain massifs, and is among the species most threatened by climate change on the continent (Brambilla et al. 2017b). Predicted changes in distribution and connectivity among suitable sites (Brambilla et al. 2017b), potential increase in the impact of human alteration to alpine habitats (Brambilla et al. 2016), modifications in snow-cover and snow-melt date (Brambilla et al., 2018b; Resano-Mayor et al., 2019) and in foraging habitat (Brambilla et al., 2018a) suggest a very concerning status of the species, at least in the Alps, where the species has been most studied.

Despite the dramatic future prospects for the species, the snowfinch had been little investigated until a few years ago and was classified as 'Least Concern' in the last Red List of European Birds (BirdLife International 2015). In recent years, evidence for range contractions and/or population declines has accumulated (Knaus et al. 2019, Scridel et al. 2017) and the snowfinch is now regarded as a flagship species for high-elevation taxa and habitats threatened by climate change. The current breeding distribution of the species is reasonably well known only for the Alps, the Pyrenees and the Cantabrian Mountains, whereas for the Italian pre-Alps and Apennines, available data are less complete and accurate; in the Balkans, data are even scarcer and knowledge of the species' occurrence is still poor in several areas (see www.snowfinch.eu).

We aimed to identify those mountain areas in Europe with suitable habitats and climates for breeding snowfinches and to compare them with the current estimated geographical range during the breeding season, in order to: *(i)* provide a better understanding of the breeding distribution over the continent; *(ii)* identify gaps in current knowledge by comparing our output with the currently known distribution as defined by BirdLife International (BirdLife International and Handbook of the Birds of the World, 2018; hereafter, "BirdLife distribution") and thus to pinpoint new, potentially important, areas to be explored (Bourg et al. 2005, Brambilla et al. 2009); and, *(iii)* compare the potential importance for conservation of the different countries hosting snowfinch populations according to current knowledge (BirdLife distribution relative to the breeding season) and to our model, respectively. All this information is essential to better understand distribution patterns for conservation-related purposes, such as identifying key areas and national responsibilities for snowfinch conservation.

Methods

Data were collected as widely as possible throughout European countries, in the framework of different studies carried out by the authors (Brambilla et al. 2017a, 2018a, Resano-Mayor et al. 2017, 2019, Strinella et al. 2007) and by national parks and local institutions. All these data were collected in the form of spatially georeferenced observations. In addition, citizen science data (i.e. collected by the public) were gathered through online databases (www.ornitho.at, www.ornitho.ch, www.ornitho.it), after official requests specific to the purposes of the project (data downloaded and received in the period December 2018–April 2019). Data were therefore occurrence-only.

We collated all data for the period 1979–2018 and removed all records not satisfying the temporal and spatial requirements. We only kept records of breeding individuals (atlas code suggesting breeding or 'territorial' behaviour), or observed during the species' breeding season (15 May–31 July, i.e. the 'core period' of the breeding season, during which most individuals are likely to be involved in reproduction). All data recorded at a resolution coarser than 1 km were discarded.

Overall, 14,574 records met the above criteria. Twenty-four observations were from elevations between 750 and 1500 m a.s.l., and 96 observations were recorded above 3000 m (but below 3700 m). Most data (14454) were collected between 1500 and 3000 m (mean 2247 ± 316 SD). Note that the recorded elevation (assigned based on the digital elevation model used for model building; see below) could be not exact, because of the resolution of the records (from one or a few meters, up to 1 km); even an approximation of a very few hundreds of meters on mountain slopes may result in elevation differences of up to hundreds of metres because of the steep terrain.

To develop the distribution model, we considered climatic, topographic and land-use/land-cover variables. Climatic data were gathered by the CHELSA database for the period 1979–2013 (Karger et al. 2017) at a 30 arc seconds (~ 1 km) resolution. Topographic variables were derived from a 30-m digital elevation model in GRASS GIS (Neteler et al. 2012). Land-cover data were derived from Corine Land Cover 2012 (European Environment Agency 2016). All environmental data were expressed at the scale of 2 x 2 km cells, taking the average values for climatic predictors, slope and solar radiation, and the proportional cover for land-use/land-cover categories.

The same grid was used to process snowfinch records and to create background points. All cells with one or more snowfinch records were considered as occupied cells and used as occurrence cells for modelling (thus avoiding duplicates and reducing the number of records from the most intensively sampled areas). We thus obtained 2473 independent 2 x 2 km cells occupied by the species. The distribution of occurrence data and hence of occupied cells was not uniform over the European range. The Alps hosted the largest amount of data, followed by the Cantabrian Mountains. There were fewer data from the Pyrenees and the Apennines, but they were nonetheless adequately sampled (Figure S2.5 in the Supplementary Material). Notably, environmental conditions in the Apennines were representative of Mediterranean mountains and this area may thus provide a test-site to check the model’s ability to predict species distribution over the poorly sampled Mediterranean mountains.

The distribution model was developed using MaxEnt (hence, a presence-background method not requiring absence data), under the package ENMeval (Muscarella et al. 2014) in R (R Core Team 2018). 150000 background cells were randomly identified within the most intensively sampled countries in the study region (irrespective of snowfinch records), i.e. Portugal, Spain, France, Italy, Switzerland, Austria and Slovenia. All those countries harbour snowfinch populations or are close to existing ones (Portugal) and hence potentially reachable by the species.

We used only the variables which did not lead to multicollinearity issues for modelling, on the basis of the generalized Variance-Inflation Factor (gVIF; Zuur et al. 2009), removing variables with values >5. Variables tested included those selected in the final model shown in Table 2.1, in addition to other climatic and land cover variables. We tested climatic variables potentially relevant for snowfinches as those related to temperature and snowfall regimes, and all land cover variables occurring within the study area, in three different combinations: *(i)* only the variables of most importance for the species according to current knowledge, *(ii)* the latter plus those more represented in mountain environments (i.e. the cover of pastures, mixed forest, moors and heathland, glaciers and permanent snow, water courses and water bodies), *(iii)* all variables listed in Table 2.1. Table S2.1 in the Supplementary Material contains further details about the potential effect of environmental variables.

We split occurrence data into four bins (using the function 'checkerboard 2'), i.e. in four partitions of spatially independent occurrence records, which were used for model training and validation over independent datasets. AUC (Area Under the Curve of the receiver operating characteristic -ROC- plot) and omission rates on test data (Muscarella et al. 2014) were considered (Table S2.1). Eight different values of the regularization multiplier were tested (from 0.5 to 4 with increments of 0.5), and the one leading to the model with the lowest AIC was selected. Then, the variables with the weakest effects (with permutation importance and percentage contribution both lower than 1) were removed from the model, which was trained again with the eight different regularization multiplier values. This process was repeated until we obtained a final best-supported model. The logistic model output was reclassified into three different suitability categories to facilitate interpretation: unsuitable (lower than maximum training sensitivity plus specificity threshold), partly suitable (between maximum training sensitivity plus specificity threshold and 10th percentile), and definitely suitable (higher than 10th percentile). These two thresholds are those generally adopted for binary reclassification of models produced using MaxEnt (Liu et al. 2005, 2013, Engler et al. 2014).

To refine the predictions at a finer scale in order to provide outputs as precise as possible, we limited the potential occurrence of suitable sites to the region-specific elevation belt inhabited by the species, by filtering out as unsuitable all areas below 1500 m (this being a conservative value, selected to exclude areas at elevations where snowfinches had never been found in recent years in Europe). The changes due to this post-modelling correction were almost imperceptible at the working scale (see Figure S2.1).

Table 2.1. Variables selected in the final MaxEnt model and their relative effect, and other variables tested but not included. Irrespective of their inclusion, variables are subdivided into two groups (potentially important predictors vs. other variables). The number before the land-cover variables represents the CORINE category. A short description of the potential importance of the variables presumed to be potentially important for the species is also provided in the last column.

Variable	Permutation importance	Effect	Potential importance
Potentially important predictors of environmental suitability for Snowfinches			
23 – broad-leaved forest	0.29	negative	unsuitable habitat locally reaching high elevation
24 – coniferous forest	1.06	negative	unsuitable habitat reaching high elevation
26 – natural grassland	0.16	positive	positive effect – important foraging habitat
31 – bare rocks	0.25	positive	positive effect – foraging and nesting habitat
32 – sparsely vegetated areas	0.09	positive	positive effect – potential foraging habitat
annual average temperature	94.27	quadratic (optimum between -3° and 0°C)	important driver of species occurrence
precipitation of the warmest quarter	1.88	positive	potential effect because of impact on vegetation (e.g. seed production)
slope	2.01	quadratic (optimum at c. 20°)	generally associated to slopes
average solar radiation			important for microclimate
precipitation of the coldest quarter			potential positive effect (snow-cover in spring is crucial for foraging)
Other variables presumably less important - tested but not included in the models			
2 – discontinuous urban fabric, 3 – industrial or commercial units, 12 – non-irrigated arable land, 13 – permanently irrigated land, 15 – vineyards, 16 – fruit trees and berry plantations, 17 – olive groves, 18 – pastures, 20 – complex cultivation patterns, 21 – land principally occupied by agriculture with significant areas of natural vegetation, 22 – agro-forestry areas, 25 – mixed forest, 27 – moors and heathland, 28 – sclerophyllous vegetation, 29 – transitional woodland-shrub, 34 – glaciers and perpetual snow, 35 – inland marshes, 40 – water courses, 41 – water bodies			

Finally, we performed a country-based comparison of the suitable breeding area as predicted by our model, with that estimated to be occupied by breeding snowfinches according to the BirdLife distribution, the most widely used and comprehensive estimation of the species' geographic range currently available. Similarly, we compared the estimated percentage of the species' European range within each country based on our models and the BirdLife distribution. These assessments are particularly relevant because the percentage of a species' population within a country (likely correlated with the percentage of range within it) is among the criteria used to define a country's responsibility for the conservation of a given species (BirdLife International 2017). This analysis was performed *(i)* using raster data and the relative approximation (resulting in an irrelevant difference over such a broad scale), and *(ii)* without any correction for elevation. In addition, the analysis was restricted to the countries hosting the species as a breeder according to the BirdLife distribution, and to those closely neighbouring snowfinch populations in other countries (Andorra and Bulgaria).

Results

The output of the distribution model was identical for the three sets of variables tested. The most supported MaxEnt distribution model performed well and was very robust, displaying the same AUC and omission rates very close to the expected values, over all the four independent bins (Supplementary Table S2.1).

Average annual temperature (bio1) was by far the most important predictor of species occurrence, having the only notable effect according to permutation importance; it had a quadratic effect, with an optimum for snowfinch occurrence between c.-3°C and 0°, and unsuitable conditions below -10° and, especially, above 4°–5°. The other climatic predictor included in the final model was precipitation of the warmest quarter (bio18); this variable was slightly positively correlated with environmental suitability for snowfinches, as were natural grassland, bare rocks and sparsely vegetated areas. Forest cover (both broadleaved and coniferous) had a negative effect on environmental suitability, whereas a quadratic relationship was identified between suitability and slope, with a peak at intermediate slope values (Table 2.1). The effect of environmental variables on habitat suitability for snowfinches is shown in Supplementary Figure S2.4.

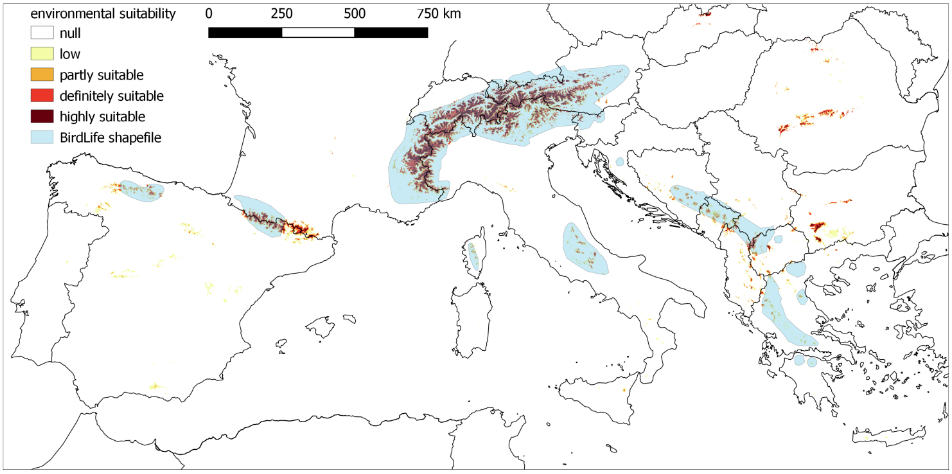


Figure 2.1. Modelled (our work) and reported (BirdLife) distribution of white-winged snowfinch in Europe. Partly suitable sites are those with suitability above the maximum training sensitivity plus specificity threshold, definitely suitable sites those higher than the 10th percentile (see text for further details); highly suitable areas are those with suitability close to the maximum value. Areas below 1500 m were considered as unsuitable (see also Supplementary Figure S2.1).

Modelled and reported (BirdLife) distributions were generally similar (Figure 2.1), although there were some important discrepancies (Supplementary Figures S2.2–S2.3). Similarly, the estimated suitable area per country displayed important differences; in general, the area inhabited by snowfinches according to the BirdLife distribution was greater (249221 km^2) than the area suitable or potentially suitable estimated by our model (91044 km^2). The percentages of the European species' range hosted by each country calculated according to the model and the BirdLife distribution were significantly correlated (Spearman's rho 0.71, P = 0.001), but revealed some important discrepancies in the relative relevance of each national population (Table 2.2).

Table 2.2. Comparison between suitable area and relative distribution share per country according to our distribution model and the BirdLife distribution, respectively. Country extent mirrors the raster resolution of the distribution model. List of abbreviations used in the table: pot_suit: area potentially suitable; def_suit: area definitely suitable; tot_suit: sum of potentially and definitely suitable area; area_BLD: extent of BirdLife distribution within the country; %_suit_model: percentage extent of the country potentially or definitely suitable; %_BLD: percentage extent of the country occupied by the species according to BirdLife distribution; %_species_model: percentage of snowfinch European range within the country according to the potentially or definitely suitable areas (considering only the countries listed in the table); %_species_BLD: percentage of snowfinch range within the country according to BirdLife distribution.

		model			BL distr	National scale		European range	
Country	country extent	pot_suit	def_suit	tot_suit	area_BLD	%_suit_ model	%_BLD	%_species_model	%_species_BLD
France	549264	4892	9860	14752	44073.4	2.7	8.0	16.2	17.7
Spain	498684	3208	2696	5904	12692.2	1.2	2.5	6.5	5.1
Italy	301152	7648	12988	20636	64509.8	6.9	21.4	22.7	25.9
Germany	357578	1084	508	1592	6088.7	0.4	1.7	1.7	2.4
Greece	132184	736	204	940	20977.2	0.7	15.9	1.0	8.4
Bulgaria	111036	1212	1120	2332	0.0	2.1	0.0	2.6	0.0
Serbia	88456	968	380	1348	5864.8	1.5	6.6	1.5	2.4
Austria	83808	7604	12436	20040	45910.0	23.9	54.8	22.0	18.4
Croatia	56488	88	8	96	622.3	0.2	1.1	0.1	0.2
Bosnia and Herzegovina	51196	1104	224	1328	6899.1	2.6	13.5	1.5	2.8
Switzerland	41320	4084	11980	16064	23795.0	38.9	57.6	17.6	9.5
Albania	28488	940	472	1412	1618.4	5.0	5.7	1.6	0.6
Macedonia	25396	924	736	1660	4641.7	6.5	18.3	1.8	1.9
Slovenia	20248	516	364	880	4146.5	4.3	20.5	1.0	1.7
Montenegro	13872	1280	348	1628	7218.0	11.7	52.0	1.8	2.9
Andorra	460	120	264	384	0.0	83.5	0.0	0.4	0.0
Lichtenstein	160	24	24	48	160.0	30.0	100.0	0.1	0.1

Discussion

For a species so highly threatened by climate change (Brambilla et al. 2018a, Resano-Mayor et al. 2019), it is essential to accurately define current and potential distribution in order to plan conservation strategies and implement measures in relevant sites; distribution modelling may help considerably in that sense (Engler et al. 2017). Our study provides a detailed and spatially explicit identification of the potentially suitable breeding areas of the nominate snowfinch subspecies *Montifringilla nivalis nivalis*, which inhabits European mountains. Analyses confirmed the primary importance of climatic (in particular temperature) and topographic (slope) parameters in determining environmental suitability and hence distribution in snowfinches (see Table 2.1 and Supplementary Figure S2.5), in concordance with assessments carried out over finer spatial scales (Brambilla et al. 2016, 2017b). As expected, environmental suitability for snowfinches increases with the cover of natural grassland and sparsely vegetated areas, which provide key foraging habitats (Brambilla et al. 2017a, 2018b), and with bare rocks, which provide potential nesting sites.

Snowfinch occurrence data mostly came from the Alps, where the species has a rather broad distribution; however, the model correctly predicted occurrence in other, more isolated mountain chains, such as the Cantabrian Mountains and the Apennines. The latter served as a test-site for model performance in the Mediterranean region; these results were encouraging, as the predicted distribution represented well the actual occurrence of the species, including some isolated habitat patches irregularly occupied by the species which were classified as potentially suitable by the model (E. Strinella and M. Brambilla pers. obs.). Despite this, we cannot exclude the possibility that the potential region-specific variations in habitat associations could to some extent affect model predictions for poorly sampled areas, such as the Balkans. Further occurrence data should be collected in south-eastern Europe to exclude such potential limitations, as well as to improve knowledge and model accuracy for this relatively poorly known portion of the European range of the species. Nevertheless, we believe that the predicted suitability *(i)* makes sense also for southeastern Europe (see below and supplementary material), and *(ii)* can be used to highlight areas requiring further investigation.

In southern European mountains, the availability of potentially suitable areas according to the model is much more restricted and fragmented than the overall species range suggested by the BirdLife distribution, and snowfinches likely occupy smaller, and more isolated, suitable patches there (Figure 2.1), in areas characterised by higher average temperatures. As a consequence, populations breeding in these mountains (Cantabrian Mountains, Apennines, Balkans) appear to be at greater risk because of climate change impacts. Future studies based on the comparison of the species' autecology and demography between large suitable areas (e.g. Alps, Pyrenees) and smaller, more marginal ones (e.g. Cantabrian Mountains, Apennines, Corsica, several areas in the Balkans) may help to understand the potential impacts of climate change by allowing the inclusion of large gradients of climate and isolation.

Despite a general concordance with the currently known distribution, modelling also highlighted some important differences with the current range of the species as defined by BirdLife International (BirdLife International and Handbook of the Birds of the World 2018), especially (but not exclusively) for eastern Europe. Generally, the BirdLife distribution includes most of the areas predicted to be suitable by our model (apart for some parts of the Cantabrian Mountains and Pyrenees), but also includes rather large unsuitable areas compared to our models. Some of these discrepancies are likely due to the different spatial resolution of the two approaches; approximate polygons surrounding occupied areas and not considering elevation are very likely to 'overpredict' occurrence compared to a dedicated species distribution model for such a species strongly linked to high elevation. Nevertheless, some discrepancies definitely require further investigation (see Supplementary Figures S2.2–S2.3 for detailed comments and comparisons). Some of the differences arose because the model identified potentially suitable sites in mountain chains currently believed not to harbour breeding snowfinches, such as the Carpathians, Rila and Rhodope mountains, and Mount Etna. In some of these sites, further investigations should be carried out (see below and supplementary material for further discussion). Suitable areas in the Balkans show only a moderate concordance with the snowfinch range according to the BirdLife distribution (Supplementary Figure S2.2). Even if this is largely attributable to the relatively low spatial resolution of the BirdLife distribution, which needs to be considered at a larger scale, most areas encompassed by it in Greece are located below 1500 m, and suitable areas are located largely outside the supposed species range. In Albania, Macedonia and Bulgaria, several suitable patches occur outside the known range of the species. Some of those sites could potentially host important populations that need to be preserved for the conservation of the species in eastern Europe. According to the BirdLife distribution, snowfinches do not breed in Bulgaria. However, our model suggested the availability of large suitable patches in the southwestern part of the country. Even if the species is currently considered as non-breeding in the country, historical records of breeding pairs in the 1960s were reported (although regarded as not reliable) for Mt. Rila (Ivanov 2011). According to our model, this site has the highest suitability in the country. Further intensive field work is needed in this key unknown area.

These differences have important implications for the supposed national responsibility for the species' conservation, and such discrepancies result also in very large differences in the expected frequency of a species within a country (Table 2.2). For example, the estimated area occupied by snowfinch in Greece according to the BirdLife distribution is 22 times higher than the suitable/potentially suitable area estimated by our model. Considering the BirdLife distribution, Greece should host a proportion of the European snowfinch breeding range that is very close to that harboured by Switzerland, whereas our model suggests that the proportion of the European snowfinch range in Switzerland is almost 18 times that found in Greece. A further example relevant to those regarding the perceived frequency of the species within each country is provided by Montenegro, where snowfinches should occur in more than half of the country according to the BirdLife distribution, whereas our model suggests that less than 12% of the country is potentially suitable for the species, and only 2.5% is definitely suitable.

The concerning situation of the species in Europe has triggered several studies on its ecology, distribution and demography in several areas in Europe, namely the Cantabrian Mountains, the Pyrenees, Corsica, the Alps and the Apennines (see ongoing initiatives on www.snowfinch.eu). Unfortunately, we are not aware of any detailed study in the Balkans. The results of our work suggest the need for new investigations on the species in the eastern portion of its European range, where the basic distribution of the species is also poorly known. In addition, such areas need to be investigated in the future, as they could provide key features for planning conservation measures for this species. Within such sites, snowfinches may experience climatic conditions that are now lacking in other European mountains, but that will be potentially much more widespread in the future. In addition, an increase in the availability of occurrence data from the Balkans could confirm or increase the accuracy of model predictions for this area. Further site-specific studies to better understand the ecology and population dynamics of the species are required across the entire geographic range to better assess snowfinch conservation status and promote management and other conservation actions for the most emblematic (and highly threatened) alpine passerine of Europe.

Supplementary Material

Preliminary modelling attempts

Before presenting in details the distribution model we obtained, we actually performed some other attempts with different number of background points (30000 – 50000 – 150000), and different criteria for their spatial location (within a 10 km buffer from sample points, within a 50 km buffer, as in the final model). Notably, all models led to generally similar outcomes, but the ones we presented led to the most reliable estimate of occurrence of suitable habitats (at least in the well known areas).

Table S2.1. Summary statistics for MaxEnt model. The model highlighted in grey represents the “final” one. Legend of abbreviation: rm: regularization multiplier; AUC: area under the curve of the ROC plot; OR10: omission rate on test data al 10th percentile; ORmin: omission rate on test data at minimum training presence.

rm	Full AUC	Mean. AUC	Var. AUC	Mean AUC DIFF	Mean OR10	AICc	ΔAICc	w.AIC	nk	AUC.1	AUC.2	AUC.3	AUC.4	OR10.1	OR10.2	OR10.3	OR10.4	ORmin.1	ORmin.2	ORmin.3	ORmin.4
0.5	0.986	0.986	0.000	0.001	0.106	48532.43	57.72	0	101	0.985	0.986	0.986	0.985	0.107	0.086	0.096	0.136	0.000	0.000	0.000	0.002
1	0.986	0.986	0.000	0.001	0.106	48506.26	31.55	0	85	0.985	0.986	0.986	0.985	0.107	0.083	0.099	0.136	0.000	0.000	0.000	0.002
1.5	0.986	0.986	0.000	0.001	0.104	48503.98	29.27	0	80	0.985	0.986	0.986	0.985	0.107	0.080	0.094	0.138	0.000	0.000	0.000	0.002
2	0.986	0.986	0.000	0.001	0.106	48511.49	36.78	0	77	0.985	0.986	0.986	0.985	0.110	0.083	0.096	0.136	0.000	0.000	0.000	0.002
2.5	0.986	0.986	0.000	0.001	0.105	48493.03	18.32	0	64	0.985	0.986	0.986	0.985	0.110	0.083	0.093	0.134	0.000	0.000	0.000	0.002
3	0.986	0.986	0.000	0.001	0.104	48474.71	0	0.62	50	0.985	0.986	0.986	0.985	0.115	0.085	0.090	0.129	0.000	0.000	0.000	0.000
3.5	0.986	0.986	0.000	0.001	0.102	48475.67	0.96	0.38	43	0.985	0.986	0.986	0.985	0.111	0.085	0.087	0.127	0.000	0.000	0.000	0.002
4	0.986	0.986	0.000	0.000	0.102	48487.93	13.22	0	40	0.985	0.986	0.986	0.985	0.111	0.085	0.090	0.124	0.000	0.000	0.000	0.002

Table S2.2. Checklist proposed by Feng et al. (2019) compiled considering the features of our work (Feng et al. 2019. A checklist for maximizing reproducibility of ecological niche models. Nature Ecology & Evolution 3: 1382-1395).

Workflow	Category	What to report	Our paper
(A) Obtaining and processing occurrence data	metadata	(A1) source of occurrence data	multiple sources, reported
		(A2) download date; version of data source	reported (approx.)/NA
		(A3) basis of records	reported
		(A4) spatial extent	reported and visually displayed in maps
		(A5) temporal range	reported
	processing	(A6) duplicate coordinates	records from the same 2 km x 2 km cells were removed
		(A6-2) spatial/environmental outlier; error	data were carefully checked before analyses
		(A6-3) spatial/coordinate uncertainty	data at 'coarse' resolution (over 1 km) were discarded
		(A7-1) sampling bias	described in text and maps
		(A7-2) spatial autocorrelation	partition of records into four spatially independent bins
(B) Obtaining and processing environmental data	metadata & processing	(B1) source	reported
		(B2) download date; version of data source	reported
		(B3) spatial resolution	reported
		(B4) temporal range	reported
(C) Model calibration	data input	(C1) modelling domain	reported
		(C2) number of background data	150 000
		(C3) sampling method for background data	randomly scattered over fully sampled countries
		(C4) variable selection	based on knowledge on species' ecology; process described; variables leading to multicollinearity issues removed (VIF>5)
	algorithm	(C5) name	reported
		(C6) version of algorithm and software	reported
		(C7) parameterization	reported

Workflow	Category	What to report	Our paper
(D) Model transfer and evaluation	evaluation	(D1) evaluation index	AUC and omission rates over independent bins
		(D2) threshold for evaluation index	MTP and 10th percentile for omission rates
		(D3) dataset used to evaluate models	different bins
	output	(D4) format/transformation	logistic; reported
		(D5) threshold	MTSS and 10th percentile
	extrapolation	(D6) novelty of projected environments compared with training environments	within the values sampled in training data (occurrence + background)
		(D7) collinearity shift between training and projected environments	very limited for variables selected in the model; VIF for removal of multicollinear variables was calculated over all the area, including that of "extrapolation"
		(D8) extrapolation strategy	simple prediction
	metadata	(D9) source	same of training data
		(D10) download date; version of data source	
		(D11) spatial resolution	
		(D12) temporal range	

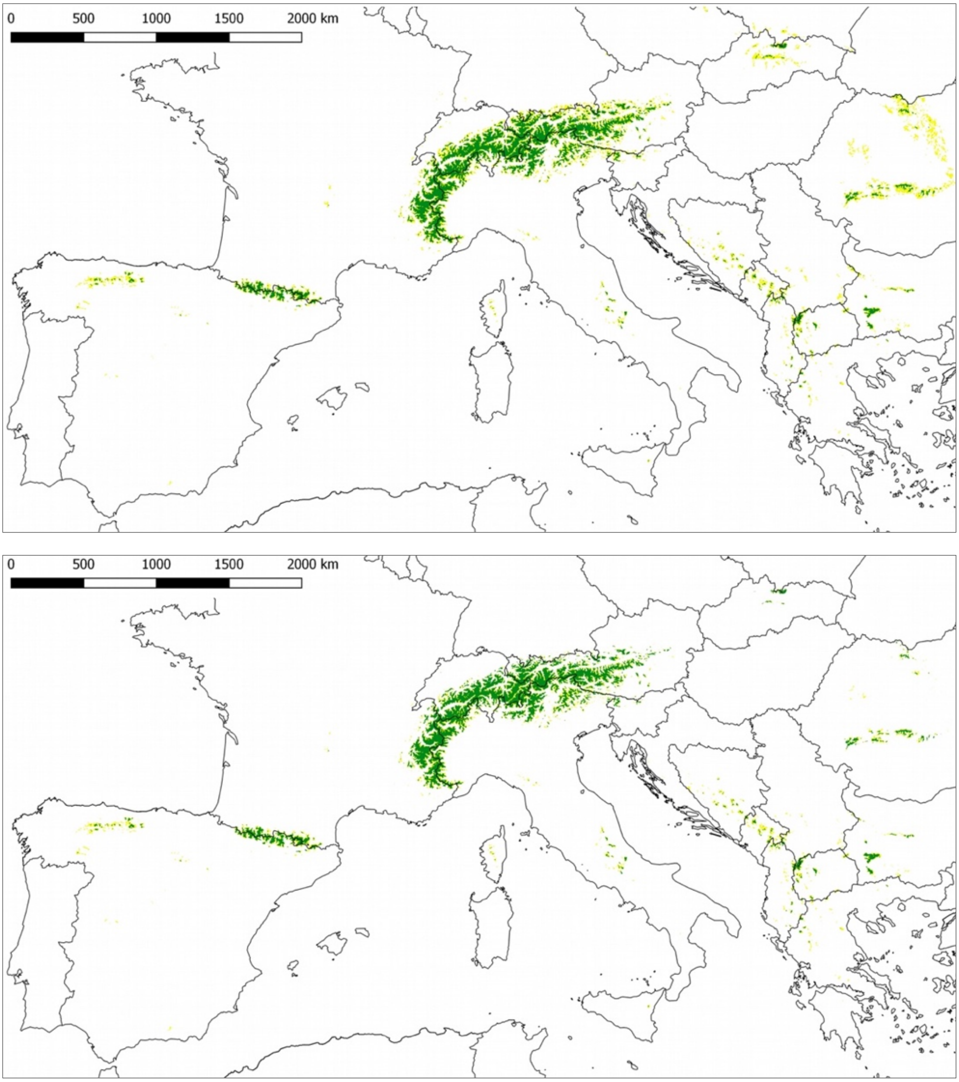


Figure S2.1. Comparison between the full model prediction (upper) and that with sites below 1500 m a.s.l. filtered as unsuitable (lower). The main differences are found for the Carpathians, which are outside the range of the species. Also a few sites along the northern edge of the Alps are regarded as potentially suitable by the model but are discarded as they are below 1500 m a.s.l. These are mostly sites located in colder valleys, and with some grassland, but in fact do not host the species (C. Schano & R. Arlettaz, pers. Obs.).

Figure S2.2. Modelled distribution and current species range according to BirdLife distribution (light blue; BLD hereafter) in southern Italy and the Balkans.

1: Central Apennines: full concordance between the two; our modelled suitable areas are more accurate, BLD includes large unsuitable portions.

2: Croatia: the species currently does not breed (K. Mikulic com. pers.) in the country (as suggested by our model, contrary to BLD).

3: Relatively good concordance in Bosnia-Herzegovina and almost so in Montenegro.

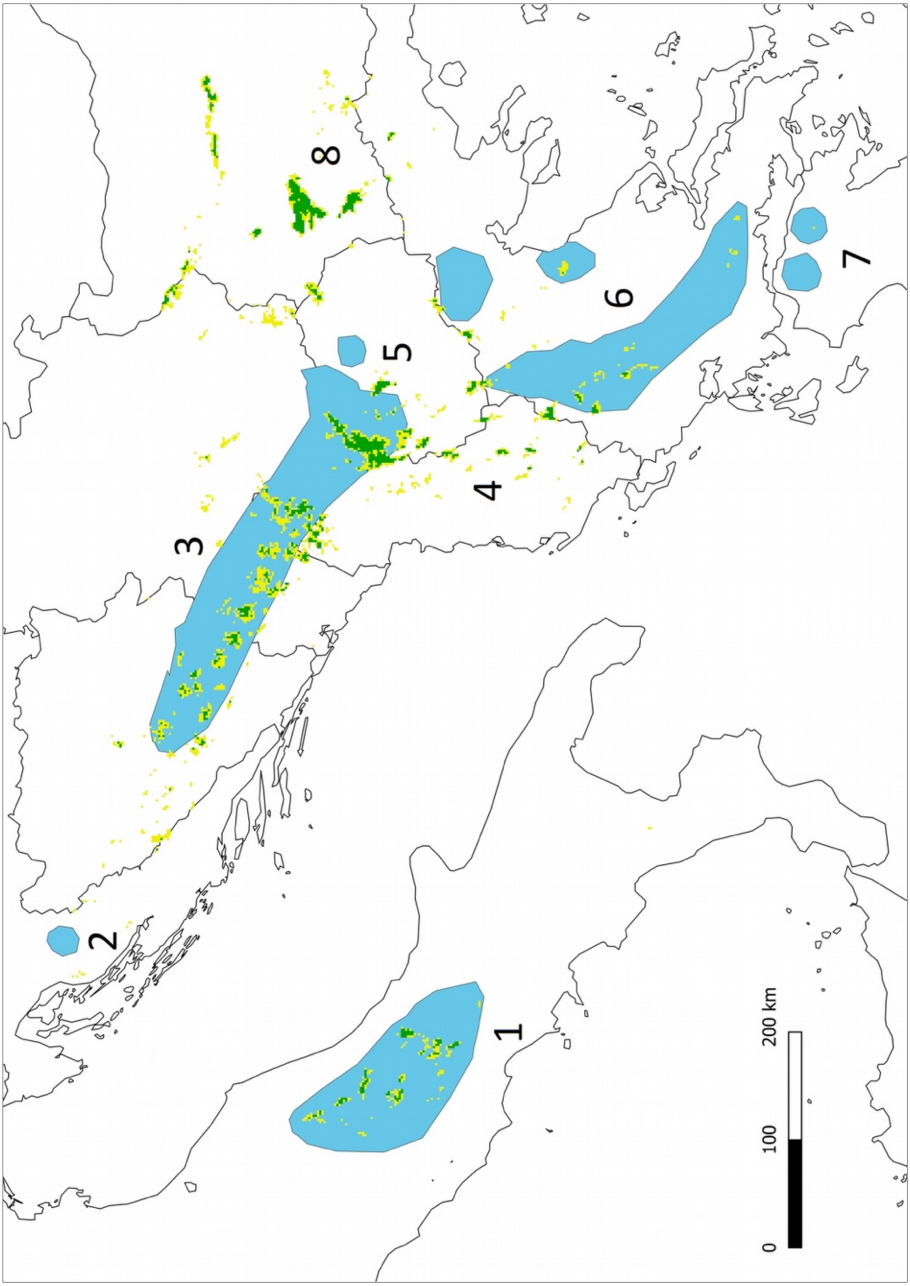
4: Albania: suitable sites occurring within the country, but largely outside the BLD. To be investigated.

5: Macedonia: suitable areas located also just outside the BLD; one isolated area occupied according to BLD apparently does not include any suitable patch. To be investigated.

6: Nothern-central Greece: BLD, which includes several areas <1500 m a.s.l., likely overestimates the real species distribution. Some suitable patches occur outside the BLD. To be investigated.

7: Southern Greece: occurring according to BLD, but almost no suitable area found there according to our model. To be investigated.

8: Southern Bulgaria: not occurring according to BLD; recently reported as non breeding in the country, but historical records of breeding pairs in 1960s (though regarded as not reliable) for Mt. Rila (Ivanov, B. 2011. The Fauna of Bulgaria. Vol. 30. Aves. Part III. Sofia, Prof. Marin Drinov Publ. House), the site with highest suitability according to our model. To be investigated.


1
2
3
4
5
6
7
8
0
100
200 km

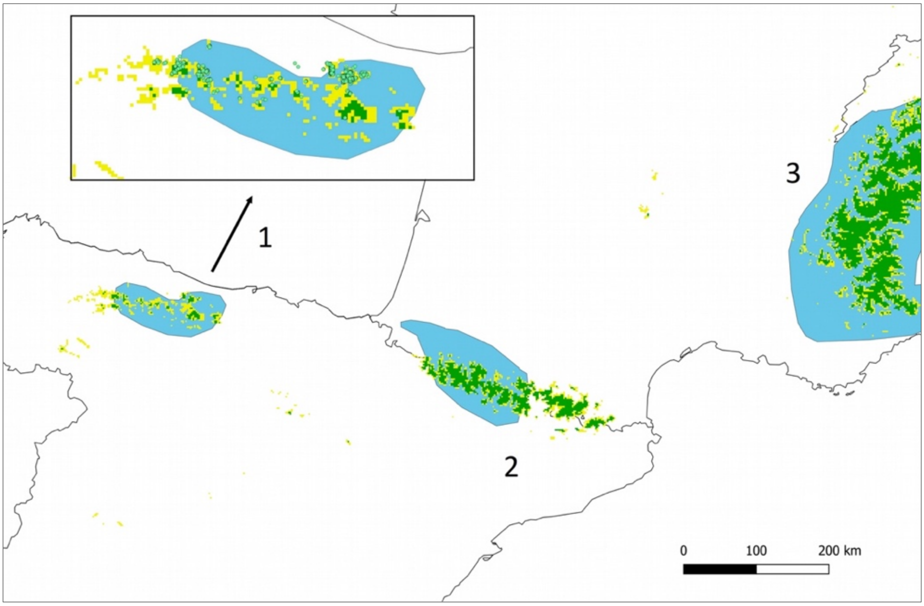


Figure S2.3. Modelled distribution and current species range according to BirdLife distribution (light blue; BLD hereafter) in western Europe.
1: Cantabrian Mountains: general concordance between BLD and model prediction, but the latter matches the occurrence data much better (plotted), especially in the west.
2: Pyrenees: the model provides a more accurate description of the local distribution of the species, which breeds in Andorra, whereas it is unlikely to occur in the NW part of the BLD, which covers a low-elevation area (largely between 30 and 500 m a.s.l.).
3: Western Alps: BLD tends to overestimate the actual species distribution, by including pre-alpine hills on both sides of the Alps, where the model depicts a total lack of suitable sites.

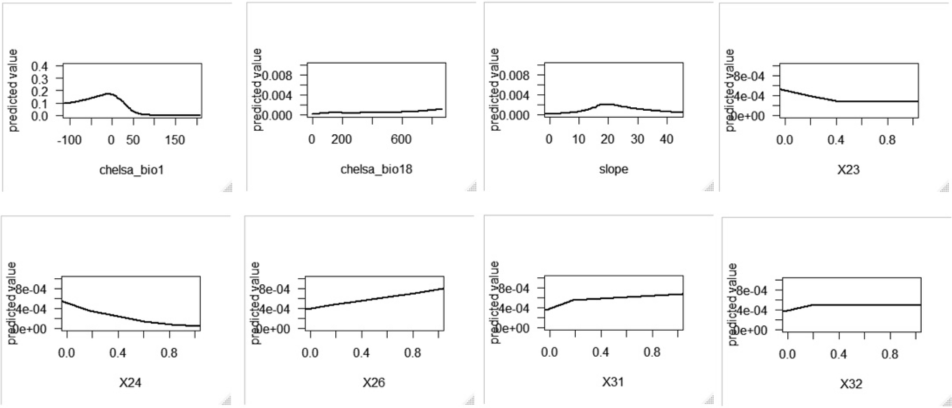


Figure S2.4. Response curves for variables included in the model (according to the full model and calculated keeping the other variables at their mean values). Note that values on the axes vary across variables.

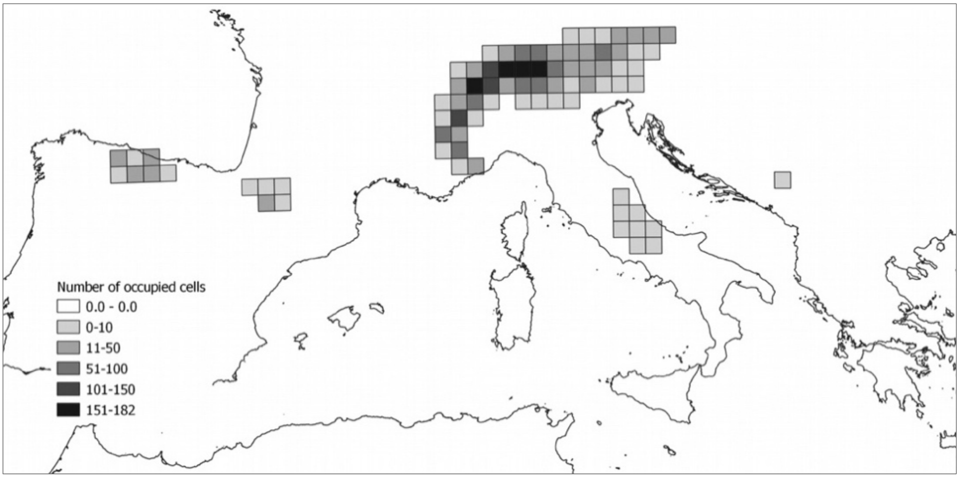


Figure S2.5. Number of independent records (occupied cells of 2 km x 2 km) for each cell of a 50 km x 50 km grid covering the entire area.

Chapter III

Circannual variation in habitat use of the white-winged snowfinch *Montifringilla nivalis nivalis*

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Summary

High mountain areas are subject to strong seasonal fluctuations and species inhabiting these particular environments show a high degree of habitat specialisation to cope with extreme abiotic conditions. Estimates of habitat use are influenced by the spatial and seasonal scales at which they are evaluated, so studies at multiple scales are important in order to explore adaptive responses to seasonal environments. In the present study, we assessed habitat use of the white-winged snowfinch *Montifringilla nivalis* subsp. *nivalis* (henceforth snowfinch) during breeding and non-breeding seasons at three different spatial scales (diameters of 100 m, 250 m and 500 m). Although snowfinches clearly used high-elevation habitats in both seasons, there was evidence that they are less specific during the non-breeding period: the variance explained by habitat and topographic factors was lower in winter compared to the breeding season. Moreover, our results suggest that the use of habitat is scale-dependent. This pattern was especially relevant in the breeding season, perhaps because habitat use might be more related to nest site selection and specific foraging sites to provide food for nestlings. Snowfinches use high mountain habitats throughout the year, probably as a consequence of physiological and morphological specialisations typical of high-elevation species, but in winter they show a certain flexibility in habitat use. Snowfinches might thus adopt a flexible specialist strategy. This could represent trade-off to overcome possible effects on survival, condition and fitness, which can be particularly strong in harsh, unpredictable environments.

Introduction

Many life-history trade-offs are mediated by environmental factors such as food abundance and climatic variables. As these factors change spatially and seasonally, species need to follow a circannual routine (McNamara and Houston 2008) that varyies at different spatial scales in order to fulfil their ecological requirements. In this regard, it is important to determine the ways in which animals select and use habitat, considering all those available (Martínez et al. 2003). While habitat selection refers to a hierarchical process of behavioral responses that may lead to the disproportionate use of habitats, habitat use is the way in which an individual uses the resources as a result of habitat selection processes (Jones 2001).

Habitat use varies according to different spatial and seasonal scales. At the seasonal scale, while food availability and predation risk are the main drivers of habitat use during the non-breeding period, other factors like breeding site characteristics (Kolbe and Janzen 2002, Forstmeier and Weiss 2004, Ciuti et al. 2006) and the use of specific foraging site to provide food for offspring (Wisenden et al. 1995, Mäntylä et al. 2015, Sprayberry and Edelman 2016) have also been shown to play an important role in determining the different patterns of habitat use. In addition, the environment is heterogeneous in space, and so individuals might rely on certain habitat features at broader scales, while changing use patterns at a finer scale (Mayor et al. 2009). For instance, among migratory land birds, the ruby-throated hummingbird *Archilochus colubris* mainly prefers flowering shrub habitats for feeding requirements at a large spatial scale, whereas the need to avoid predation drives the use for higher, denser tree cover at a finer spatial scale (Deppe and Rotenberry 2008). Similarly, the scale-dependent trade-off between food requirements and low predation risk has been described for example in the Brewer's sparrow *Spizella breweri* (Chalfoun and Martin 2007) as well as in the Eurasian woodcock *Scolopax rusticola* (Braña et al. 2013). In addition, organisms can show multi-scale responses to a single resource, as for instance the different pattern of human avoidance in bald eagles *Haliaeetus leucocephalus* at finer and coarser spatial scales (Thompson and McGarigal 2002). Therefore, the study of habitat use requires the consideration of multiple spatial scales, in order to avoid misleading inferences regarding species-habitat relationships (Boyce 2006) and to find the scale that best explains a species' occurrence (Quevedo et al. 2006).

High mountain areas are subject to strong seasonal fluctuations (Lloret 2017) and species inhabiting these particular environments have evolved complex life-history strategies to cope with extreme abiotic conditions, generally exhibiting a high degree of habitat specialisation (Reif et al. 2016). Considering Hutchinson's representation of a species' ecological niche as an n-dimensional space, where the axes correspond to environmental variables or resources (Hutchinson 1957), habitat specialisation can be defined as the breadth occupied by a species on niche axes (Vamosi et al. 2014). The concept of ecological specialisation is, however, versatile and dependent on the spatial and seasonal scales at which it is evaluated (Devictor et al. 2010). In their work on habitat specialisation and traits in European breeding birds, Reif et al. (2016) suggested that, at large spatial scales, species can be habitat specialists but have a wide diet niche within the selected habitat. As for seasonal scales, in frugivorous birds, species that are highly specialised within a season might show a certain degree of flexibility across seasons in order to, for example, respond to resource fluctuations (Bender et al. 2017). Similarly, in unpredictable mountain ecosystems, citril finches *Carduelis citrinella* exhibit higher seasonal variability in food preferences compared to lowland finches (Förschler 2007). Therefore, in order to better understand the adaptive response of a species to seasonal and heterogeneous alpine environments (Laiolo and Obeso 2017), it is important to study habitat use at multiple seasonal and spatial scales.

To date, the few studies on habitat selection of the snowfinch, a charismatic Palearctic mountain bird, have focused on a single spatial scale (micro- or mesohabitat) during the breeding season (Resano-Mayor et al. 2019). These studies have highlighted the importance of snow patches, grassland and sward height for foraging during chick rearing (Strinella 2007, Brambilla et al. 2017a, 2018a, 2018b), as well as the detrimental effects of climate-induced alteration of their microhabitat (Brambilla et al. 2018a). However, little is still known about the habitat used by wintering snowfinches, as well as possible differences between seasons and variation among scales. As winter is a challenging period in which individuals need to cope with harsh conditions that can affect individual survival (Marra et al. 2015), condition and fitness (Harrison et al. 2011, López-Calderón et al. 2017), a deeper understanding of habitat use at different spatial and seasonal scales is needed. In the present study, we aimed to study circannual variations in habitat use patterns of snowfinches at three different spatial scales (diameters of 100, 250 and 500 meters). We first compared habitat use between breeding and non-breeding seasons in order to detect possible seasonal differences. Second, we compared habitat use versus habitat availability at the above mentioned seasonal and spatial scales to characterize year-round habitat use and identify possible differences between seasons. During the breeding season habitat use might be more related to nest site selection and specific foraging sites to provide food for nestlings, hence we might expect snowfinches to be more specific in their habitat requirements than in the non-breeding season. For the same reasons, we might expect breeding snowfinches to be more specific at small spatial scales.

Methods

The species

The snowfinch is a cold-adapted, Palearctic passerine species distributed from the Iberian peninsula to the Himalaya with different subspecies (del Hoyo et al. 2009), that usually breeds above 1900 m a.s.l. in the Alps (Knaus et al. 2019) and above 1700 m a.s.l. in the Spanish Cantabrian Mountains (Fernández-González 2014). The range of the subspecies object of the present study extends from the Spanish Cantabrian Mountains eastwards through the Pyrenees, the Alps, Corsica, the Apennines, to the Dinaric Alps and Pindo Mountains in Greece (Cramp and Perrins 1994). The snowfinch is classified as a species of Least Concern by the Global IUCN Red List, yet the status of the population in Europe is unknown, due to insufficient available data (EIONET, European Environment Information and Observation Network, https://nature-art12.eionet.europa.eu/article12).

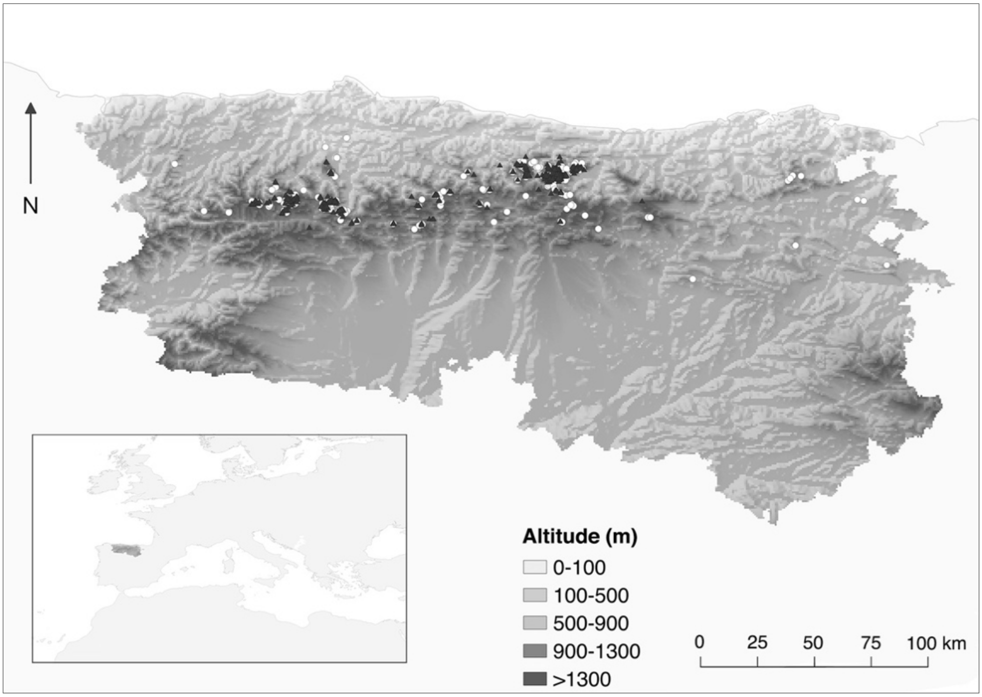

Figure 3.1. Map of the study area. White dots refer to the observations recorded during the non-breeding season and black triangles refer to the observations recorded during the breeding season.

Study area and data collection

The Cantabrian Mountains are a mountain system located in the north of Spain (Figure 3.1), that represents the western limit of the snowfinch distribution (Barquín et al. 2018). We used a database of 3720 observations collected in the Cantabrian Mountains from 1979 to 2018, by means of both formal surveys and birders' observations. Out of those, 195 observations were found in the literature (see Supplementary Data 3.1). With regards to the birders' observations, we are aware that there could be a spatial bias due to clustering. We note, however, that any potential biases could not have been avoided by using a formal survey only, due to the intrinsic constraints of working in high mountain environments where transects, point counts or sample plots are limited by accessibility and terrain characteristics.

In order to study spatial and seasonal differences in habitat preference, we first divided the database into two periods, i.e. breeding (from 1st of May to 31st of July based on personal observations; n = 3150) and non-breeding (encompassing the rest of the year; n = 570), and created plots of different diameters (100 m, 250 m and 500 m, corresponding to areas of respectively 0.78, 4.91 and 19.62 hectares) around each observation using QGIS software (QGIS, Quantum GIS Development Team 2016). Considering that during the breeding season snowfinches can occasionally forage beyond 300 m from the nest (Strinella 2007), we limited the maximum diameter to 500 m. We used plots of 100 m diameter as the smallest scale due to the resolution of the land cover and digital elevation layers, and we established an intermediate plot in order to detect possible further differences in habitat use. This multi-scale approach is also based on Johnson's (1980) conceptual framework, which assumes that animals make decisions regarding basic resources (e.g. breeding sites, food) at hierarchically smaller scales. The identification of the scales at which particular environmental variables influence habitat use is essential for understanding habitat suitability patterns as perceived by animals in heterogeneous landscapes.

To avoid pseudoreplication, we removed any observation that had respectively a distance of less than 100 m, 250 m and 500 m from any other, obtaining three datasets of 597 (337 breeding and 260 non-breeding), 297 (148 breeding and 149 non-breeding) and 158 (64 breeding and 94 non-breeding) observations, respectively. Considering the habitat used by snowfinches (Strinella 2007, Brambilla et al. 2017a, 2018a), we estimated the following land cover features within each plot (Supplementary Table S3.1): bare rock (hereafter 'rock'), natural grassland (hereafter 'grass') and a third category encompassing sparsely vegetated areas, sclerophyllous vegetation, transitional woodland shrubs and moors and heathland (hereafter 'shrubland'). We grouped these latest vegetation types into a single category because in the area of the Cantabrian Mountains containing the snowfinch observations, the moors and heathland cover feature is by far the most dominant.

The habitat variables were derived from Corine Land Cover data 2012 (European Environment Agency 2016) shapefiles with 100 m resolution, using the QGIS Intersect tool and obtaining the percentage of land cover in each plot at the different spatial scales. In addition, from 90 m resolution SRTM raster files (http://srtm.csi.cgiar.org), we extracted for each observation (plot centres) the following topographic features, by means of the QGIS Raster Terrain Plugin and Point Sampling tool (Supplementary Table S3.1): elevation, slope, orientation and Terrain Ruggedness Index (hereafter 'ruggedness') which expresses the amount of elevation difference between adjacent cells of a Digital Elevation Model (Riley et al. 1999).

Finally, to detect possible habitat differences between seasons, we selected a set of random points equal to the number of observations during the breeding and non-breeding periods, respectively. We ensured that each point had a distance higher than 100 m, 250 m and 500 m from any other, and from the corresponding observation. For each random point, and at the three spatial scales, we estimated the abovementioned habitat characteristics. To generate the random points, we first created a shapefile polygon around the study area, by means of QGIS Vector Creation tool (Supplementary Figure S3.1). Inside the polygon and for each spatial scale, we created a plot with the corresponding radius around each observation and afterwards we removed from the polygon the areas inside the plots (basically making a 'Swiss cheese' out of the polygon, Supplementary Figure S3.2). Random points were created inside the 'Swiss cheese' polygon, controlling for the minimum elevation (1000 m for random points related to observations recorded in the breeding season, 900 m for random points related to observations recorded in the non-breeding season; see range of elevations of both real observations and random points in Supplementary Table S3.2). Custom R script for random points creation is provided in Supplementary Data 3.2.

Some observations or random points fell in areas where there was also a different habitat (mainly woodland) to those considered for the study. As this type of habitat represented less than 0.1% of the total habitat, we deleted it. We retained our full dataset for all analyses after finding no significant differences (see Tables S3.6-S3.7 in Supplementary Material) when applying the 2012 land cover data to all data or to a subset from 2000 (deleting observations previous to 2000, n = 464).

Statistical Analyses

Because habitat variables were correlated to differing extents, we first performed a principal component analyses (PCA) for each season and at the three considered spatial scales, including all three land cover variables (rock, grass and shrubland; Table S3.1) and four topographic variables (elevation, slope, orientation and ruggedness; Table S3.1). Variables were scaled to standard deviation of 1, with prior logarithmic transformation of land cover variables. Following Kaiser's criterion (Kaiser 1958), for both PCAs, only components with eigenvalues >1 were retained. A varimax rotation with Kaiser normalisation was applied to the retained components (McGarigal et al. 2000). This involves rotating the subspace defined by selected Principal Components, so that a small number of the coefficients in the loading vectors have much greater values than the remaining coefficients, thus facilitating the interpretation of the PCA as it associates each variable with one – or few – components.

Since semi-variograms showed some spatial autocorrelation (gstat package version 2.0; Pebesma 2004), we computed an autocovariate (spdep package version 1.1; Bivand and Wong 2018) with the matrix of the spatial coordinates and the response variable (observed and random points). The retained principal components and the autocovariate were then included as explanatory variables in a logistic regression model (GLM), including observed (1) and random (0) points as the response variable.

After generating the sets of competing models, we selected the best models by means of model averaging on the 95% confidence set to derive values of AICc, ΔAICc, Weighted AICc and parameter coefficients as well as the relative importance values (RIV) of each explanatory variable using the full-model averaging approach (Burnham and Anderson 2002). We considered models with ΔAICc values lower than 2 as equally competitive. We also calculated the adjusted coefficient of determination to describe model performance.

All analyses were performed in R 3.4.4 (R Development Core Team 2018), using the lme4 package (Bates et al. 2015). Multimodel inference and model averaging were run using the MuMIn package (Barton 2009).

Results

The habitat used by snowfinches showed no significant differences among spatial scales in either season (see mean and standard deviation in Supplementary Table S3.3). There was a different scenario when comparing habitat use with habitat availability (i.e. observed versus random points). For both seasons, three principal components were retained in the PCA at the 100 m and 500 m spatial scales, accounting for more than 70% of the total variance in habitat features (Supplementary Table S3.4). At the 250 m scale, three principal components were retained for the breeding season (75.4% of the total variance, Supplementary Table S3.4) and four principal components (87% of the total variance, Supplementary Table S3.4) were retained for the non-breeding season.

The first component (PC1, 32.7-37.8% of the variance explained) was related to topographic features at all scales regardless of the season, and showed a strong correlation with slope and ruggedness. The second principal component (PC2, 21.9-23.4% of the variance explained) was related to grass and shrubland at the 250 m and 500 m scales respectively. At the 100 m scale, PC2 was related to rock and elevation during the breeding season, while in the non-breeding season grass appeared to be the most important variable. The third component (PC3, 14.6-16.5% of the variance explained) was related to elevation and rock at almost all spatial scales and regardless of the season; however, the breeding season at the 100 m scale exhibited a different pattern, grass having a high correlation with PC3. During both seasons, at the 500 m scale, PC3 was also related to orientation. Furthermore, this topographic variable was related to PC4 at the 250 m scale during the non-breeding season (14.4% of the variance explained).

All principal components and the autocovariate entered into the best models with high relative importance values (Table 3.1, Supplementary Table S3.5). In the breeding season, we found that at the 100 m scale snowfinches preferentially selected higher elevation sites with steeper, rugged terrain (Table 3.1, Figure 3.2a). In addition, snowfinches selected areas characterised by a prevalence of rock but less grass. At the 250 m and 500 m scales, Snowfinches selected rugged, steep areas, with grass cover while avoiding shrubland (Table 3.1, Figure 3.2c), whereas rock and high elevation had a weaker, positive effect. Moreover, at the 500 m scale snowfinches preferably selected areas with north oriented slopes (Supplementary Figure S3.3c). During the non-breeding season (Table 3.1. Figures 3.2d-f), and at the three spatial scales, snowfinches selected steeper, rugged terrain, with prevalence of rock and grass. There was also a positive, though less important, association with elevation (PC3), which confirmed the use of high mountain habitats throughout the year. Orientation entered PC3 and PC4 at the 500 m and 250 m scales respectively, where snowfinches seemed to prefer north-west and south-east facing areas (Figure S3.3b-c).

Table 3.1. Model-averaged coefficients (b), standard errors (SE) and relative importance values (RIVs) of the best models (see Table S3.5) comparing habitat preferences with habitat availability in breeding (a) and non-breeding (b) seasons, at the three spatial scales considered. The explanatory variable 'ac' corresponds to the autocovariate.

Spatial scale	Explanatory variables	Model-averaged coefficients and relative importance values			
	Breeding vs. random	β	SE	p	RIV
100 m	Intercept	-7.3812	1.3951	<0.001	
	ac	0.0251	0.0043	<0.001	1
	PC1	1.7433	0.1878	<0.001	1
	PC2	-0.5495	0.1296	<0.001	1
	PC3	0.6795	0.1220	<0.001	1
250 m	Intercept	-7.8040	2.1475	<0.001	
	ac	0.0578	0.0150	<0.001	1
	PC1	1.4284	0.2386	<0.001	1
	PC2	-0.4791	0.1767	0.007	0.95
	PC3	0.7448	0.1755	<0.001	1
500 m	Intercept	-7.8103	2.5213	0.002	
	ac	0.1332	0.0417	0.001	1
	PC1	0.6298	0.2429	0.010	0.94
	PC3	0.4443	0.2167	0.042	0.77
	PC2	0.1078	0.2118	0.614	0.28

Spatial scale	Explanatory variables	Model-averaged coefficients and relative importance values			
	Non-breeding vs. random	β	SE	p	RIV
100 m	Intercept	-2.3275	0.6686	<0.001	
	ac	0.0120	0.0028	<0.001	1
	PC1	-1.1804	0.1664	<0.001	1
	PC2	0.4533	0.1126	<0.001	1
	PC3	-0.6327	0.1274	<0.001	1
250 m	Intercept	-1.3124	0.8046	0.104	
	ac	0.0128	0.0052	0.015	0.90
	PC1	0.9912	0.1812	<0.001	1
	PC2	0.2193	0.1443	0.130	0.54
	PC3	-0.6531	0.1468	<0.001	1
	PC4	-0.0304	0.1355	0.823	0.27
500 m	Intercept	-1.7851	1.0316	0.085	
	ac	0.0270	0.0111	0.016	0.90
	PC1	-0.8234	0.2026	<0.001	1
	PC3	1.0084	0.2046	<0.001	1
	PC2	0.1684	0.1994	0.401	0.34

Values of R-squared during the non-breeding season were lower than during the breeding season at all spatial scales, except for the 500 m scale, where the values were the same (Supplementary Table S3.5), indicating that, overall, the winter period exhibits higher variability than the breeding season. That is, snowfinches appeared to be more specific in their habitat requirements during breeding, regardless of the spatial scale considered, than during the non-breeding season. Finally, we also found that R-squared values tended to be generally lower when increasing spatial scale (Supplementary Table S3.5), indicating that the use of habitat might be scale-dependent.

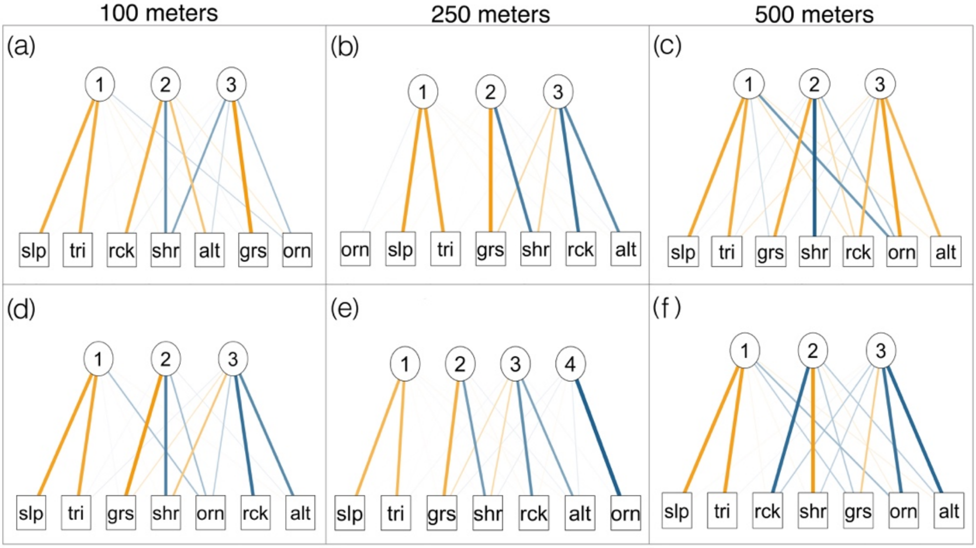

Figure 3.2. Correlations between varimax rotated variables (in square boxes) and the principal components (numbers in circles) selected in the breeding season (a, b and c) and in the non-breeding season (d, e and f) at the three spatial scales. Orange lines correspond to positive correlations and blue lines denote negative correlations. The thickest lines represent high loadings.

Discussion

By studying habitat use by snowfinches during breeding and non-breeding seasons at different spatial scales, we found that snowfinches were more specialised in their habitat requirements during the breeding season and that the use of habitat features during this season varies depending on the spatial scale considered.

The 100 m scale may represent the nesting sites. snowfinches breed preferentially in rock crevices of steep cliffs, thus explaining the positive correlation we found with topographic features and rock, as well as the negative correlation with grass. The foraging area of snowfinches normally falls within a distance of 100-200 m from the nest, whereas foraging beyond that distance (e.g. 300 m or more) is occasional (Strinella 2007, Grangé 2008, Brambilla et al. 2019); therefore, the main foraging area falls between our two largest spatial scales. We do not think that snowfinches strictly avoid nesting sites for foraging, but that they forage in the surrounding areas where they can easily find more resources. This is because they nest in cliffs, i.e. in rocky areas where there are fewer insects and seeds compared to the surrounding grasslands. At the two largest spatial scales, we detected a positive correlation with grass, slope and ruggedness index, indicating that snowfinches tend to feed in irregular terrain with a mixture of grass and rocks.

With respect to grass cover, our findings are in line with those of Strinella (2007) and Brambilla et al. (2017a, 2018b), who found that snowfinches preferably feed in grassy areas. These authors, as well as Resano-Mayor et al. (2019), also found a strong correlation with snow patches during the nestling period. It was not feasible to consider snow in our set of habitat variables due to the impossibility of having good quality information about snow cover at a wider scale, especially during the breeding season in the Cantabrian Mountains, where only small snow patches or glacial ice patches (Serrano et al. 2011) are present at this time. Indeed, the preference for northerly exposed areas at the 500 m scale might be related to the presence of those small snow patches, which can persist in less exposed sites throughout the summer and represent extremely important sources of arthopods (Antor 1995). This is consistent with the preference for cooler sites - with lower solar radiation and thus longer persistence of snow patches and soil moisture - for foraging as the season progresses recorded in the Italian Alps (Brambilla et al. 2017a). However, we need to stress that at the 500 m scale, the R-squared value was not only half the value of the 250 m scale, but also corresponded to the value in the non-breeding season. Thus, during the breeding season snowfinches seem to be more selective at the 100 m and 250 m scales than at the 500 m scale, probably because foraging is more intense at the 250 m scale, and the 100 m scale is linked to the specific nesting requirements of the species.

Between the end of July and the beginning of August, snowfinches aggregate in large flocks and wander in a nomadic manner, probably depending on the availability of food, which gradually changes as the season progresses. While at first they tend to move upslope following flowering phenology and insect eclosions and fallout, during winter their movements become completely erratic and, depending on the amount of snow cover, they can occupy lower elevations (Fernández-González and Fernández 2012, Resano-Mayor et al. 2017). According to our results, during the non-breeding season, snowfinches still select steeper and rugged areas, with an availability of grass, whereas rock and elevation tend to be less important. Importantly, the lower R-squared values of habitat variables when comparing non-breeding vs. random plots than when comparing breeding vs. random plots might be an indication of a reduced tendency of snowfinches to be selective during the non-breeding season. Birds are generally more specialised during the breeding season (Cramp and Perrins 1994), due to the increasing energetic requirements of nestlings (e.g. Förschler 2007, Booth et al. 2018). In snowfinches, the diet during the breeding season is mainly composed of dipteran larvae (Brambilla et al. 2017a), while after breeding the diet becomes more diverse, including a wider range of arthropod species and arachnids, as well as seeds (Strinella, unpubl. data) and human food remains when available (Cramp and Perrins 1994). In our study population, the attraction to anthropogenic resources during winter might be less evident, or even absent, due to the scarcity of refuges and the absence of ski resorts. Moreover, due to the temperate climatic conditions, snow storms in the Cantabrian Mountains are more unpredictable and the snow cover is less persistent and more variable during the winter compared to the Alps. Therefore, we think that snowfinches in our area might find – and thus use - suitable habitat throughout the year more easily than their Alpine conspecifics. However, there might be an effect due to livestock in areas where snowfinch flocks have been seen foraging (pers. obs.). For example, livestock enhances the presence of coprophagpous insects, which might be an extra source of food for wintering snowfinches.

Snowfinches might have physiological and morphological specializations to high-elevation environments (Heiniger 1991a, Martin 2001, Lei et al. 2002), that restrict them to a high mountain habitat throughout the year. Nevertheless, they exhibit a plasticity that allows them to be more generalist in their habitat use during the non-breeding season. However, we should also stress that there might be specific habitat requirements during winter that we have not considered in our models, as for example snow conditions. Further investigations are needed in order to better understand the degree of plasticity of snowfinches during winter.

Interestingly, in both seasons the value of R-squared when comparing observation plots with random plots tended to decrease with increasing spatial scale. Thus, this pattern of snowfinch flexibility seems to be space-sensitive and has a stronger effect at larger scales than at small ones. This result seems to be in accordance with Reif et al. (2016), who found a positive correlation between habitat specialisation and diet specialisation, but the relationship was weak at a coarse spatial scale.

Snowfinches are known to undertake erratic movements throughout the winter (Fernández-González and Fernández 2012, Resano-Mayor et al. 2017), but the scale and extent of this behaviour in the species are still poorly investigated. Nomadism is driven by the variability of resources in space and time (Teitelbaum and Mueller 2019) and in semi-arid and arid enviroments it is linked to diet (Davies 1984, Woinarski 2006). Because their unpredictability and harshness, high mountain ecosystems may be comparable to arid zones and in fact erratic movements driven by diet in alpine birds have already been recorded in chough *Pyrrhocorax pyrrhocorax* and alpine chough *Pyrrhocorax graculus* (Laiolo and Rolando 1999). We may therefore speculate that the nomadic movements of snowfinches are similarly governed by diet, as well as by the need to find suitable nocturnal shelters in rock crevices not blocked by ice. However, given the broader diet of snowfinches after breeding, the mechanism might be more complex and also involve the physiological and morphological adaptations which constrain populations to specific elevation zones. During winter, they might be forced to move to lower elevations in search of suitable foraging patches and nocturnal shelters because of snow cover. However, they cannot cross certain elevation zones (usually below 900 m) because of both species-specific adaptations (Martin 2001) and unsuitable habitats (although anthropogenic food resources might alter snowfinches behaviour, attracting them to unsuitable habitats, as happens in some Alpine areas). Therefore, nomadic movements might be necessary to reach suitable areas in terms of both resource availability and physiological constraints.

In our study, we did not explicitly consider climatic variables. However, a strict correlation exists between temperature and elevation, so that the preference for high-elevations exhibited by snowfinches throughout the year suggests that they select areas with lower temperatures. Given the important role that climatic variables play in mountain ecosystems (Catalan et al. 2017), reproductive phenology (Martin and Wiebe 2004), ecotypic responses (Delgado et al. 2019) and range size (Scridel et al. 2017) of cold adapted species, it would be interesting to investigate their role in habitat use more thouroughly, especially during the non-breeding season.

We do not expect changes in nesting sites in the study period considered, especially taking into account that in our study area there are no houses or skilifts and snowfinches nest in rock crevices only. However, we cannot discard the possibility that there could have been variation in grass and shrubland coverage over the period of time encompassed by our observations. Further studies investigating the potential effects of land cover changes on snowfinch distribution and abundance are particularly needed.

To our knowledge, this is the first study comparing habitat use across seasons at different spatial scales in a high-elevation bird species. We showed that snowfinches adopt a more general tolerance for overwintering sites compared to the use of the habitat during the breeding season. snowfinches might have evolved this plasticity as a strategy to cope with the unpredictability and harshness of the non-breeding season at high elevations. How this strategy is influenced by climatic variables, the way it is expressed in the different European populations of snowfinches and to what extent it could help them to face the variations triggered by climate change are questions that need further investigation.

Supplementary Material

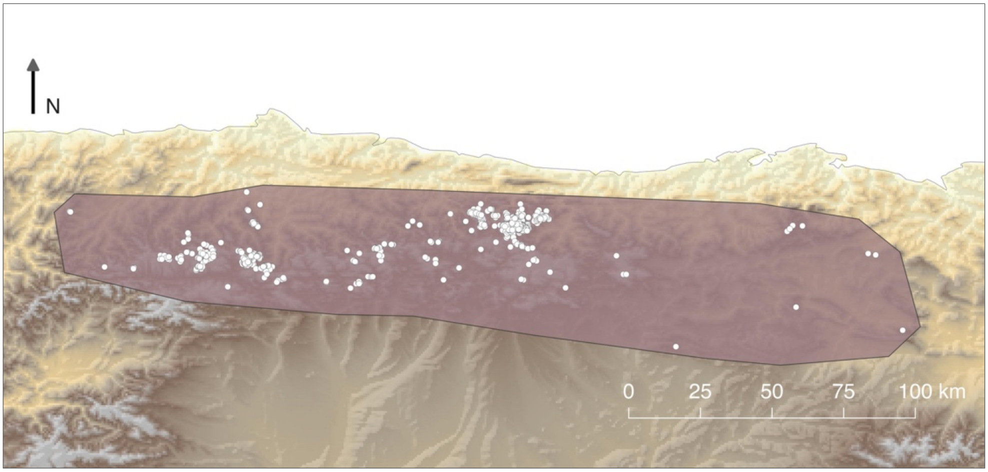

Figure S3.1. Shapefile polygon created around the study area by means of QGIS Vector Creation Tool. White dots correspond to the observations. The polygon was used for the creation of the random points (see followed method in the main text).

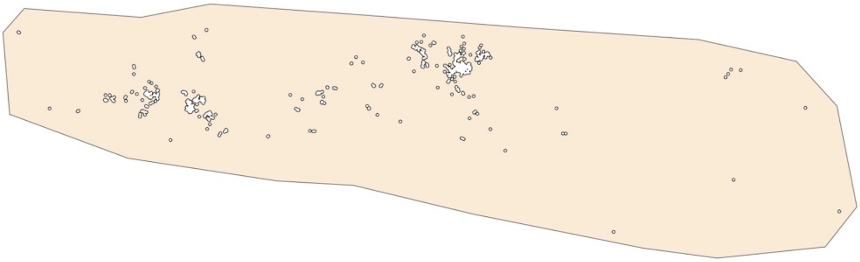

Figure S3.2. "Swiss cheese" created by removing the plot areas around the observations from the shapefile polygon. Random points were subsequently created inside the remaining area.

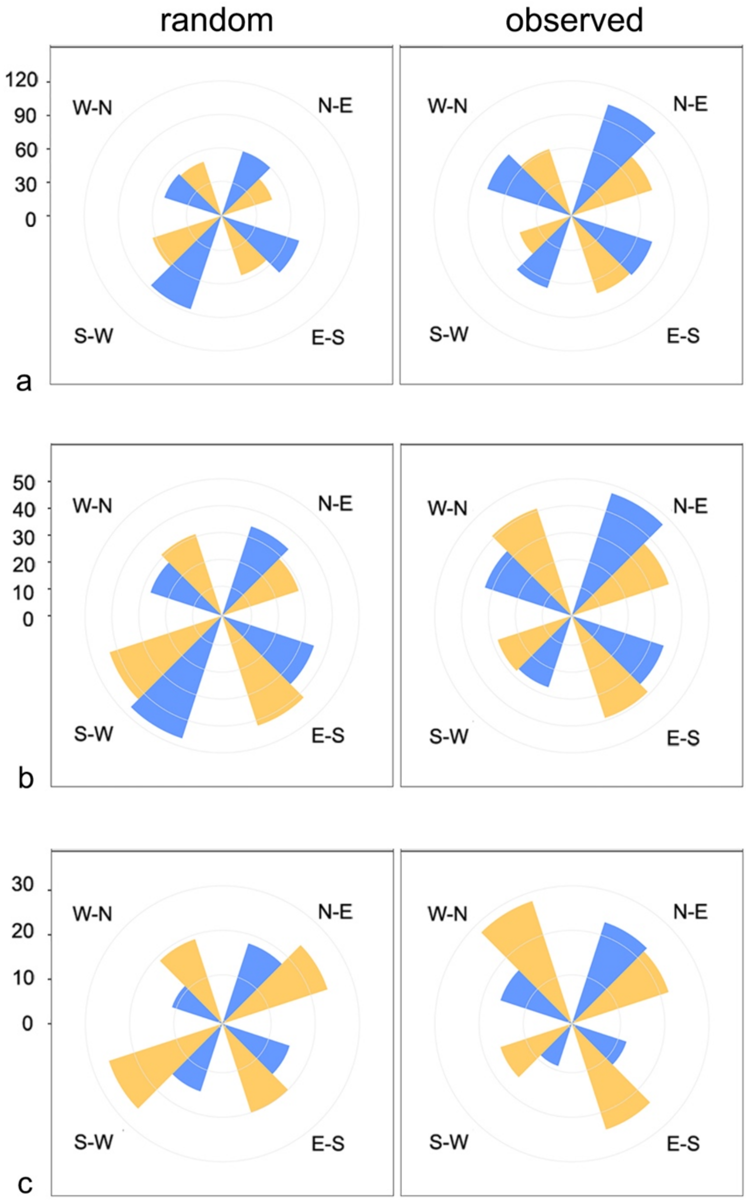

Figure S3.3. Distribution of orientation (N-E=0-90°; E-S=90-180°; S-W=180-270°; W-N=270-360°) in observed vs. random points at the scales of a) 100 meters, b) 250 meters and c) 500 meters. Blue areas refer to breeding season, yellow areas to non-breeding season.

Table S3.1. Habitat variables extracted from observed and random plots at the three spatial scales with the diameter of 100, 250 and 500 meters

Variable	Abbreviation	Description	Source
rock	rck	% cover of bare rock	Corine Land Cover 2012 shapefile
grass	grs	% cover of natural grassland	
shrubland	shr	% cover of sparsely vegetated areas, moors, heathland and slerophyllous vegetation	
orientation	orn	slope aspect, expressed as degrees from north	SRTM raster (90 m)
slope	slp	slope as percentage	
TRI	tri	Terrain Ruggedness Index	
elevation	alt	altitude in meters above sea level	

Table S3.2. Range of elevations of real observations and random points.

Season	Real observation	Random
Breeding	1336 m – 2473 m	1004 m – 2287 m
Non-breeding	942 m – 2478 m	900 m – 2157 m

Table S3.3. Descriptive statistics (mean±SE) for the habitat variables of observation plots at the three spatial scales with diameter of 100, 250 and 500 meters

Spatial scale (diameter)	Variable	Mean ± SE Breeding	Mean ± SE Non-breeding
100 m	rck	45.479 ± 2.630	36.682 ± 2.878
	grs	7.047 ± 1.347	16.396 ± 2.219
	shr	47.168 ± 2.634	46.432 ± 2.960
	orn	167.157 ± 6.233	168.809 ± 6.843
	slp	20.486 ± 0.570	17.465 ± 0.558
	tri	31.055 ± 0.820	26.486 ± 0.782
	alt	1932.429 ± 11.060	1821.277 ± 18.120
250 m	rck	37.204 ± 3.693	31.048 ± 3.537
	grs	9.046 ± 2.244	10.988 ± 2.277
	shr	52.599 ± 3.767	52.975 ± 3.755
	orn	159.761 ± 9.457	182.572 ± 8.962
	slp	20.934 ± 0.827	17.465 ± 0.716
	tri	31.309 ± 1.283	26.750 ± 0.982
	alt	1875.540 ± 19.934	1789.148 ± 27.638
500 m	rck	22.927 ± 4.701	23.195 ± 4.064
	grs	11.548 ± 3.506	9.330 ± 2.338
	shr	61.594 ± 5.403	58.955 ± 4.481
	orn	157.248 ± 14.985	186.951 ± 11.818
	slp	18.704 ± 1.324	17.270 ± 0.893
	tri	29.230 ± 2.254	26.505 ± 1.196
	alt	1824.234 ± 30.211	1741.425 ± 39.795

Table S3.4 Principal component analyses of the habitat variables extracted from observation and random plots after varimax rotation.

Spatial scale	Variable	Breeding			Non-breeding			
		PC1	PC2	PC3	PC1	PC2	PC3	PC4
100 m	rck	-0.031	**-0.657**	0.092	0.010	0.020	**-0.661**	
	grs	-0.049	0.063	**-0.811**	0.044	**0.742**	0.181	
	shr	0.079	0.562	0.442	-0.042	-0.589	0.409	
	orn	-0.191	-0.151	0.318	0.285	-0.305	-0.230	
	slp	**0.696**	-0.001	-0.048	**-0.692**	0.004	0.006	
	tri	**0.675**	-0.051	0.000	**-0.658**	-0.042	-0.083	
	alt	0.117	**-0.472**	0.187	-0.056	-0.083	**-0.551**	
	Eigenvalues	2.643	1.640	1.079	2.598	1.595	1.105	
	Cumulative explained variance	37.763	61.199	76.620	37.110	59.903	75.692	
250 m	rck	-0.045	-0.064	**0.681**	-0.040	0.087	**-0.692**	0.077
	grs	0.002	**-0.773**	-0.289	0.052	**0.772**	0.289	-0.102
	shr	0.066	**0.622**	-0.354	0.051	**-0.621**	0.353	-0.109
	orn	-0.082	-0.049	0.001	-0.017	0.009	-0.050	**-0.977**
	slp	**0.710**	-0.052	-0.012	**0.716**	0.020	0.028	0.015
	tri	**0.692**	-0.021	0.037	**0.689**	-0.017	-0.058	-0.006
	alt	0.066	0.072	**0.572**	0.076	-0.098	**-0.553**	-0.129
	Eigenvalues	2.568	1.639	1.068	2.436	1.532	1.110	1.009
	Cumulative explained variance	36.688	60.105	75.360	34.797	56.685	72.546	86.964
500 m	rck	0.247	0.294	0.440	-0.070	**0.639**	0.214	
	grs	-0.181	**0.578**	-0.084	0.213	0.230	-0.338	
	shr	-0.007	**-0.708**	-0.127	-0.066	**-0.690**	0.195	
	orn	-0.414	-0.253	**0.731**	0.285	-0.114	**0.605**	
	slp	**0.600**	-0.070	0.012	**-0.650**	0.000	-0.047	
	tri	**0.579**	-0.080	0.131	**-0.655**	-0.010	0.050	
	alt	0.198	0.053	**0.480**	-0.107	0.221	**0.657**	
	Eigenvalues	2.500	1. 631	1.021	2.289	1.620	1.153	
	Cumulative explained variance	35.717	59.014	73.605	32.700	55.839	72.308	

Table S3.5. Best models or sets of candidate models comparing habitat preferences with habitat availability in breeding and non-breeding season, at the three spatial scales considered. The explanatory variable “ac” corresponds to the autocovariate, while PC1, PC2 and PC3 to the three principal components.

Dependent variable	Spatial scale	Competing models	AICc	ΔAICc	Weighted AICc	R_2
Breeding vs random	100	**ac+PC1+PC2+PC3**	**484.75**	**0.00**	**1**	**0.4406**
	250	**ac+PC1+PC2+PC3**	**255.58**	**0.00**	**0.95**	**0.4000**
		ac+PC1+PC3	261.41	5.82	0.05	
	500	**ac+PC1+PC3**	**141.97**	**0.00**	**0.52**	**0.2426**
		ac+PC1+PC2+PC3	**143.84**	**1.87**	**0.20**	
		ac+PC1	144.37	2.39	0.16	
		ac+PC1+PC2	146.32	4.35	0.06	
Dependent variable	Spatial scale	Competing models	AICc	ΔAICc	Weighted AICc	R_2
Non-breeding vs random	100	**ac+PC1+PC2+PC3**	**481.50**	**0.00**	**1**	**0.2863**
	250	**ac+PC1+PC2+PC3**	**333.78**	**0.00**	**0.34**	**0.2168**
		ac+PC1+PC3	**333.92**	**0.13**	**0.32**	
		ac+PC1+PC2+PC3+PC4	335.83	2.05	0.12	
		ac+PC1+PC3+PC4	335.94	2.15	0.12	
		PC1+PC2+PC3	337.46	3.68	0.05	
	500	**ac+PC1+PC3**	**205.68**	**0.00**	**0.61**	**0.2448**
		ac+PC1+PC2+PC3	**207.15**	**1.47**	**0.29**	
		PC2+PC3	**210.54**	**4.86**	**0.05**	

The land cover data used in our analyses were derived from 2012 layers (see Table S3.1), while our dataset dated back to the 1980s. Therefore, we performed the entire set of analyses (see "Methods" in the main text) considering only the observations recorded since 2000, and the results are reported in the tables below. Deleted observations (from 1979 to 1999) were only one tenth of the whole database and the results did not show any significative difference. We thus retained the full dataset and the results as reported in Tables S3-S5.

Table S3.6. Principal component analyses of the habitat variables extracted from observation and random plots (reduced dataset).

Spatial scale	Variable	Breeding			Non-breeding		
		PC1	PC2	PC3	PC1	PC2	PC3
100	rck	-0.005	**-0.627**	0.166	0.089	-0.052	**-0.715**
	grs	-0.146	-0.034	**-0.715**	0.010	**0.783**	0.215
	shr	0.130	**0.611**	0.316	-0.076	-0.572	0.414
	orn	-0.233	-0.135	**0.596**	0.039	-0.229	-0.019
	slp	**0.668**	-0.020	-0.021	**-0.716**	0.058	0.033
	tri	**0.660**	-0.051	-0.005	**-0.675**	0.003	-0.076
	alt	0.156	**-0.459**	0.074	-0.129	-0.048	**-0.513**
	Eigenvalues	2.721	1.668	1.070	2.587	1.661	1.064
	Cumulative explained variance	38.877	62.700	77.989	36.960	60.686	75.882
250	rck	-0.074	0.074	**-0.566**	0.017	0.070	**-0.667**
	grs	0.154	**0.634**	0.040	-0.020	**0.768**	0.221
	shr	-0.069	-0.581	0.429	-0.062	-0.579	0.443
	orn	-0.501	0.487	0.486	-0.426	0.224	0.315
	slp	**-0.576**	-0.094	-0.119	**-0.641**	-0.035	-0.045
	tri	**-0.592**	-0.092	-0.119	**-0.619**	-0.053	-0.141
	alt	-0.179	-0.016	-0.478	-0.140	-0.125	**-0.433**
	Eigenvalues	2.850	1.556	1.017	2.550	1.474	1.117
	Cumulative explained variance	40.719	62.953	77.491	36.426	57.487	73.451
500	rck	0.437	0.289	0.231	-0.079	**0.655**	-0.115
	grs	-0.170	**0.587**	-0.160	0.406	0.170	-0.146
	shr	-0.109	**-0.718**	-0.087	-0.111	**-0.721**	-0.111
	orn	0.063	0.069	**-0.945**	0.212	-0.091	-0.817
	slp	**0.546**	-0.142	-0.075	**-0.588**	0.052	-0.042
	tri	**0.572**	-0.131	-0.101	**-0.611**	0.044	-0.112
	alt	0.373	0.114	0.056	-0.228	0.090	-0.521
	Eigenvalues	2.606	1.612	1.000	2.402	1.593	1.116
	Cumulative explained variance	37.227	60.263	74.539	34.321	57.074	73.022

Table S3.7. Model-averaged coefficients, R2 and RIV values of the best models or sets of models (ΔAICc < 2) comparing habitat preferences with habitat availability in breeding and non-breeding season, at three spatial scales (reduced dataset).

Dependent variable	Spatial scale	Competing models		AICc	ΔAICc	Weighted AICc	R_2
Breeding vs random	100	**ac+PC1+PC2+PC3**		**303.69**	**0.00**	**0.90**	**0.4934**
		ac+PC1+PC2		308.18	4.49	0.1	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-10.4335	3.2219	0.00124		
		ac	0.0535	0.0156	0.00066	1	
		PC1	1.8993	0.2360	<2e-16	1	
		PC2	-0.8794	0.1526	9e-09	1	
		PC3	0.3691	0.1470	0.01233	0.9	
	250	**ac+PC1+PC2+PC3**		**163.53**	**0.00**	**0.84**	**0.4153**
		ac+PC1+PC3		167.56	4.03	0.11	
		ac+PC1+PC2		169.52	6.00	0.04	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-7.0988	2.2929	0.00210		
		ac	0.0822	0.0252	0.00120	1	
		PC1	-1.6182	0.2969	6.1e-08	1	
		PC2	0.4662	0.1924	0.01611	0.88	
		PC3	-0.5698	0.2117	0.00749	0.95	
	500	**ac+PC1**		**93.75**	**0.00**	**0.42**	**0.2322**
		ac+PC1+PC2		**94.85**	**1.10**	**0.24**	
		ac+PC1+PC3		95.85	2.10	0.15	
		ac+PC1+PC2+PC3		97.01	3.26	0.08	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-6.3267	2.3695	0.00853		
		ac	0.1756	0.0623	0.00549	1	
		PC1	0.7068	0.3009	0.02072	0.89	
		PC2	0.2783	0.2748	0.31871	0.36	
		PC3	-0.0864	0.2589	0.74268	0.26	

Dependent variable	Spatial scale	Competing models		AICc	ΔAICc	Weighted AICc	R_2
Non-breeding vs random	100	**ac+PC1+PC2+PC3**		**323.90**	**0.00**	**0.97**	**0.3285**
		ac+PC1+PC2		330.88	6.97	0.03	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-2.3904	0.8285	0.00404		
		ac	0.0178	0.0052	0.00074	1	
		PC1	-1.4245	0.2165	<2e-16	1	
		PC2	0.7015	0.1448	1.38e-06	1	
		PC3	-0.4631	0.1617	0.00432	0.97	
	250	**ac+PC1+PC3**		**231.38**	**0.00**	**0.37**	**0.1704**
		PC1+PC3		**232.84**	**1.46**	**0.18**	
		ac+PC1		**233.35**	**1.97**	**0.14**	
		ac+PC1+PC2+PC3		233.42	2.04	0.13	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-0.9499	0.9424	0.3150		
		ac	0.0181	0.0097	0.0638	0.69	
		PC1	-0.9652	0.2086	4.3e-06	0.27	
		PC3	-0.3299	0.1637	0.0452	0.74	
		PC2	-0.0281	0.1637	0.8646	0.34	
	500	**PC1+PC3**		**132.66**	**0.00**	**0.37**	**0.2139**
		ac+PC1+PC3		**132.75**	**0.09**	**0.36**	
		ac+PC1+PC2+PC3		134.79	2.13	0.13	
		PC1+PC2+PC3		134.80	2.15	0.13	
		Explanatory variables	Model-averaged coefficients and relative importance values				
			β	SE	p	RIV	
		Intercept	-0.6262	0.9840	0.52692		
		PC1	-1.0157	0.2598	0.00011	1	
		PC3	-0.7274	0.2326	0.00198	0.99	
		ac	0.0308	0.0218	0.16254	0.49	
		PC2	-0.0460	0.2381	0.8485	0.26	

Data 3.1. References from where 195 observations out of the total 3720 were extracted.

1. De Juana E. 1996. Noticiario Ornitológico. Ardeola 43(2):239-259
2. Anuario ornitológico asturiano, 1993. El Draque 1 (1996): 53-102
3. García Sánchez E. 1997. Annuariu Ornitolóxicu d'Asturies, 1994 y 1995. *El Draque* 2: 61-256
4. García Sánchez E. 1998. Annuariu Ornitolóxicu d'Asturies, 1996. *El Draque* 3: 13-185
5. García Sánchez E. 2003. Annuariu Ornitolóxicu d'Asturies, 1997. *El Draque* 4: 27-234
6. García Sánchez E. 2004. Annuariu Ornitolóxicu d'Asturies, 1998. *El Draque* 5: 15-198
7. García Sánchez E. 2006. Annuariu Ornitolóxicu d'Asturies, 1999. *El Draque* 6: 17-201
8. García E., Alonso L.M., Arce L.M., Marín J.M., Menéndez P.J., Peón P. 2007. Annuariu Ornitolóxicu d'Asturies, 2000. *El Draque* 7: 35-255

Data 3.2 R script for creating random points

```
#packages
library(scales)
library(rgdal)
library(plyr)
library(rgeos)
library(raster)
library(maptools)

#set directory
setwd("address of directory that contains the dataset")
#reading the dataset
snowfinch <- read.csv2("name of the dataset file",
dec=".")
#set longitude (x) and latitude (y) as numeric
```

```
snowfinch$x<-as.numeric(snowfinch$x)
snowfinch$y<-as.numeric(snowfinch$y)

#create groups
snowfinch$unit <- factor(substr(snowfinch$unit.id, 1,
nchar(as.character(snowfinch$unit.id))-5))
n.groups <- length(levels(snowfinch$unit))
palette(rainbow(n.groups))
require(scales)

#plot the observations by Long and Lat and colored by unit
group
with(snowfinch, plot(x,y, bg=alpha(as.integer(unit),0.5),
pch=21, col="grey"))
legend("topleft", pch=19, legend = levels(snowfinch$unit),
col=1:n.groups, cex=0.5, ncol=5)
require(rgdal)
s.hab <- readOGR(dsn = "XXX_shp", layer = "XXX")#load the
shapefile (dsn=folder where the shp is; NB: the shapefile
#must be saved from QGIS directly to the folder, it can't
be opened from an external USB memory)
plot(s.hab)
axis(1); axis(2)
with(snowfinch, points(x,y, pch=19,
col=alpha(as.integer(unit),0.5)))

#Select random points
palette("default")
x <- c(0,5,6); y <- c(4,10,0)
z <- x + 1i*y
plot(z, pch=19, col=2:4, cex=2)

#The next simple function draws a circle of radius r
around points z.
#It returns a two-column x-y matrix of coordinates of the
circle (made of 100 points):
getCircle <- function(z, r){
  circle <- complex(mod = r, arg = seq(0,2*pi,length=100))
  z.circle <- z + circle
  return(cbind(x = Re(z.circle), y = Im(z.circle)))
}
plot(z, xlim = c(-2,8), ylim = c(-2,12), pch=19, col=1:3,
asp=1)
for(i in 1:length(z)) for(r in c(1,2,3)){
  lines(getCircle(z[i], r = r), col=i, lty = r)
}
```

```
#Now, to select random points from within the circle (and
also later for the polygon)
#maybe the best tool is spsample - a function in sp.
#To do this, your polygon has to be a "Polygon" class
object (from sp).
xy.circle1 <- getCircle(z[1], r = 2)
circle1.polygon <- Polygon(xy.circle1)

plot(xy.circle1, type="l", asp=1)
random.points1 <- spsample(circle1.polygon, n=10,
type="random")
points(random.points1, cex=2, col=4, pch=19)

#We can loop this to create a single spatial polygon list
with random points:
circle.polygons <- list()
random.points <- list()

for(i in 1:length(z)){
  circle.polygons[[i]] <- Polygon(getCircle(z[i], r = 2))
  random.points[[i]] <- spsample(circle.polygons[[i]],
n=10, type="random")
}

#Now we have two lists - one of the circles, and one of
the random points
plot(z, xlim = c(-2,8), ylim = c(-2,12), pch=19, col=1:3,
asp=1)
for(i in 1:length(z)){
  lines(circle.polygons[[i]], col=i)
  points(random.points[[i]], col=i, pch=4)
}

#to get just the coordinates of the random points (as a
list)
(points.list <- lapply(random.points, coordinates))

#Or - to convert that into a data frame where the index of
the coordinates is a column,
#we can use ldply (small note: the list must be "named").
So:
require(plyr)
names(points.list) <- paste0("snowfinch",
1:length(points.list))
points.df <- ldply(points.list)
```

```
head(points.df)

#Intersecting polygons
z.snowfinch <- 200000 + 1i*4772277
xy.circle <- getCircle(z.snowfinch, r = 3e3)#r=2000m

plot(s.hab, xlim = c(19e4, 21e4),
ylim=c(475e4,478e4),col="antiquewhite")
axis(1); axis(2)
points(z.snowfinch, col = "darkred", pch=19)
lines(xy.circle, col=2)

require(rgeos)
circle.spatialpolygons <-
SpatialPolygons(list(Polygons(list(Polygon(xy.circle)),
"circle")))

# it helps to give the new spatial polygons the same
projection as the habitat data
(myproj <- proj4string(s.hab))
proj4string(circle.spatialpolygons) <- myproj

plot(s.hab, xlim = c(19e4, 21e4),
ylim=c(475e4,478e4),col="antiquewhite")
plot(circle.spatialpolygons, add=TRUE,
col=rgb(0.5,0.5,0,.2))

# key intersection command
inCircleOnLand <- gIntersection(circle.spatialpolygons,
s.hab)
plot(inCircleOnLand, add=TRUE, lwd=3)

#But now that we have the polygon, we can sample points
from it easily:
plot(s.hab, col="wheat",
     xlim = bbox(inCircleOnLand)[1,],
     ylim = bbox(inCircleOnLand)[2,])
plot(inCircleOnLand, add=TRUE, col="antiquewhite")
random.points <- spsample(inCircleOnLand, 20,
type="random")
points(random.points, cex=2, pch=21, bg="white",
col="red")
points(z.snowfinch, lwd=2, cex=3, pch=4, col="darkblue")

require(raster)
gClip <- function(shp, bb){
```

```
  if(class(bb) == "matrix") b_poly <-
as(extent(as.vector(t(bb))), "SpatialPolygons")
  else b_poly <- as(extent(bb), "SpatialPolygons")
  gIntersection(shp, b_poly, byid = T)
}
s.hab.crop <- gClip(s.hab, bbox(inCircleOnLand))

plot(s.hab.crop,col="antiquewhite"); axis(1); axis(2)

#Now, we will add some random points, and make a list of
their 1 km circles:
s.x <- 19e4 + c(7280.4, 7635.4, 9572.9)
s.y <- 477e4 + c(1000, 3700, 2425)
s.z <- s.x + 1i*s.y
points(s.z, col=2, pch=19, cex=2)

circles <- list()
for(i in 1:length(z)) circles[[i]] <- getCircle(s.z[i],
1e3)
lapply(circles, lines)

#Now we want to draw n points (say, 100) outside of the
circles but inside of the polygon.
#1. Make a SpatialPolygons list for the circles
# first - make a list of "Polygons" ... IMPORTANT, hole
must be "FALSE"
circles.listOfPolygon <- lapply(circles, Polygon,
hole=FALSE)

# next make it a "Polgons" object:
circles.Polygons <- Polygons(circles.listOfPolygon,
"circle")

# make is a "Spatial Polygons" object
circles.sp <- SpatialPolygons(list(circles.Polygons))
proj4string(circles.sp) <- proj4string(s.hab.crop)

#2. Remove these circles from the habitat polygon
require(maptools)
swisscheese <- gDifference(s.hab.crop, circles.sp)
plot(swisscheese, col="antiquewhite")

#3. Sample random points from the remainder
#Finally get random points out of this piece of cheese:
points(spsample(swisscheese, n = 100, type="random"),
col="blue", pch=19)
```

```
# all data locations
z.snowfinch <- snowfinch$x + 1i*snowfinch$y
# radius = write the radius (for example 500 m)
r <- 500
# collect ALL the circles
circles <- list()
for(i in 1:length(z.snowfinch)) circles[[i]] <-
getCircle(z.snowfinch[i], r = 500)
# convert ALL the circles to a single SpatialPolygons
circles.listOfPolygon <- lapply(circles, Polygon,
hole=FALSE)
circles.Polygons <- Polygons(circles.listOfPolygon,
"circle")
circles.sp <- SpatialPolygons(list(circles.Polygons))
proj4string(circles.sp) <- proj4string(s.hab.crop)
# delete the circles from the habitat
superswisscheese <- gDifference(s.hab, circles.sp)
# get for example 100 random points
randompoints <- spsample(superswisscheese, 100,
type="random")
xy.randompoints <- randompoints@coords

# Draw the final plot
plot(superswisscheese, col="antiquewhite")
points(xy.randompoints, col="darkred", cex=0.5, pch=19)
myrandomPoints <- data.frame(x = xy.randompoints[,1],
                             y = xy.randompoints[,2])
#save the list of random points with their coordinates
write.csv2(myrandomPoints, "name of the file.csv")
```

Chapter IV

Partial migration of white-winged snowfinches is correlated with winter weather conditions

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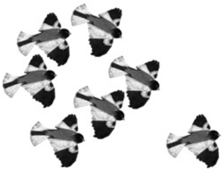


Summary

Seasonal movements are a response to variability in resource availability and result from a complex interaction between the behavioral and physiological traits of a species and its prevailing environment. A widespread bird migration strategy is partial latitudinal migration, where some proportion of the population moves from breeding to winter grounds, while the remaining individuals stay year-round on the breeding grounds. Deciphering how and why some individuals migrate while others stay is essential to understanding population and community structure and dynamics. Little is known about the drivers of partial migration strategies of high-mountain birds that are subjected to strong seasonal environmental fluctuations and count among the species most threatened by climate change. In this study, we investigated the migratory pattern of an alpine songbird, the white-winged snowfinch (*Montifringilla nivalis nivalis*), through the analysis of stable hydrogen isotopes of feathers (δ^2H_f), and how it relates to weather factors. First, values of δ^2H_f were used to assess the probability that snowfinches wintering in the Spanish Pyrenees and Cantabrian Mountains have a breeding origin in the Alps. Second, we analysed whether winter weather conditions (ambient temperature and precipitation) in the Alps may play a role in migratory movements towards the southern wintering grounds. Overall, ca 98% and 86% of the individuals sampled in winter in the Spanish Pyrenees and Cantabrian Mountains, respectively, were likely to originate from breeding populations in the Alps. Snowfinches also had a higher propensity for large-scale movements to the South in winters where the average monthly temperature was particularly low in the Alps, typically < –2°C (i.e., in the 42% coldest winters). Our results suggest that snowfinches adopt a partial migratory strategy, with different patterns among and within populations that have important implications in terms of population connectivity, spatio-temporal dynamics and structuring. Considering the role of cold winter conditions in migration propensity of snowfinches, there is a risk of increased isolation of the southern populations under a scenario of global warming, insofar as the hypothetical settling of winter immigrants could no longer contribute to a demo-genetic rescue. Future research should decipher how these risks affect alpine species that are particularly exposed to climatic shifts, and how they adapt and evolve.

Introduction

Animal migration consists of spatial movements that result from a complex interaction between the behavioral and physiological traits of a species and its prevailing environment (Newton, 2008). Migration is defined as a movement between geographically distant breeding and non-breeding areas that aims at tracking seasonally fluctuating environmental conditions, in particular food supplies, year-round (Berthold, 2001; Newton, 2008). Different factors such as age, sex, habitat quality, risk of predation or weather conditions may influence animal migration strategies (Berthold, 2001; Webster et al., 2002), which can differ not only among species (Chapman et al., 2011) but also between populations (Newton, 2008). Alpine populations can exhibit both latitudinal or elevational migration in order to moderate environmental stressors. Whereas latitudinal migration involves individuals moving relatively long distances from breeding to wintering grounds, elevational migration is often a very short distance movement along mountain slopes and can occur many times throughout the year in response to inclement weather and the strong inherent seasonality of these environments (Borras et al., 2010; Boyle, 2017; Hsiung et al., 2018; Newton, 2008).

A widespread migration strategy is partial latitudinal migration, where only a proportion of a population migrates from breeding to wintering grounds, whereas another subset remains in or next to the breeding areas throughout the year (Chapman et al., 2011; Newton, 2008). Partial latitudinal migration can be obligate (i.e., a specific proportion of individuals migrates every year), or irruptive/facultative (i.e., migration only occurs some years depending on prevailing environmental conditions on the breeding grounds). In obligate partial migration, the migratory strategy seems to be under endogenous control (Berthold and Helbig, 1992), with individuals from any given population adopting the same strategy (staying or migrating) every year. In irruptive or facultative partial migration, individuals may stay or migrate according to directly perceived environmental conditions at the time (Borras et al., 2010; Boyle, 2017; Newton, 2008; Watts et al., 2018).

Migration strategies ultimately affect individual survival and reproduction (Chapman et al., 2011; Fudickar et al., 2013). Therefore, determining how and why animals migrate within their range is fundamental to a deeper understanding of population and community structures and dynamics (Morales et al., 2010). High mountain ecosystems are subject to strong seasonal fluctuations (Lloret, 2017) and species inhabiting such challenging environments have evolved complex life-history strategies to cope with extreme abiotic conditions (Hille and Cooper, 2015). For instance, some alpine animal populations remain as high as possible close to the breeding grounds for the competitive advantage of arriving and breeding earlier the following year (Winger et al., 2019), moving to wintering areas or lowlands only in the case of extreme disruption of food resources (Watts et al., 2018). Weather can indeed strongly impact food availability in these environments (e.g. while precipitation and temperature influence insect activity and abundance, snow and ice may cover seeds) and thus trigger large-scale movements (Mittelhauser et al., 2012). Therefore, in high mountain ecosystems, animal migration strategies may form a continuum from obligate to irruptive migratory movement behaviours that, together with elevational movements, may enhance the capability of individuals, populations and species to cope with seasonally varying environments (Fudickar et al., 2013; Newton, 2008; Reid et al., 2018).

Despite the information accrued from bird ringing and species monitoring programs, bird movement strategies in high mountain ecosystems remain poorly documented. Indeed, high elevations can be important over-wintering sites for short-distance migrants, as well as migration corridors and refueling sites for long-distance migrants (Boyle and Martin, 2015). Yet, little is known about how weather factors may influence the movements of alpine species (Laplante et al., 2019; Macdonald et al., 2016). This is particularly important since alpine ecosystems are forecasted to be among the most impacted by climate change, with temperature warming being double of what is estimated globally (Brunetti et al., 2009). The analysis of the stable hydrogen isotope ratios of feathers (δ^2H_f) has proven to be a useful tool for investigating the breeding origins of latitudinal and elevational migrants (Boyle et al., 2011; Hobson et al., 2003). This is facilitated by continental-scale gradients from lower δ^2H values in precipitation and surface waters with higher latitudes and elevations, which is transferred through the foodweb into animal tissues (Hobson, 2011). Metabolically inert tissues, such as feathers, integrate and maintain the hydrogen isotopic composition of the environment where they were grown (Rubenstein and Hobson, 2004). For most migratory bird species, the timing and extent of moulting is sufficiently well described (Jenni and Winkler, 1994) that the analysis of δ^2H_f values in targeted feathers may allow individuals to be assigned probabilistically to the regions where their feathers were grown, relative to their breeding grounds (Cardador et al., 2015; Rubenstein and Hobson, 2004). In recent years, a few studies analyzing δ^2H_f have elucidated seasonal elevational movements in both temperate and tropical bird species that would have been difficult to assess by conventional methods (Boyle et al., 2011; Gadek et al., 2018; Hobson et al., 2003). In the Western Palearctic, even fewer studies have investigated the applicability of δ^2H_f for the assessment of mountain songbird migratory movements (but see Arizaga et al., 2015; Resano-Mayor et al., 2017). Compared with conventional migratory tracking methods, the analysis of δ^2H_f presents the advantage that an individual only needs to be captured and sampled once (Hobson, 2011).

Here, we investigated the migratory movement patterns of an emblematic songbird of high-alpine European ecosystems, the white-winged snowfinch (*Montifringilla nivalis nivalis*; hereafter snowfinch), through the analysis of δ^2H_f. We aimed to elucidate whether snowfinches wintering on their southwesternmost European grounds (i.e., Spanish Pyrenees and the Cantabrian Mountains) may originate from breeding grounds in the Alps. More specifically, we investigated whether δ^2H_f measured in the most outer rectrices differed between breeding grounds in the Swiss Alps and those in other southwestern European populations such as the Spanish Pyrenees, Cantabrian Mountains and Italian central Apennines. Due to the general pattern of lower δ^2H with increasing latitude and elevation, we predicted that breeding individuals in the Swiss Alps should have distinctively lower δ^2H_f compared to those in the southwestern breeding populations. In addition, we assessed the pattern of δ^2H_f in several wintering populations and estimated the proportion of wintering birds with a high probability of having a breeding origin in the Alps. Finally, we investigated the extent to which weather factors, such as winter ambient temperature and precipitation in the Swiss alpine region might correlate with southward movement of snowfinches breeding in the Alps. We predicted that under harsh wintering weather conditions (lower temperature and greater snowfall) in the Alps, a greater proportion of the snowfinch breeding population in this mountain region would exhibit southward migration.

Methods

The species

The snowfinch is an emblematic, high-alpine bird. In Western Europe, the subspecies *M. n. nivalis* has a patchy breeding distribution, ranging from the Cantabrian Mountains in northwestern Spain, through the Pyrenees, the Alps, Corsica and the Apennines east to northern Greece (Brambilla et al., 2020; Cramp and Perrins, 1994). Snowfinch occurs above the tree-line, in barren rocky habitat interspersed with grasslands. During the breeding season (May-August), it commonly forages on invertebrates next to patches of melting snow (Bettega et al., 2020; Jaime Resano-Mayor et al., 2019; Strinella, 2007). Snowfinch breeds in cliffs, buildings and skilift pylons. After fledging, family groups gather in large flocks, ascending above breeding grounds up to glaciers. They move to lower elevations with first snow falls (Cramp and Perrins, 1994). The species has long been considered as resident in Europe with only elevational downward movements depending on weather severity (Géroudet and Cousin, 1998); yet, individuals have been sighted in winter a few hundred kilometers away from their breeding grounds (Cramp and Perrins, 1994) and the origin of these birds has long remained a mystery. For instance, the French Central Massif, situated midway between the Alps and the Pyrenees, is regularly visited in winter (Cheylan, 1973), suggesting that birds from the Alps may move south towards the Pyrenees (Albouy and Riols, 2018). A few ring recoveries in the Spanish Pyrenees have established that some snowfinches wintering in Spain actually come from the Alps (Resano-Mayor et al., 2017). Nonetheless, the magnitude and frequency of this partial latitudinal migration is still poorly understood, especially given the limited ringing effort deployed so far in the difficult mountainous terrain and often adverse weather conditions.

Study sites and feather collection

Between 2006 and 2018, we collected primary and tail feathers from 382 snowfinches in four populations across Western Europe (Figure 4.1). Between May and August, we captured and sampled 109 individuals on their breeding grounds in the Cantabrian Mountains (CM, northwestern Spain; n = 63, 1800 to 2100 m a.s.l), Spanish Pyrenees (SP, northern Spain;

n = 8, 2500 m a.s.l.), Swiss Alps (SA, southwestern Switzerland; n = 27, 2200 to 2800 m a.s.l.) and Italian central Apennines (AP; n = 11, 2200 m a.s.l.). Individuals were mist-netted either on passes, while commuting from their foraging grounds to nesting cliffs (CM and SP), or next to breeding sites in buildings and skilift pylons (SA), and near nestboxes (AP). All winter captures (January-March; n = 273) resulted from mist-netting (CM: n = 9, 1400 m a.s.l.; SA: n = 100, 1500 m a.s.l.) or whoosh-netting (SP: n = 164, 1850 m a.s.l.) at foraging sites, often next to artificial seed feeders. Every individual was ringed and we collected either the innermost primary (wing feather P1; n = 227) or the outermost rectrice (tail feather R6; n = 244) for subsequent isotopic analysis. Feathers were stored in sealed plastic or paper bags at -20°C until analyzed. From 89 individuals we collected both a P1 and a R6 each to run tests of variation in δ^2H_f between primaries and rectrices. As the difference in δ^2H_f values between the SA population and all other populations was more pronounced for R6 than P1, we conducted all the analyses with rectrix material (Supplementary Figure S4.1 and Table S4.1). The reason is probably that snowfinches moult their R6 later in the season (generally, September to October) than P1 (July to August, Strinella et al., 2011; Winkler and Winkler, 1985), typically when social flocks aggregate at the highest elevations. Indeed, in the Alps, these late summer gatherings can take place at much higher elevation than in the other mountain massifs investigated because the Alps are much higher, potentially leading to more negative δ^2H_f.

Stable isotope analysis

A total of 471 feathers (including both P1 and R6) were prepared and analysed for δ^2H following standard procedures. All samples were cleaned using a 2:1 chloroform-methanol solvent soak (24 h) and rinsed, followed by drying in a fume hood for 48 h. We corrected for "exchangeable" hydrogen by conducting δ^2H analyses with the comparative equilibration method described by Wassenaar and Hobson (2003), thus using three calibrated keratin hydrogen isotope reference materials (CBS: -197‰, SPK: -121‰, KHS: -54.1‰). Approximately 0.35 mg of feather material was weighed into a silver cup, crushed, and then loaded into a zero-blank carousel. Pyrolytic combustion of samples under helium flow (1350 °C) produced H_2 gas that was separated in an elemental analyser (Eurovector, Milan, Italy) and analysed using continuous-flow isotope-ratio mass spectrometry (Isoprime, Manchester, UK). Isotope measurements are expressed in the delta (δ) notation as parts per thousand (‰) relative to Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP). Within-run analytical precision was estimated to be ±2‰ based on 5 replicate measurements from each of the three keratin reference standards for every 84 sample unknowns. Measurements of δ^2H were performed at the National Hydrology Research Centre of Environment Canada in Saskatoon, Canada. Note that for individuals captured at artificial feeders during the winter, supplemental feeding would not influence isotope measurements because feather growth was already completed.

Weather data

To test the hypothesis that the movements of snowfinches from the Alps to SP in winter might correlate with the prevailing winter weather conditions in the Alps in a given year, we correlated our proxy for an apparent yearly influx of snowfinches from the Alps into SP with mean monthly ambient temperature (°C) and monthly total precipitation (mm) in SA and in SP, recorded from October to March 2004-2015 (for SA: MeteoSwiss, data were averaged from n = 24 weather stations, 1300-2300 m a.s.l., Supplementary Figure S4.2; for SP: AEMET, data averaged from n = 11 weather stations, 1300-2300 m a.s.l.).

Statistical analysis

To investigate the differences in δ^2H_f between breeding populations, we performed a linear regression model, including δ^2H_f as the response variable and two predictors, population and season, as well as their interaction. Note that the AP population could not be included in this model because it lacked data for wintering birds. Once we generated sets of competing models, we applied the Akaike information criterion (AIC), using the values of $\Delta AIC < 2$ as the criterion for selecting the most parsimonious models (Burnham and Anderson, 2002). Following standard procedures, we calculated the Akaike weight for each candidate model *(wi)* as the relative strength of evidence, i.e., the probability of model *i* being the best-approximating model from the entire set of candidate models, and evidence ratios of the best models as the ratio of model weights.

The previous linear regression model showed that δ^2H_f differed between SA and the other breeding populations to an extent that allowed us to estimate the proportion of individuals captured on the wintering grounds in CM, SP and even SA having a breeding origin in the Alps. To do so, we used a finite mixture model for the stable isotope measures y_i. We defined the likelihood $p(y_i|\lambda) = \lambda * Normal(-98.11,8.70) + (1-\lambda) * Normal(-67.05,7.79)$, where λ is the proportion of birds originating from the Alps. The first normal density function is defined by the mean and standard deviation of the stable isotope measurements of the breeding population in the Alps and the second one by the combined measurements from the Pyrenees and the Cantabrian Mountains. We fitted the model to each data from the three mountains (Cantabrian, Pyrenees and Alps) separately by Hamiltonian Monte Carlo as implemented in Stan (Carpenter et al., 2017) using the R-interface rstan (Stan Development Team, 2019). We simulated 4 chains with 4000 iterations of which the last 2000 were used to describe the posterior distribution of λ. We assessed convergence by diagnostic statistics and graphical exploration of the Markov chains using shinystan (Gabry, 2018).

To test whether harsh winter weather conditions in the Alps may be associated with more snowfinches moving from the Alps to SP, we used bird ringing data obtained at one station in the Pyrenees from 2005-2015 (Supplementary Table S4.2). We first performed a logistic regression where the response variable was binary: 1 meaning snowfinches were captured during a single capturing attempt in the Pyrenees, and 0 meaning no capture, in relation to the weather conditions in the Swiss Alps and in the Pyrenees (i.e., mean temperature and mean precipitation) during the two months preceding each capture attempt. We also modelled weather conditions during the three preceding months, but the results did not qualitatively differ (Supplementary Table S4.3). Correlations between monthly mean temperature and total precipitation, both in the Alps and in the SP, and over the years, are shown in Supplementary Figure S4.3. Based on field observations, we assumed that the probability of snowfinch capture is a good measure of snowfinch presence/absence at this particular wintering site (in most cases when snowfinches were not captured, they were also not observed), which was visited regularly and under different weather conditions. As a second step, we built a further model, in which we included the number of snowfinches captured as a function of the above weather variables. We treated the number of snowfinches captured as a count data. As we had overdispersion in our data, we fitted a negative binomial model. Model selection followed the same criteria as for δ^2H_f ($\Delta AICc < 2$). We could not include the variable year as a random factor in these last two models because of singularity problems.

All analyses were performed in R 3.4.4 (R Core Team, 2018), using the lme4 package (Bates et al., 2015). Multimodel inference and model selection were run using the MuMIn package (Barton, 2009).

Results

Among population δ^2H_f differences and breeding origins of snowfinches

Breeding individuals of the SA population had significantly lower δ^2H_f (mean ± SD = -98.2 ± 8.4‰; range = -116.6‰, -84.6‰) compared to individuals from the breeding grounds in SP (-66.9 ± 9.0‰; range = -79.7‰, -52.0‰), CM (-67.1 ± 7.5‰; range = -84.6‰, -52.8‰) and AP

(-60.6 ± 10.1‰; range = -76.8‰, -45.9‰; Figure 4.1 and Supplementary Table S4.1). However, a different pattern emerged in the values of δ^2H_f of wintering individuals. Snowfinches captured in the SA during winter had similar values to those captured during the breeding period (-94.9 ± 8.9‰; range = -130.2‰, -76.5‰), while individuals at both SP (-95.7 ± 10.7; range = -115.7, -65.6) and CM (-85.9 ± 15.0‰; range= -102.2‰, -62.5‰) showed the widest ranges of δ^2H_f. That is, wintering individuals at the SP and CM encompassed the entire isotopic values of all breeding populations, although their δ^2H_f values were closer to the SA breeding birds than to the breeding individuals of the two Iberian populations. There were also larger differences in δ^2H_f between breeding and wintering individuals in the SP population compared to the CM population (Table 4.1A, Figure 4.1 and Supplementary Figure S4.4).

The breeding origin assignment of wintering birds suggests that 99% (CI: 96-100%) of the individuals sampled during the winter in SA had a high probability to belong to the SA breeding population, with the remaining 1% (CI: 0-3%) showing a breeding origin other than SA (Figure 4.1). Similarly, 98% (CI: 92-99.8%) of the wintering birds from SP were assigned to a breeding origin from the Alps, compared to 2% (CI: 0.2-8%) for which a breeding origin other than SA was obtained (Figure 4.1). The 86% (CI: 55-99%) of the wintering birds captured in the CM had a high probability to belong to the breeding population from the Alps, while for 14% (CI: 1-45%) a breeding origin other than the Alps was assigned (Figure 4.1). It is important to note, however, that with only 9 individuals captured in winter in the Cantabrian Mountains, these estimates should be taken with caution.

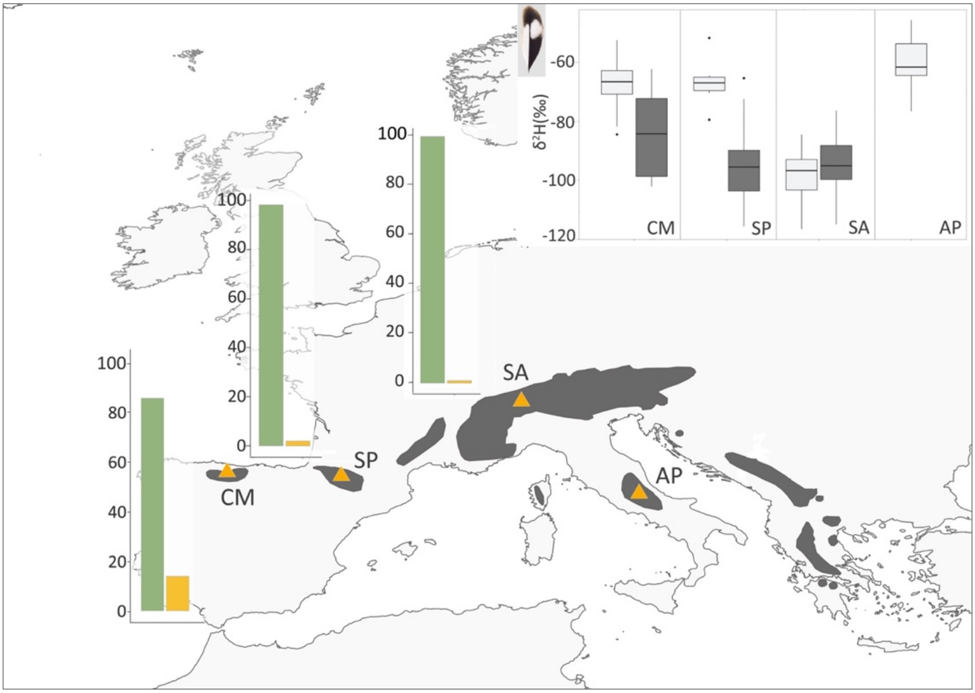


Figure 4.1. Distribution (grey shaded area) of the subspecies *Montifringilla nivalis nivalis* (Birdlife International, 2017). Monitored snowfinch breeding populations (orange triangles) in the Cantabrian Mountains (CM), Spanish Pyrenees (SP), Swiss Alps (SA) and Italian central Apennines (AP). The investigated wintering populations are in CM, eastern SP and SA. Insert: differences in δ^2H_f values of rectrices per population during the breeding (light grey boxes) and wintering (dark grey boxes) seasons. The bar charts show the probability of a breeding origin from the Alps (green bar) or other than the Alps (orange bar) for wintering birds sampled at CM, SP and SA.

Winter weather conditions and migratory propensity

Finally, the probability of capturing snowfinches at the SP wintering site was related to the mean temperature in the Alps and to the mean precipitation in the SP during the previous two months: the lower the temperature in the Alps and the higher the precipitation in the SP, the greater the number of snowfinch were captured (Table 4.1B). Combining the information on δ^2H_f and captures, this suggests that snowfinches from SA may be more prone to move to SP when low winter ambient temperature prevailed in the Alps (< -2°C, i.e., in the 42% coldest winters. Table 4.1B and Figure 4.2) and high level of precipitation in the SP (Table 4.1B). Mean precipitation of the previous two months in the Alps also entered the most parsimonious models but with no significative effect. In contrast, the number of wintering snowfinches captured per capturing attempt in SP was not related to any weather variables: correlations with weather variables could not be measured due to large uncertainty and/or low sample size (Supplementary Table S4.4).

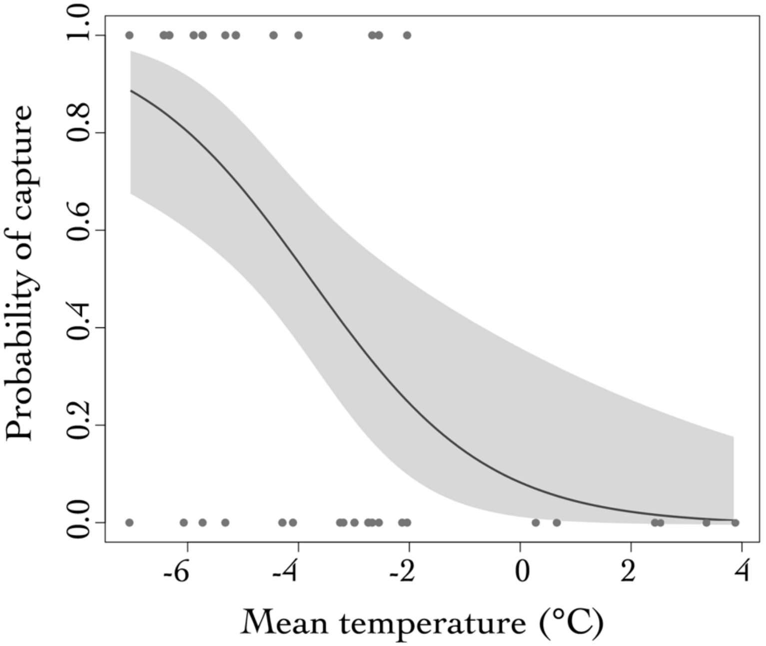


Figure 4.2. Model prediction for the probability of capturing wintering snowfinches in SP from 2005 to 2015 in relation to the mean ambient temperature (°C) of the two months preceding each capture, recorded in the Swiss Alpine massif.

Table 4.1. AICc, ΔAICc, AICc weight and goodness-of-fit values of the most parsimonious models (for which coefficients and confidence intervals are shown), for: (A) comparing pattern of δ2H for the outer rectrix in breeding vs. wintering populations; and (B) investigating the influence of weather variables on the success (i.e., binary response variable, with 1 = snowfinches were captured during one session, and 0 = no snowfinches were captured; total number of capture attempts = 49) of capturing snowfinches in SP during every winter capturing attempt (predictor variables: MeanTemp_CH = mean ambient temperature in the Swiss Alps of the two months preceding each capture; MeanPrec_CH = mean precipitation in the Swiss Alps of the two months preceding each capture; MeanPrec_SP = mean precipitation in the Spanish Pyrenees of the two months preceding each capture). Models shown here are those with ΔAICc < 2 (see all other alternative models in the Supplementary Table S4.5).

(A) Models	AICc	ΔAICc	AICc weight	Adjusted-R^2	β	SE	RIV	Confidence Interval	
								2.5%	97.5%
Season + Population + Season*Population	**1719.76**	**0.00**	**1**	**0.56**					
Intercept					-67.09	1.66		-70.36	-63.81
Season: Winter					-18.84	3.50	1	-25.74	-11.95
Population: SP					0.21	4.12	1	-7.92	8.33
Population: SA					-31.07	2.61	1	-36.22	-25.92
Winter * Population SP					-9.92	5.27	1	-20.31	0.47
Winter * Population SA					22.43	4.15	1	14.26	30.60

(B) Models	AICc	ΔAICc	AICc weight	Deviance	β	SE	Confidence Interval	
							2.5%	97.5%
MeanTemp_CH + MeanPrec_SP	**51.55**	**0.00**	**0.42**	**0.33**				
MeanTemp_CH + MeanPrec_CH+MeanPrec_SP	**53.40**	**1.85**	**0.17**					
Intercept					0.13	0.38	-0.66	0.89
MeanTemp_CH					-2.25	0.73	-4.07	-1.06
MeanPrec_SP					1.34	0.62	0.26	2.75

Discussion

The breeding population of snowfinch in the Swiss Alps (SA) showed a distinctive lower δ^2H_f in rectrices compared to southern populations such as those in the Apennines (AP), Spanish Pyrenees (SP) and Cantabrian Mountains (CM), which did not differ between them. Here, we assume that δ^2H_f of the sampled breeding populations were representative of the respective breeding population. This isotopic pattern allowed us to estimate the probability of a breeding origin (Alps *vs.* other) for wintering birds in the SA, SP and CM. When assessing the probabilities of having a breeding origin from the Alps within a wintering snowfinch population in the SA, not surprisingly we found that ca 100% of the individuals were estimated to be local breeders. Astonishingly, as many as 98% and 86% of the individuals sampled in winter in the SP and CM, respectively, also had a high probability of originally stemming from the breeding population in the Alps. These results not only support previous evidence suggesting that latitudinal wintering movements exist in the European snowfinch (Albouy and Riols, 2018; Cheylan, 1973; Resano-Mayor et al., 2017) but also suggest that such wintering movements from the Alps to the SP could reach the westernmost distribution limit represented by the CM massif.

Snowfinches from the Alps apparently adopt a partial latitudinal migratory strategy, which leads to southern, resident populations potentially merging with northern populations in winter. Among extrinsic drivers, winter ambient temperature seems to play a role in partial migratory movements of snowfinches from the Alps, as documented for other species (Watts et al., 2018). For instance, in Europe some northern populations of the European robin (*Erithacus rubecula*) migrate longer distances when winter temperatures in the breeding areas are cold, although large geographical variation in response to climate seems to exist (Ambrosini et al., 2016). Interactions between an individual's physiological balance (homeostasis sensu Arlettaz et al., 2015; Wingfield et al., 2017) and its ability to acquire food (social status, Mckinnon et al., 2019) are likely to be the mechanisms at play when deciding whether to stay or move in non-obligate migrants (Singh et al., 2012). Our results raise the question of which are the key triggering factors determining the snowfinch flexible partial migration from the Alps towards southern Iberian populations. Snowfinches might move in response to low temperatures because of allostatic stress, or because low temperatures prevent snow melting and thus reduce food availability, or as a combination of both. Yet, factors other than extrinsic (e.g. food availability and weather) can motivate birds to migrate. Intrinsic factors linked to social rank and/or physiological performance may constrain subordinate individuals to leave breeding territories in the cold season (Chapman et al., 2011; Macdonald et al., 2016; Reid et al., 2018). In this regard, migration propensity in partially migratory populations may be dependent on the sex, age, size or individual internal state (Chapman et al., 2011; Fudickar et al., 2013; Hegemann et al., 2015). However, more research is still needed to better understand how extrinsic and intrinsic factors may determine migratory strategies, and whether different movement patterns may ultimately affect population viability.

We do not really know from our results whether the sampled wintering individuals at the southern populations with high probability of a breeding origin from the Alps are migrating or dispersing (i.e., we do not know if they return). Based on ring recoveries, both South-West movements in autumn-winter and North-East movements in spring indicate that migrating individuals move in both directions (from and to the breeding grounds in the Alps, although quantitative analyses are still missing). Our results could also indicate a case of irruption, which is common for many North American finches, particularly during harsh winters, when birds that are unable to stay farther North migrate South (Strong et al., 2015). Snowfinches' movements between the Alps and the Spanish Pyrenees and Cantabrian Mountains, as well as the exchanges of individuals between different sectors of the Alps described earlier (Scridel, 2019), may be important for the overall genetic structure of the snowfinch west European metapopulation (see Resano-Mayor et al., 2017). If we assume that winter migrants from the Alps settle from time to time to breed in the Iberian populations, then gene flow could help to maintain genetic diversity across the western European range of the snowfinch. This would help preventing the potential negative impacts of a demo-genetic isolation due to habitat loss (Cote et al., 2017; Jacob et al., 2017; Procházka et al., 2008), which will be more acute in high-alpine ecosystems than anywhere else because of both the pyramid shape of mountains and rapid climate warming (Brunetti et al., 2009; Urban, 2018). In our case this concerns, in particular, the small CM population for which an occasional settling of winter immigrants might represent a unique demo-genetic rescue option. Although according to our findings a good proportion of birds wintering in the CM may come from the Alps, we need to point out that our sample size was low, what might have overestimated the result. In effect, this population shows signs of genetic isolation, having a specific and predominant haplotype not shared by other European populations (Resano-Mayor et al., 2017). Nevertheless, further genetic studies would be needed to better understand if the CM snowfinch population became more isolated since the last ice age because of the use of a different refuge compared to the other populations, or whether the higher genetic isolation currently observed has increased overtime. Future studies employing individual tracking devices (e.g., GPS-based system) and high-resolution genetic markers would help to test the hypotheses raised in this study to better understand whether or not, and to what extent, wintering birds in the SP and the CM are actually residents, migrants or dispersers.

Climate change influences movement strategies in different ways. For instance, in long-distance migrants, it can affect the onset of migration and the arrival date on the breeding grounds (Bókony et al., 2019). In short-distance migrants, milder winters may induce a progressive reduction of seasonal journeys (Singh et al., 2012), which may eventually lead to permanent residency (Pulido and Berthold, 2010). Alpine ecosystems are particularly vulnerable to climate change (Brunetti et al., 2009). Warmer temperatures cause an upwards elevational shift of the treeline, resulting in higher fragmentation and isolation of alpine habitats (Holtmeier and Broll, 2007). For species adapted to live in such environments, this could have detrimental effects on population connectivity. An upward shifting treeline can lead to the shrinkage of alpine habitat so animals would need to move farther to find suitable patches, with such movements having the importance of enhancing metapopulation functioning (Cote et al., 2017; Roland et al., 2000). In species like the snowfinch, if the decision to migrate is triggered by adverse climatic conditions, warmer winters might reduce the frequency of latitudinal migration. If the latter occurs in the long run with snowfinches breeding in the Alps (i.e., if they progressively reduce migration propensity), and the viability of the smaller, potentially more isolated populations (e.g. CM) relies on immigrants from the Alps, then those populations may eventually become extinct. In effect, the latter would not only be massively impacted by global warming given their southern latitude, but they may in addition lose the demo-genetic rescue benefits provided by potential immigrants coming from the North for overwintering. Conversely, the migrant portion of the breeding population in the Alps, by becoming less mobile, might experience an increase in competition. As the dynamics of migrant and non-migrant subpopulations might be linked through density-dependent effects (Griswold et al., 2011), warming conditions might affect population demography, structure and heterogeneity of species living in alpine environments. More generally, future research should decipher how these sorts of risks affect high-alpine species that are particularly exposed to climatic shifts, but show flexible migration behaviour in space and time, to better understand how they may respond to rapidly changing environments.

Our study suggests that snowfinches adopt a partial latitudinal migratory strategy probably determined by climatic conditions such as the temperature in the Alps over the winter. The different movement patterns suggested by the analysis of δ^2H_f could have important implications in terms of population connectivity, spatio-temporal population dynamics and structuring. The consequent eco-evolutionary responses to environmental perturbations might be similarly multi-faceted, especially under uncertain future climate change scenarios. Long-term studies, considering the metapopulation structure of the species in western Europe, are thus required to better disentangle the complexity of the movement strategies of alpine species, and its potential consequences in the light of global warming for conservation purposes. The analysis of δ^2H_f may thus offer unique opportunities for research about migratory strategies and population connectivity in high-alpine birds.

Supplementary Material

Table S4.1. Descriptive stable hydrogen isotope ratios (δ^2H_f; ‰) in primary and rectrice snowfinch feathers sampled at different breeding (Cantabrian Mountains, Spanish Pyrenees, Swiss Alps, Apennines) and wintering (Cantabrian Mountains, Spanish Pyrenees, Swiss Alps) populations. Sampling period (years), minimum (Min), maximum (Max), mean and standard deviation (sd) values are shown together with sample size (n).

Feather	Season	Population	Period	Min	Max	Mean	sd	n
Primary	Breeding	C. Mountains	2012-2015	-84.3	-41.7	-59.8	9.0	42
		Pyrenees	2012-2015	-80.7	-45.2	-59.0	14.4	7
		Swiss Alps	2013-2015	-125.0	-54.3	-84.0	18.5	21
	Wintering	Pyrenees	2013-2015	-100.3	-41.3	-65.6	12.2	119
		Swiss Alps	2015	-119.7	-63.7	-88.8	14.4	38
Rectrice	Breeding	C. Mountains	2013-2018	-84.6	-52.8	-67.1	7.5	31
		Pyrenees	2012-2015	-79.7	-52.0	-66.9	9.0	6
		Swiss Alps	2015-2016	-116.6	-84.6	-98.2	8.4	21
		Apennines	2012	-76.8	-45.9	-60.6	10.1	11
	Wintering	Pyrenees	2006-2015	-115.7	-65.6	-95.7	10.7	66
		Swiss Alps	2015-2018	-130.2	-76.5	-94.9	8.9	100
		C. Mountains	2018	-102.2	-62.5	-85.9	15.0	9

Table S4.2. Number of visits (capture attempts), mean and standard deviation (sd) of the number of snowfinches captured in winter in the Spanish Pyrenees during the years 2005 to 2015.

Year	No. of visits	No. of snowfinches captured	
		Mean	SD
2005	3	4.3	7.5
2006	8	40.4	51.5
2007	1	0.0	0.0
2008	4	1.0	2.0
2009	7	62.0	60.5
2010	8	50.6	53.6
2011	4	0.7	1.5
2012	2	0.0	0.0
2013	5	24.2	19.3
2014	3	0.0	0.0
2015	4	4.5	9.0

Table S4.3. AICc, ΔAICc, weighted AICc and goodness-of-fit values of models (for which coefficients and confidence intervals are shown) for: (A) investigating the influence of weather variables (three months preceding each capture attempt) on the snowfinch capture success over winter in the Spanish Pyrenees. The response variable is binary: 1 = snowfinches were captured, and 0 = no snowfinches were captured; total number of capture attempts = 49; (B) investigating the influence of the same weather variables on the number of snowfinches captured in the SP during winter. Predictor variables: MeanTemp_CH = mean ambient temperature in the Swiss Alps; MeanPrec_CH = mean precipitation in the Swiss Alps; MeanTemp_SP= mean temperature in the Spanish Pyrenees; MeanPrec_SP = mean precipitation in the Spanish Pyrenees.).

(A) Models	AICc	ΔAICc	Weighted AICc	β	SE	Confidence Interval	
						2.5%	97.5%
MeanPrec_SP+ MeanTemp_CH	**57.01**	**0.00**	**0.35**				
MeanPrec_SP+ MeanTemp_SP+ MeanTemp_CH	**57.87**	**0.84**	**0.23**				
MeanPrec_SP+ MeanPrec_CH+ MeanTemp_CH	59.32	2.30	0.11				
MeanPrec_SP+ MeanTemp_SP+ MeanPrec_CH+ MeanTemp_CH	59.88	2.86	0.08				
MeanPrec_SP+ MeanTemp_SP	60.22	3.20	0.07				
MeanTemp_CH	61.74	4.72	0.03				
MeanTemp_SP	62.50	5.47	0.02				
MeanPrec_SP+ MeanTemp_SP+ MeanPrec_CH	62.56	5.53	0.02				
MeanPrec_CH+ MeanTemp_CH	63.17	6.15	0.02				
Null	63.38	6.36	0.01				
MeanPrec_SP	63.77	6.75	0.01				
MeanTemp_SP+ MeanTemp_CH	63.93	6.91	0.01				
MeanTemp_SP+ MeanPrec_CH	64.55	7.53	0.01				
MeanPrec_SP+ MeanPrec_CH+MeanPrec_CH	65.09	8.07	0.01				
MeanPrec_CH	65.48	8.46	0.01				
Intercept				0.34	0.35	-0.35	1.05
MeanTemp_CH				-2.63	1.26	-5.31	-0.26
MeanPrec_SP				1.23	0.48	0.37	2.33
MeanTemp_SP				1.41	1.16	-0.79	3.92

(B) Models	AICc	ΔAICc	Weighted AICc	β	SE	Confidence Interval	
						2.5%	97.5%
Null	**176.87**	**0.00**	**0.27**				
MeanPrec_SP	**177.49**	**0.62**	**0.20**				
MeanPrec_SP+ MeanPrec_CH	179.07	2.20	0.09				
MeanTemp_SP	179.38	2.52	0.08				
MeanTemp_CH	179.39	2.52	0.08				
MeanPrec_CH	179.54	2.67	0.07				
MeanPrec_SP+MeanTemp_CH	180.17	3.30	0.05				
MeanPrec_SP+MeanTemp_SP	180.32	3.45	0.05				
MeanPrec_CH+MeanTemp_CH	182.15	5.28	0.02				
MeanTemp_SP+MeanPrec_CH	182.31	5.44	0.02				
MeanPrec_SP+MeanTemp_SP+MeanPrec_CH	182.37	5.50	0.02				
MeanPrec_SP+MeanTemp_CH+MeanPrec_CH	182.54	5.67	0.02				
MeanTemp_SP+MeanTemp_CH	182.55	5.68	0.02				
MeanPrec_SP+MeanTemp_SP+MeanTemp_CH	183.75	6.88	0.01				
MeanTemp_SP+MeanPrec_CH+MeanTemp_CH	185.63	8.76	0.00				
MeanPrec_SP+MeanTemp_SP+MeanPrec_CH+MeanTemp_CH	186.32	9.45	0.00				
Intercept				3.25	0.17	2.93	3.61
MeanTemp_CH				0.38	0.76	-1.20	1.95
MeanPrec_CH				-0.33	0.29	-0.89	0.17
MeanTemp_SP				-0.46	0.66	-1.87	0.97
MeanPrec_SP				0.60	0.25	-0.01	1.19

Table S4.4. Model-averaged coefficients of the models investigating the influence of weather variables on the number of snowfinches captured in the Spanish Pyrenees during winter (predictor variables: MeanTemp_CH = mean ambient temperature in the Swiss Alps of the two months preceding each capture; MeanPrec_CH = mean precipitation in the Swiss Alps of the two months preceding each capture; MeanTemp_SP = mean temperature in the Spanish Pyrenees of the two months preceding each capture MeanPrec_SP = mean precipitation in the Spanish Pyrenees of the two months preceding each capture).

Models	AICc	ΔAICc	Weighted AICc	β	SE	p
Null	**176.87**	**0.00**	**0.37**			
MeanPrec_CH	179.18	2.31	0.12			
MeanTemp_CH	179.50	2.63	0.10			
MeanTemp_SP	179.61	2.74	0.09			
MeanPrec_SP	179.66	2.79	0.09			
MeanPrec_CH+ MeanTemp_CH	180.27	3.40	0.07			
MeanTemp_SP+ MeanPrec_CH	181.68	4.81	0.03			
MeanPrec_SP+ MeanPrec_CH	182.30	5.43	0.02			
MeanTemp_SP+ MeanTemp_CH	182.61	5.74	0.02			
MeanPrec_SP+ MeanTemp_CH	182.65	5.78	0.02			
MeanPrec_SP+ MeanTemp_SP	182.77	5.90	0.02			
MeanPrec_SP+ MeanPrec_CH+ MeanTemp_CH	183.64	6.77	0.01			
MeanTemp_SP+ MeanPrec_CH+ MeanTemp_CH	183.79	6.92	0.01			
MeanPrec_SP+ MeanTemp_SP+ MeanPrec_CH	185.18	8.31	0.01			
MeanPrec_SP+ MeanTemp_SP+ MeanTemp_CH	186.21	9.34	0.00			
MeanPrec_SP+ MeanTemp_SP+ MeanPrec_CH+ MeanTemp_CH	187.71	10.84	0.00			
Intercept				3.27	0.18	<0.001
MeanTemp_CH				0.56	0.41	0.174
MeanPrec_CH				-0.48	0.31	0.122
MeanTemp_SP				-0.11	0.37	0.769
MeanPrec_SP				0.10	0.20	0.601

Table S4.5. Alternative models (A) comparing pattern of δ^{2}H for the outer rectrix in breeding vs. wintering populations; and (B) investigating the influence of weather variables on the success of capturing snowfinches in the Spanish Pyrenees during winter for every capturing attempt (see Table 1 in the main text for the most parsimonious models; predictor variables: MeanTemp_CH = mean ambient temperature in the Swiss Alps of the two months preceding each capture; MeanPrec_CH = mean precipitation in the Swiss Alps of the two months preceding each capture; MeanTemp_SP = mean temperature in the Spanish Pyrenees of the two months preceding each capture; MeanPrec_SP = mean precipitation in the Spanish Pyrenees of the two months preceding each capture).

	Models	AICc	ΔAICc	Weighted AICc
A	Season+Population	1769.63	49.88	0.00
	Population	1783.42	63.67	0.00
	Season	1830.36	110.61	0.00
	Null	1896.96	177.21	0.00
B	MeanPrec_SP+MeanTemp_SP+MeanTemp_CH	53.79	2.24	0.14
	MeanTemp_CH	55.04	3.48	0.07
	MeanPrec_SP+MeanTemp_SP+MeanPrec_CH+MeanTemp_CH	55.74	4.19	0.05
	MeanPrec_SP+MeanTemp_SP	56.80	5.25	0.03
	MeanTemp_SP	57.00	5.45	0.03
	MeanTemp_SP+ MeanTemp_CH	57.25	5.69	0.02
	MeanPrec_CH+MeanTemp_CH	57.29	5.73	0.02
	MeanPrec_SP+MeanTemp_SP+MeanPrec_CH	57.79	6.24	0.02
	MeanTemp_SP+MeanPrec_CH	59.16	7.61	0.01
	MeanTemp_SP+MeanPrec_CH+MeanTemp_CH	59.60	8.04	0.01
	MeanPrec_CH	67.36	15.81	0.00
	MeanPrec_SP+ MeanPrec_CH	69.25	17.70	0.00
	Null	69.83	18.28	0.00
	MeanPrec_SP	71.90	20.35	0.00

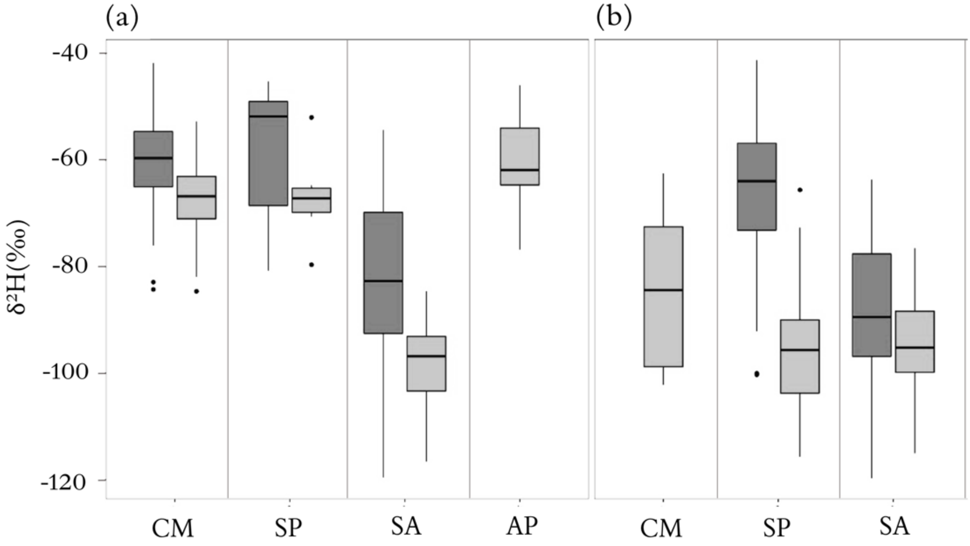


Figure S4.1. Box plot with δ^2H_f values in the primaries (dark grey boxes) and rectrices (light grey boxes) for each population/season. Feathers were samples at the Cantabrian Mountains (CM; P1 = 42 and R6 = 31 individuals), the Spanish Pyrenees (SP; P1 = 7 and R6 = 6), the Swiss Alps (SA; P1 = 21 and R6 = 21) and the Italian central Apennines (AP; R6 = 11) during the breeding season (a), and the Cantabrian Mountains (CM; R6 = 9), the Spanish Pyrenees (SP; P1 = 119 and R6 = 66) and the Swiss Alps (SA; P1 = 38 and R6 = 100) during the wintering season (b).

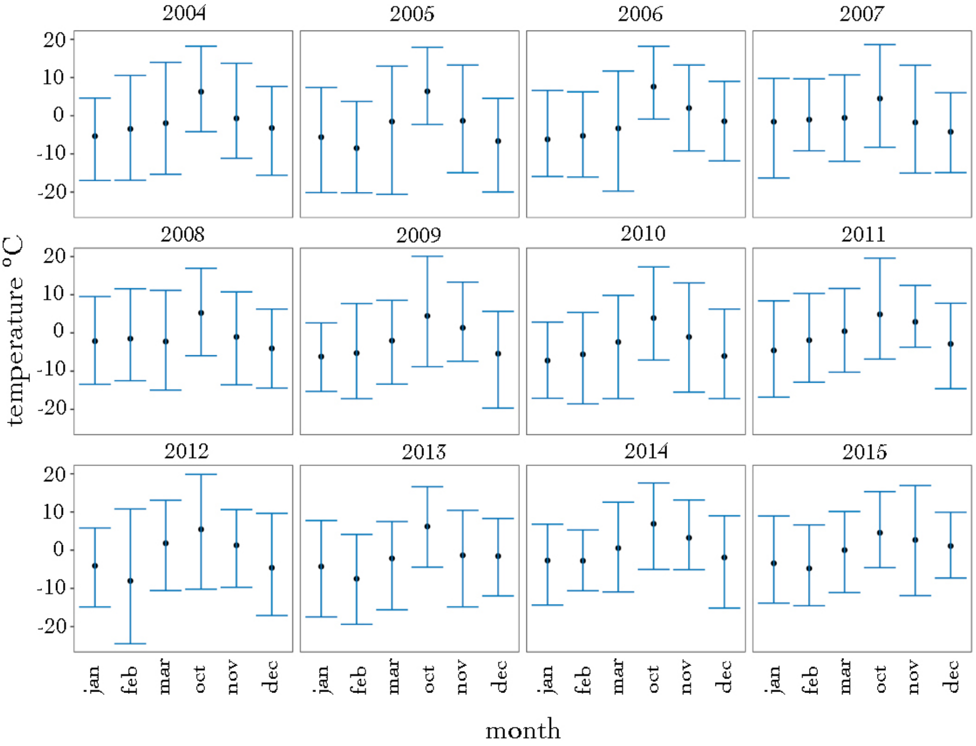
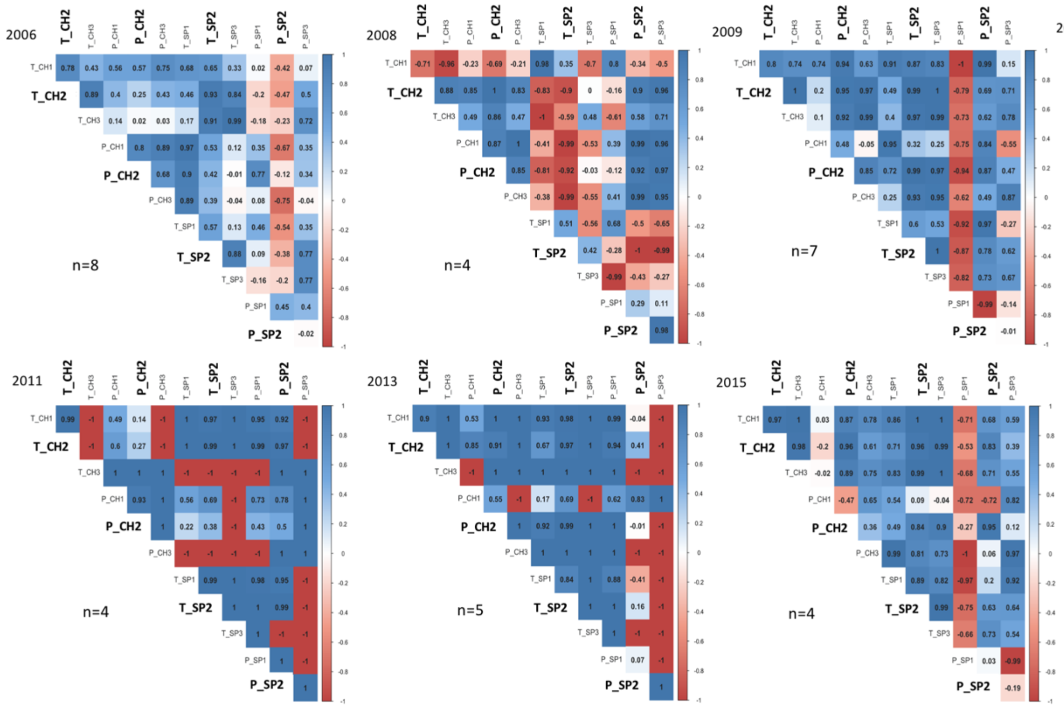


Figure S4.2. Mean (blue dots) and range (min, max; vertical lines) temperature (°C) in the Swiss Alps (n = 24 weather stations, 1300-2300 m a.s.l.) for each month considered in the analysis (January to March and October to December) across the study period (2004-2015).

Figure S4.3. Correlation between monthly mean temperature and total precipitation, both in the Swiss Alps and in the Spanish Pyrenees, and over the years (n = number of capture attempts; only years when n > 3 are shown). Climatic variables legend: T and P refer to mean temperature and precipitation respectively; CH refers to the Swiss Alps, SP to the Spanish Pyrenees; numbers 1 to 3 refer to the number of months (preceding the captures) for which the mean temperature and precipitation were calculated. Bold labels refer to the variables considered in the main analyses.



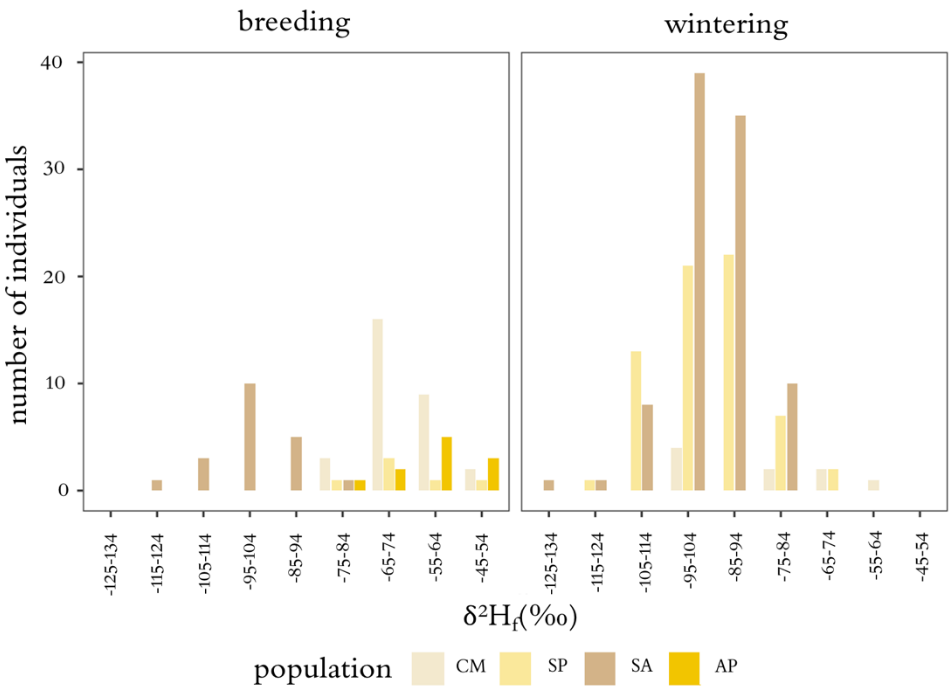


Figure S4.4. Number of individuals classified into nine different categories according with their stable hydrogen isotopes (δ^2H_f; ‰) from lower (-134‰) to higher (-45‰) values (x-axis). Samples correspond to rectrices collected during the breeding and wintering seasons at the Cantabrian Mountains (CM), the Spanish Pyrenees (SP), the Swiss Alps (SA) and the Italian central Apennines (AP, only during the breeding season).

Chapter V

Spatio-temporal variation in the wintering associations of an alpine bird

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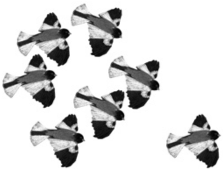


Summary

Many animals, in particular cold-adapted temperate species, make behavioural changes to cope with winter conditions, the development of gregariousness being a common strategy. Several ultimate and proximate factors have been invoked to explain why gregariousness may evolve during winter, with individuals coming together and separating as they trade off the different costs and benefits of living in groups. These trade-offs may however change over space and time as a response to e.g. varying environmental conditions. Despite its importance, little is known about the factors triggering gregarious behaviour during winter and its change in response to variation in weather conditions is poorly documented. Here, we aimed at quantifying large-scale patterns in wintering associations over 23 years of one of the most emblematic songbird species of alpine ecosystems in Europe, the white-winged snowfinch *Montifringilla nivalis nivalis*. Our results highlight that individuals gather in larger groups especially at sites with harsh wintering conditions. Moreover, individuals at colder sites generally reunite later and separate earlier than at warmer sites. However, the magnitude and phenology of wintering associations are ruled by changes in weather conditions during the winter. In particular, when temperature increased or the levels of precipitations decreased, the size of snowfinch wintering associations substantially decreased, and individuals stayed united in groups for shorter time. These results shed light on factors driving gregariousness and points to shifting winter climate as an important factor influencing this behaviour. This indicates that gregariousness should be monitored to assess whether global warming may have consequences on the social behaviour of alpine species, ultimately affecting its population dynamics.

Introduction

Winter represents a major challenge for a large number of animal species. Even cold-adapted species of temperate regions face challenges like reduction in food availability and have to seek for shelter when snowfall arrives. For sedentary species, such as mammals, there is little alternative other than to hibernate (Delgado et al., 2018a), whereas in other species migration represents a good strategy for overwintering (Newton, 2008). Yet, there are other behavioural adaptive responses to harsh winter conditions, the most common of these being the adoption of gregarious behaviour (Evans and Morand-Ferron, 2019; Spencer, 1982). Individuals that are extremely territorial throughout the breeding season may in contrast adopt an extended social way of life during the winter.

Gregariousness during winter is such a common strategy in temperate zones that must have marked advantages (Evans and Morand-Ferron, 2019; Mcfarland et al., 2015). A variety of ultimate and proximate factors have been proposed to explain why gregariousness may evolve during winter. Among birds, apart from reduced predation (Riipi et al., 2001), wintering association confers considerable advantages when it comes to locating suitable feeding areas (e.g. patches free of snow or with food abundance) (Newton, 2008). Drawbacks of living in groups include, however, increased competition for resources or spread of diseases (Altizer et al., 2011). Therefore, group size can be dynamic and fluctuate over time and space (Dhanjal-Adams et al., 2018; Sueur et al., 2011), with individuals gathering together or separating (i.e. fission-fusion dynamics) as they trade off the costs and benefits of living in a group (Delgado et al., 2018b; Sueur et al., 2011). Fission-fusion dynamics (Dhanjal-Adams et al., 2018) certainly influence many ecological and evolutionary aspects, such as habitat selection, space use and migration (Covas and Griesser, 2007; Delellis et al., 2014; Loretto et al., 2017; Teitelbaum et al., 2016), ultimately affecting the dynamic and persistence of animal populations (Delgado et al., 2018b). Despite its importance, little is known about the dynamics of gregariousness during winter and, especially, about its spatio-temporal responses to varying climatic conditions.

Animal life-history strategies are adapted to local and global climate conditions (Ovaskainen et al., 2013; Parmesan and Yohe, 2003; Root et al., 2003; Thackeray et al., 2010). In birds, there is good evidence that the changes in climatic conditions (e.g. temperature, precipitation) affect the migratory behaviour of many species in several ways, including changes in (1) the proportion of individuals migrating or staying in local populations, (2) migration distance, and (3) the timing, direction and speed of migratory movements (Both and Visser, 2001; Cotton, 2003; Gordo, 2007; Knudsen et al., 2011). Also, the timing of reproduction is affected by climatic changes (Forchhammer et al., 1998; Halupka and Halupka, 2017; Møller et al., 2010). Such behavioural adjustments in migration strategies and breeding phenology frequently have severe negative effects on species distribution, abundances and may lead to local extinctions (Forchhammer et al., 1998; Parmesan and Yohe, 2003). Notably, other behavioural adaptations to new local climatic conditions are key adaptive responses for maintaining populations in a changing world (Bellard et al., 2012; Koh et al., 2004). As individual decisions are context-dependent (Delgado et al., 2018b), we could anticipate that gregariousness may change over space and time as a response to e.g. varying environmental conditions. Yet, theoretical studies on animal aggregation have primarily focused on methods to detect the underlying mechanisms leading its emergence

(Sumpter, 2006), whereas empirical works on gregariousness have often been restricted to small spatial (single location) and short temporal (from few days to few months) scales (Cavagna et al., 2010; Nagy et al., 2013). Yet, discerning a consistent pattern and revealing the geographic scope of the locally observed dynamic in gregariousness behaviour may require spatially and temporally extensive data. Although gregariousness responses to local weather conditions certainly help to understand the short-term impacts of changes in environmental conditions, assessing differences in natural groups along a geographic and climatic gradient can offer better insights into how gregariousness may respond to long-term changes in climate.

Here, by profiting from a long-term dataset, we quantified large-scale patterns in wintering associations of one of the most emblematic songbird species of alpine ecosystems in Europe, the white-winged snowfinch (*Montifringilla nivalis*; hereafter snowfinch). The snowfinch is a Palearctic alpine species, with a subspecies (*M. n. nivalis*) distributed in Europe from the Spanish Cantabrian Mountains in the northwest of the Iberian Peninsula, through the Pyrenees, the Alps, Corsica, the Apennines, eastwards to the Dinaric Alps and the south-western Balkans (Brambilla et al., 2020; Keller et al., 2020). Even though the snowfinch is classified as a Least Concern species by the Global IUCN Red List Category Criteria, data for population and trend estimation is currently unknown and remain poorly known in more than 90% of the European countries (Brambilla et al., 2020). Surveys conducted in part of its range however point to recent range contractions (Knaus et al., 2019; Scridel et al., 2017), at the same time that high-elevation ecosystems in Europe are facing dramatic changes induced by global warming (Grunewald and Scheithauer, 2010; Haeberli et al., 2007; López-Moreno, 2005; Rixen and Wipf, 2017). Little is known about whether variation in climate affects the social behaviour of cold-adapted species, and the snowfinch, with its marked gregarious behaviour (Bettega et al., 2020) during the non-breeding season (hereafter winter), is an ideal biological model for the purposes of this study. Specifically, the aims of our study were to address: 1) to what extent does the variation in fission-fusion and in wintering group size follow abiotic gradients such as latitude or elevation (here represented by mean site temperature and mean site precipitation over the extent of the study period)?; and 2) have wintering group size and fission-fusion dynamics changed as a response to varying weather conditions?

Methods

Data collection

From 1990 to 2013, 10843 observations on snowfinches were collected in Switzerland, Italy and Spain, in the framework of different studies carried out by the authors (Bettega et al., 2020; Brambilla et al., 2018a; Resano-Mayor et al., 2019; Strinella et al., 2020) and by national parks and local institutions. In addition, data collected by the public (citizen science) and gathered through online databases (www.ornitho.at, www.ornitho.ch, www.ornitho.it, www.ornitho.cat), were obtained after official requests for the purpose of the study. All data were collected in the form of spatially georeferenced observations.

To study the spatio-temporal variation in group separation and group formation (i.e. fission–fusion dynamics) we modelled the number of snowfinches within groups (Q) as a function of the Julian date for each particular site and year (Supplementary Figure S5.1). We treated Q as a Gamma distributed response variable, and fitted a General Additive Model (GAM) to allow the relationship to be nonlinear, i.e. the smoothing function f(Q) could potentially take any shape. For each model, we estimated the two internal knots of the linear regressions, representing the inflection points where the linear regression could be separated into different segments with different slopes (Supplementary Figure S5.1). We used these knots as a proxy of the fission–fusion dynamic, representing the time when individuals separate (fission), and when individuals come together in large flocks during the non-breeding season (fusion). Further, for studying the spatio-temporal variation in group size during winter, we considered only those observations where more than 5 individuals were simultaneously observed (total number of observations = 6164), and selected the 1295 observations collected from September to March, both included.

To study the potential influence of weather conditions in wintering group fission-fusion and group size dynamics, we used the potentially relevant weather data for the snowfinch as those related with mean ambient temperature and mean precipitation gathered by the CHELSA database at a 30 arc sec-resolution (Karger et al., 2017). In particular, we estimated two different types of weather variables: (1) for each area, we estimated the mean temperature over the observation period (hereafter mean site temperature) and the mean precipitation over the observation period (hereafter mean site precipitation). Thus, we characterized each area by one mean site temperature and one mean site precipitation over the observation period; and (2) for each observation, we recorded the mean monthly temperature (hereafter mean temperature) and mean monthly precipitation (hereafter mean precipitation).

Statistical analysis

To quantify the dynamics of wintering associations, we fitted three generalized additive mixed models (GAMMs), treating the number of snowfinches within a group observed during winter as a Gamma and the internal knots (representing group fission and fusion) as two Normal distributed response variables. To account for both snowfinch fission-fusion and wintering group size varying with abiotic gradients, we included the linear effect of mean site temperature and mean site precipitation. These variables were standardized using a z-score transformation with a mean of 0 and a standard deviation of 1. To measure how fission-fusion dynamic and the size of groups are changing as a response to temporal varying weather conditions during the winter, we further included mean temperature, mean precipitation and year, as well as its interactions as smoothing variables using the default thin-plate regression spline in the GAMM4 package in R (Wood and Scheipl, 2014; Zuur et al., 2014). When adding the non-linear effects, we always checked the effective degrees of freedom (EDF) of the variables. Those variables showing an EDF < 2 were otherwise included as a linear effect (Zuur et al., 2014).

It is important to note that the different areas considered here vary in snowfinch population sizes, and therefore differences in population size could potentially influence the upper limits of flock size. However, as the observed maximum flock sizes were always well below the size of populations in each area, we consider that differences in this variable could not directly affect the results of this study. Yet, to account for any potential bias due to differences in the number of observations collected among years and areas, we included both the area ID and year ID as random factors. Doing so, we accounted at the same time for any other potential influential factor varying with site or year that could otherwise be overlooked. Yet, because of the structure of the data for fission-fusion group dynamic, area ID and year ID were estimated as zero. Thus, in these cases we proceeded with linear models without random effects.

Once we generated the sets of competing models, we employed the Akaike information criterion (AIC), using the values of $\Delta AIC < 2$ as the criterion for selecting the most parsimonious model (Burnham and Anderson, 2002). Following standard procedures, we calculated the Akaike weight for each candidate model *(wi)* as the relative strength of evidence, i.e. the probability of model *i* being the best-approximating model from the entire set of candidate models, and evidence ratios of the best models as the ratio of model weights. Models were finally evaluated by checking diagnostic plots. All analyses were performed using R 3.5.0 (R Core Team, 2018).

Results

Snowfinches show a marked seasonal pattern in group size (Supplementary Figure S5.1A). While fusion takes place at the beginning of July, i.e. around the mean (±SD) Julian day of 220.6 ±17.9 days (range = 181-268.8 days;

Supplementary Figure S5.1), fission occurs in April, i.e. around the mean (±SD) Julian day of 147.3 ±44.3 days (range = 46-217.5 days; Supplementary Figure S5.1). Overall, group fission-fusion dynamic tends to follow the abiotic gradient among the study sites, with group formation slightly occurring earlier at warmer sites with abundant precipitations (Supplementary Table S5.1) and group separation occurring later at warmer sites with low precipitations. During the winter, the mean size (±SD) of snowfinch group is 31 ± 34 individuals (range = 6 to 350 individuals), being the number of individuals within a group also related to the mean site temperature and mean site precipitation (Supplementary Table S5.1). At sites with lower temperatures, especially when associated with abundant precipitation, winter groups tend to be larger (Figure 5.1A).

Yet, weather covariates show that the different mountain regions here considered have experienced an uneven increase in temperature, especially outside the breeding season, while precipitation remained stable or declined (Figure 5.2). We observed that group separation occurs later when temperatures increased (Figure 5.1B; Supplementary Table S5.1), whereas group formation shifts earlier when the level of precipitations increased (Figure 5.1C; Supplementary Table S5.1). The resulting models provided an adequate description of the data, as evidenced by a moderate mean explanatory power (fission: adjusted R-squared = 49%; fusion: marginal R-squared = 22%). Further, when weather conditions result in higher temperatures, independently of the amount of precipitation, snowfinches form smaller groups (Figure 5.1D; Supplementary Table S5.1). Notably, beyond the observed influence of weather, the low mean explanatory power (adjusted R-squared = 4%) of the resulting model evidences that other factors not accounted here likely rule group size variation.

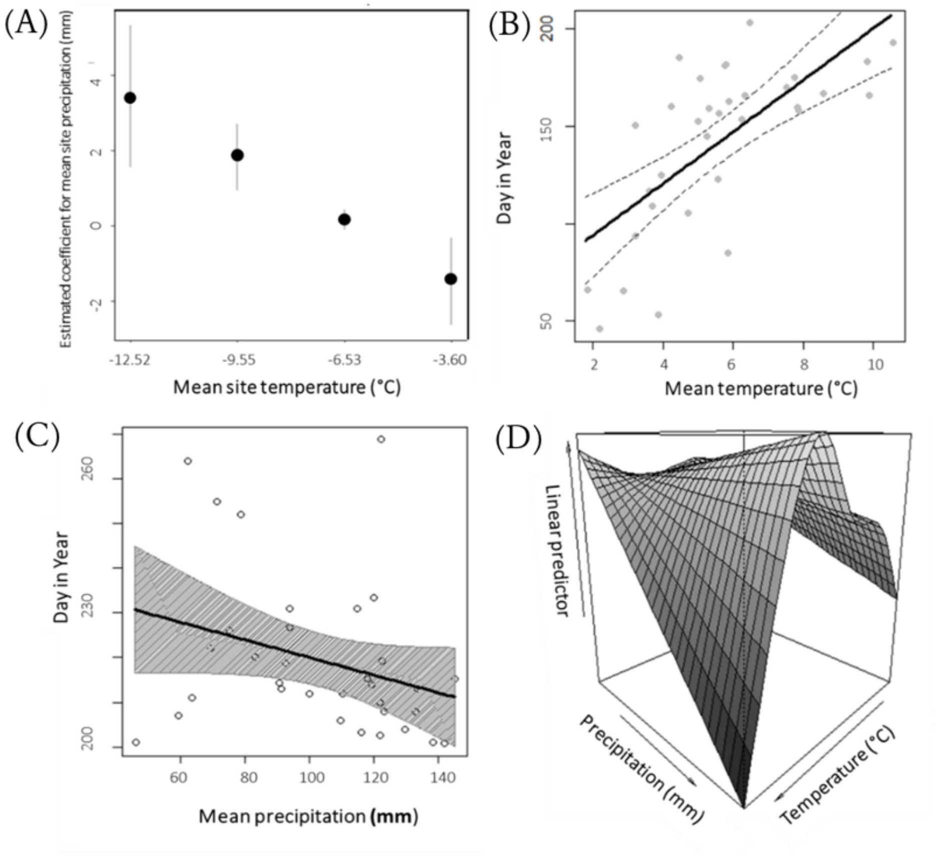
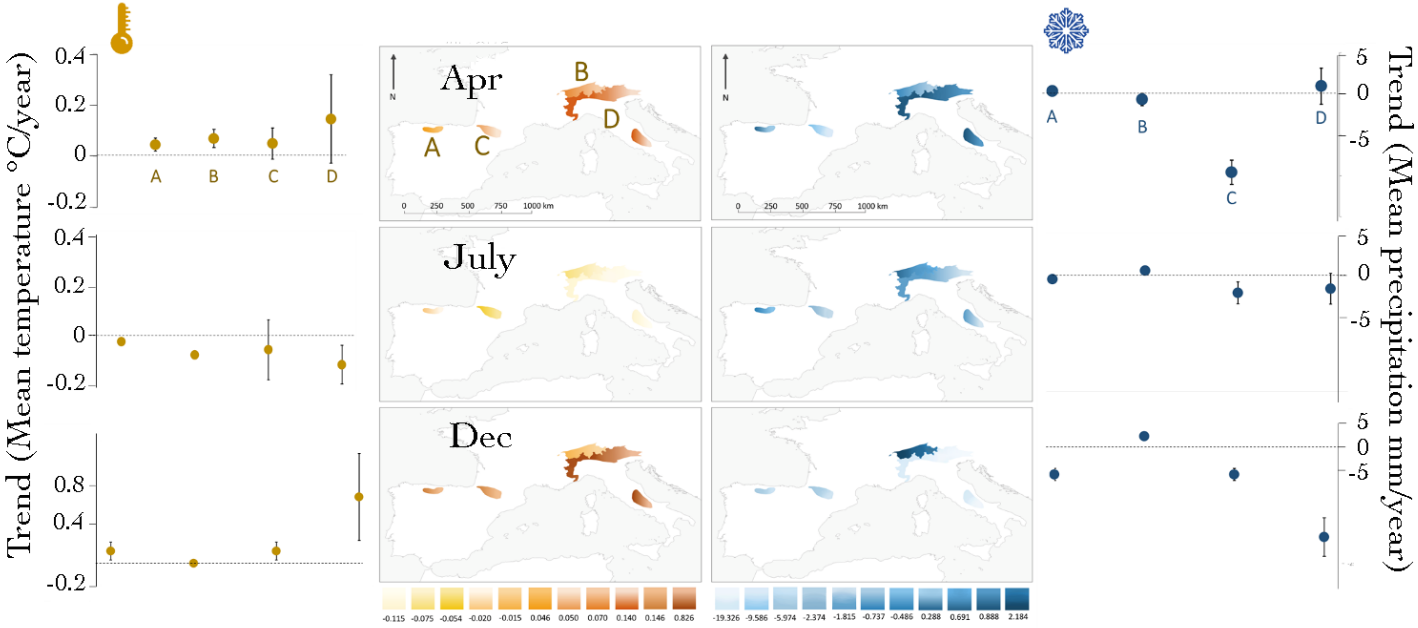


Figure 5.1. (A) Plot of marginal effects of the interaction between mean temperature and mean precipitation on wintering group size showing that at colder sites, especially when associated with high levels of precipitation, winter groups tend to be larger; Linear effect of temperature (B) and precipitation (C) on group fission and fusion dates, respectively. When average temperature increased and the average level of precipitation decreased, individuals stayed united in groups shorter time; (D) Group size and the interaction surface between mean temperature and mean precipitation from a generalized additive mixed model. Values on the y-axis represent the partial residuals of the tensor product (ti) smoother accounting for the influence of the other predictors in the model.

Figure 5.2. Site-specific trends in mean temperature and precipitation obtained by fitted linear models with year as a fixed effect at any of the locations considered (A: Cantabrian Mountains; B: Swiss Alps; C: Pyrenees; and D: Italian Alps) for the months of April (spring), July (summer) and December (winter). The overall mean site-specific coefficients are respectively the mean temperature and mean precipitation trends.



Discussion

Gregariousness is essential in allowing individuals to interact, transfer information and cope with changing environmental conditions (Teitelbaum et al., 2016). Here we found that individuals belonging to an alpine species gather in larger groups especially at sites where wintering conditions are harsher, i.e. under cold ambient temperature and high levels of precipitation. At these sites, individuals reunite later and separate earlier than at warmer sites. However, our results revealed that temporary changes in wintering associations (i.e. group size and fission-fusion dynamic) are affected by weather conditions. Specifically, we found that when temperatures are high and the level of precipitations is low, the size of wintering groups substantially decreased, with the group separation occurring later when temperature increased and the group formation shifting to earlier dates when the level of precipitation increased. Together, this sensitivity of flocking behaviour to climate variation across winter indicates that ongoing changes in climate, which are particularly affecting high-elevation ecosystems, will likely impact on the gregarious behaviour of alpine species.

Our results highlight that the variation in snowfinch group size and its fission-fusion dynamics substantially follow an environmental gradient, importantly confirming the basic expectation of a general pattern of variation in wintering associations along latitudinal or elevational gradients. The pattern that wintering associations tend to be larger at colder site with high levels of precipitations (typically higher latitude or elevation) is in accordance with the hypothesis that living in group might help individuals to locate prime feeding grounds (Dhanjal-Adams et al., 2018), which are unpredictable as well as patchily and heterogeneously distributed in alpine environments during the winter (Bettega et al., 2020). By maintaining long-term groups during the non-breeding period, the benefits of gregariousness may increase individual fitness and reduce the levels of stress (Dhanjal-Adams et al., 2018).

However, while part of the variation in wintering associations can be attributed to a simple environmental gradient, we observed that winter association responses to weather conditions are peculiarly varying within local regions. Certainly, variations in climatic events may depend on average temperature and mean levels of precipitations and change as well differently over time. Therefore, we could expect site-specific variation in wintering associations attributable to changes in average temperature and/or levels of precipitation. In areas where changes in climate have increased temperatures, resources probably occur broadly over larger areas, such that the costs of living in a group are not compensated by the benefits of cooperation (Delellis et al., 2014; Loretto et al., 2017). Moreover, as climates improves by the spring, winter-sport activities come to an end, and those snowfinch populations relying on food provided by humans in refugees and ski-areas likely split into smaller flocks searching for natural food sources at this time. This may further contribute to differences among sites in flocking phenology. Taken as whole, however, our results suggest that, as climate warming continues, large wintering associations could revert to smaller groups.

As the costs of living in a group are not compensated by the benefits of cooperation, individuals might coordinate decisions to fuse into a short-term group. Although increasing temperatures might positively influence food availability, temporary changes in group fission-fusion dynamics, such as when and why groups separate and reunite, could result in individuals having to re-establish their social relationships, thus taking time away from other tasks like foraging or breeding (Maldonado-Chaparro et al., 2018). These relationships are worthy exploring by future studies, to assess whether fission-fusion dynamics generated by e.g. varying climatic conditions might lead to group instability, ultimately disrupting the social organization of populations (Conradt and Roper, 2005).

Even though our data cannot directly measure breeding activity, we could expect that the latter may be linked with the observed delay in the timing of group separation. In a warming climate, mild winters and early springs are associated with unpredictable extreme weather events, resulting in unexpected cold temperature episodes later in spring (Penteriani et al., 2014). This is particularly common in alpine environments, which are among the most affected by climate change (IPCC, 2007). Staying together longer during winter might indeed represent an adaptive response of alpine bird species to cope with these extreme climatic events. However, snowfinches might need to adjust their breeding period to match the peak of particular food resources (Resano-Mayor et al., 2019). If the spring arrives early but wintering groups separate later, birds might be delayed in relation to the phenology of food resources (Both and Visser, 2005), consequently shortening their reproductive activity and/or lowering their breeding performance.

Variation in the duration of the reproductive season in birds as a response to climate change has been previously reported (Halupka and Halupka, 2017; Møller et al., 2010). Notably, elevational clines have generally received far less attention than latitude (Hille and Cooper, 2015), though alpine birds are declining more severely than other passerine birds – except farmland birds. Given the ongoing rapid environmental change, more studies disentangling the relative role of climatic factors in driving wintering associations and its effects on breeding activity of alpine birds could help understand how these species might maintain viable populations in changing environments.

Supplementary Material

Table S5.1. Model coefficients, AICc, ΔAICc, and weighted AICc values for group fission-fusion and size dynamic features against abiotic gradients and weather variables. Competing models showed are those with ΔAIC<2. Temperature is measured in °C and precipitation in mm.

Dependent variable	Competing models		AICc	ΔAICc	Weighted AICc
Group separation (fission)	**Mean site precipitation + Mean temperature**		309.19	0.00	0.48
	Explanatory variables	*β*	*SE*	*t-value*	*CI*
	Intercept	142.24	4.15	34.30	[133.77,150.71]
	Mean site precipitation	-23.55	5.75	-4.96	[-33.25,-13.84]
	Mean temperature	39.93	4.75	8.40	[30.23,49.63]
Group formation (fusion)	**Mean site temperature**		279.44	0.00	0.26
	Mean precipitation + **Mean site temperature**		280.64	1.20	0.14
	Mean site precipitation + **Mean site temperature**		281.17	1.73	0.11
	Explanatory variables	*β*	*SE*	*t-value*	*CI*
	Intercept	219.37	2.74	80.18	[213.10,224.97]
	Mean site precipitation	-0.73	5.97	0.12	[-11.48, 12.93]
	Mean site temperature	-9.01	5.91	-1.25	[-21.10, 3.08]
	Mean precipitation	-2.85	4.11	-0.69	[-11.27, 5.56]
Group size	**Mean site temperature*Mean site precipitation+t2(Mean temperature, Mean precipitation)**		11353.14	0.00	0.24
	Mean site temperature*Mean site precipitation +t2(Mean temperature, Mean precipitation)+year		11353.59	0.45	0.19
	Mean site temperature*Mean site precipitation +t2(Mean temperature, Mean precipitation)+s(Mean temperature)		11354.05	0.91	0.15
	Mean site temperature*Mean site precipitation +t2(Mean temperature, Mean precipitation)+year+s(Mean temperature)		11355.07	1.93	0.09
	Explanatory variables	*β*	*SE*	*t-value*	*CI*
	Intercept	3.59	0.07	49.68	[3.45, 3.73]
	Mean site precipitation	-0.28	0.13	-2.16	[-0.55, -0.03]
	Mean site temperature	-0.59	0.19	-3.07	[-0.97, -0.21]
	Mean site precipitation:Mean site temperature	-0.37	0.12	-3.13	[-0.60, -0.13]
		edf	*Ref.df*	*F*	*p-value*
	t2(Mean temperature, Mean precipitation)	9.17	9.17	3.24	0.0007

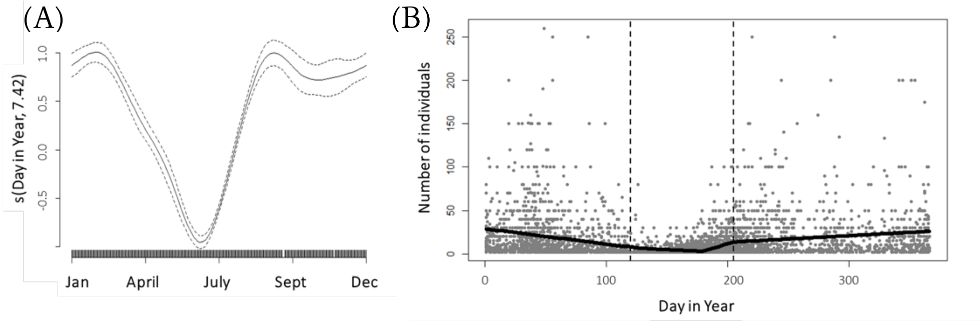
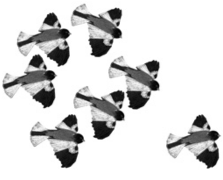


Figure S5.1. (A) Snowfinches show a marked fission–fusion dynamics across the annual cycle, resulting in a strong social seasonality. In particular, once the nestlings fledge, family groups gather in large flocks during the non-breeding season (i.e. from July to early April); (B) Representation of the internal knots estimated by fitting the model of the number of snowfinches within groups as a function of the smoothing factor for Day in Year (i.e. Julian dates).

Chapter VI

Patience is a virtue of the strong: what we have learnt in five years studying the most peripheral snowfinch population of Western Europe.



In Spring 2016, when we started to study the snowfinch population of Ubiñas-La Mesa and Babia in the western Cantabrian Mountains (Figure 6.1), what we knew about the species was essentially what you can find in any bird handbook. We also had a database of historical observations recorded in the Cantabrian Mountains, which proved to be essential throughout the development of our project. Based on those observations, we could outline our study area (Figure 6.1).

During that first breeding season, we walked a lot. And observed, but more often did not observed, a lot. The most important first step was to become familiar with the massif, find out the right places to capture the birds and collect preliminary information about the population. After that first season, we had identified our future breeding ringing sites and we made a first estimation of the size of the breeding population, based on the sightings we recorded over the summer. By then, we already understood that working with this species in this area would have been very important but physically challenging.

Five years later, leading towards the end of the project and having finished our last breeding field season, we can tell another part of the story, but surely – and fortunately - not put an end on it. This chapter falls outside the objectives of this doctoral thesis. However, a small part of the data used in the previous chapters comes from the hard work we carried out during the snowfinch project in the western Cantabrian Mountains. It was the first research project undertaken in the area focusing on this species, which meant we had to start from scratch and means, today, that we are still exploring the tip of the iceberg, and the results are still too scarce to be published. Therefore, we thought that devoting a chapter of this thesis to share some preliminary results, as well as some anecdotes and thoughts about what we achieved while working with this species, was mandatory .

Logistical challenges

The mountains of Ubiñas-La Mesa and Babia are located at the western boundaries of the Cantabrian Mountains (Northern Spain) and represent the western limit of the snowfinch distribution. Apart from the utilization of high altitude pastures for cattle and sheep, the area is not affected by the anthropogenic leisure activities common in the adjacent massif of Picos de Europa or, even more, in the Pyrenees or in the Alps. Ski pistes and resorts are absent there, and there is only a mountain hut located at 1560 m a.s.l.

This scenario gave us the unique opportunity to study a less human-habituated population. In fact, snowfinches in the Alps are known to nest also in artificial cavities such as ski-pilons, crags in buildings or even in nest-boxes (Cramp and Perrins, 1994), and they are regularly seen in the proximity of mountain huts or ski resorts, looking for anthropogenic food. However, the extraordinary privilege of working with such a wild population had its downside: no infrastructures for the snowfinches, no infrastructures for us. In the breeding season, with the exception of the site of La Mesa, reachable by car and a short 10-minutes walk, working with the snowfinch in this study area meant careful planning, a lot of walking with heavy loads and many cold hours with no shelters to rely on. In winter, we were lucky enough that the one site regularly visited by snowfinches during snowfalls was very close to a shepherds cabin.

Otherwise, it would have been impossible to do any field work during winter.

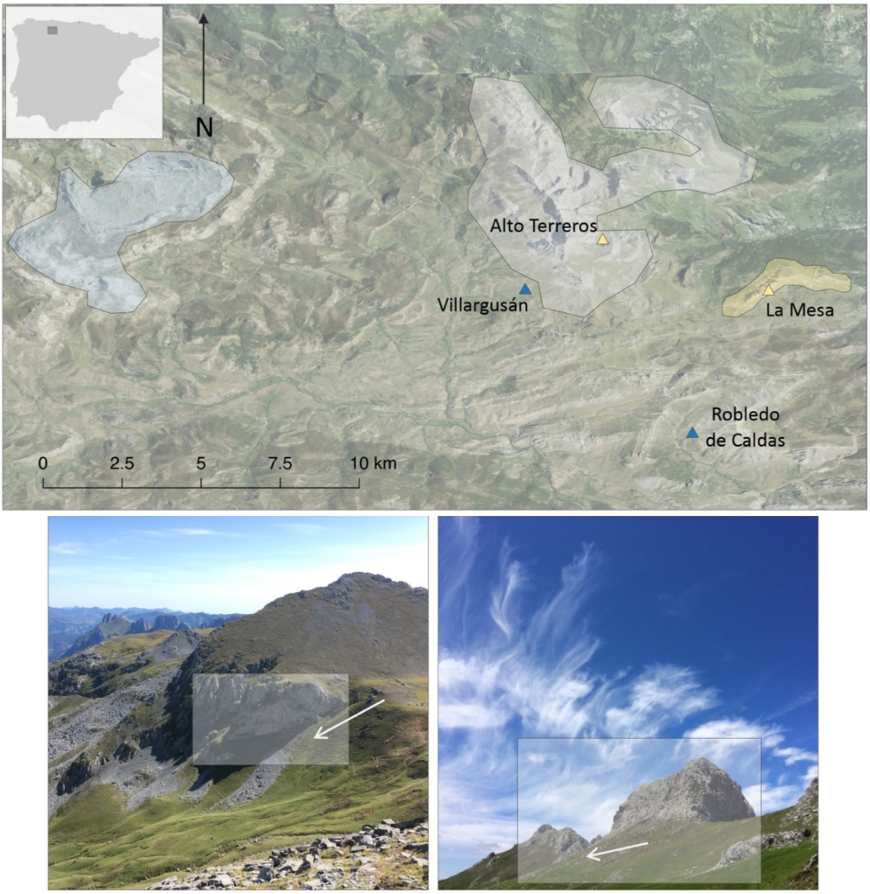


Figure 6.1. In the upper panel, the study area located in the massif of Las Ubiñas (light grey area), La Mesa (yellow area) and Babia (light blue area). Yellow and blue triangles show the sites where respectively the breeding and winter captures of snowfinches were carried out. The bottom pictures show the nesting sites of Alto Terreros (on the left) and La Mesa (on the right), with the capture site highlighted by the arrows.

Working with this species means also a good combination not only of knowledge and intuition, but also luck. It is a high mobile species and therefore its presence is not always predictable, even during the breeding season. For example, we happened to spend an entire morning close to a nesting cliff with almost no birds around, when few days before and later, at the same site we spotted three couples flying back and forth the rocky wall for hours. Therefore, it is often a matter of being at the right place at the right time, like the day we found what it would be our main ringing site during winter. We went to explore an area where snowfinches had been seen during winter in the past. We had been walking for a while under a light snowstorm, when we suddenly spotted a flock of 10-15 snowfinches foraging on some snowless patches. We were so lucky that at a hundred of meters away stood a cabin used by the shepherd during the summer (Figure 6.2). Then, we set up our winter field station there. During the following winters, we understood that during snowstorms: *(i)* snowfinches may forage in some particular areas, but not always (and still we do not fully understand when do they visit those places); *(ii)* when they are around those area, they seem to follow a quite regular pattern in time and space, but again, sometimes they do not, and *(iii)* most of the time they come in flock ranging from 15 to 50 individuals, but sometimes you see only 1 or 2 individuals around. Therefore, you really need to be at the right place at the right time, and being right does not depend on you.

Breeding and non-breeding field seasons

We carried out the breeding ringing season at two sites in the study area (Figure 6.1): the first on the southern slope of La Mesa (1750 m a.s.l.) and the second on the north-west slope of Alto Terreros (Ubiñas, 1850 m a.s.l.). Both sites were located in the foraging area of breeding individuals, but only the site of Alto Terreros was adjacent to the nesting wall, so that we could actually follow the birds in their foraging activity and we could locate at least two active nests. From the beginning of May to the end of July, capturing sessions were carried out at both sites at least once a week, avoiding days with heavy rains. Sessions started at dawn and usually ended around midday. Birds were captured by means of mist nets during the first year, while in the following seasons we also used clap nets manually triggered, but only at the site of La Mesa, since the slope of Alto Terreros was too steep for this type of nets.

Together with the ringing activity, we also carried out yearly census during the breeding season, covering not only the area of Ubiñas-La Mesa, but also the neighbours mountains of Babia. We tried to cover as much as possible all the potential favourable habitat in the area (which lies above 1800 m a.s.l. during the breeding season), by means of altitudinal point transects. Transect lengths averaged 1.8 km, with approaching distances of ~9.6 km (thus a mean walking distance of 11.4 km per transect).

Captures during winter took place mainly at a location near the village of Robledo de Caldas, 6 km south from La Mesa, at 1425 m a.s.l. (Figure 6.1 and 6.2). We also performed some captures at a location near the village of Villargusán, situated near the area of Ubiñas at 1520 m a.s.l. In winter birds are not strictly bounded to a site as during the breeding season, and therefore their movements are more unpredictable. Moreover, under favorable weather conditions, snowfinches remain high in inaccessible cliffs (especially in winter, when most mountain passes are closed), descending to lower pastures only during snowfalls. Therefore, the beginning and duration of the winter ringing season were not fixed, nor the field work days were constant, but limited to snowy days. Sessions started after dawn, usually ending in the afternoon. Birds were captured with white mist nets, using a recorded call to attract the flocks, and ringed inside the cabin located nearby.

Figure 6.2. The winter ringing site. The picture on the left shows the area where the nets were set up. On the right, the cabin used to ring the birds.

Ringing data, population estimates and survey methods

Overall, we ringed 111 snowfinches during the 4-years project, of which 92 during the breeding season and 19 in winter. With respect to the breeding season, 62 were adults and 30 juveniles. We installed 49 GPS. Out of these, we could recapture the ca. 47% of the GPSs. However, as some birds lost them and few devices did not properly work, we could only get information from five individuals in two years.

We believe that this figure is the result of an intense and systematic capturing effort throughout the breeding season. Moreover, the methods used to capture – and specially to recapture – the birds needed to be constantly monitored and adapted, since snowfinches learn quickly how to avoid any kind of net. Above all, great patience is required. Although the daily number of captures seemed small, at the end of the season they were enough decent, and when taken together they motivate us to do not give up.

We could also draw some considerations from the attempts of estimate the breeding population size through yearly census. During the first year of census, we applied the standard method of point counts, i.e. points separated ~300 m one from the other and always above 1800 m, and in each point any bird detected within a 100 m buffer around the point in 10 minutes was recorded. This method proved to be inadequate for snowfinches census. First of all, most of the times it is difficult to adequately select the points, given the difference in height and the fact that paths are constrained due to the roughness of the terrain. Moreover, the high mobility of the species might lead to double counting of the same individuals or to erroneously consider the species absent. For these reasons, in the following seasons we simply walked through the whole study area, stopping at the most suitable sites (both in terms of nesting and foraging) for at least 30 minutes and, even though we recorded the number of individuals, we considered the survey as a proxy of the population size.

Therefore, we think that in order to estimate the size of the snowfinches populations the best method is to monitor as many breeding sites as possible, and trying to mark as many individuals as possible. Sightings recorded just after the breeding season (August and September), when snowfinches families gather together in bigger flocks and move to higher elevations, might be a useful add-on to the estimation of the size of breeding populations. Long-term monitoring schemes combined with capture-recapture methods are essential, and require not only appropriate funding, but also – or especially – great physical effort and motivation. Yet, the reward may be more than greater.

Back to our population, we started our project estimating a breeding population of 200) individuals in the Ubiñas-La Mesa massif. After four breeding seasons, combining both ringing activity and surveys, and with bigger knowledge of the species and the territory, the estimation changed dramatically to 50-60 individuals (including both adults and juveniles), which also corresponds to the size of the biggest group that we recorded every year in August. Intriguingly, the size of the group sighted at the same time of the year and in the same area, but 20 years ago, was of 120 individuals, three times bigger than today (García et al., 2007). Another example of a deep change in population size comes from the north slope of Tapinón, a peak in the Ubiñas massif. The site is a massive rocky wall, historically considered a colony of snowfinches. In 1999, for example, at least 15 pairs were spotted entering the wall crevices to feed the nestlings (García, 2006). Instead, during each year of our monitoring we could only observe one breeding pair. We lack of a regular monitoring of the population during the last decades, but this numbers could reflect that the population size has decreased considerably. Thus, continuing with what we started in this project is crucial for understanding the dynamic and trends of our population.

From what we have seen until now, the difficulties of collecting data have been great and we could not build a doctoral thesis with the information gathered in those years. For this reason, the development of this thesis has been possible thanks to a historical dataset of observations not only of the Cantabrian Mountains but also of other mountain areas of Europe *(Chapters III and V)*, to the collaboration with the European Snowfinch Group *(Chapters II and IV)* and to a literature review *(Chapter I)*.

Interesting data from the field work

Both breeding and non-breeding biology and behaviour of the snowfinch are still poorly known. Information about natal dispersal are absent, and data about winter movements - derived from ringing records - are scarce. Moreover, the knowledge of their social system is limited to the gathering of family groups in bigger flocks after the breeding season. Under this perspective, we think that the small collection of data that follow may represent an interesting source of information, that of course does not solve any puzzle. Instead, it leaves many open questions that will surely stimulate future studies.

Breeding season

In 2018 we ringed a male at the breeding site of La Mesa. Two days later we recaptured him at the breeding site of Alto Terreros, almost 6 km away (Figure 6.1). Considering that the foraging area of breeding adults during nestling rearing usually falls within 100-200 m from the nest (only occasionally 300 m or more, Strinella, 2007), it seems unlikely that the bird would be nesting in one of the two sites and foraging in the other. This finding opened interesting questions as, for example, *is the bird nesting in both places (i.e. male snowfinches may be polygamous)?*, *is the bird a floater?* or *is the bird a helper (provided that this social structure would be present in snowfinches)?*

In 2017 we ringed a female as a juvenile at the nesting site of La Mesa and she was recaptured in the following breeding season at the other nesting site of Alto Terreros. We could not confirm whether she was breeding or not. Moreover, the age at which snowfinches reach the sexual maturity is unknown. The sister species white-rumped snowfinch *Onychostruthus takzanowskii* can breed at the second year after hatching (Lu et al., 2013). If that would be the case for snowfinches too, the role of this female in the nesting area of Alto Terreros is more uncertain. In fact, after that second season, we never recaptured or sighted her again. Of course, she could have died during the winter. But she could also have been a floater. (i.e. a prospector visiting the area to gather public information (i.e. information derived from the breeding performances of conspecifics) about potential breeding sites (Pärt and Doligez, 2003) or a helper.

Non-breeding season

During the winter 2017/2018 we captured 11 birds, 9 of which were females and 2 were males. In the following winter (2018/2019) we captured 5 birds, all of them being females. Very interestingly, we never recaptured during the winter any of the individuals ringed during the breeding season, neither found a bird ringed during the winter breeding in our study area. Data are still too scarce to draw any conclusion, yet they might suggest the existence of some nomadic movements with individuals segregated in winter flocks, i.e. adult females separating from adult males and moving together with young individuals (see also section 6.5).

First data on movements

We fitted adult individuals captured during the breeding season with dataloggers, set to record a localization every 10 days over an entire year, in order to track snowfinches movements during their full annual cycle. Due to the size of the birds (weight ~ 40 g), we could not use GPS tracking systems, a technology not yet developed for small species. Dataloggers must be retrieved in order to download the data. For us, that was probably one of the trickiest parts of the job (see section 6.3). Still, we could retrieve information from five dataloggers. In 2019 we retrieved 3 dataloggers from male birds (Figure 6.3 A-C), while in 2020 we recaptured the first female (Figure 6.3 E), as well as another male (Figure 6.3 C-D).

Although they bred in two different sites, from the beginning of August until the first snow storm they all used the same areas, visiting the highest peaks of the massif. The four males were quite sedentary, only making altitudinal movements during snow storms. Interestingly, the two males which shared the same breeding site (M0C and M38 in Figure 6.3) used also the same wintering area, while the other male (M30) used a different one. Considering that snowfinches usually move in groups during winter, it could be possible that M0C and M38 moved together.

The female bred in the same nesting site of male M30. However, she overwintered in a completely different area, moving easterly ~ 25-35 km and coming back to the same breeding area at the end of February. We need to collect movement data from more females, in order to understand if this is a clear pattern in our population. It is in fact intriguing that *(i)* most of the individuals ringed during winter are females, *(ii)* we never recaptured any female of the breeding season during winter and *(iii)* female M33 moved a further distance than males during the winter. We still don’t know the composition and dynamics of winter flocks. However, the data we collected through the dataloggers, together with data from ringing activity, not only bolster the hypothesis that there might be some kind of sex and/or age segregation in winter flocks, but also could suggest a higher mobility in females than in males.

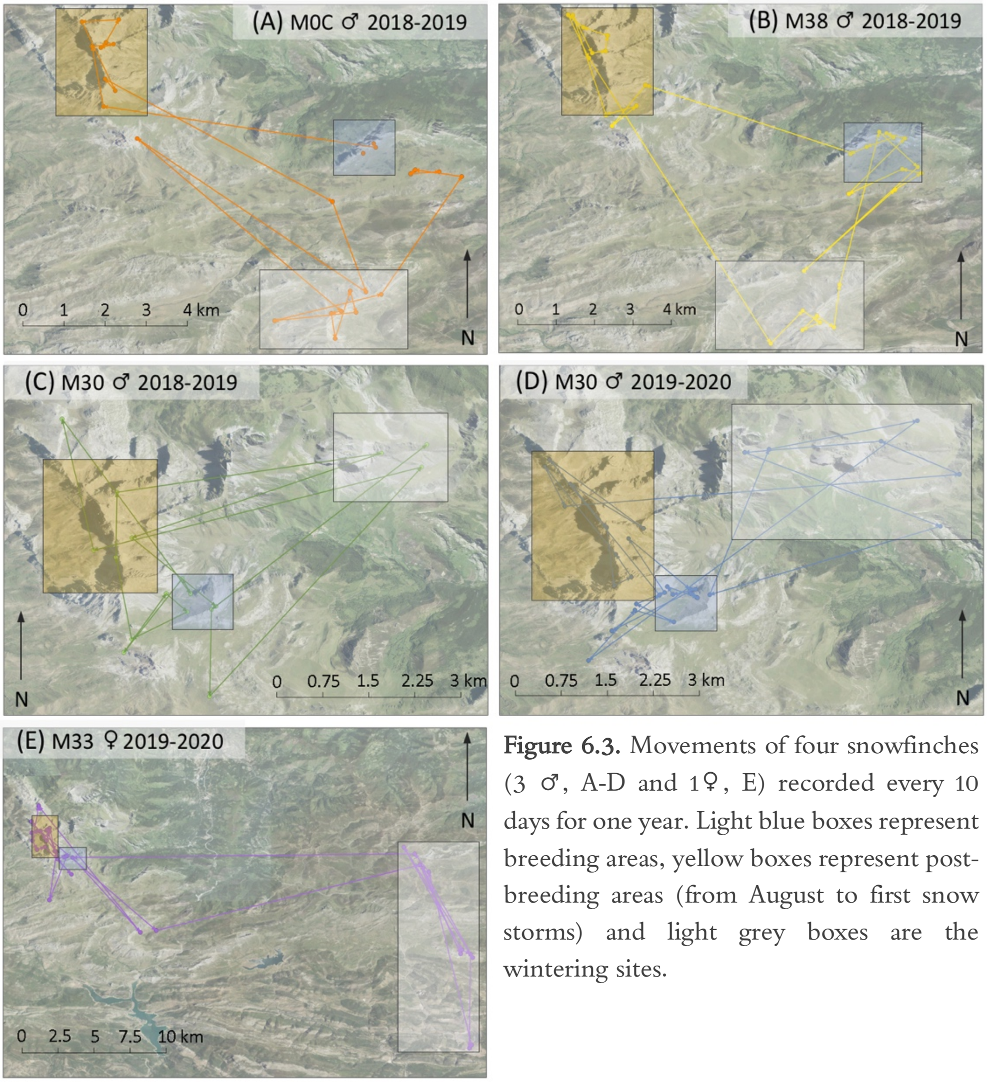


Figure 6.3. Movements of four snowfinches (3 ♂, A-D and 1♀, E) recorded every 10 days for one year. Light blue boxes represent breeding areas, yellow boxes represent post-breeding areas (from August to first snow storms) and light grey boxes are the wintering sites.

What mountains have taught me, in the end

When I started to write this thesis, I thought that we were bringing novel insights into the ecology of the snowfinch. At the present time, having reached almost the end of the writing process, I guess I should go further and say that it brings more questions than answers: *what are the driving factors of partial migration strategies?, what is the degree of connectivity among the different European populations?, how is the species responding to a changing environment?, do more or less human-habituated populations differ in their behaviour?,* just to list a few. I go through our results and I keep finding pieces and possible connections, like a Rubik's cube that needs to be turned again and again. With this thesis we have certainly opened the Pandora's box for a bulk of future research, of which not only the snowfinch itself but mountain biodiversity in general, will benefit.

To me, beyond the relevance of *what* we obtained through our study and the resulting future inspirations that it brings, it lies the importance of *how* we could do it, which is the way science – and not only science – should be always done. That is, through networking and collaboration, through sharing data as much as ideas, knowledges and experiences. This becomes even more valuable when you work with such a challenging species in such a challenging environment. As much as we try to understand the connections in our study systems we should connect ourselves as scientists. Either way there will be benefits.

Last but not least, being able to communicate *why* we do what we do is key determinant of good science and conservation activity, and it certainly helps when it comes to fundraising our research. In the case of the snowfinch and high-elevation species in general, it might be a tricky job, since first of all, people need to know that *there are species*, up there. They need to see them, and while spotting a chamois or a marmot may be easy and exciting, it is harder to notice the astonishing diversity of the smallest. And once we have trained people to see this diversity in a place they would not expect it, they need to know why it matters. Like in a feedback loop, the more we do our research, the more we can explain people why, so that the more they will rely on what we do and ultimately, the more we will be able to keep doing what we do.

General Discussion

In this doctoral thesis we explored some crucial aspects of the ecology of a high-elevation bird species, the snowfinch. By studying its current vs. potential distribution in Europe *(Chapter II)*, its pattern of habitat use at multiple scales *(Chapter III)*, the migration strategies and group dynamics and their relationship with climate *(Chapter IV and V respectively)*, this thesis brings novel insights, which may help implementing the EBVs framework to monitor and manage mountain biodiversity. The effects of global change on biodiversity are manifold and species' responses are not always linear. In that sense, the complexity of mountain ecosystems adds further obstacles for disentangling the cause-effect-response relationships. Consequently, there are many gaps in our understanding not only of the capacity of response and the viability of the responses of mountain species, but also of basic ecology and biology of many high-elevation organisms, which hamper monitoring strategies themselves.

Traditionally, because of logistical constraints, research has focused on common species, being *common* in relation to the abundance of the species in the community (Lyons et al., 2005). However, commonness and rarity are multifaceted concepts that can be viewed under a functional perspective (Violle et al., 2017). In *Chapter I* we showed that species uniqueness in terms of both vital rates and morphological traits is independent on the geographic distribution of mountain species and that it increases with elevation, i.e. species living at higher elevations have more peculiar traits. Bird assemblages above the treeline are indeed different from those below it, and despite having lower species richness, they show a high degree of specialization in their adaptations (Altamirano et al., 2020). However, an important point emerging from our study is that we do not know to what extent the uniqueness of high-elevation species may contribute to the functioning of the ecosystem. Are unique traits simply the result of adaptations to a life in extreme environments, or do they play a specific role for the ecosystem? And if so, how essential would that role be? The disproportionate effect of rare species on ecosystem processes is increasingly reported for a variety of systems (Bracken and Low, 2012; Mouillot et al., 2013). But with respect to mountain habitats, we completely lack of information in this sense and we could only make speculations, rather than conclusions.

Indeed, morphological distinctiveness might also relate to a stronger propension to move in response to a highly seasonal environment (Sheard et al., 2020). As we could see in *Chapter III*, habitat specialization of high-elevation organisms can extend beyond the breeding season, and the need to find suitable foraging areas while remaining in harsh environments throughout the year may condition the decisions that individuals take with respect to its movement strategies and its social behaviour during winter *(Chapter IV and V)*.

One of the most interesting finding of this doctoral thesis is perhaps the partial migratory strategy that the snowfinch seems to adopt *(Chapter IV)*, especially considering that the species had traditionally been considered resident. This observed movement of snowfinches between the Alps and the Spanish mountain ranges have potentially important consequences for the genetic diversity of populations. Gene flow stemming from connected populations reduces genetic differentiation between them and, at the same time, increases the genetic diversity within a given population, preventing genetic drift (Cayuela et al., 2018) and enhancing population persistence. Gene flow generally hinders local adaptation (Morjan and Rieseberg, 2004); yet, if individuals do not move (and mate) randomly, but actively select the habitat that matches their phenotypes (Clobert et al., 2009), the effect of gene flow might instead facilitate local adaptation and positively affect the ability to adapt to new environments (Jacob et al., 2017). This could have important implications for the resilience and persistence of species living in mountain ecosystems, considering the alteration and loss of habitats and the effects of climate change affecting these areas.

Understanding the magnitude and randomness of these movements is of particular concern for the more isolated populations. In southern European mountains, the availability of potentially suitable areas is more restricted and fragmented, and populations living in these ranges are likely more isolated *(Chapter II)*. The population of the Cantabrian Mountains that we are currently studying *(Chapter VI)*, could represent a surrogate of other isolated populations (Caro et al., 2005), for example the Balkans', that are still poorly monitored *(Chapter II)*. Given its position at the westernmost limit, the population of the Cantabrian Mountains can only receive incoming flows from the East. The population is also probably experiencing a size contraction, especially in its western sector *(Chapter VI)*. As we have seen, in winter this population seems to be composed of individuals coming from the Alpine breeding population mixing with individuals having another breeding origin *(Chapter IV)*, most probably local, as suggested by the preliminary results of our project *(Chapter VI)*. The simultaneous presence of a specific and predominant haplotype in the population of the Cantabrian Mountains, together with the most common haplotypes (Resano-Mayor et al., 2017), is an indicator of a potential asymmetrical gene flow. A source-sink dynamic might be occurring (Hauser et al., 2019), with the populations of the Alps and the Cantabrian Mountains acting as source and sink, respectively. Source-sink dynamics are common in heterogeneous landscapes, where variations in habitat quality and structure, as well as in population conditions and conspecific densities within patches, exist (Pulliam, 1988; Dias, 1996). Increasing environmental heterogeneity and habitat fragmentation caused by anthropogenic changes makes source-sink systems even more relevant for species conservation and management (Heinrichs et al., 2019). Sources (i.e. populations with positive growth rate) provide propagules to sinks (i.e. populations with negative growth rate), preventing them from local extinction (Hauser et al. 2019). In addition, source-sinks are often considered as a particular case of metapopulation, where sinks might also contribute to the stability of the system with both negative and positive effects (Howe et al., 1991). High emigration rates from sources to sinks might drive source populations to negative growth (Gundersen et al., 2001). Conversely, if an opposite flux of individuals from sinks to sources also exists (Foppen et al., 2000), and possible environmental perturbations are spatially asynchronous, sink populations can promote larger metapopulations size. Our results are a starting point for future investigations, since we have just identified the existence of a flux of individuals among populations. The large differences in survival rates apparently found between Alpine and Mediterranean snowfinch populations (Strinella et al. 2020) concur to suggest a possible source-sink structure of snowfinch populations. In fact, the correct identification of source-sink systems requires long time series data about survival, reproduction and, importantly, emigration and immigration through natal or breeding dispersal (Heinrichs et al., 2019).

Another interesting finding of this thesis is the role that weather plays – or might play – in shaping snowfinches' movement and social behaviours. Like other cold-adapted species, snowfinches are well adapted to winter harsh and unpredictable climates, so that low temperatures and abundant precipitations should not represent a constrain in terms of physiology and physical tolerance (although specific studies in the species have not been undertaken yet). During winter they actually take advantage of strong winds to save energy in flight, and they sleep in rock crevices that can be placed up to 3000 m, where interior temperature and humidity conditions are far better than outside (Heiniger, 1991b). In *Chapter III*, although we did not specifically consider climatic variables in our analysis, we confirmed the dependence of snowfinches on high-altitude habitats throughout the year. Yet, they also show a higher plasticity during winter, probably determined by a more generalist diet compared to that of the breeding season. In fact, snowfinches rely almost entirely on invertebrates while rearing chicks and their foraging microhabitat selection is intimately linked to the snow melting process, which affects vegetation phenology and creates diverse prey-habitat associations (Resano-Mayor et al., 2019). Conversely, during winter snowfinches are less constrained by diet and the extreme unpredictability of the environment makes them less dependent on a specific habitat. Indeed, under unfavourable weather conditions they move in flocks to lower elevations – although rarely below 1000-1500 m a.s.l. – to look for resources in an erratic manner. Thus, unlike long-distance latitudinal migrants that spend the winter at milder climates, snowfinches winter movements might be essentially prompted by tracking food availability. Other cold-adapted species, e.g. snow buntings *Pletrophenax nivalis*, spend the winter in highly stochastic and cold weather conditions, moving in a nomadic manner that allows utilization of suitable foraging patches (Snell et al., 2018). This species can also adopt flexible migration strategies driven by weather, where cold tolerance and food abundance determine a different spatial arrangement between sexes and, in general, between larger *vs.* smaller individuals (Macdonald et al., 2016; Mckinnon et al., 2019) The migration patterns we found in snowfinches *(Chapter IV)* and the preliminary results of our research project showed in *Chapter VI* give us a hint that similar dynamics might occur in our study species, with possible differential migration by sex and age. If that would be the case, different groups of individuals might experience different environmental conditions, risks and energy expenditures, with carry-over effects on body condition, reproductive success and survival, with ultimate effects on population dynamics and resilience (Briedis and Bauer, 2018). Survival is indeed lower in snowfinch females than males (Strinella et al., 2020; a similar pattern was also found in alpine cough *Pyrrhocorax graculus*, see Chiffard et al., 2019), and one possible explanation is food availability and accessibility in winter which may affect inter-individual competition in flocks. Therefore, females might be forced to migrate, experiencing higher energetic loss and higher predation risks (Chapman et al., 2011).

Although in *Chapter IV* we could only describe a possible link between partial migration and weather conditions, we have hypothesized that climate change might reduce migratory propensity. This could happen through the alteration of social dynamics in wintering flocks. In fact, we found that weather conditions seem to deeply interact with both the timing and the magnitude of snowfinches' gregarious behaviour *(Chapter V)* and we identified a trend caused by a changing climate. Snowfinches seem to respond to warmer conditions through shifts in social dynamics phenology and flock size, i.e. smaller and more ephemeral flocks. This could diminish social hierarchies and thus lower the differential pressure that might be the trigger of seasonal movements.

One of the most ubiquitous response to climate change is phenological adaptation, i.e. adjusting the timing of life cycle events, with individuals responding through a shift in time trying to keep synchrony with cyclical abiotic factors (Bellard et al., 2012). Yet, phenological changes can be disruptive, when species interactions are involved. Indeed, species differ in their physiological tolerance, life-history strategies and dispersal abilities, determining a high variability of responses to climate change. Therefore, the variation in phenological response between interacting species may jeopardize synchrony in predator-prey and insect-plant systems (Parmesan, 2006). The phenological adjustment that snowfinches seem to undertake in response to a warming climate *(Chapter V)* might be an attempt to match delayed phenology of alpine plants. In fact, although springs are shifting earlier in mountains, warmer winters disrupt the dormancy-breaking process of some plants, causing the delaying of spring phases (Yu et al., 2010). Increasing frequency of extreme events such as spring snowstorm might further delay plants phenology (Dorji et al., 2020). This in turn may affect the peak of insects availability. It would therefore seem that splitting up flocks later, and thus breeding later, could benefit snowfinches. Yet, the effect might be opposite as well. In fact, because breeding snowfinches are highly specialized for a specific microhabitat where the presence of snow patches, low sward height and soil moisture is essential (*Chapter III* and Resano-Mayor et al., 2019), the peak of resources availability might not match that of their accessibility. Because of a short peak of food availability, birds breeding at high elevation generally show a higher investment in offspring quality, through the production of small clutches and a low re-nest potential (Hille and Cooper, 2015). If snowfinches fail to synchronise with prey abundance and accessibility, later breeding could result in decreased reproductive success and recruitment rate, with detrimental effects on the persistence of smaller populations.

* * *

When we started to work with the snowfinch in western Cantabrian Mountains, we soon realized that a doctoral thesis would be an utopia and we actually did not think of it at all. Data were hard to collect and we had to face with the ineluctability of intrinsic slow progress when starting a research project from zero. However, going slow does not mean going nowhere. After a couple of years we still had not enough data to build a thesis, but through the collaboration with our European colleagues we could contribute with our information and start producing some results. These results prompted who will then be my PhD supervisor to a still risky, challenging proposal, to which I gave an equally risky answer. That is how the adventure started and this thesis is the result of how far we could go.

I believe that this thesis represents an advancement in our understanding of the ecology of the snowfinch, which can help implementing future monitoring plans and conservation strategies. We demonstrated that the status of the species is far from being well-defined, and its strict dependence on mountain habitats makes it potentially at risk. Climate change and anthropogenic activities are increasing the fragmentation of high-elevation habitats, and species inhabiting them need to either adapt or disperse. One of the most striking findings was that the snowfinch is capable of latitudinal movements that connect fragmented populations and that could potentially represent the salvation for the more isolated ones. This high mobility that does not involve only altitudinal movements might also help snowfinches to find new suitable areas. On the other hand, we discovered that climate change is acting on phenological responses of the species through changes in their social behaviour that could have not only consequences on their breeding performances, but affect their movement strategies as well. Mountains are indeed complex systems. The snowfinch as a species seems to reflect such a complexity, although this perception might depend on the fact that the dark side of its ecology is still bigger than the bright one.

In order to understand the impact of global change on mountain biodiversity, we need to consider different levels of organization, from individuals to populations and communities, with a multidisciplinary approach. Emerging tools like the EBVs framework can help in that sense. In my opinion, with our results we have offered an important starting point for future research aimed at better understanding population connectivity and dynamics, identifying more isolated populations and deepening the knowledge about the species' responses to climate change and habitat reduction.

Conclusions

1. Functional uniqueness is independent from the geographical distribution of mountain species, but linked to the pool of species of each community. Moreover, for both morphological and vital rate traits it increases along the elevational gradient, following increasing specialization in high-elevation taxa adaptations.
2. The role of species with unique traits and their potential contribution to the functioning and processes of mountain ecosystems are unknown. This in turn hinders our understanding of the effects of their possible disappearance as a consequence of global change and calls for future research.
3. Climatic and topographic parameters are of primary importance in determining environmental suitability and hence distribution in snowfinches. As expected, suitability increases with natural grassland cover and sparsed vegetated areas, as well as with bare rock.
4. There are important discrepancies between the current distribution of the species estimated by BirdLife International and the breeding range classified as potentially suitable by our model. Differences are particularly evident in Eastern Europe, where the species is poorly monitored and for Southern populations that are likely more isolated and fragmented and therefore at major risk because of global warming.
5. Snowfinches use high-elevation habitats throughout the year, probably as a consequence of physiological and morphological specializations typical of high-elevation species. Nevertheless, they

seem to be more flexible during the winter, perhaps because of a combination of a more diverse diet and the need to cope with unpredictable environments.

6. The use of habitat is more constrained by the spatial scale during the breeding period than during the non-breeding season, possibly because birds are more constrained by nest-site selection and specific foraging sites to provide food for nestlings.
7. Snowfinches adopt a partial migratory strategy, with different patterns among and within populations: the majority of the birds captured in winter in the Alps belonged to the alpine breeding populations, and the 98% and the 86% of the birds wintering in the Spanish Pyrenees and the Cantabrian Mountains respectively, had a high probability of belonging to the alpine breeding population.
8. The movements of individuals between the Alps and the Iberian massifs may be important for the overall genetic structure of west European metapopulations. In particular, they could prevent the potential negative impacts of a demo-genetic isolation due to habitat loss, which might especially concern small and more isolated populations like the one of the Cantabrian Mountains.
9. The migratory propensity of snowfinches was higher in winters with low average monthly temperature in the Alps. This suggests that climate may play a role in partial migratory movements of snowfinches from the Alps. Under a scenario of global warming, migratory propensity could be disrupted, with consequences for population connectivity, spatio-temporal dynamics and structuring.

10. Winter climate is an important factor influencing gregarious behaviour in snowfinches. As a general pattern, individuals gather in larger groups especially at sites with harsh wintering conditions, and generally reunite later and separate earlier than at warmer sites.
11. The extent and phenology of wintering associations are ruled by changes in weather conditions during the winter, i.e. when temperature increases or the levels of precipitations decreases, the size of snowfinch wintering associations substantially decreases, and individuals stay united in groups for shorter time.
12. Since climate warming is especially affecting mountain environments, there could be consequences on the snowfinches' group dynamics which might lead to group instability, disruption of social organization and mismatches between breeding phenology and the peaks of resource availability and abundance.

Resumen

La biodiversidad, definida como la diversidad taxonómica, genética y ecológica medida a todas las escalas espaciales y temporales, está íntimamente conectada al funcionamiento del ecosistema, y por tanto también con el bienestar humano. Tradicionalmente, la biodiversidad se ha medido a través de la riqueza de especies que ocurren en un lugar en un determinado momento. Sin embargo, se trata de una medida que puede llevar a resultados muy diferentes en función de la escala espacial que se considere. Por esta razón, en los últimos años se ha comenzado a medir la biodiversidad teniendo en cuenta *(i)* la función de cada especie en el ecosistema (rasgos funcionales), y *(ii)* cuántos y cuáles de estos rasgos funcionales son necesarios para mantener el funcionamiento del ecosistema (diversidad funcional).

Medir la biodiversidad de la manera más precisa posible es necesario y urgente, dado que una multitud de cambios están ocurriendo a una velocidad preocupante como consecuencia de la sobreexplotación, la contaminación, la invasión de especies, la fragmentación y alteración del hábitat y el cambio climático. Las respuestas de las especies no son siempre lineares o instantáneas, como tampoco son similares en todas las escalas espaciales. Debido a la complejidad intrínseca de la biodiversidad, a menudo los cambios se detectan cuando las respuestas efectivas no son viables y los daños a los ecosistemas irreversibles. Es entonces necesario identificar las señales precoces de alarma, para lo que se propuso en 2013 el concepto de "variables esenciales de la biodiversidad" (EBVs), como herramienta para identificar los componentes clave constituyentes del cambio de biodiversidad. Las EBVs están organizadas en cinco clases:

composición genética, poblaciones, rasgos, composición de las comunidades y estructura y función del ecosistema, siendo la propuesta original monitorizar al menos una de ellas por cada categoría. De esa forma, las EBVs pueden verse como un marco conceptual para organizar datos complejos de biodiversidad de diversos ecosistemas y especies en diferentes partes del mundo en un conjunto limitado de variables biológicas para documentar el cambio de biodiversidad. En esta tesis doctoral se investigan algunas de estas variables (distribución de las especies, rasgos morfológicos y reproductores, movimiento y diversidad taxonómica), abarcando diferentes niveles de organización de la biodiversidad y del ecosistema. Para ello, consideramos uno de los hábitats más ricos en términos de biodiversidad y más amenazados por el cambio global, las montañas.

Las montañas son ecosistemas cuya complejidad y heterogeneidad dependen de una amplia combinación de factores. En primer lugar, los eventos geológicos originan una topografía variada y dinámica. Por otro lado, los procesos orogénicos determinan la heterogeneidad edáfica, y por ultimo elevación, orientación y topografía dan lugar a climas peculiares caracterizados por una alta estacionalidad y marcada variacionón diarias. Debido a estas características, las montañas pueden actuar como cunas, barreras, puentes o refugios para las especies, además de influir en la biodiversidad a escala continental.

La modificación antropogénica de los hábitats de montaña y el cambio climático están amenazando seriamente estos ecosistemas. Las especies que los habitan están respondiendo a través de cambios fenológicos o migratorios hacia altitudes mayores. Sin embargo, la velocidad a la que el clima está cambiando, junto con la alteración del hábitat, pueden desafiar sus capacidad de respuesta. Debido a la complejidad de la dinámica de las especies y de las comunidades, los efectos reales del cambio climático sobre la biodiversidad de montaña, especialmente cuando interactúa con otras fuentes de estrés, son extremadamente difíciles de prever. Además, la dureza del ambiente de montaña obstaculiza las actividades de investigación. Por este motivo, a menudo falta conocimiento sobre la ecología de las especies, esencial para un monitoreo y una conservación rigurosos. Falta también investigación sobre las relaciones entre los rasgos funcionales de las especies y el funcionamiento del ecosistema. En concreto, la identificación de especies raras cuyo papel en la dinámica ecosistémica trasciende a su abundancia, es esencial para establecer prioridades de conservación.

El modelo biológico utilizado en esta tesis doctoral es el gorrión alpino (*Montifringilla nivalis*), un ave de alta montaña, estrictamente vinculada a estos ambientes. Tiene una amplia distribución en toda Eurasia y por eso aparece catalogada como LC (Preocupación menor) en la Lista Roja de las Aves europeas. Sin embargo, en Europa la subespecie *M. nivalis nivalis* tiene una distribución reproductiva irregular y parcheada, desde la Cordillera Cantábrica en el noroeste de España hasta el norte de Grecia pasando por los Pirineos, los Alpes, Córcega y los Apeninos. Esta especie está sufriendo de un declive poblacional debido a alteraciones del hábitat, perturbaciones antropogénicas, contracción del rango de distribución y reducción de la conectividad, además del cambio climático. Sin embargo, a pesar de lo anterior se desconocen todavía muchos aspectos de su biología y ecología.

El objetivo de esta tesis doctoral es ampliar el conocimiento sobre *(i)* el rango de distribución, *(ii)* la especificidad del hábitat, *(iii)* las estrategias de movimiento y *(iv)* las dinámicas de grupo de una de las especies de aves alpinas más emblemáticas, el gorrión alpino *Montifringilla nivalis nivalis*, a través del estudio de las poblaciones de los Alpes, Apeninos, Cordillera Cantábrica y Pirineos españoles. Además, hemos introducido nuestro estudio con una exploración de las comunidades de aves de montaña del Holártico, atendiendo a su diversidad funcional y a la rareza funcional de sus especies.

En el capítulo I analizamos la diversidad funcional de las comunidades de aves de montaña del Holártico, utilizando rasgos morfológicos y aquellos relacionados con la reproducción, para identificar así qué especies, dentro de cada una de ellas, son únicas, con el objetivo de averiguar si estas especies son efectivamente las que habitan cotas más altas. Los resultados indican que la comunidad más diversa es aquella que habita los sistemas montañosos del Himalaya y China, en aspectos como la riqueza de especies y riqueza funcional. Sin embargo, esta comunidad es la que presenta menor diferenciación en cuanto a reparto de nicho trófico. La comunidad que presenta una mayor redundancia de especies es la del Cáucaso, y las comunidades de Asia son las que presentan el numero más alto de especies únicas. Además, comprobamos como según aumenta la altitud las especies se hacen más exclusivas en cuanto a sus rasgos morfológicos y vitales. Confirmamos entonces el papel importante de las montañas como reservas de biodiversidad, pero también identificamos los ambientes más elevados como más vulnerables frente a la pérdida de funciones ecológicas.

En el capítulo II comparamos las areas potenciales de reproducción del gorrión alpino en Europa con la distribución actual definida por BirdLife International, que corresponde a la estimación más completa y utilizada del rango de distribución de la especie. Para determinar las areas potenciales de reproducción empleamos observaciones georreferenciadas recogidas durante la estación reproductora en diferentes macizos de Europa y diferentes variables climáticas y de cobertura del suelo. Encontramos que la distribución actual del gorrión alpino determinada por BirdLife International es considerablemente mayor que la potencial. Las discrepancias resultan particularmente evidentes en el este de Europa, donde hay una importante falta de monitoreo. Además, en las montañas del sur de Europa, la disponibilidad de areas potencialmente favorables para la reproducción del gorrión alpino resultan más fragmentadas y restringidas en comparación con la distribución sugerida por BirdLife International. Como consecuencia, las poblaciones que habitan estas áreas - entre ellas la de la Cordillera Cantábrica - ocupan parches más pequeños y aislados y podrían sufrir un mayor riesgo debido al calentamiento global.

En el capítulo III estudiamos las variaciones circanuales del uso del hábitat a diferentes escalas espaciales en la población de gorrión alpino de la Cordillera Cantábrica. Encontramos que la especie no solo depende de los ambientes de alta montaña durante la estación reproductora, como era esperable, sino también durante la estación no reproductora. Sin embargo, mientras que durante la reproducción el gorrión alpino es más especifico en el tipo de hábitat que utiliza, sobre todo a escalas espaciales más pequeñas, durante el invierno la especificidad disminuye. El ambiente más duro en invierno hace que la especie se mueva más, de manera errática y descendiendo a menores altitudes si es preciso, para buscar recursos, que sin embargo son más diversos en esta estación. La especie muestra entonces un mayor grado de plasticidad durante el invierno, que sin embargo se ve limitada en las cotas más bajas, debido probablemente a las adaptaciones fisiológicas y morfológicas de la especie y a la escasez de hábitat adecuado. Esta mayor plasticidad invernal podría ser una estrategia para hacer frente a la imprevisibilidad y dureza de la estación no reproductora en ambientes de alta montaña. Queda por investigar cómo esta estrategia podría verse afectada por el cambio climático en las diferentes poblaciones de Europa.

En el capítulo IV exploramos los patrones de movimiento invernal del gorrión alpino, a través del análisis de los isótopos de plumas de individuos pertenecientes a varias poblaciones europeas. Estimamos la probabilidad de un origen reproductivo (Alpes vs. Otros) para aves invernantes en los Alpes suizos, en el Pirineo español y en la Cordillera Cantábrica. Encontramos que el 99% de los individuos capturados en invierno en los Alpes pertenecen a la población reproductora alpina, y hasta el 98% y el 86% de los individuos muestreados en invierno en el Pirineo y en la Cordillera Cantábrica, respectivamente, tienen una alta probabilidad de provenir originalmente de la población reproductora en los Alpes. Los gorriones alpinos, tradicionalmente considerados residentes, parecen entonces adoptar una estrategia de migración invernal parcial. Estos resultados no solo respaldan evidencias previas que sugieren que existen movimientos latitudinales de invernada en el gorrión alpino, sino que también sugieren que tales movimientos invernales desde los Alpes hasta el Pirineo podrían alcanzar el límite de distribución más occidental representado por la Cordillera Cantábrica. Encontrándose esta población más aislada de las demás, el movimiento invernal de individuos de los Alpes podría potencialmente reducir la deriva genética, con consecuencias importantes para su resiliencia y persistencia. Posteriormente analizamos si las condiciones climáticas en invierno en los Alpes pueden jugar un papel en los movimientos migratorios hacia los macizos ibéricos. Estos movimientos parecen desencadenados por las condiciones climáticas, es decir, los gorriones alpinos migrarían cuando las condiciones invernales en los Alpes son más duras. Bajo un escenario de calentamiento global, la propensión a migrar podría reducirse, con efectos sobre la demografía, estructura y heterogeneidad de las diferentes poblaciones, y un mayor riesgo de aislamiento de las poblaciones más periféricas.

En el capítulo V analizamos las dinámicas de los bandos que la especie forma en invierno. Los resultados sugieren que los gorriones alpinos se reúnen en grupos más grandes especialmente en sitios donde las condiciones de invernada son más duras, es decir, con baja temperatura ambiente y alto nivel de precipitación. En estos lugares los bandos se disgregan más temprano y se forman más tarde que en zonas más cálidas. Sin embargo, los resultados revelan que los cambios temporales en las asociaciones de invernada (es decir, el tamaño del grupo y la dinámica de separación y reunión) se ven afectados por las condiciones climáticas. Específicamente, encontramos que cuando las temperaturas aumentan y el nivel de precipitaciones disminuye, el tamaño de los grupos de invernada disminuye, y los individuos permanecen en grupo durante menor tiempo. Esto podría provocar desajustes potenciales entre el inicio de la reproducción y los picos máximos de disponibilidad y accesibilidad de recursos, afectando potencialmente a la supervivencia y la reproducción. Estos resultados nos indican que el efecto del cambio climático sobre la dinámica de los grupos invernales podría alterar la organización social de las poblaciones, con consecuencias también en la actividad reproductora.

Esta tesis doctoral aporta información novedosa de la ecología del gorrión alpino, que puede ayudar a la hora de implementar monitoreo y planes de conservación futuros. Los resultados demuestran que el estado en el que se encuentra la especie está lejos de ser definido, y cómo su estricta dependencia de los hábitats de montaña lo pone potencialmente a riesgo. Uno de los resultados más interesantes es la estrategia de migración parcial que caracteriza la especie, estrategia que puede conectar poblaciones fragmentadas, facilitando el rescate de las más aisladas. Sin embargo, el clima tiene un papel importante en desencadenar estos movimientos, como también determinar el comportamiento social de la especie, propiciando cambios en la dinámica de los grupos que podrían tener consecuencias en la reproducción y supervivencia y en la misma estrategia migratoria. Esta tesis representa también el punto de partida para futuras investigaciones, que permitan comprender mejor la dinámica y conectividad de las poblaciones, identificar fenómenos de aislamiento y profundizar el conocimiento de las respuestas de la especie al cambio climático.

Conclusiones

1. La rareza funcional de las especies de montaña es independiente de sus rangos de distribución, estando asociada al conjunto de especies que forman cada comunidad. Además, la rareza funcional en los rasgos morfológicos y vitales aumenta a lo largo del gradiente altitudinal, siguiendo el incremento de especialización de las adaptaciones de las especies de alta montaña.
2. El papel de las especies con rasgos únicos y su contribución potencial al funcionamiento y a los procesos de los ecosistemas de montaña son desconocidos. Consecuentemente, eso dificulta nuestra comprensión de los efectos que la desaparición de estas especies, como consecuencia del cambio global, podría tener sobre el ecosistema de montaña, y requiere futuras investigaciones.
3. Los parámetros climáticos y topográficos resultan importantes para determinar la idoneidad del hábitat del gorrión alpino, y por tanto su distribución. Como era esperado, la idoneidad aumenta en areas con vegetación dispersa y pastizales naturales, así como en zonas rocosas.
4. Se encontraron importantes discrepancias entre la distribución de la especie estimada por BirdLife International y la distribución potencial identificada por nuestro modelo. En particular, las diferencias son evidentes en el este de Europa, donde la especie está escasamente monitorizada, y en las poblaciones sureñas, que se encuentran más aisladas y fragmentadas y por tanto en mayor riesgo debido al calentamiento global.

5. Los gorriones alpinos utilizan ambientes de alta montaña a lo largo de todo el año, posiblemente como consecuencia de las adaptaciones fisiológicas y morfológicas típicas de las especies de alta montaña. Sin embargo, parecen tener una mayor flexibilidad en invierno lo que parece deberse a la dieta más variada y a la necesidad de enfrentarse a un ambiente impredecible.
6. El uso del hábitat resulta más dependiente de la escala espacial en la estación reproductora que respecto al invierno, probablemente porque los individuos están limitados por la selección del sitio de nidificación y de áreas específicas de forrajeo para la alimentación de los pollos.
7. Los gorriones alpinos adoptan una estrategia de migración parcial, con patrones diferentes tanto entre poblaciones como dentro de una misma población. Así, la mayoría de los individuos capturados en invierno en los Alpes pertenecen a la población reproductora alpina, y el 98% y 86% de los individuos invernantes respectivamente en el Pirineo español y en la Cordillera Cantábrica tienen una alta probabilidad de pertenecer a la población reproductora de los Alpes.
8. Los movimientos de individuos entre los Alpes y los macizos ibéricos pueden ser importantes para la estructura genética de la metapoblación europea. En particular, podrían prevenir potenciales efectos negativos de un aislamiento genético debido a la pérdida de hábitat, siendo esto particularmente importante para las poblaciones más pequeñas y aisladas como la de la Cordillera Cantábrica.

9. La propensión migratoria de los gorriones alpinos resultó superior en los inviernos con temperatura media mensual más baja en los Alpes. Esto sugiere que el clima podría ser determinante en los movimientos de migración parcial de los gorriones alpinos de los Alpes. Bajo un escenario de calentamiento global, la propensión migratoria podría verse afectada, con consecuencias sobre la conectividad de las poblaciones y sobre las dinámicas y estructura espacio-temporal de las mismas.
10. El clima invernal es un factor importante que influye en el comportamiento gregario de la especie. Como patrón general, los individuos forman grupos más grandes especialmente en aquellos lugares con condiciones invernales más duras, y además se congregan más tarde y se separan más temprano que en áreas más cálidas.
11. La magnitud de las asociaciones invernales y su fenología están reguladas por cambios en las condiciones del tiempo a lo largo del invierno. Así, cuando las temperaturas aumentan o las precipitaciones disminuyen, el tamaño de los grupos se reduce considerablemente, y los individuos permanecen en grupo durante un tiempo más breve.
12. Debido a los efectos que el calentamiento global tiene sobre los ambientes de montaña, podrían esperarse consecuencias sobre las dinámicas de los grupos invernales. Éstas incluyen la inestabilidad y la perturbación de la organización social y los desajustes entre la fenología de la reproducción y los picos de disponibilidad y abundancia de recursos.

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